

To the Graduate Council:

I am submitting herewith a dissertation written by Marie Turner entitled "Mechanisms Structuring a Guild of Raptorial Spiders." I have examined the final copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Zoology.

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MECHANISMS STRUCTURING A GUILD
OF RAPTorial SPIDERS

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Presented for the
Doctor of Philosophy
Degree
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ABSTRACT

Resource utilization patterns of a guild composed of four syntopic species of raptorial ambush spiders were investigated over a three year period. Coefficient of similarity values were calculated for six species pairs based on exploitation of four niche dimensions (phenology, microhabitat, prey taxa and prey size). Differences in seasonal patterns were evident for all guild members. Microhabitat distribution indicates that when the space resource (flowerheads) is not in limited supply, each spider species utilizes a separate component of the habitat. There was a large amount of overlap in prey size among all four species but only moderate overlap in prey taxa taken. Overall results show that species overlap in resource use varies from year to year with no obvious pattern in the magnitude or direction of change.

To test for interspecific competition controlled field experiments were conducted wherein the dominant species, Peucetia viridans, was removed over a two year period. Removal of P. viridans did not produce any of the expected effects on the species remaining (Misumenops lepidus, M. californicus, M. deserti). There was no significant increase in fecundity, altered pattern of food resource use or habitat utilization, and the population density of the remaining species did not increase. Thus, interspecific exploitation competitive interactions appear to be minimal among the guild members. However, the available evidence suggests that interference competition in the form of cannibalism and intraguild predation is important in structuring the guild when resources are in limited supply.

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CHAPTER 1

INTRODUCTION

During the last few decades ecologists have paid a great deal of attention to the supposition that interspecific competition is a primary selective force leading to species differences and community organization. This concept is based on several tenets: 1) species are likely to compete if they require similar resources such as food, habitat, nest sites, etc., and if these resources are present in limited supply 2) competition for limited resources will eventually lead to the exclusion of one species by another 3) coexistence of ecologically similar species when it does occur is the result of co-evolved divergence in the species' use of resources over evolutionary time 4) species may experience interference competition (e.g., cannibalism, agonistic territorial behavior) as well as exploitative competition 5) communities exist at competitive equilibrium (i.e., the species making up a community are in balance with their resources and with one another).

Initial interest in the role of competition in structuring communities has been further fueled by the formulation of numerous mathematical models (Hutchinson and MacArthur 1959; MacArthur and Levins 1967; May 1973, 1976) which attempt to describe how resources are divided between species and the degree of difference needed between species to allow coexistence. Several predictions resulted from these models, and since the early 1960's there has been a

plethora of ecological studies oriented towards testing these predictions.

The majority of these studies have focused on the detection of competition in terrestrial vertebrate communities: birds (Grant 1966; Cody 1973, 1974; Pulliam 1975; Wiens and Rotenberry 1980); reptiles (Pianka 1973, 1975; Huey and Pianka 1974; Dunham 1980; Tinkle 1982); amphibians (Jaeger 1970, 1971; Fraser 1976; Hairston 1980, 1981); and rodents (Brown and Lieberman 1973; Joule and Cameron 1975; Schroeder and Rosenzweig 1975). Unfortunately there have been far fewer studies dealing with invertebrate communities, and the importance of competition in the evolution of species differences and community organization of arthropods seems especially unclear.

Although there is circumstantial evidence for the importance of interspecific competition in structuring communities, very few studies have demonstrated experimentally that the presence of one species affects the abundance, distribution and resource utilization of similar species that coexist in nature. Before the role of interspecific competition can be properly ascertained, carefully designed field experiments need to be carried out (Reynoldson and Bellamy 1971; Connell 1975). Under ideal field conditions both the limiting resource and the competing populations should be manipulated separately. However, experimental studies of competition are often difficult to conduct. Further, the data resulting from them are often hard to interpret for a number of reasons: 1) The majority of field studies are short term. Therefore, the results may have little relevance to evolutionary processes that may have brought about the

present structure and diversity of the system, and may lead to incorrect conclusions on the possible degree of interaction between species. 2) Long term experiments on unconfined populations are most likely to demonstrate realistic community responses to competition. However, they are often impractical because of the difficulty in maintaining reduced population densities in the face of continual immigration. 3) Field experiments may be difficult to replicate because of habitat heterogeneity and/or constraints in terms of manpower and time limitations.

In order to circumvent these problems an ecologist should first choose a system which is amenable to resource and density manipulations; and second, one where the model organism has relatively short generation times allowing the experiments to be replicated over time. Many invertebrate populations exhibit such characteristics, but spiders are a particularly good model system for a number of reasons. Spiders are important carnivores in terrestrial communities in terms of biomass, energy flow and numbers of species (Van Hook 1971; Moulder and Reichle 1972). Most species have a generation time of less than one year. Local populations generally occur in very high densities thus facilitating field manipulations. Since spiders are predators of other arthropods they may play a significant role in determining the densities of insect populations and as such may prove to be effective biocontrol agents (Riechert and Lockely 1984).

Initial studies of spider communities were primarily descriptive and provided only indirect evidence as to the extent of inter- or intraspecific competition. Uetz (1975, 1977), in an observational

study of a guild of wandering spiders, hypothesized that possible interspecific competition was reduced primarily by temporal segregation of foraging and breeding activity. Post and Riechert (1977) showed that structure of a spider community occupying a woodlot could be explained in terms of habitat heterogeneity. Gertsch and Riechert (1976) demonstrated that closely related species of several spider families were separated by spatial and temporal differences and others were not. Turner and Polis (1979) found no evidence for exploitative competition in a guild of raptorial spiders but suggested that coexistence and patterns of guild structure among similar species were a product of interference competition. Enders (1974) observed that the coexistence of two species of orb weavers, Argiope aurantia and Argiope trifasciata, was a consequence of high mortality in the vertically stratified immature stages.

Experimental field studies have shown that resource shortages such as prey and suitable web sites can limit the growth, fecundity, distribution and survival of spiders. Schaefer (1978) concluded that the ultimate factor limiting the population size of the linyphiid spider, Floronia bucculenta, was the availability of suitable web sites. Intraspecific competition for attachment sites forced inferior competitors to emigrate thus reducing the population density. Other investigators (Colebourne 1974; Riechert 1981) have also found that structural features of the habitat are potential limiting factors. Riechert (1976, 1978, 1979, 1981, 1982) in a long term study of the funnel web spider, Agelenopsis aperta, demonstrated that intraspecific competition for web sites occurred in the form of agonistic

interactions. Thus, territorial behavior in this species produces patterns of spacing that eliminates competition for prey. Wise (1975, 1983) obtained conflicting results as to whether or not spider populations are regulated by the level of food supply. Adults of Linyphia marginata apparently compete for food and thus Wise (1975) concluded that food supply acts as a density dependent limiting factor for this species. However, in a study of two species of orb weavers involving the manipulation of prey density, he concluded that although food is a limited resource for both species, exploitative competition is weak or absent. Riechert and Cady (1983) conducted removal experiments in a community of cliff-dwelling spiders, but found no evidence for interspecific competition in the form of competitive release. They offer the suggestion that interspecific effects in spider communities may be masked and/or offset by other impinging factors such as interspecific predation and intraspecific competitive effects.

Spider species can easily be divided into three major guilds based on methods used to capture prey. (A guild, sensu Root 1973, is a group of organisms exploiting a single resource or type of resource in a similar manner. The three guilds of spiders are the web spinners, cursorial forms and ambush predators (Balogh 1946). Each of the three groups generally consists of closely related taxa). To date most experimental investigations attempting to detect competitive effects in spider communities have been focused on one major guild type--the web building spiders, particularly orb weavers (e.g., Wise 1983; Riechert and Cady 1983). With the exception of an experimental study by Schaefer (1975) on the importance of interspecies competition

for three Lycosid species in a salt marsh, there have been almost no in-depth field studies which attempt to discern the role of competition, if any, in structuring communities of non-web spinning spiders. This is in large part due to the numerous difficulties encountered in trying to manipulate population densities and potentially limiting resources of the cursorial species. However, there does exist a moderately large guild of non-web builders, the ambush spiders, that are relatively sedentary. These spiders do not actively hunt for food, but rather capture their prey by employing a sit and wait foraging tactic. Their sedentary habits and the fact that they often occur in very high densities make them particularly amenable to field experiments. The majority of ambush spiders are species belonging to the crab spider family Thomisidae, but a few species of Oxyopidae and Lycosidae are also included.

This study deals with a sagescrub dwelling guild of coexisting raptorial spiders located in Riverside County, California. The guild is composed of three species of crab spider (Thomisidae) and one oxyopid species, the green lynx spider. Previous work (Turner and Polis 1979) provided circumstantial evidence that competitive interactions (primarily intraspecific) may be important in determining guild structure and coexistence in this habitat. The objectives of this present study were: 1) To determine and describe the resource utilization patterns of each guild member. If these spiders exhibit a high degree of similarity in resource use, it may be possible that they are experiencing exploitative competition. 2) To see if guild structure (in terms of niche characteristics, density and diversity)

is constant from year to year. 3) To delineate any competitive interactions (exploitative or interference) that may exist among guild members. 4) To complete replicated experimental removals of the dominant species.

CHAPTER 2

NATURAL HISTORY

Introduction

The ambush spider guild in the study location is composed of three species of Thomisidae: Misumenops lepidus (Thorell), Misumenops californicus (Banks) and Misumenops deserti (Schick). There is also one species of Oxyopidae, Peucetia viridans (Hentz), which belongs to the guild. These spiders are all relatively sedentary and can usually be found sitting on flowers or inflorescences from which they forage. They are all diurnal predators and are equipped with relatively keen eyesight. During periods of inactivity they often move to the underside of the flower head and remain quiescent.

Oxyopidae

The green lynx spider, Peucetia viridans, is a large (length 14-16 mm) spider with a high, oval cephalothorax and a rounded abdomen tapering to a point behind. The legs are covered with long black spines which are retrocurved. It is a broad ranging species and can be found from Virginia south to Florida and west to California. Local populations in Southern California are characteristically bright green in color and are often marked with red spots on the dorsal surface of the cephalothorax, abdomen and legs. This species is capable of extremely fast movement and often leaps great distances (10-50 cm) to escape predators. However, like other members of the

guild, Peucetia generally captures prey items by using a sit and wait foraging strategy, lying in ambush for potential food. Foraging individuals located in the study area are most commonly found on Eriogonum fasciculatum and Corethrogne filangifolia.

The mating behavior of an Arkansas population of P. viridans has been described in detail by Whitcomb and Eason (1965). Mating in California may be observed in April but is most common in June and July. Probably only one mating occurs in this species since the epigynum of a mated female is covered with a hard blackish layer which Gertsch (1979) describes as being composed of dried semen and collateral fluid. Subsequent insertion of a male palpus is inhibited by the presence of such a plug. Often a small process from the male palpus, broken off during mating, is also present in the epigynum.

The female generally constructs her egg sac 21-28 days after mating (Whitcomb et al. 1966). The egg sac is straw-colored and is attached to leaves, stems and inflorescences of a number of different shrub species. After constructing the egg sac the female guards it by covering it with her body and assuming a threatening posture whenever a potential predator (including conspecifics) enters her field of vision. Eggs hatch into a first instar spider known as a deutovum. The deutovum remains in the egg sac until it molts into a second instar at which time it emerges. Emergence usually takes place when the female tears a hole in the egg sac. Egg sacs which are not protected and opened by a female can be opened by the spiderlings themselves. Newly emerged spiders remain with the female for approximately seven days often feeding on prey the female

has captured. Cannibalism does not appear to be an important mortality factor at this time. Dispersal is generally by ballooning.

Sexual differences begin to appear during the sixth instar with the palpi of males becoming slightly swollen (Whitcomb et al. 1966). In Southern California males are smaller than females, and adults are first observed in early April. Females can be found as late as December. Under California sagescrub field conditions there are often widely overlapping stages of development. For example, it is not uncommon for second, fifth and adult instars to occur in the study area all in the same period of time.

Thomisidae

The crab spiders are members of the moderately large family Thomisidae. The common name "crab spider" refers to the crab-like appearance of the majority of species and the fact that they move sideways and backwards in the same manner as crabs. The body is short and broad and the legs are oriented at right angles to the longitudinal axis--a condition often referred to as laterigrade. All three species involved in this study belong to the genus Misumenops. Unlike other species of Thomisidae these spiders are generally found on blossoms or inflorescences of woody shrubs or the flowers of annual herbs. They are capable of changing body color, usually from white to yellow and vice versa such that their coloration often matches that of the substrate they are found upon. Capture of prey is effected by means of ambush. Often the spider holds the front legs outstretched in readiness and when a prey item comes within reach the

spider quickly encloses it with the first two pairs of legs and inflicts a bite with its fangs. The venom of crab spiders has been noted to be particularly toxic to arthropods (Gertsch 1979) as evidenced by the fact that insects much larger than the spider (e.g., butterflies) are often quickly subdued and fed upon.

These spiders are capable of diapause (Schick 1965). This generally occurs in the fall and/or winter months. During this period of time the spider feeds only occasionally and does not undergo ecdysis.

Sexual dimorphism is marked in these species. The males are smaller and darker than the females and have much longer legs. There do not appear to be any complex rituals in the mating process. When a male finds a female he touches her with his front legs briefly and if she appears receptive, he almost immediately "leaps" upon her dorsum and inserts his palpi which have been charged with semen (personal observation). As in Peucetia, females are prevented from mating more than once by an epigynal plug--a waxy coating which forms over the atrium in the epigynal plate (Schick 1965). Once an egg sac is laid the female will guard it, but she usually dies before the spiderlings emerge.

The smallest of the Misumenops species in this study is M. lepidus. Females average five mm in length and males average three mm. Mature individuals occur from March to May, but are most abundant in April. Misumenops californicus is the second smallest guild member. Females average five to six mm in length and males average three to four mm. Adults can usually be found in April and

May. The third and largest crab spider species in this guild is M. deserti, which was declared a new species by Schick in 1965. Mature males average four mm in length and females average six to seven mm. Adults occur from May through September.

There are no detailed life history data available for these three species, but a study of a closely related species, M. celer, revealed that males reach maturity after four or five instars and females attain the adult stage after six to seven instars (Muniappan and Chada 1970). Like P. viridans, the first instar (deutovum) remains within the egg sac and emerges as a second instar spiderling. Upon emergence the spiderlings are very white in color with no markings and they quickly disperse via ballooning.

CHAPTER 3

DESCRIPTION OF STUDY SITE

The study was conducted at Lake Perris State Recreation Area located 40 km southeast of Riverside, California. The vegetation in the area is typical of a dry coastal sagescrub dominated by several species of perennial shrubs: Eriogonum fasciculatum (Benth) (California buckwheat); Artemisia tridentata Nutt.; Encelia farinosa Nutt.; and Corethrogne filangifolia (H. and A.) Nutt., a purple-flowered composite. Also commonly found in the spring and early summer months is a species of wild mustard, Brassica nigra L.

The study was conducted over a three year period from 1980 to 1982 during the spring and summer months (April through August). Day time temperatures (highs) at the study site range from 16°C in early April up to 47°C in July and August. Spiders actively forage throughout this range of temperatures. Rainfall averages 15.4 cm per year (Lake Perris Ranger Station) and precipitation occurs mostly between late fall and early spring. Occasionally heavy rainfall in January and February causes flooding in the study area. However, water levels are never high enough to cover the existing vegetation.

CHAPTER 4

RESOURCE UTILIZATION PATTERNS

Introduction

Before the validity of models of community structure can be tested it is necessary to be able to detect and measure the extent of biological interactions. One method of measuring these interactions is to examine the distribution, food habits, microhabitat, etc. of closely related species to see how much their resources overlap. This method is very useful in detecting patterns of resource utilization and suggesting hypotheses for testing.

Methods and Materials

During the course of the 1980 field season I assessed the resource utilization patterns of this spider guild. Since the spiders comprising the guild often blend cryptically with the plants they inhabit, surveys were carried out by systematically searching each shrub encountered within a specified area. Each time a spider was observed the following data were recorded: its species, sex (male, female or immature) and instar stage (immature, penultimate or adult); and microhabitat categorized as the species of plant on which it was sighted. When a spider was found feeding, the spider and prey item were collected, preserved in 70% ethanol and the prey item was later identified to family. Prey length was also measured using a standard metric ruler (± 0.5 mm). Surveys were conducted at

least three times a week between 0800 and 1300 hours from April until early August.

As part of an ecomorphology study, spiders of each species were collected semi-monthly from a similar sagescrub area located 0.8 km from the study site. An effort was made to collect a minimum of 30 specimens of each species each time, but this was not always possible. In 1980 samples were collected only for the months of July and August but in 1981 and 1982 collections were made from April through August. Following procedures set by Dondale (1961) and Whitcomb et al. (1966), carapace width (rather than body length or volume) was measured with an ocular micrometer on specimens that had been preserved in 70% ethanol. As all four spider species feed by capturing prey with the first pair of legs, trophic organ size was determined by measuring the length of the right first leg (± 0.5 mm) with a standard metric ruler.

To obtain information on fecundity, egg sacs of representatives of each guild member were collected in 1981 and 1982 from the same area used in morphometric sampling. Egg sacs were collected along with the female spider and both were placed into a vial containing 70% ethanol. Each vial was numbered separately. Data recorded included date of collection and the shrub species the egg sac was attached to. Preserved egg sacs were opened in the laboratory and the number of eggs counted using a dissecting microscope. To determine if there was a correlation between body size and the number of eggs produced, the carapace width of the female was measured (± 0.1 mm) using an ocular micrometer.

Analysis

Factors which could be used in resource selection and partitioning were considered to be microhabitat (plant species), food (prey taxa and prey size) and time (phenology). The extent of species' similarity in resource exploitation was calculated for each resource category using the measure proposed by Schoener (1968):

$$D = 1 - 0.5 \sum^n |p_{ih} - p_{jh}|$$

where p_{ih} equals the proportion of species i in resource state h and p_{jh} equals the proportion of species j in the same resource states, and n equals the total number of resource states. This measure is preferred over other similarity or overlap indices (e.g., Pianka 1973; Horn 1966; Hurlbert 1978; MacArthur and Levins 1967) because it is easy to calculate, it makes no assumptions about the competitive process (Abrams 1980), it is not affected by sample size (Leviten 1981), it produces estimates which are most consistent with the true overlap except at overlaps approaching unity (Linton et al. 1981), and it is not changed by the subdivision of resource states not distinguished by the potential competitors. As pointed out by Abrams (1980) and Greene and Jaksic' (1983) this last reason is important, since human investigators may distinguish categories which the animals under study do not. The values obtained from this equation are not considered to be competition coefficients (sensu MacArthur and Levins 1967 and May 1975), but rather an indication of the degree of

similarity in the utilization of some of the same resource types by two or more species (=overlap).

Estimating overall similarity in resource utilization along several dimensions is often difficult (Pianka 1976; May 1975) because organisms usually integrate resource use over space and time. However, when niche dimensions are entirely dependent upon each other one can estimate overall multidimensional utilization by calculating the arithmetic mean of the similarity coefficients along component dimensions (Pianka 1976; May 1975):

$$\Sigma D = \frac{\sum^n (D_{jh} R)}{n}$$

where $D_{jh} R$ is the total resource utilization similarity of species j on species h for n resource dimensions. When niche dimensions are independent then the best estimator of overall utilization is the product of the separate unidimensional utilizations (Pianka 1976; May 1975):

$$\Pi D = \Pi^n (D_{jh} R)$$

where $D_{jh} R$ and n are as above.

The measure used to determine species-specific diversity of resource use was the normalized version of Levins' (1968) niche breadth formula based on information theory:

$$B_n = \frac{1}{R \sum_i^n p_i^2}$$

where p_i is the proportion, out of all those resources used by the

population, that consists of items in resource state i . The index is normalized by R , the number of resource states available. Then B_n varies from $1/R$, when the population uses one resource state exclusively, to 1.0, when the population uses all resource states in equal proportions.

Results

Phenology

Differences in seasonal patterns were evident among all three species of Misumenops during each year of the study (see Fig. 1 for a typical season). Mature males and females of M. lepidus were observed during the early spring months, with the males appearing in early April and females most prevalent about mid-April. No egg sacs of M. lepidus were ever found so information on timed emergence of spiderlings was not available. Adults of M. californicus were observed during late April and May. Females of this species laid their egg sacs in early June with spiderlings emerging a few weeks later. Misumenops deserti had the longest activity period. Both males and females were abundant from late May through the end of the study period (mid-August). Spiderlings began to emerge from egg sacs in July. Previously published data (Turner and Polis 1979) indicate that female M. deserti occur in this area through September and have been observed guarding egg sacs in late August.

Instars of P. viridans were observed throughout the spring and summer months with adults first appearing in May. Adult females have been found as late as December (Turner and Polis 1979). However,

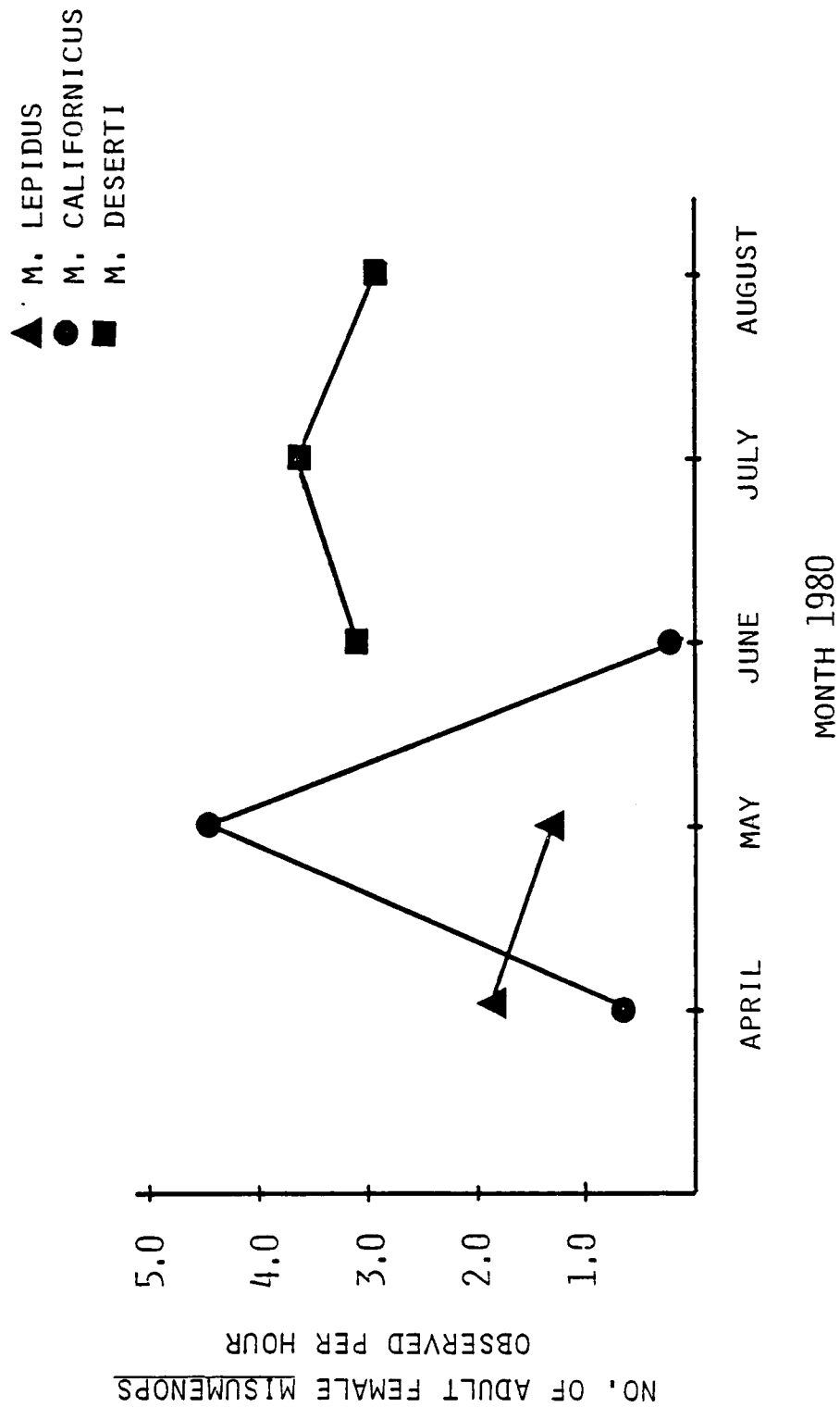


Figure 1. Phenology of three species of adult female Misumenops over a five month period. There is a seasonal overlapping succession of peak abundance among the three species.

unlike the three species of Misumenops, P. viridans was noted to have overlapping generations, particularly during the summer months (June-August) which is the time that females lay their egg sacs.

Coefficient of similarity (CS) values for seasonal activity (1980-1982) were calculated for both immatures and adults. Tables 1 and 2 indicate that the greatest similarity in seasonal distribution occurred between P. viridans and M. deserti during 1980 (.67) and 1982 (.69). However, in 1981 overlap for this species pair decreased more than 30% to .47. The highest overlap in temporal activity for 1981 occurred between M. lepidus and M. californicus (.75). Low CS values were obtained in 1980 for P. viridans x M. californicus and P. viridans x M. lepidus (.20, .30) and for P. viridans x M. lepidus (.33) in 1982. Average CS values were approximately the same with 1981 being slightly higher than the other two years.

Microhabitat

The analysis of microhabitat distribution (Table 3) shows differences in the percent utilization of the major shrub species by immatures and adults of each guild member. In 1980 about half of the immatures of each species were observed on California buckwheat (E. fasciculatum). This shrub species attracts numerous pollinators (Hymenoptera, Diptera and Coleoptera) as well as seed gatherers (Formicidae) during its flowering period (late May-September). Thus, there is abundant prey for the immature spiders. Female P. viridans were found almost exclusively on either Corethrogne filangifolia (58%) and E. fasciculatum (35%). Corethrogne filangifolia is bright green

Table 1. Coefficient of similarity values between four species of raptorial spiders (P. = Peucetia, M. = Misumenops) based on exploitation of four niche dimensions over a three year period. Species pairs are arranged in order of decreasing size from top to bottom.

Species Pairs	Phenology			Microhabitat (Shrub Species)			Prey Taxa			Prey Size		
	1980	1981	1982	1980	1981	1982	1980	1981	1982	1980	1981	1982
<u>P. viridans</u> x <u>M. deserti</u>	.67	.47	.69	.70	.81	.63	.51	.46	.65	.78	.84	.81
<u>P. viridans</u> x <u>M. californicus</u>	.20	.30	.45	.49	.67	.33	.41	.35	.29	.73	.65	.68
<u>P. viridans</u> x <u>M. lepidus</u>	.30	.31	.33	.56	.75	.68	.26	.30	.13	.76	.61	.52
<u>M. deserti</u> x <u>M. californicus</u>	.56	.64	.42	.72	.72	.66	.44	.33	.29	.84	.61	.67
<u>M. deserti</u> x <u>M. lepidus</u>	.54	.67	.47	.76	.64	.87	.40	.35	.17	.78	.72	.57
<u>M. californicus</u> x <u>M. lepidus</u>	.65	.75	.51	.81	.86	.64	.43	.20	.40	.81	.62	.53
Average ($\bar{X}$)	.49	.52	.48	.67	.74	.64	.41	.33	.32	.78	.67	.63

Table 2. Summation (ΣD) and product (ΠD) coefficient of similarity values between four species of raptorial spiders (P. = Peucetia, M. = Misumenops) based on exploitation of four niche dimensions over a three year period. Species pairs are arranged in order of decreasing size from top to bottom.

Species Pairs	ΣD			ΠD		
	1980	1981	1982	1980	1981	1982
<u>P. viridans</u> x <u>M. deserti</u>	.66	.64	.70	.19	.15	.23
<u>P. viridans</u> x <u>M. californicus</u>	.46	.50	.44	.03	.05	.03
<u>P. viridans</u> x <u>M. lepidus</u>	.47	.49	.42	.03	.04	.02
<u>M. deserti</u> x <u>M. californicus</u>	.64	.58	.51	.15	.09	.05
<u>M. deserti</u> x <u>M. lepidus</u>	.62	.60	.52	.13	.11	.04
<u>M. californicus</u> x <u>M. lepidus</u>	.68	.61	.52	.18	.08	.07
Average ($\bar{X}$)	.59	.57	.52	.10	.09	.06

Table 3. Microhabitat distribution of four species of raptorial spiders (P. = Peucetia, M. = Misumenops). Data represent the percent utilization of the major shrub species by immature and adult spiders.

	<u>P. viridans</u>			<u>M. deserti</u>			<u>M. californicus</u>			<u>M. lepidus</u>		
	Imm.	F	M	Imm.	F	M	Imm.	F	M	Imm.	F	M
1980												
<u>Corethrogne</u>	19.51	57.64	12.50	1.63	11.64	5.76	0.83	-----	-----	5.68	-----	-----
<u>Eriogonum</u>	60.96	34.97	78.12	51.63	64.38	82.73	45.00	30.38	36.84	57.95	23.53	24.49
<u>Encelia</u>	8.13	2.96	3.13	23.10	13.01	5.03	30.83	56.96	39.47	10.23	39.22	28.57
<u>Artemisia</u>	0.54	0.49	6.25	-----	2.05	0.72	-----	2.53	-----	-----	-----	-----
<u>Brassica</u>	0.81	-----	-----	18.48	4.11	5.03	19.17	8.86	23.68	19.32	25.49	28.57
<u>Other</u>	10.03	3.94	-----	5.16	4.79	0.72	4.17	1.27	-----	6.82	11.76	18.37
1981												
<u>Corethrogne</u>	43.68	33.08	26.67	23.85	20.00	14.93	14.41	11.76	12.90	18.98	-----	3.64
<u>Eriogonum</u>	37.21	44.62	53.33	30.28	38.18	64.18	40.54	5.88	25.81	38.69	15.22	29.09
<u>Encelia</u>	6.18	6.92	4.00	22.02	1.82	7.46	18.92	50.00	45.16	18.25	69.57	49.09
<u>Artemisia</u>	8.38	6.92	13.33	6.42	36.36	5.97	5.41	17.65	-----	5.84	-----	-----
<u>Brassica</u>	1.18	1.54	-----	13.76	-----	5.97	13.51	11.76	12.90	15.33	4.35	9.09
<u>Other</u>	3.38	6.92	2.67	3.67	3.64	1.49	7.21	2.94	3.23	2.92	10.87	9.09
1982												
<u>Corethrogne</u>	62.08	48.85	43.55	29.33	31.53	28.33	16.67	-----	7.69	57.97	9.09	-----
<u>Eriogonum</u>	21.32	41.22	29.03	32.21	12.61	43.33	8.82	6.45	-----	15.94	-----	10.00
<u>Encelia</u>	3.21	1.53	4.84	15.38	9.91	16.67	51.96	67.74	61.54	21.74	72.73	70.00
<u>Artemisia</u>	11.32	5.34	14.52	10.10	40.54	1.66	13.73	16.13	7.69	17.39	9.09	20.00
<u>Brassica</u>	0.38	-----	-----	10.10	3.60	6.67	4.90	6.45	19.23	4.35	-----	-----
<u>Other</u>	1.70	3.05	8.06	2.88	1.80	3.33	3.92	3.23	3.85	4.35	9.09	-----

in color and provides excellent camouflage for the green lynx spider. Eriogonum fasciculatum offers a wide variety of potential prey items. The majority of male P. viridans (78%) were associated with Eriogonum.

Adults of the three Misumenops species appear to utilize shrubs which have the greatest number of blossoms during the spiders' peak activity periods. Encelia farinosa is an early bloomer (March-April) and in 1980 females of M. lepidus (39%) and M. californicus (57%) occurred most often on this plant. Males of both these species wander during the mating season and this factor is correlated with their approximately equal distribution on three of the major shrub species (E. fasciculatum, E. farinosa and B. nigra). Misumenops deserti does not appear until later in the season and by this time the only shrubs in flower are E. fasciculatum and C. filangifolia. Both female (64%) and male (83%) M. deserti were associated most commonly with Eriogonum in 1980 with about 13% of the females on Encelia and 12% on Corethrogne.

In 1981 a period of extremely high temperatures (up to 47°C) occurred during the last week of May and first two weeks of June. This had the effect of destroying all the blossoms on Encelia and the early inflorescences of Eriogonum. In addition, all B. nigra withered and died within the first week of the heat wave. As a result, the patterns of microhabitat utilization for P. viridans and M. deserti were affected. Almost half of P. viridans immatures were found on Corethrogne and about 49% on Eriogonum. The highest proportion of adults also occurred on these two shrub species (45% males, 53% females). Significantly more M. deserti were associated with

Artemisia and Corethrogne than had been the previous year. Females increased their use of Artemisia by 34% and immatures on Corethrogne went from about 2% to 24%.

The peak activity period of M. lepidus and M. californicus occurred before the severe temperatures. Percent habitat utilization of these two species resembled 1981 with the exception of an increase of female and male M. lepidus on Encelia (30% and 20% respectively).

Again in 1982 there was a shift in habitat preference for each guild member. All instars of P. viridans increased their utilization of Corethrogne over that of 1981. As had been observed in 1980 and 1981 the largest percentage of M. deserti immatures occurred on Eriogonum, but females shifted from buckwheat to Artemisia and Corethrogne. The most notable habitat shift occurred in M. lepidus with almost 60% of the immatures occupying Corethrogne as compared to 6% in 1980 and 19% in 1981. 1982 was a normal year in terms of flowering periods. As a result, the majority of M. californicus shifted back to Encelia farinosa.

Examination of CS values for microhabitat utilization (Table 1) reveals high overlaps ($>.50$) for all species pairs during each year. The single exception was a moderately low overlap (.33) in 1982 between P. viridans and M. californicus. Year to year differences in CS values are evident for each species pair. The only species that did not have a definite increase in microhabitat overlap were M. deserti and M. lepidus. The situation was reversed in 1982 with all species pairs except M. deserti x M. lepidus exhibiting a substantial decrease in microhabitat overlap.

When the CS values were averaged for all species pairs the highest overlap occurred in 1981. This is an expected result since the loss of flowers on Encelia and Brassica early in the season caused guild members to converge on shrub species which survived the May-June heat wave.

Prey Taxa and Prey Size

The spiders that comprise the ambush guild are euryphagous predators. During the three years of this study over 900 prey items were recorded, representing 81 different insect and arachnid families (Table 4). Pollinators, primarily Hymenoptera and Diptera, were the major diet items for P. viridans and the three species of Misumenops. Conspecifics and other spiders were also important diet items as were species of Heteroptera and Coleoptera.

Closer examination of each species' diet for each year (Figs. 2-5), shows that Hymenoptera made up the largest percentage of prey items in the diet of P. viridans each year (>50% in 1980 and 1982) (Fig. 5). However, the percentage of bees and wasps taken in 1981 dropped about 20% compared to the other two years. Diptera comprised the second major prey type taken in 1980 (23%), but this dropped to about 14% in 1981 and 1982.

Figure 5 indicates that in 1981 there was a shift in the percentage of prey utilized from pollinators to other available prey, particularly species of Araneae and Heteroptera (19% and 15% respectively). This shift probably reflects the decrease in blossoms available to pollinators as a result of high temperatures in late May-early June.

Table 4. Prey taxa of four species of raptorial spiders over a three year period. The number in parentheses after an order name represents the percent composition of each major order into the diet. Numbers refer to the number of prey items observed.

Prey Taxa	1980	1981	1982
<u>Peucetia viridans</u>			
Hymenoptera	(54.84%)	(31.44%)	(52.15%)
Apidae	22	23	55
Halictidae	9	17	21
Anthophoridae	4	2	1
Colletidae	4	14	3
Pompilidae	4	2	2
Sphecidae	2	8	3
Eurytomidae	2		
Megachilidae	1	3	
Andrenidae	1	4	3
Pteromalidae	1	4	
Vespidae	1	4	2
Formicidae		3	
Mutillidae		1	1
Braconidae		4	1
Chalcidoidea		5	3
Ichneumonidae			2
Diptera	(22.58%)	(17.73%)	(13.98%)
Tachinidae	7	17	4
Chironomidae		10	4
Calliphoridae	2	3	
Syrphidae	3	3	5
Muscidae		7	2
Tipulidae	1		
Pipunculidae		1	
Mycetophilidae		1	
Chloropidae		1	3
Asilidae		1	
Stratiomyidae		1	
Tephritidae			1
Acalyptrate muscoids	7	7	7

Table 4 (Continued)

Prey Taxa	1980	1981	1982
Heteroptera	(4.30%)	(13.38%)	(5.91%)
Cercopidae		9	2
Cicadellidae		6	2
Tingidae	1	6	
Pentatomidae		4	
Rhopalidae		3	
Anthocoridae		3	2
Miridae	2		1
Reduviidae		2	2
Berytidae		2	
Lygaeidae	1		
Unknown		5	2
Coleoptera	(7.53%)	(6.69%)	(9.68%)
Dascillidae	4	2	7
Curculionidae	2	4	
Chrysomelidae	1	3	
Scarabidae		4	5
Mordellidae		1	
Coccinellidae		1	2
Carabidae			2
Unknown		5	2
Araneae	(6.45%)	(19.06%)	(13.44%)
<u>Peucetia</u>	4	26	7
<u>Misumenops</u>		20	8
Araneidae	2	5	4
Salticidae		6	4
Unknown			2
Miscellaneous	(4.30%)	(11.71%)	(4.84%)
Larvae	1	12	2
Orthoptera	3	3	
Neuroptera		3	1
Lepidoptera		5	5
Dermaptera			1
Unknown		10	

Table 4 (Continued)

Prey Taxa	1980	1981	1982
<u>Misumenops lepidus</u>			
Hymenoptera	(50.00%)	(25.00%)	(28.57%)
Formicidae	5	6	3
Apidae	1		2
Pteromalidae	1		1
Halictidae	2		
Diptera	(38.89%)	(16.67%)	(33.33%)
Tachinidae	3	4	4
Muscidae	4		
Chironomidae			1
Dolichopodidae			1
Tephritidae			1
Thysanoptera		(16.67%)	(9.52%)
Heteroptera	(11.11%)	(8.33%)	(19.05%)
Araneae		(16.67%)	(9.52%)
<u>Misumenops</u>		4	2
Lepidoptera		(16.67%)	
<u>Misumenops californicus</u>			
Hymenoptera	(27.03%)	(33.33%)	(13.33%)
Apidae	4	5	2
Formicidae	2	2	
Sphecidae	1		
Pteromalidae	1		
Braconidae			1
Halictidae	2	1	1

Table 4 (Continued)

Prey Taxa	1980	1981	1982
Diptera	(45.95%)	(37.50%)	(46.67%)
Tachinidae	5	1	5
Muscidae	5	4	3
Syrphidae	4	2	2
Tipulidae	1	1	2
Bombyliidae	1		
Chironomidae			2
Unknown	1	1	
Heteroptera	(5.40%)	(12.50%)	(16.67%)
Cicadellidae	1	3	1
Tingidae			1
Rhopalidae	1		
Unknown			3
Araneae	(16.22%)	(16.67%)	(3.33%)
<u>Misumenops</u>	5	3	1
Linyphiidae		1	
Salticidae	1		
Miscellaneous	(5.40%)		(20.00%)
Coleoptera	1		
Lepidoptera			1
Thysanoptera			3
Unknown	1		2
<u>Misumenops deserti</u>			
Hymenoptera	(54.76%)	(42.86%)	(51.35%)
Apidae	10	4	23
Formicidae	6	6	6
Halictidae	7	5	4
Chalcidoidea		1	2
Vespidae			1
Anthophoridae		1	2
Braconidae		1	

Table 4 (Continued)

Prey Taxa	1980	1981	1982
Diptera	(21.43%)	(19.05%)	(13.51%)
Chironomidae		4	1
Muscidae	3	2	2
Tachinidae	4	1	4
Syrphidae	2		
Conopidae			1
Calliphoridae		1	
Empididae			1
Chloropidae			1
Heteroptera	(11.90%)	(9.52%)	(13.51%)
Lepidoptera	(4.76%)	(4.76%)	(5.41%)
Noctuidae	2	2	4
Araneae	(7.14%)	(7.14%)	(10.81%)
<u>Misumenops</u>	2	2	4
<u>Peucetia</u>	1	1	4
Miscellaneous		(16.66%)	(5.40%)
Coleoptera		2	2
Thysanoptera		1	1
Unknown		4	1

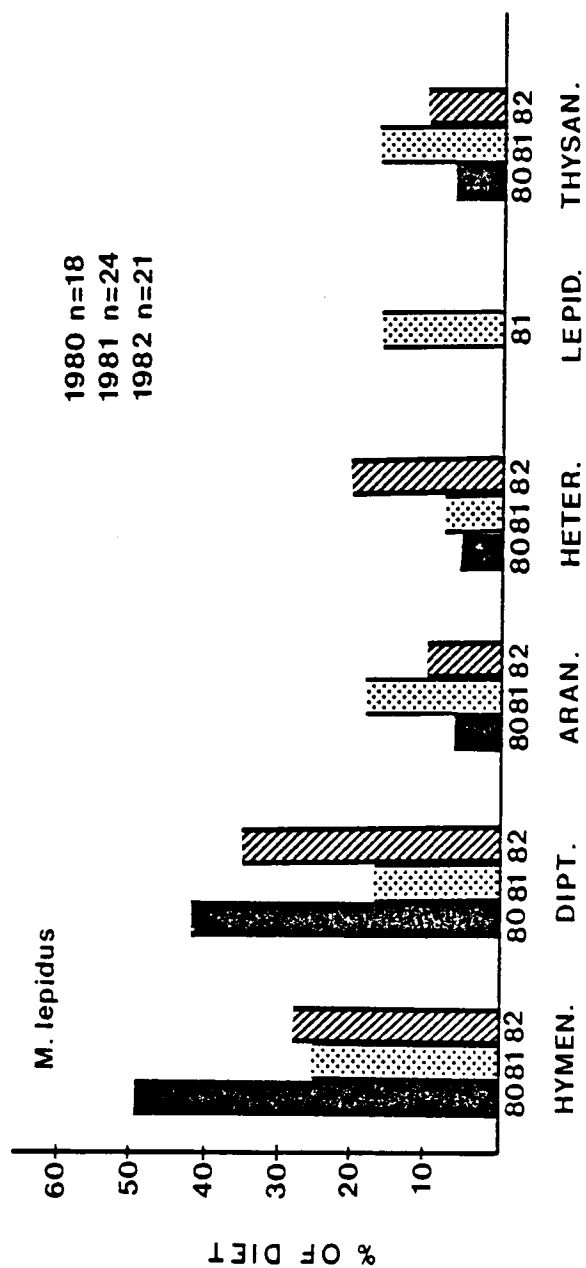


Figure 2. Percentage of major arthropod orders incorporated into the diet of Misumenops lepidus from April through August over a three year period. Abbreviation of arthropod orders: Hymen. = Hymenoptera; Dipt. = Diptera; Aran. = Araneae; Heter. = Heteroptera; Lepid. = Lepidoptera; Thysan. = Thysanoptera.

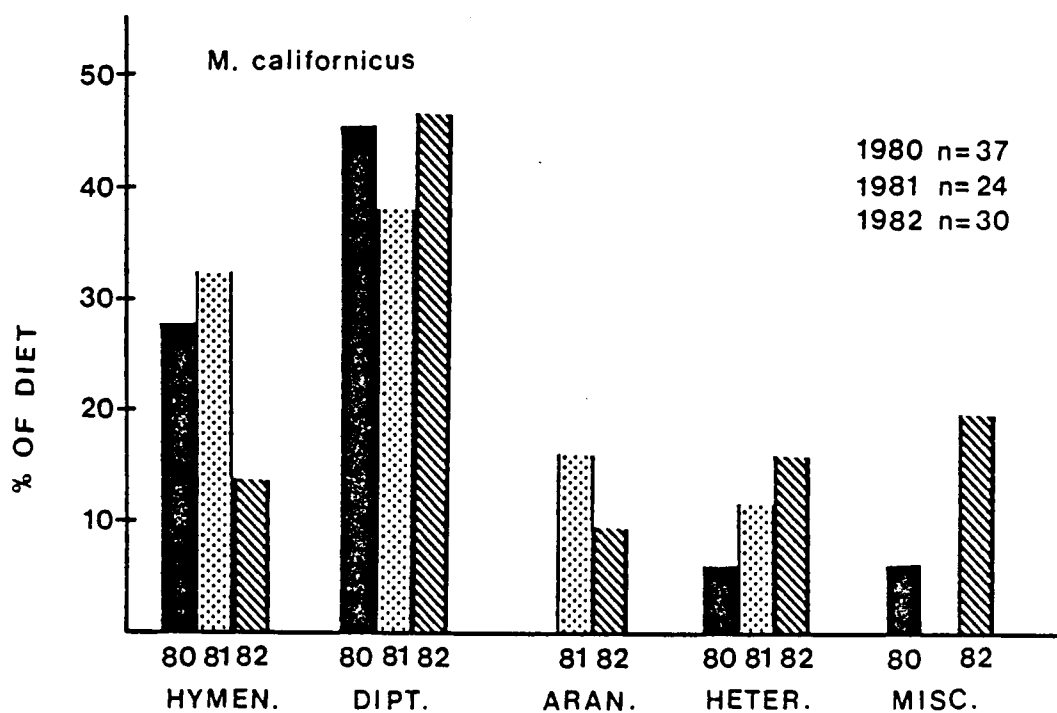


Figure 3. Percentage of major arthropod orders incorporated into the diet of Misumenops californicus from April through August over a three year period. Abbreviation of arthropod orders: Hymen. = Hymenoptera; Dipt. = Diptera; Aran. = Araneae; Heter. = Heteroptera; Misc. = Miscellaneous.

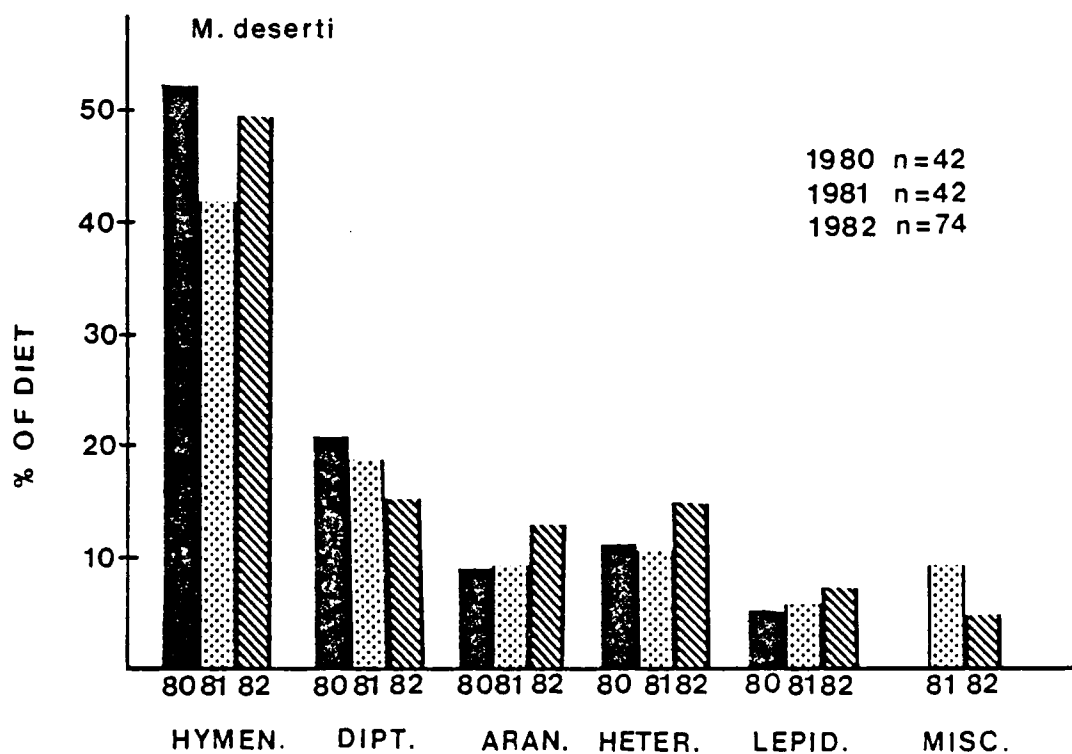


Figure 4. Percentage of major arthropod orders incorporated into the diet of Misumenops deserti from April through August over a three year period. Abbreviation of arthropod orders: Hymen. = Hymenoptera; Dipt. = Diptera; Aran. = Araneae; Heter. = Heteroptera; Lepid. = Lepidoptera; Misc. = Miscellaneous.

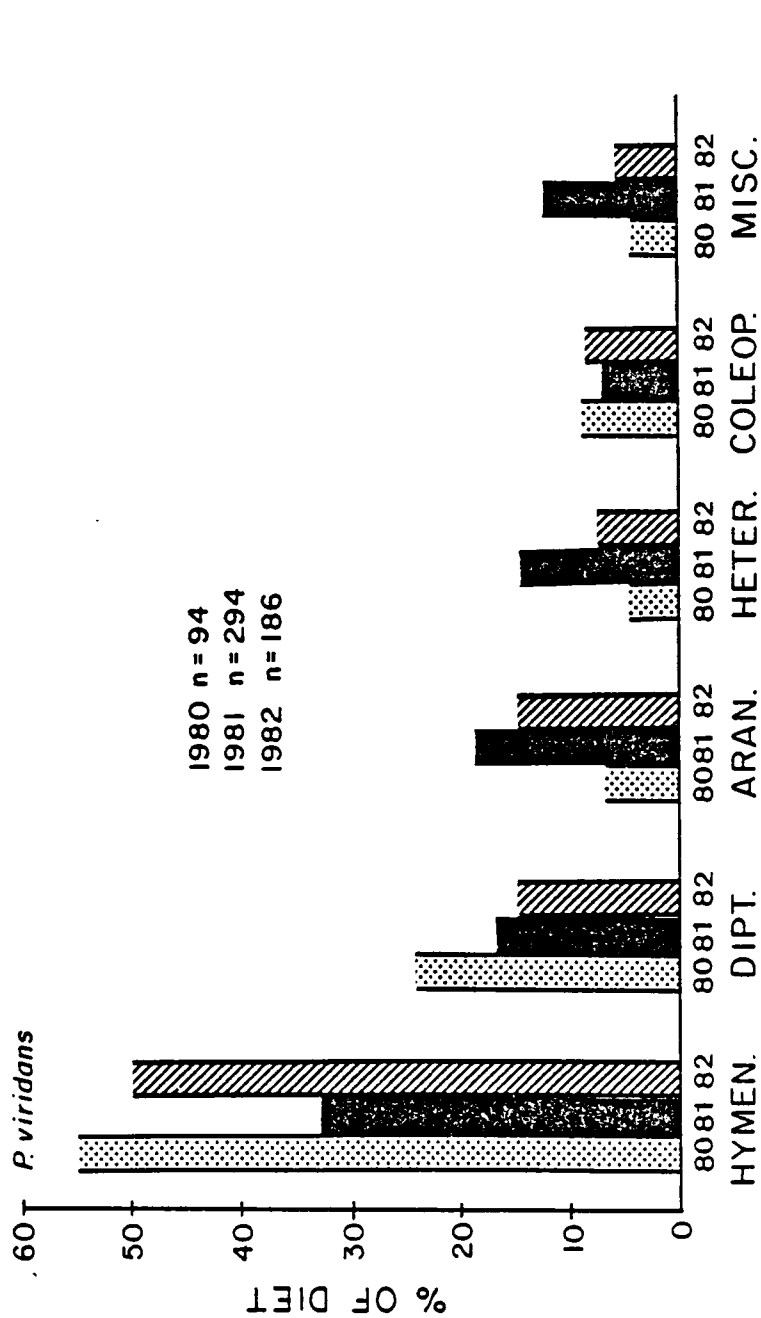


Figure 5. Percentage of major arthropod orders incorporated into the diet of *Peuceetia viridans* from April through August over a three year period. Abbreviation of arthropod orders: Hymen. = Hymenoptera; Dipt. = Diptera; Aran. = Araneae; Heter. = Heteroptera; Coleop. = Coleoptera; Misc. = Miscellaneous.

Both M. lepidus and M. deserti (Figs. 2 and 4) took more hymenopteran prey than any other category in 1980, while species of Diptera were the primary diet item for M. californicus (Fig. 3). For all three species of Misumenops there was a dramatic decrease (Fig. 6) in the percentage of pollinators eaten in 1981 compared to 1980 and 1982 with a concomitant increase in the percentage of Araneae, Heteroptera and Thysanoptera captured.

Conspecifics and other spiders made up 19% of the diet of P. viridans in 1981 (Table 4), a 13% increase over 1980. Cannibalisms accounted for 8.36% of the diet (Fig. 7), up from 4.30% the previous year. This rather large increase in cannibalism and intraguild predation (IGP) was probably directly related to the convergence of spiders onto shrubs with available flowers after the May-June heat wave. Thus, there was an increased possibility that a spider would encounter a conspecific or other spider species relative to an alternative prey item. In 1982 the incidence of other Araneae in the diet decreased back to 13% with 3.76% of these cases attributed to cannibalism.

The data for the Misumenops species (Table 4) indicate that the percentage of Araneae diet items was about the same in 1980 and 1981 for M. californicus and M. deserti. There was a slight increase in 1982 for M. deserti, up from 7.14% to 10.81%. However, M. californicus demonstrated a decrease in the percentage of Araneae in its diet from 16.67% to 9.52%. It should be noted that the sample size of prey items collected for the latter two spider species was rather small. These low sample sizes may obscure true dietary trends.

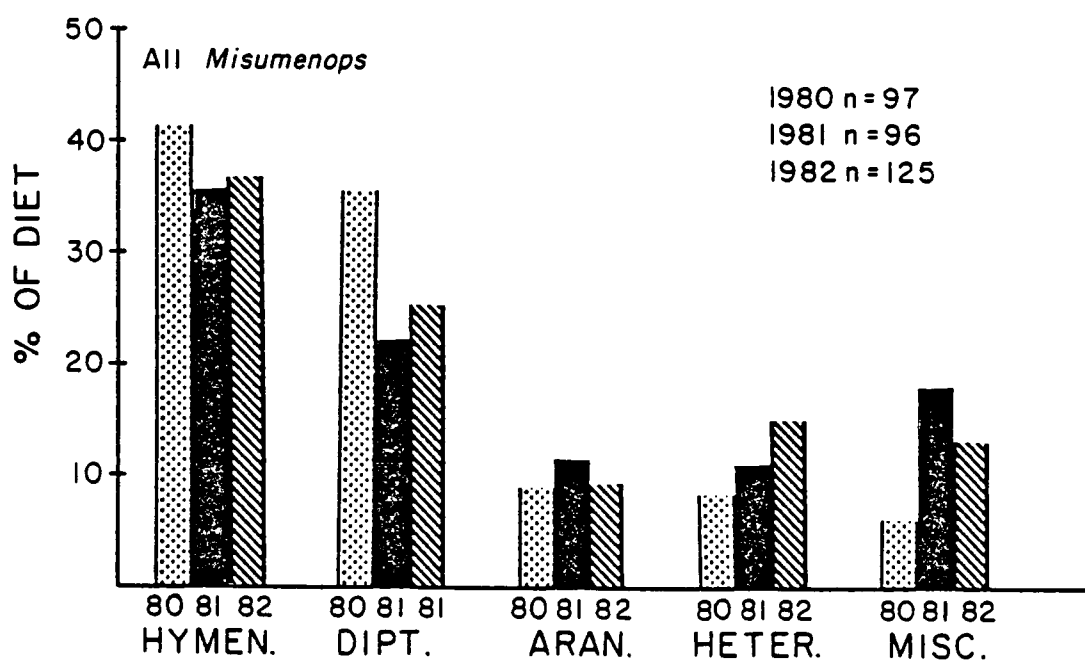


Figure 6. Percentage of major arthropod orders incorporated into the diet of three species of *Misumenops* (*M. lepidus*, *M. californicus* and *M. deserti*) from April through August over a three year period. Abbreviation of arthropod orders: Hymen. = Hymenoptera; Dipt. = Diptera; Aran. = Araneae; Heter. = Heteroptera; Misc. = Miscellaneous.

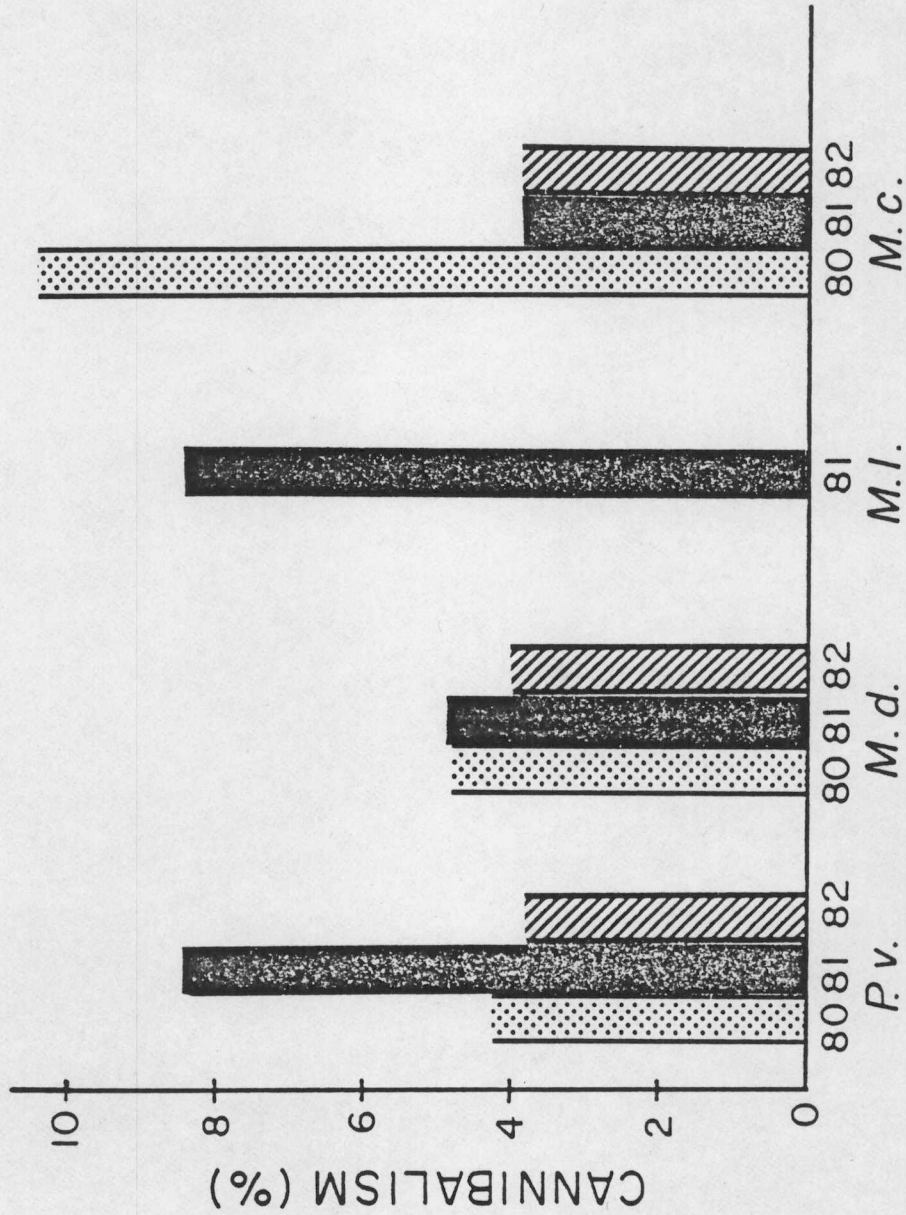


Figure 7. Percentage of cannibalism occurring over a three year period in a guild of raptorial spiders. Species names are abbreviated: P.v. = *Peuceetia viridans*; M.d. = *Misumenops deserti*; M.l. = *Misumenops lepidus*; M.c. = *Misumenops californicus*. No cannibalism was observed in *M. lepidus* in 1980 or 1982.

Therefore, the data for all three Misumenops species were pooled (Fig. 6). Here it can be seen that other spiders made up a substantial proportion of the diet each year. They were the third most important prey item in 1980 and 1981 and the fourth most common in 1982.

Spiders with prey items were most often observed on those shrub species which possess the greatest number of blossoms. For example, early in the season E. farinosa, B. nigra and E. fasciculatum are the most common flowering plants. As would be expected, the majority of M. lepidus and M. californicus with prey items were observed feeding on these shrubs (Table 5). When the heat wave in 1981 eliminated most of the available flowers (particularly of E. farinosa and the early inflorescences of E. fasciculatum) there was a decrease in the numbers of spiders found feeding on these shrubs. This is especially evident for P. viridans which went from 70% feeding on E. fasciculatum in 1980 to 46% in 1981, and increased to 73% in 1982. Many individuals of this species were also observed to take prey items while inhabiting C. filangifolia (21.6%) and A. tridentata (14.4%). A similar shift in feeding microhabitat in 1981 can be seen for M. deserti with a greater percentage observed feeding on B. nigra and miscellaneous uncommon plants. Interestingly, there was also a change in 1982 with fewer spiders of M. deserti feeding on E. fasciculatum than the previous two years.

There was little to moderate dietary overlap in terms of prey taxa among these four species (Table 1). Peucetia viridans and M. deserti exhibited the highest degree of similarity in diet

Table 5. Percent of spiders (P. = Peucetia, M. = Misumenops) feeding on each of the major shrub species.

Spider Species	Shrub Species	1980	1981	1982
<u>P. viridans</u>	<u>Corethrogne</u>	11.70	21.60	8.04
	<u>Eriogonum</u>	70.21	45.60	73.21
	<u>Encelia</u>	4.26	12.80	7.14
	<u>Artemisia</u>	-----	14.40	11.61
	<u>Brassica</u>	-----	3.20	-----
	Other	13.83	2.40	-----
<u>M. deserti</u>	<u>Corethrogne</u>	4.76	7.14	13.51
	<u>Eriogonum</u>	69.05	54.76	48.65
	<u>Encelia</u>	9.50	7.14	9.46
	<u>Artemisia</u>	-----	2.38	5.41
	<u>Brassica</u>	14.29	23.81	5.41
	Other	2.38	4.76	16.22
<u>M. californicus</u>	<u>Corethrogne</u>	-----	8.33	3.33
	<u>Eriogonum</u>	40.54	41.67	23.33
	<u>Encelia</u>	45.95	29.17	46.47
	<u>Artemisia</u>	-----	-----	10.00
	<u>Brassica</u>	10.81	8.33	10.00
	Other	-----	8.33	6.67
<u>M. lepidus</u>	<u>Corethrogne</u>	-----	4.17	4.76
	<u>Eriogonum</u>	61.11	33.33	23.81
	<u>Encelia</u>	33.33	50.00	47.62
	<u>Artemisia</u>	-----	-----	14.29
	<u>Brassica</u>	5.56	12.50	9.52

($\bar{X}$ CS=.54) while P. viridans and M. lepidus had the least amount of overlap ($\bar{X}$ CS=.23). When all species pairs were averaged for each year the greatest overlap in diet occurred in 1980 (.41) and decreased each succeeding year (.33 in 1981 and .32 in 1982).

Conversely, analysis of prey size indicates very high CS values for all species pairs all three years. Again, the highest overlap occurred between P. viridans and M. deserti. Overall CS values for prey size show that there was also a decreasing amount of overlap as was found for prey taxa from 1980 to 1982.

Niche breadth values (Table 6) for prey taxa and prey size indicate that P. viridans was a more generalized predator relative to the other guild members. It is interesting to note that the two species most affected by the heat wave in June of 1981, P. viridans and M. deserti, appeared to expand the range of prey items taken as evidenced by higher niche breadth values for prey taxa. Both M. californicus and M. lepidus appear to be specialists in terms of prey taxa taken, but generalists in the size of the food they feed upon.

Further analysis of prey size (Table 7) shows that the mean prey length of P. viridans and M. deserti was less in 1981 compared to data for 1980 and 1982. This result may have been a function of an overall decrease in spider body size and leg length measurements (see section on Ecomorphology); or it may have been due to a change in the prey size spectrum. For statistical purposes prey size data for all four spider species were transformed logarithmically (base e) to homogenize the variances and make them independent of the means. The mean prey size of both M. californicus and M. lepidus also decreased between 1980

Table 6. Niche breadth values for four species of raptorial spiders (P. = Peucetia, M. = Misumenops) over three niche dimensions.

Niche Dimension	1980	1981	1982
Microhabitat (Shrub Species)			
<u>P. viridans</u>	.359	.367	.417
<u>M. deserti</u>	.340	.489	.747
<u>M. californicus</u>	.523	.639	.427
<u>M. lepidus</u>	.413	.565	.606
Prey Taxa			
<u>P. viridans</u>	.272	.380	.164
<u>M. deserti</u>	.214	.243	.143
<u>M. californicus</u>	.309	.193	.292
<u>M. lepidus</u>	.138	.134	.200
Prey Size			
<u>P. viridans</u>	.446	.535	.588
<u>M. deserti</u>	.495	.457	.601
<u>M. californicus</u>	.473	.281	.446
<u>M. lepidus</u>	.330	.386	.455

Table 7. Mean prey length (mm)* of four species of raptorial spiders (P. = Peucetia, M. = Misumenops).

Spider Species	Sample Size	$\bar{X} \pm \text{S.D.}$
1980		
<u>P. viridans</u>	83	2.02 $\pm$.68
<u>M. deserti</u>	42	1.83 $\pm$.65
<u>M. californicus</u>	37	1.66 $\pm$.65
<u>M. lepidus</u>	18	1.60 $\pm$.55
1981		
<u>P. viridans</u>	125	1.69 $\pm$.68
<u>M. deserti</u>	41	1.48 $\pm$.81
<u>M. californicus</u>	24	1.55 $\pm$.62
<u>M. lepidus</u>	24	1.18 $\pm$.91
1982		
<u>P. viridans</u>	111	1.97 $\pm$.63
<u>M. deserti</u>	72	1.99 $\pm$.74
<u>M. californicus</u>	30	1.33 $\pm$.94
<u>M. lepidus</u>	20	1.00 $\pm$.56

*Prey length has been logarithmically transformed (base e).

and 1981, but was even lower in 1982. This may have been a result of relatively low sample sizes.

Regression analyses indicate that there was a highly significant relationship between body size (carapace width) and prey length as well as between trophic organ size (leg length) and prey size (Table 8). Data from each year were analyzed separately for P. viridans, but data for the Misumenops species were pooled because of the low sample sizes. For all four guild members carapace width was a better predictor of prey size than was leg length.

Complementary Niche Dimensions

The unidimensional overlap values obtained in this study probably do not reflect the actual extent of overlap between species (Levins 1968). Niche separation and overlap are generally multidimensional, and there are usually two or three important complementary dimensions along which species compete and resources are divided (Cody 1974; Schoener 1974). For this guild of ambush spiders the important dimensions include time, microhabitat, prey taxa and prey size. High similarity between two species along one niche dimension may be correlated with distinctness (low CS) along a complementary dimension. For example, P. viridans and M. californicus had a high degree of similarity in the size of the prey utilized (CS=.73), but they overlapped very little in their phenology (CS=.20). Thus, if food resources are limiting, competition is avoided by the fact that these two species are segregated in time. Similarly, in 1981, M. californicus and M. lepidus had a very high CS value in terms of

Table 8. Prey size* as a function of body size (carapace width = C.W.) and trophic organ size (leg length = L.L.) for four species of raptorial spiders.**

Spider Species	C.W. (1980)	L.L.	C.W. (1981)	L.L.	C.W. (1982)	L.L.
<u>Peucetia viridans</u>						
R^2	0.313	0.237	0.461	0.424	0.159	0.006
F value	32.80	22.32	101.80	87.51	11.43	0.36
Probability	<.0001	<.0001	<.0001	<.0001	<.01	>.5
<u>Misumenops species</u>						
R^2	0.218	0.178	0.383	0.313	0.400	0.407
F value	20.95	16.27	34.77	25.57	36.58	37.77
Probability	<.0001	<.0001	<.0001	<.0001	<.0001	<.0001

*Log transformations (base e) have been performed on prey length.

**Data for the three Misumenops species have been pooled.

microhabitat ($CS=.87$), but there was almost no similarity in the prey taxa they fed upon ($CS=.17$). This same complementarity of niche dimensions can also be seen for M. californicus and M. lepidus in 1981.

When all resource dimensions are considered by averaging CS values for each species pair (Table 2, p. 22) overall similarity in resource use is reduced. During each year of the study two species pairs, P. viridans x M. deserti and M. californicus x M. lepidus, exhibited moderately high ($>.6$) overall overlap in resource use. The lowest overall similarity occurred between P. viridans x M. californicus and P. viridans x M. lepidus. Since real niche dimensions are seldom perfectly independent or perfectly dependent of each other, actual overall niche similarity might best be estimated as a value falling between the results obtained from the summation and product indices.

Average CS values (Table 1, p. 21) were obtained for each resource dimension. The highest average CS values were obtained for microhabitat and prey size. A low mean similarity for prey taxa each year suggests that separation of guild members by the type of prey they feed upon may be the most important factor in allowing coexistence.

Ecomorphology

Mean carapace width of at least 30 adult females of each species was calculated for 1980-1982 (Fig. 8). There were significant decreases ($p<.0001$) in the carapace width in 1981 for the three largest guild members, P. viridans, M. deserti and M. californicus (Table 9).

The leg length of each species was also measured (Table 9). Again, mean leg length was less in 1981 than in 1980 and 1982 with

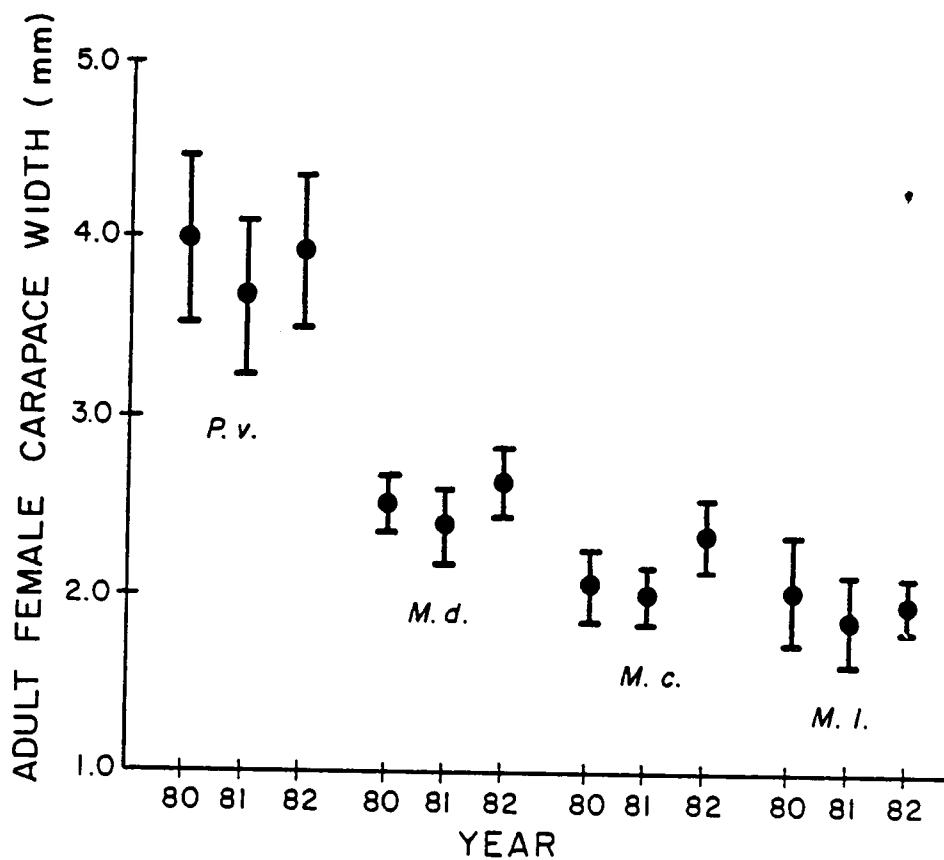


Figure 8. Mean body size represented by carapace width for four species of raptorial spiders over a three year period. Central dots represent the mean and the vertical bar one standard deviation. Species names are abbreviated: P.v. = Peucetia viridans; M.d. = Misumenops deserti; M.c. = Misumenops californicus; M.l. = Misumenops lepidus.

Table 9. Mean carapace width and leg length of adult females for four species of raptorial spiders (P. = Peucetia, M. = Misumenops).

Spider Species	1980	1981	1982
Carapace Width			
<u>P. viridans</u>	3.99 $\pm$.47	3.63 $\pm$.43**	3.88 $\pm$.38**
<u>M. deserti</u>	2.57 $\pm$.12	2.38 $\pm$.21**	2.63 $\pm$.23**
<u>M. californicus</u>	2.15 $\pm$.19	2.07 $\pm$.10	2.35 $\pm$.23**
<u>M. lepidus</u>	2.10 $\pm$.24	1.86 $\pm$.26	1.95 $\pm$.18
Leg Length			
<u>P. viridans</u>	24.97 $\pm$ 3.33	22.95 $\pm$ 2.92*	24.56 $\pm$ 3.11
<u>M. deserti</u>	11.28 $\pm$ 1.09	10.67 $\pm$ 1.18*	11.93 $\pm$ 1.42*
<u>M. californicus</u>	9.50 $\pm$ 0.92	9.43 $\pm$ 0.80	10.25 $\pm$ 0.96
<u>M. lepidus</u>	9.58 $\pm$ 1.53	9.40 $\pm$ 0.88	8.82 $\pm$ 0.70

*p<0.01 Student's t-test results between pairs indicated by lines.

**p<0.001

the exception of M. lepidus which demonstrated a further decrease in leg size in 1982. Results of student t-tests indicate that the difference in means for P. viridans and M. deserti was significant ($p < .01$). However, there was no significant difference between years for either M. californicus or M. lepidus.

Adult female mean carapace width of P. viridans was graphed over time (Fig. 9). Results demonstrate that there is a decrease of more than 0.20 mm from May to June in both 1980 and 1981, followed by an overall increase in the months of July and August. However, in 1982, there is a continual increase in carapace growth from April through August.

Adult male P. viridans showed very little change in mean carapace width over time in 1981 (Fig. 10). In May of 1982 the mean carapace width was similar to that of 1981, but increased almost 0.40 mm by July. Data for 1980 are only from July and August and depict a slight increase in growth between the two months.

Using patterns of femoral spination (Randall 1978), instar determinations were made on the P. viridans collected and preserved. Carapace width was also measured for each specimen using an ocular micrometer. Data on spider growth with age are presented in Table 10. The mean carapace width of succeeding instars two through seven are almost identical for both 1981 and 1982, suggesting a constancy in growth patterns. One first sees a difference between the two years in the carapace widths of both penultimate males and females. Measurements for 1981 are approximately 0.20 mm less for penultimate females and 0.15 mm for penultimate males. An even greater difference is

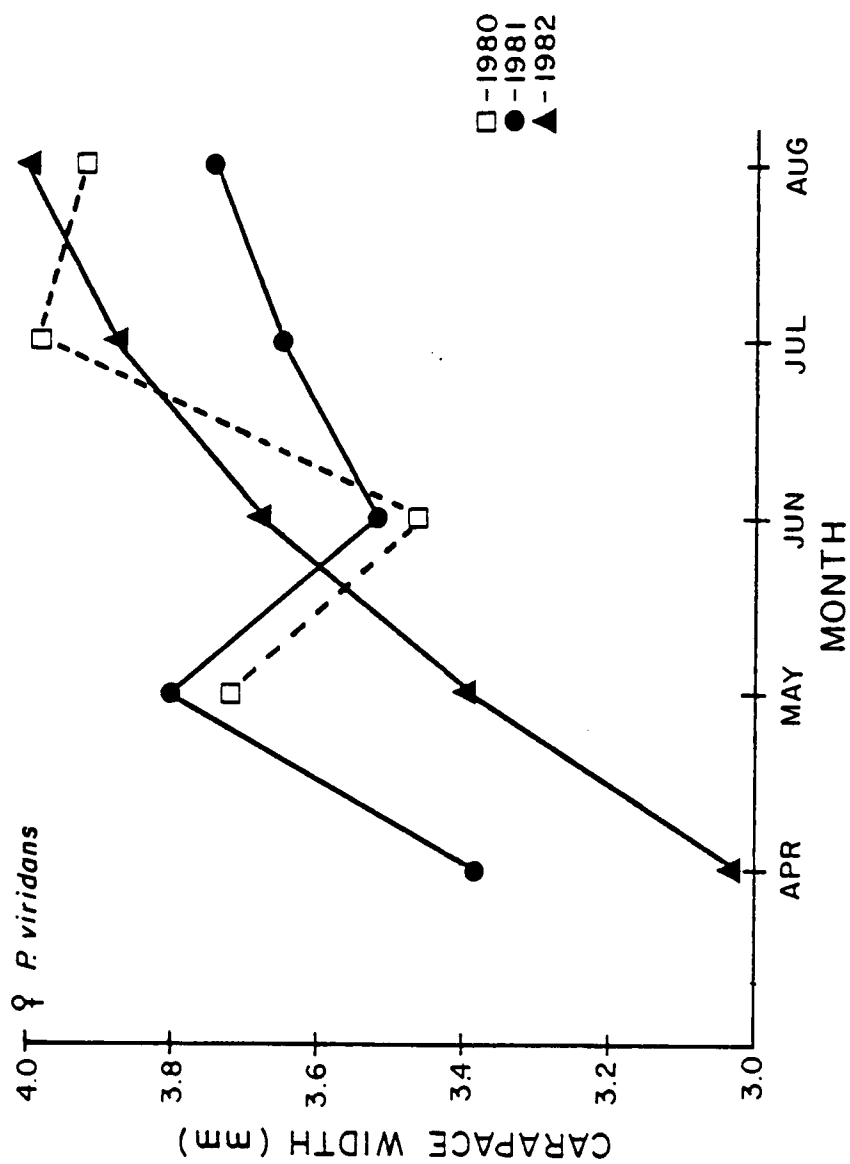


Figure 9. Mean carapace width of adult female Peuceitia viridans from April through August over a three year period.

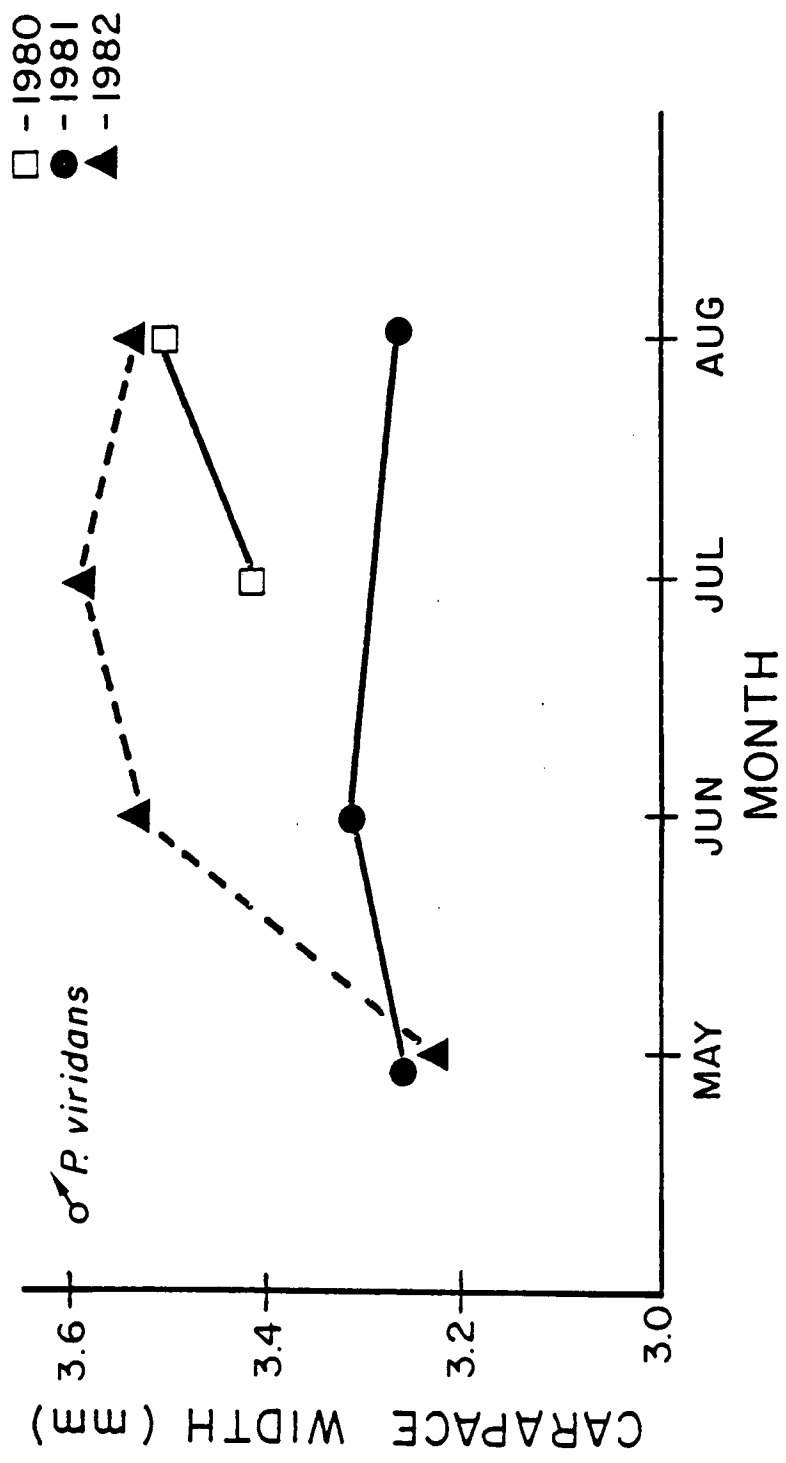


Figure 10. Mean carapace width of adult male *Peuceitia viridans* from May through August over a three year period.

Table 10. Mean carapace width (mm) of successive instars of Peucetia viridans over a three year period. Numbers in parentheses represent sample size.

Instar	1980	1981	1982
Second	0.84 $\pm$.11 (3)	0.83 $\pm$.09 (34)	0.82 $\pm$.10 (43)
Third	1.19 $\pm$.07 (5)	1.04 $\pm$.13 (37)	1.09 $\pm$.15 (81)
Fourth	1.58 $\pm$.12 (4)	1.48 $\pm$.21 (66)	1.46 $\pm$.20 (57)
Fifth	1.84 $\pm$.26 (8)	2.01 $\pm$.26 (61)	2.05 $\pm$.24 (54)
Sixth	2.49 $\pm$.34 (19)	2.39 $\pm$.18 (97)	2.44 $\pm$.27 (34)
Seventh	2.83 $\pm$.31 (26)	2.69 $\pm$.18 (84)	2.70 $\pm$.19 (34)
Penultimate male	3.01 $\pm$.23 (18)	2.86 $\pm$.22 (88)	3.00 $\pm$.26 (48)
Penultimate female	3.55 $\pm$.24 (25)	3.03 $\pm$.25 (72)	3.25 $\pm$.35 (60)
Adult male	3.47 $\pm$.22 (30)	3.29 $\pm$.22 (36)	3.53 $\pm$.25 (33)
Adult female	3.99 $\pm$.47 (30)	3.63 $\pm$.43 (45)	3.88 $\pm$.38 (38)

seen in the mean carapace widths of adults (<0.25 mm for both males and females). Again, this difference in size can probably be attributed to lower feeding rates in 1981 which resulted in slower, decreased growth for these last instar stages.

Unfortunately, there is no published technique for determining instar stages of Misumenops. I was therefore unable to complete similar analyses on other members of the guild.

Fecundity

Table 11 and Figs. 11 and 12 contain data obtained from the collected egg sacs of three guild members (P. viridans, M. deserti and M. californicus) during 1981 and 1982. No information was available for M. lepidus. In 1981 25 P. viridans egg sacs were collected from mid-May to early August. The number of eggs/sac ranged from 25-137 with a mean of 73.56 ± 6.70 S.E.. Mean female carapace width was 3.26 ± 0.29 mm. The majority of egg sacs (68%) were found on Corethrogne filangifolia. This shrub is often bright green with small purple flowers and P. viridans blends in well with the coloration. Egg sacs were also found on Eriogonum fasciculatum (28%) and Encelia farinosa (4%).

During that same year only 19 egg sacs of M. deserti were collected. Mean number of eggs/sac was 110.68 ± 16.24 with a range of 51-347. Over half (53%) of the egg sacs were collected from Artemisia tridentata. Four egg sacs each (22%) were found on C. filangifolia and E. fasciculatum and one (5%) on Brassica nigra. Sixteen of the egg sacs were collected in July and early August ($n=7$ and $n=9$,

Table 11. Comparison of reproductive output (no. of eggs/sac) in 1981 versus 1982 for three spider species (P. = Peucetia, M. = Misumenops). Mean values are accompanied by + one standard error.

Spider Species	N	Mean	S.E.	Range	Mean Female Carapace Width
1981					
<u>P. viridans</u>	25	73.56	6.70	25-137	3.26±0.12
<u>M. deserti</u>	19	110.68	16.24	51-347	2.39±0.05
1982					
<u>P. viridans</u>	55	122.91	5.66	47-238	3.96±0.05
<u>M. deserti</u>	70	163.30	8.52	64-434	2.65±0.03
<u>M. californicus</u>	6	133.33	11.51	85-172	2.26±0.76

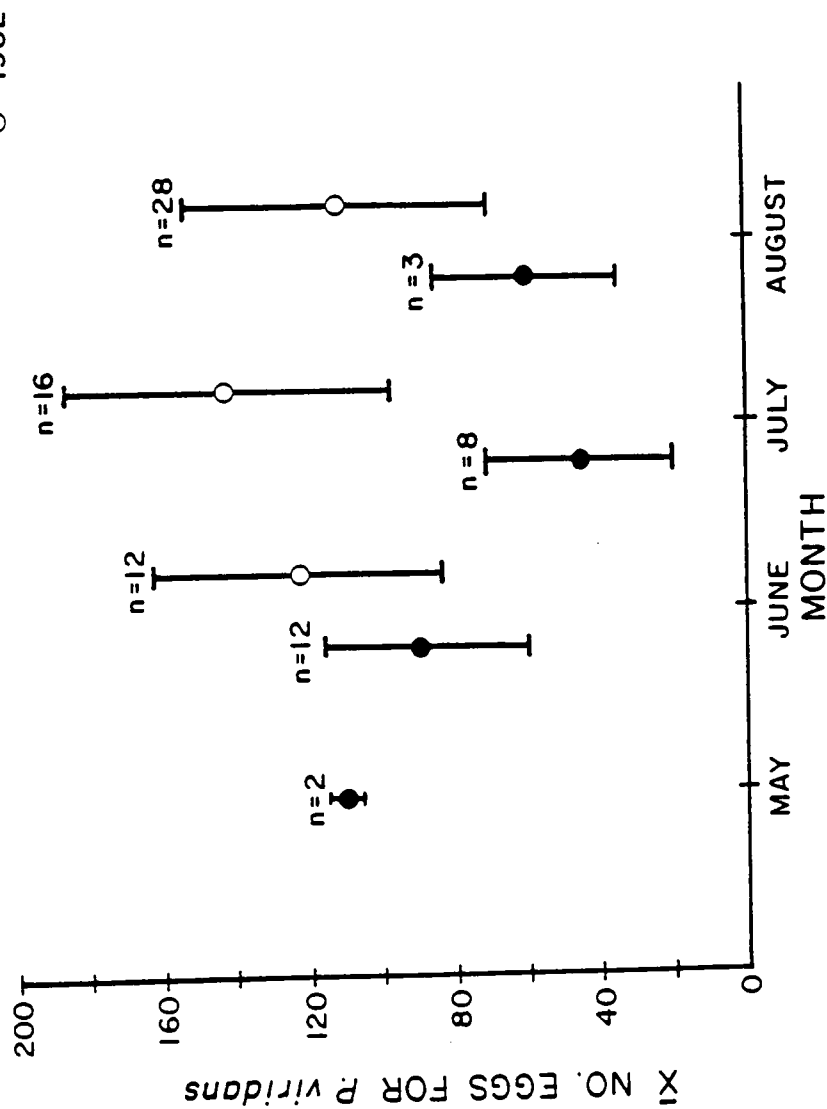


Figure 11. Mean number of eggs/egg sac for female *Peuceetia viridans* for 1981 and 1982. Center dots represent the mean and vertical bars one standard deviation.

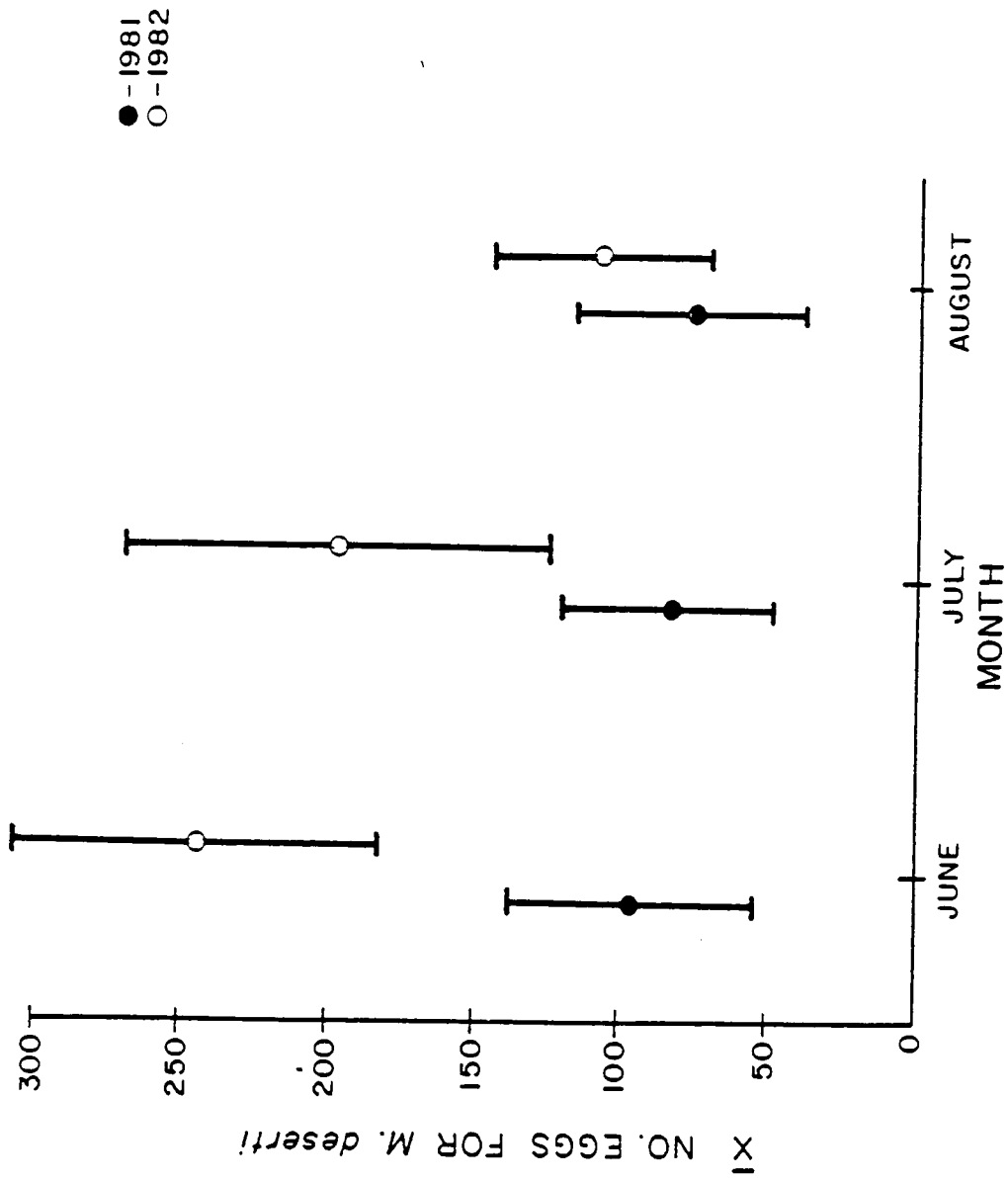


Figure 12. Mean number of eggs/egg sac for female *Misumenops deserti* for 1981 and 1982. Center dots represent the mean and vertical bars one standard deviation.

respectively). It is interesting to note that the single egg sac found in May contained over three times as many eggs ($n=347$) as those collected in June, July and August ($\bar{X}=97.5$, 80.57 and 110.78, respectively). Mean female carapace width was 2.39 ± 0.5 mm.

Twice as many ($n=56$) P. viridans egg sacs were found in 1982, 48% of which were located on C. filangifolia. Twelve (22%) were collected from A. tridentata, 14 (25%) on E. fasciculatum and three (5%) on E. farinosa. The number of eggs/sac ranged from 47-238 with a mean of 122.91 ± 5.66 , significantly larger from 1981 ($t=5.63$, $p<.001$). Mean female carapace width was 3.96 ± 0.08 mm.

The regression of carapace width on number of eggs/sac in 1982 demonstrated no significant relationship between these two variables ($F=0.46$, $p>.5$).

Seventy M. deserti egg sacs were collected from June through mid-August in 1982. The number of eggs/sac for this species ranged from 63-434 with a mean of 163.30 ± 8.52 which is significantly larger than 1981 ($t=2.87$, $p<.001$). The mean female carapace width (2.65 ± 0.03 mm) also differed significantly from 1981 ($t=4.33$, $p<.001$). The mean number of eggs/month ranged from a high of 231 in June ($n=7$ sacs) down to 196 in July ($n=34$ sacs) and 109 in August ($n=29$ sacs). Thus, it appears as if fecundity is higher in the early summer months compared to later in the reproductive season.

Regression analysis on the relationship between carapace width and number of eggs/sac in this species was highly significant ($F=50.16$, $p<.0001$) indicating that the number of eggs a spider produces was a function of spider size during this year.

Most female M. deserti inhabit flowering shrubs such as E. fasciculatum, C. filangifolia and B. nigra, since prey density is higher on these plants. However, when it is time for gravid females to lay their eggs a large number move from flowering plants to A. tridentata which at this time of year (June-August) is lacking flowers and has turned from bright green to a grayish brown. The change in habitat from flowering shrubs to one that is devoid of blossoms essentially removes M. deserti from an area of high prey availability; but, at the same time this change in habitat effectively removes the spider from predators and potential conflicts with conspecifics and other guild members.

Only six M. californicus egg sacs were collected during the study period, all in June of 1982 and all from A. tridentata. The number of eggs/sac ranged from 85-172 with a mean of 133.33 ± 11.51 .

Discussion

The extent of niche overlap is often assumed to be positively correlated with the intensity of competition (MacArthur 1972; Cody 1974; Rathcke 1976). Thus, the higher the overlap value for a given resource the greater the degree of competition. However, Colwell and Futuyma (1971), Sale (1974), Pianka (1974) and others have commented that overlap in resource use need not result in competition. This is because resources may not be in short supply or because factors such as predation (Vandermeer 1972; Connell 1975) and/or environmental variability (Andrewartha and Birch 1954; Wiens 1977; Wiens and Rotenberry 1980) maintain populations below the carrying capacity set by

available resources. Thus, the extension of resource overlap data to competitive effects has its uncertainties.

The results obtained in this study show that species overlap in resource use varies from year to year. Potentially, the time of greatest competition should have occurred in 1981 because of the marked decrease observed in available resources (blossoms and prey items) in that year, resulting from the heat wave which occurred mid-way through the season. The small increase in microhabitat overlap observed in 1981 can therefore be attributed to the sudden convergence of spiders onto the few remaining flowers on those shrubs that were not killed by the heat. In this case then, the higher overlap values obtained could be equated with competition for space. Power (1981) also found that there was a relatively high overlap in microhabitat among similar species of tropical stream catfish during the dry season. He suggests that the high overlap results from the fact that all species converge on the habitat that is safest from predators.

Contrary to the findings for microhabitat utilization, the data on prey taxa and prey size indicate that average overlap decreased in 1981 along these two resource dimensions. Similar findings have been made by researchers working with stream insects (Townsend and Hildrew 1979), rainforest frogs (Toft 1980), hummingbirds (Feinsinger 1976), herbivorous mammals (Jarman 1971) and bats (Heithaus et al. 1975). These studies have all shown that similar species overlap less during the lean season often because they become specialized in terms of microhabitat and food.

The prey taxa and prey size data for the raptorial spider guild indicate low overlap in times of stress and higher overlap in times of plenty. Yet, these data are in direct contradiction to the predictions of optimal foraging theory. One of the major tenets of optimal foraging theory is that a decrease in food availability will lead to decreased diet selectivity (=diet expansion); thus resulting in higher overlap (Schoener 1971; MacArthur 1972; Curio 1976; Krebs 1978). Diet expansion with decreased prey availability may manifest itself in two different ways: an increase in the niche breadth of prey taxa eaten or an increase in the niche breadth of prey size eaten.

When niche breadth values for prey taxa and prey size are reviewed (Table 6) it can be seen that both P. viridans and M. deserti had expanded niche breadths in 1981. The overlap and niche breadth results then seem to be contradictory. On the one hand, low overlap values in 1981 indicate that these spiders became more specialized in the prey items they fed upon, while niche breadth data indicate that there was, at least for P. viridans and M. deserti, an expansion in the range of prey taxa utilized.

The year of stress (1981) was followed by a relatively benign year wherein resources again became abundant. Therefore, one would expect to observe increased diet selectivity and specialization (=decreased niche breadth) resulting in lower overlap between species. And, the 1982 overlap data for prey taxa and prey size bear this prediction out with values slightly below those of 1981. However, niche breadth data indicate that only two species, P. viridans and M. deserti,

became more specialized in terms of prey taxa and all four species showed an increase in the size range of prey items rather than a decrease.

The lack of dietary specialization in M. californicus and M. lepidus in 1982 may be the result of a paucity of profitable or preferred items in the prey spectrum. Therefore, in order to maintain energy and nutritional requirements a wider range of prey taxa was incorporated into the diet. Conversely, the available prey in 1982 may have offered P. viridans and M. deserti a greater spectrum of preferred prey resulting in greater selectivity and thus a decrease in niche breadth.

The results of this study suggest that some caution and skepticism are in order before one can interpret niche overlap and niche breadth data in terms of broad generalizations. The conclusions that emerge may not really apply to the system as a whole and the generality of their application to other systems may not hold true. What seems to be more important is an understanding of the complexities of supply and demand as they relate to species at the local population level.

CHAPTER 5

FIELD EXPERIMENTS

Introduction

Resource partitioning studies often reveal patterns of resource allocation and degree of niche overlap among syntopic closely related species as well as delineating the distribution and relative abundance of animal species. However, at best, the intensity of biological interactions can only be inferred from these studies, and they provide only indirect evidence for the role of competition in developing and maintaining community structure.

Recently a number of ecologists (Reynoldson and Bellamy 1971; Connell 1975; Wiens 1977) have called for more reliable methods of detecting interspecific competition. The method most utilized to date has been the controlled field experiment, whose essential aspect is that everything varies in the same way between treatment and control except for the factor being tested. The two factors most often manipulated are the densities of potentially competing species and resource availability. Density manipulations generally entail removal of the dominant species. If interspecific competition is a primary force in organizing a guild or community, then removal of the dominant species should result in one or more of the following effects on the species remaining: 1) increased density, 2) increased fecundity, 3) altered patterns of habitat utilization, 4) altered patterns of food resource use, 5) faster growth resulting in larger body size.

Methods

Field Experiments

Preliminary data obtained in 1977 (Turner and Polis 1979) and 1980 revealed that the dominant guild member in terms of numbers and biomass was Peucetia viridans. The following field experiments were therefore conducted in 1981 and repeated in 1982 to determine the effects, if any, of the removal of this dominant species.

The removal experiments were performed on four contiguous plots, 3 x 20 m each for a total area of 240 m². Another four plots of the same size and with similar vegetation patterns were set up 100 m away and designated as controls. A two meter perimeter surrounding both the experimental and control plots was cleared of all vegetation to reduce the possibility of spider immigration into the areas.

Surveys in the experimental plots were conducted two to three times a month (with the exception of fewer surveys in July) and consisted of removing all P. viridans from the area each time. The spiders were captured by knocking them into a jar containing 70% ethanol. Thus, any P. viridans found in the area after each removal was a result of migration into the plots.

Before each lynx spider was captured, data on its sex and age, along with the species of shrub and position on the plant were collected as previously described. Also measured was the distance in cm to the nearest spider neighbor, regardless of species. Similar data were obtained for each Misumenops species encountered.

Control plots were surveyed in a similar manner with the exception that no Peucetia were removed. Surveys took place on either the same day as the removals were done or on the following day. As in 1980 removals and surveys were conducted on clear days between 0800 and 1300 hours. All spiders found feeding in either set of plots had the prey removed and preserved in 70% ethanol. If a P. viridans was found feeding in an experimental plot both the spider and prey were collected.

Prey Availability

Each time a survey was conducted the abundance of available prey was estimated in both the experimental and control plots by counting the number of arthropods associated with the flowers of each shrub. (Excluded from the arthropod count were those insects which have never or rarely been documented as prey items for these spiders; e.g., mites, some noxious hemipterans and small hard-winged beetles.) Also counted were the number of blossoms on each bush which I subsequently categorized as falling within a particular range (0-25, 25-50, etc.). Prey abundance for each set of plots was then estimated by calculating the mean number of arthropods per number of available blossoms. Also calculated was the mean number of spiders per available blossom (see Table 1-A).

Results

Population Density of P. viridans

High immigration kept populations of P. viridans above zero in the removal plots. Densities of adults and immatures were continually

reduced throughout the experiment and despite immigration, densities remained lower than in the control plots (Fig. 13 a and b). The total number of immatures and adults in the control plots was approximately the same at the beginning of the experiment each year. Population density reached a high of 150 individuals in June of 1981 and remained relatively stable from that time until August. In 1982, however, the population density decreased markedly in June, but then recovered and reached a peak of over 200 by early August. The continual increase in density from June through August is probably a result of spiderling emergence from egg sacs in the case of both experimental and control plots.

Fig. 14 shows the population density of adult P. viridans on the control plots. In 1981 adults reached their highest density in June, decreased slightly in mid-June and then remained at basically the same level for the remainder of the experiment. This pattern is similar to the one observed for all instars of P. viridans. The adult population density did not peak until July in 1982. Numbers of adults increased from 18 in mid-June to almost 60 two weeks later. This was probably a result of penultimate instars molting into the adult stage. By August numbers of adults had decreased back down to about 35.

Population Density of Misumenops Species

Removal of P. viridans in 1981 and 1982 did not seem to affect the population density of adult female M. lepidus or M. californicus (Figs. 15, 16). The overall patterns of control plot population size of these two species relative to that in the removal plots remained

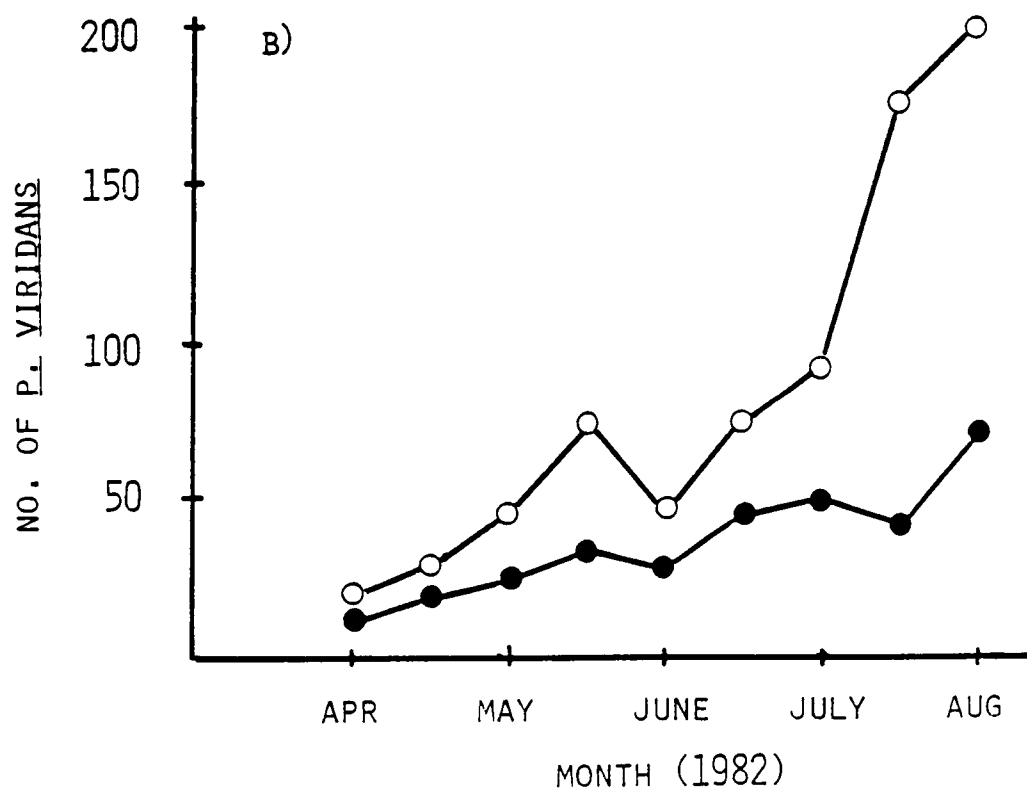
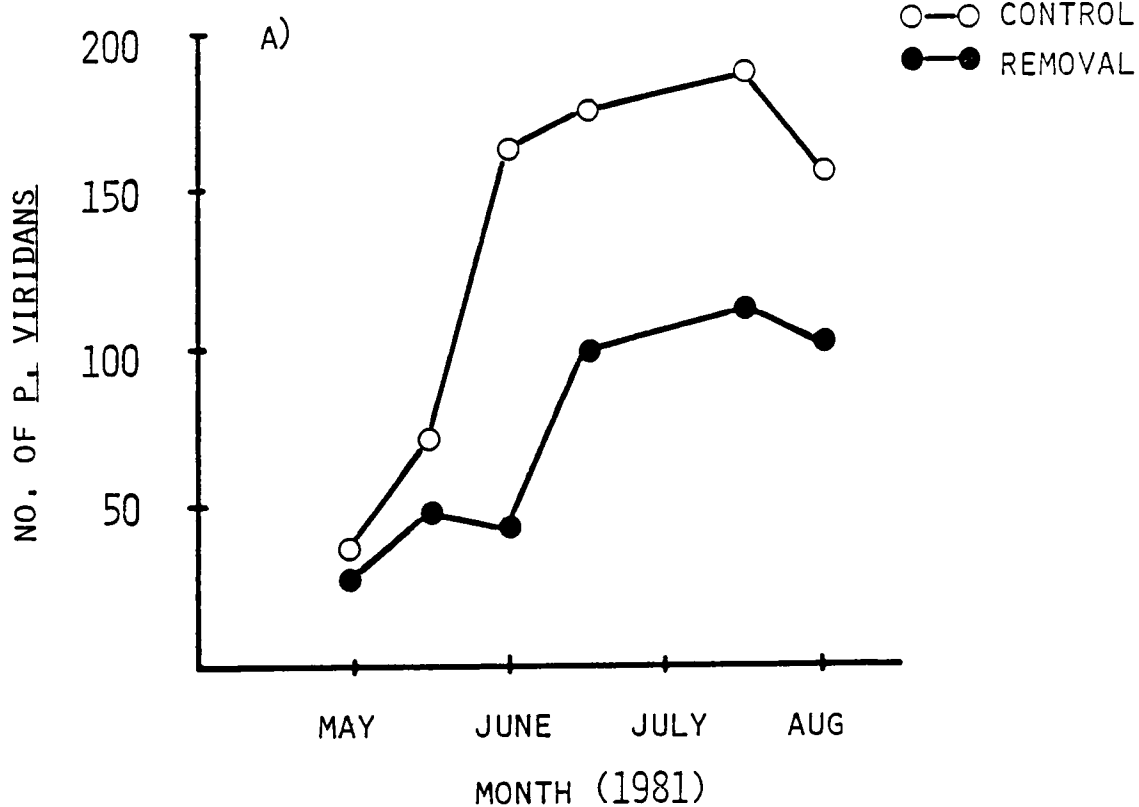


Figure 13. Density of adult *Peuceetia viridans* in control and removal plots over a four month period in 1981 and over a five month period in 1982.

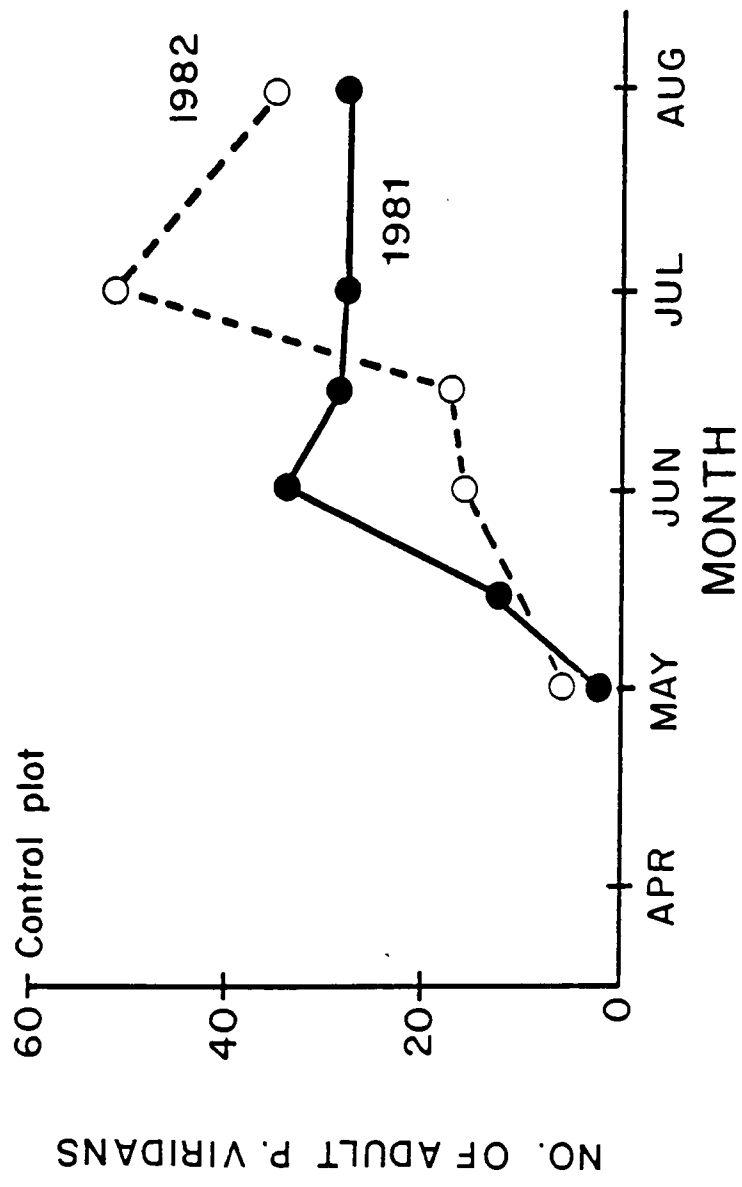


Figure 14. Density of adult *Peuceetia viridans* in the control plots in 1981 and 1982.

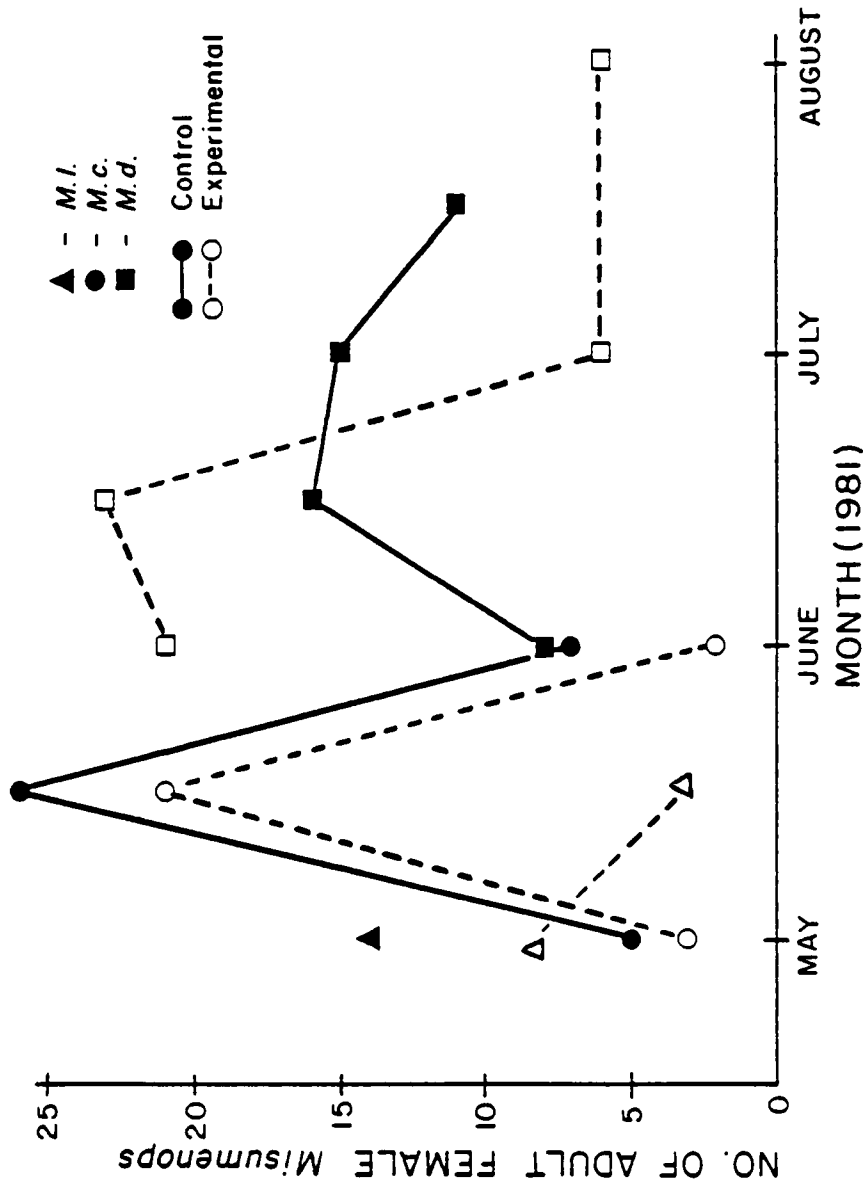


Figure 15. Absolute density of three species of *Misumenops* adult females in control and experimental plots from May through August in 1981. Species names are abbreviated: *M.l.* = *M. lepidus*; *M.c.* = *M. californicus*; *M.d.* = *M. deserti*.

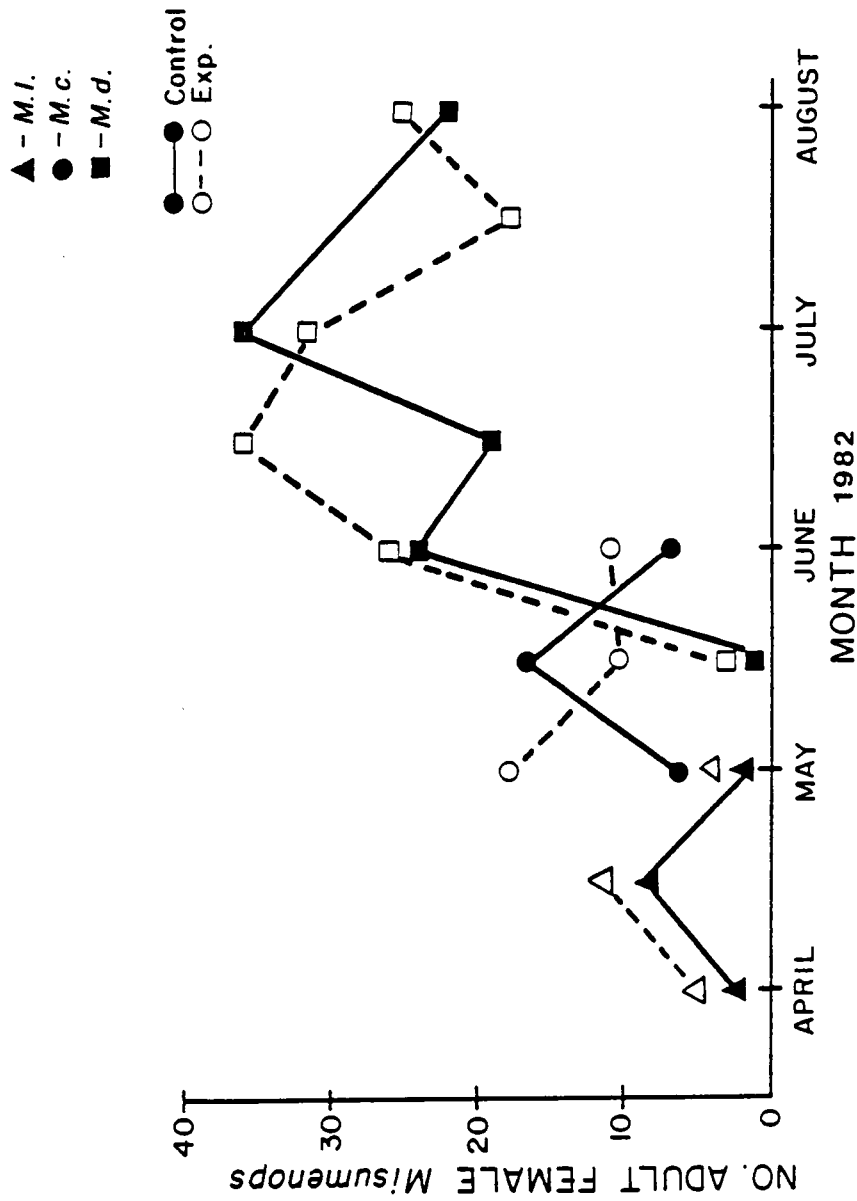


Figure 16. Absolute density of three species of Misumenops adult females in control and experimental plots from April through August in 1982. Species names are abbreviated: M.l. = M. lepidus; M.c. = M. californicus; M.d. = M. deserti.

relatively constant. There is an indication, however, that removal of P. viridans resulted in an increased density of adult female M. deserti in June of both years. However, by July the number of females in the removal plots had decreased to levels below those for the control plots. This was especially evident in 1981. Also, it should be noted that the densities of M. lepidus and M. californicus in both control and experimental plots were essentially the same each year, but that of M. deserti was twice as much in June of 1982 compared to 1981 and three times greater during the months of July and August.

The same patterns in population density occurred for immatures of all three Misumenops species. There was no overall positive response in numbers of juvenile M. lepidus to removal of P. viridans either year (Fig. 17). In contrast, control plot densities in 1981 were higher than in the removal plots in May, June and August. The density of immature M. californicus fluctuated throughout the season (Fig. 18a). There was a marked decrease in numbers from April to May (1982) (Fig. 18b) in both control and experimental plots. Both years showed an increase in density from May to June followed by a subsequent decrease from June to July. This fluctuation in density was also observed for M. deserti juveniles (Fig. 19 a and b) with no real evidence of any competitive release. July of 1981 and 1982 demonstrated a six-fold increase in numbers in the experimental plots which was most probably a result of egg sacs hatching and spiderlings emerging.

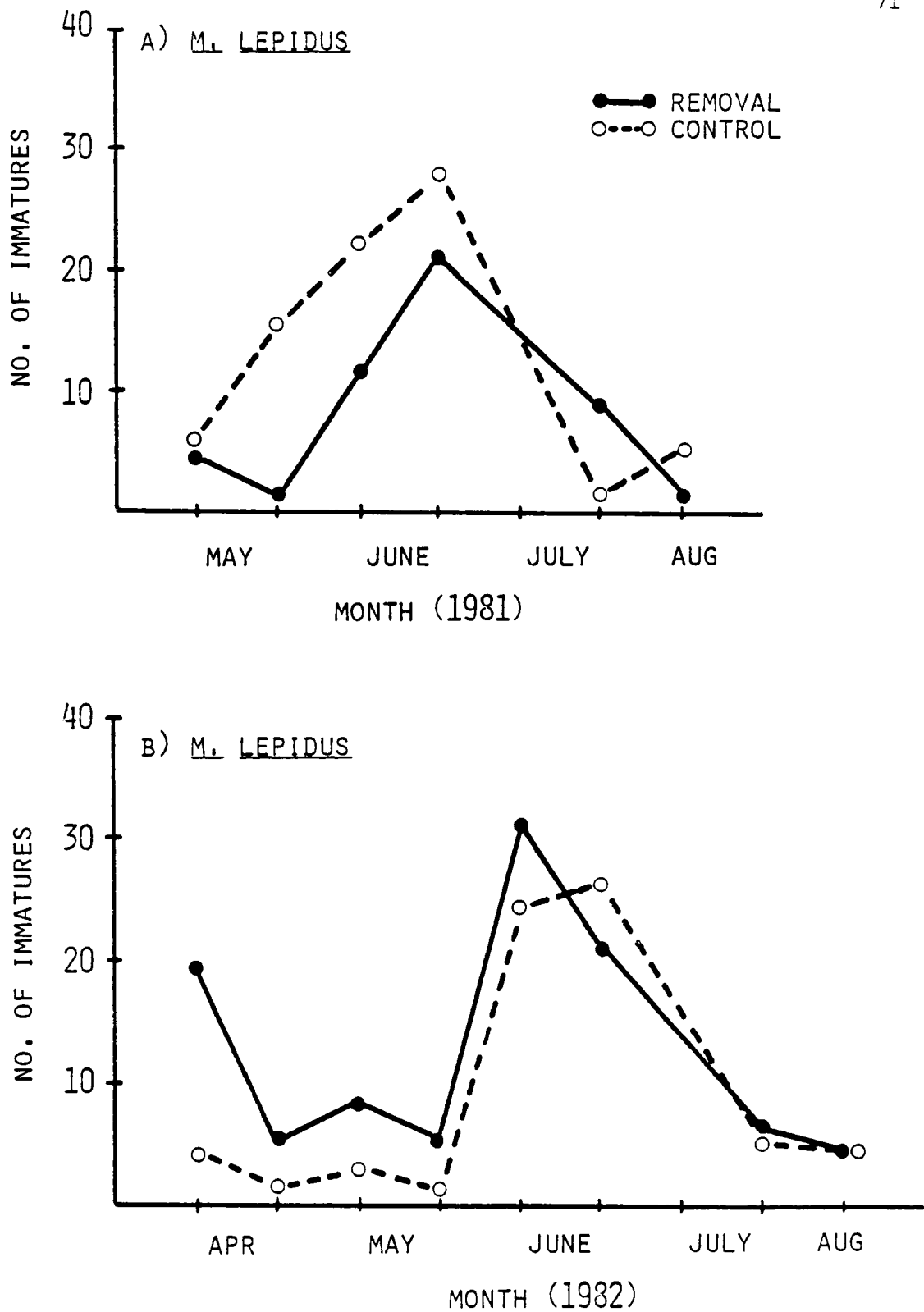


Figure 17. Absolute density of immature individuals of Misumenops lepidus in removal and control plots.

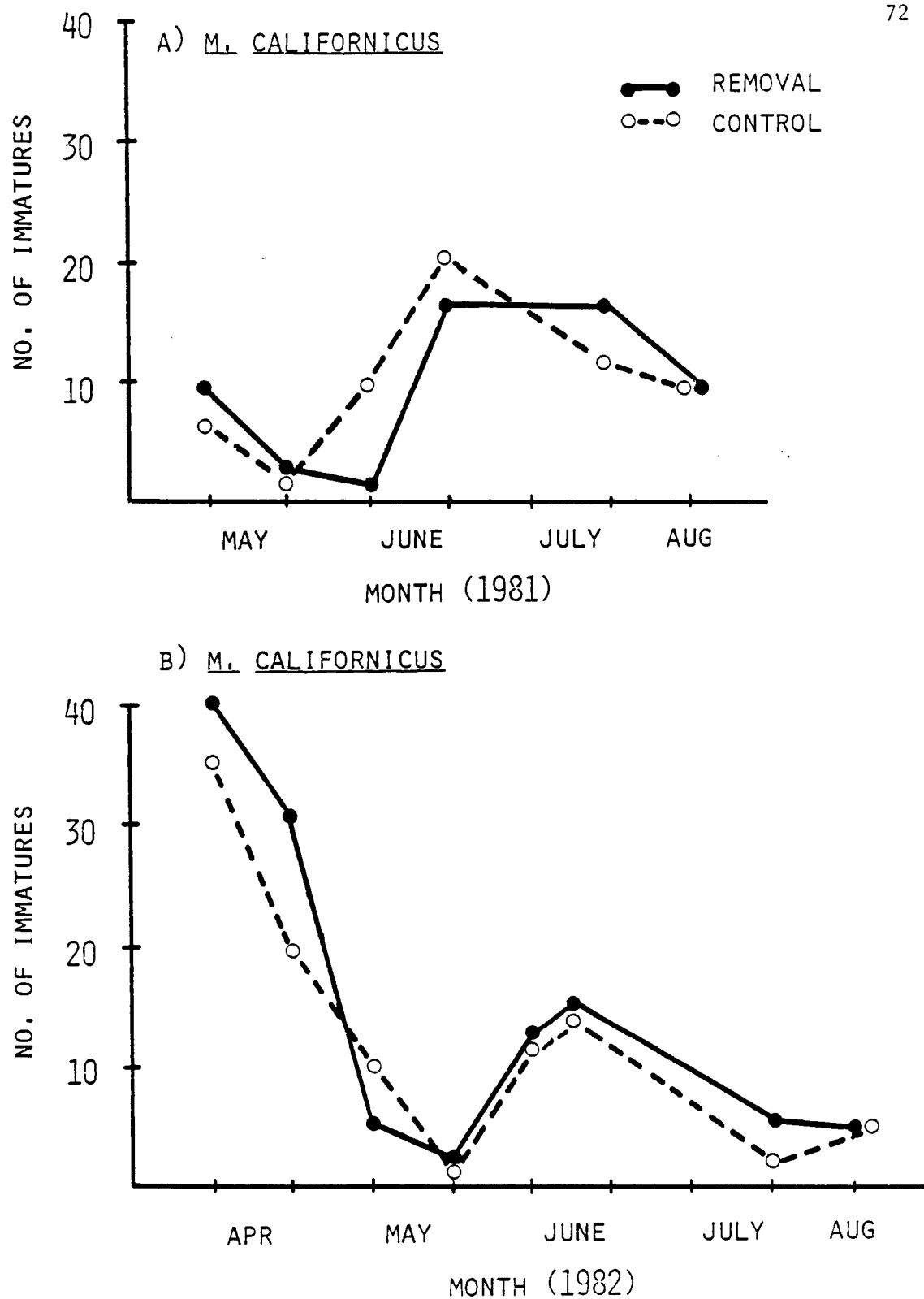


Figure 18. Absolute density of immature individuals of Misumenops californicus in removal and control plots.

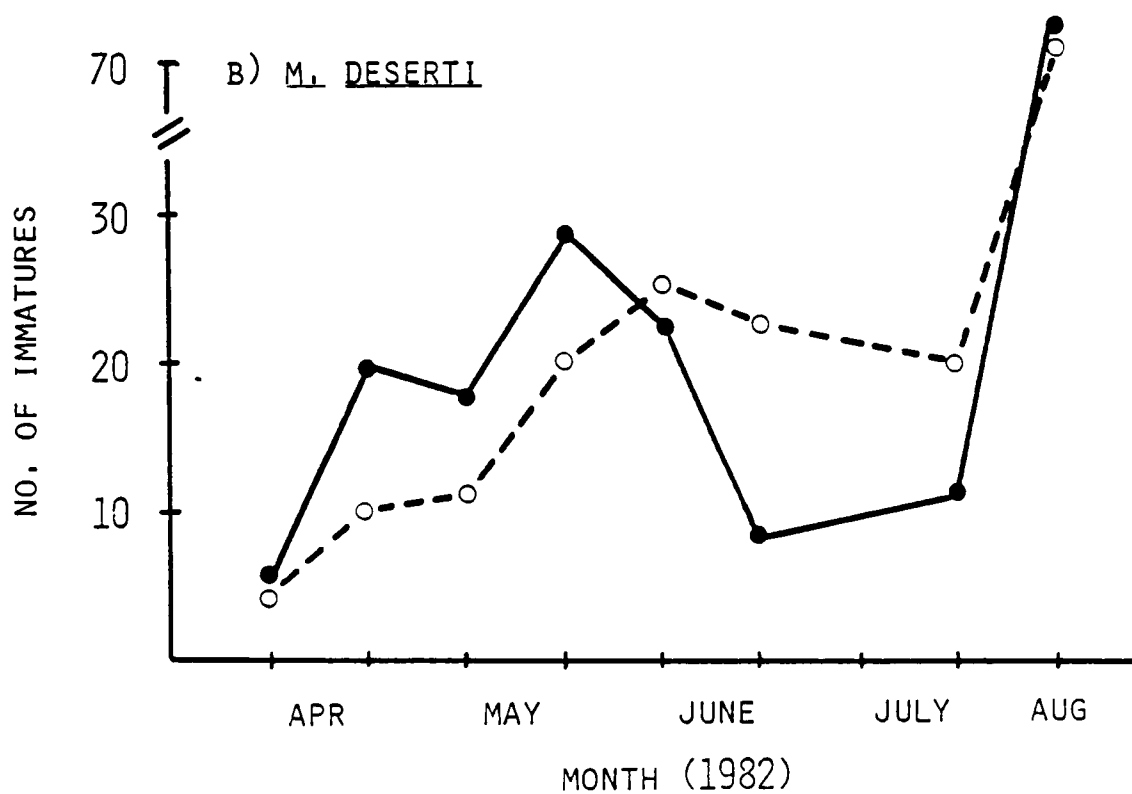
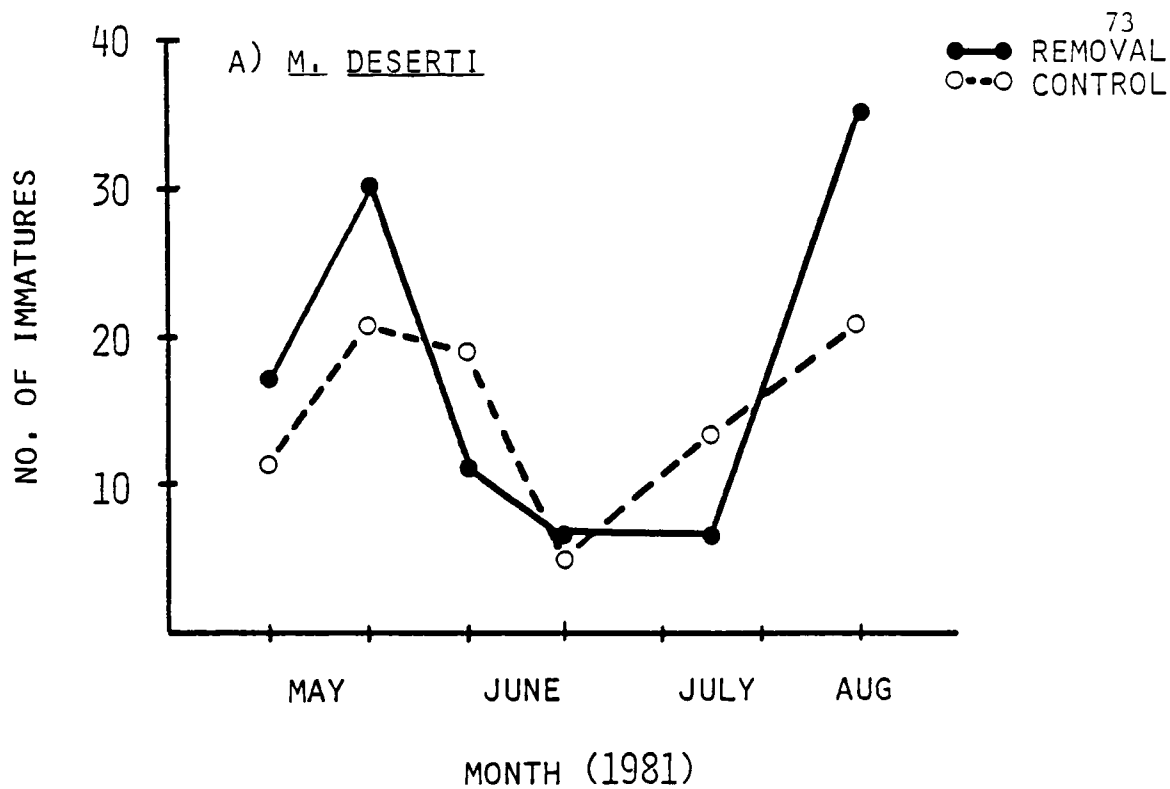


Figure 19. Absolute density of immature individuals of Misumenops deserti in removal and control plots. Note change of scale for 1982.

Prey Abundance

Pairwise Mann-Whitney U comparisons of the mean estimates of prey availability reveal that arthropod abundance was significantly greater in 1982 than in 1981 ($U=77$, $p<.01$), but there was no significant difference between the experimental and control plots in either 1981 ($U=87$, $p>.10$) or 1982 ($U=62$, $p>.10$). This particular method of assessing prey abundance does not provide an unbiased quantitative estimate of the availability of food resources at any given time. Some taxa, orthopterans for example, tend to move off a shrub when approached by a large object. Also, many pollinators do not stay on some shrubs long enough to be included in the counting procedure. However, this method proved to be far superior to sticky trap estimates which were conducted at the same time because it did a better job of sampling the prey types and sizes which are normally included in the diets of members of the raptorial spider guild.

Fecundity

Interspecific competition should result in reduced levels of egg sac production of the species most affected regardless of whether the competition is of an exploitative or interference nature. Table 12 presents data on the number of Misumenops egg sacs found in the control versus experimental plots. All egg sacs observed belong to M. deserti. Although there were more egg sacs produced in the removal plots both years, a chi-square test indicates that this increase was not significant. The number of egg sacs produced in 1982 greatly exceeded that of 1981 (almost 200% in the control plots and 150% in

Table 12. Number of Misumenops egg sacs found in control versus experimental plots.

Year	Control	Experimental	Chi-Square
1981	16 (.38)*	26 (.62)	2.38, N.S.
1982	45 (.41)	64 (.59)	3.31, N.S.

*Relative proportion of egg sacs is in parentheses.

the experimental plots). The lower levels of egg sac production in 1981 may have resulted for one or more of the following reasons:

1) there were fewer Misumenops females in the removal plots in 1981 compared to 1982, 2) fewer egg sacs/female were laid. Under ideal field conditions female Misumenops can lay up to three egg sacs during the reproductive season (Muniappan and Chada 1970). However, because of decreased levels of prey availability in 1981, female spiders were probably energy deficient and capable of laying only one egg sac.

Foraging

If interspecific competition occurs among guild members, then removal of the dominant species may result in various niche shifts of the remaining species ("competitive release"). One might expect microhabitat shifts or an increase in the number and type of available prey. Consequently, there may be an increase in the number of spiders consuming prey.

Data for immature and adults of the three species of Misumenops were pooled because of low sample sizes. There were no differences (Table 13) in the percent of individuals observed feeding in the experimental versus the control plots for either 1981 or 1982 (t test for difference in proportions; $t=4.21$, $p>.10$). There was also little yearly variability in this parameter (Table 13).

A note of interest is that the data for P. viridans are basically the same as those obtained for the Misumenops species. There was no difference in the percent of this species feeding between the experimental and control plots in 1981. However, in 1982, there was a small

Table 13. Percent of Misumenops* and Peucetia viridans feeding in experimental versus control plots.

Spider Species	Experimental	Control
<u>Misumenops</u> - 1981		
No. Feeding	23	22
Total No. in Plot	450	439
Percent Feeding	5.00%	5.00%
<u>Misumenops</u> - 1982		
No. Feeding	38	25
Total No. in Plot	597	379
Percent Feeding	6.00%	7.00%
<u>Peucetia viridans</u> - 1981		
No. Feeding	43	72
Total No. in Plot	547	788
Percent Feeding	8.00%	9.00%
<u>Peucetia viridans</u> - 1982		
No. Feeding	34	44
Total No. in Plot	351	731
Percent Feeding	10.00%	6.00%

*Feeding data for all three Misumenops species have been pooled.

increase in spiders feeding in the experimental plots (10% feeding) relative to the control plots (6% feeding).

These results indicate that individual foraging success for the three Misumenops species is not affected by the removal of P. viridans. However, the slight increase in foraging frequency observed in Peucetia in the experimental plots (1982) suggests that perhaps the density of this species may limit its own foraging success (Table 13). Reduction in the population due to the continual removals may have resulted in intraspecific competitive release.

Discussion

No evidence was found in this study for interspecific exploitative competition among the spider species of this ambush guild. If competitive interactions were occurring, then removal of the dominant species (Peucetia viridans) over long periods of time, should have resulted in an increase in available resources with a concomitant increase in the body size, fecundity, foraging success and/or density of the remaining Misumenops species.

Body sizes of spider species are difficult to compare among years because growth in spiders varies depending on factors such as diet, humidity, temperature and photoperiod. However, any differences in body size of the Misumenops species between the experimental and control area in the same year would be of interest because they would provide direct evidence of competitive release. In an attempt to obtain such data I collected all spiders from both the experimental and control plots at the end of the 1982 season. Due to circumstances

beyond my control (the specimens were stolen from my car) body size data were not available. However, since none of the other predictions of competitive release were evidenced (see below), I consider it doubtful that any of the Misumenops species increased in size because of the removal of P. viridans. Tinkle (1982) in a density manipulation study of an Arizona lizard community, also noted that body size was not different between lizards from experimental and control areas during the same year.

Data on body size are available from outside the study area for each year and these data demonstrate a significant decrease in mean carapace width for all four species in 1981. Turnbull (1962) found that when prey availability becomes scarce, a spider will still continue to mature as long as it has the energy to molt. Thus, a spider can complete a molt, but emerges from the exuvium in the subsequent stage smaller than it was in the previous stage. The availability of prey was greatly decreased in 1981 due to the heat wave which destroyed the majority of flowers in the area. Thus, the number of pollinators fell far below normal levels and the availability of optimal prey decreased. As a result, when penultimate females molted during that period of time, they emerged as adults but smaller in size. Prey were more available in the 1982 season and mean carapace width increased for each species accordingly.

The data on fecundity provided no significant evidence for a competitive effect. For the two years of the study, differences in egg sac production were in the direction predicted by a competition hypothesis, i.e., a greater number of egg sacs were laid in the

removal plots compared to the controls. However, these observed differences were not statistically significant.

If resources are limiting, then removal of a potential competitor could increase the availability of resources to other species. This might lead to increases in the foraging success of the remaining species. Yet, the data on foraging do not indicate any significant differences in the percentage of spiders feeding between the experimental and control plots for either year.

This is a surprising result because prey availability was much greater in 1982 than in 1981. Indirect evidence that these spiders were food limited in 1981 comes from fecundity data which show that the number of eggs/egg sac was significantly smaller in 1981 relative to 1982. In a study of two syntopic species of forest orb weavers, Wise (1979) also found that natural prey levels can limit egg production. However, when he manipulated spider densities he obtained results similar to those of this study; i.e., there was no evidence of an interspecific competitive effect.

The densities of Misumenops species on the experimental plots after the removal of P. viridans did not show significant changes except for an abrupt increase in the numbers of adult female M. deserti in the removal plots in June of each year. This increase may be evidence of a short term competitive release. However, the following month there was a marked density decrease in the experimental plots below that of the controls. There are a number of explanations as to why population density may have dropped so dramatically: 1) emigration of individuals to other areas in

response to high population density, 2) mortality due to disease or parasitism, 3) mortality due to predation, 4) mortality due to abiotic factors, 5) mortality due to cannibalism and/or interspecific guild predation (IGP).

The first explanation is a plausible one since spiders are known to migrate away from areas of high population density (Gertsch 1979; Kayashima 1961; Ross 1977; Kaston 1978; Riechert 1981). However, it is difficult to determine if this was the case for these spiders since the recovery rate of marked individuals was almost nonexistent (personal observation).

Little is known about the diseases of spiders and their effect on spider population size, but field observations over a three year period never gave any indication that these ambush spiders were afflicted with debilitating diseases. Neither does parasitism appear to have much effect, if any, on the density of these spiders. The females of all four species guard their egg sacs continuously, effectively preventing potential parasites from invading the egg sac. Although hundreds of egg sacs were opened and inspected there was never any evidence of parasitism. It should be noted also here that out of almost 800 hours of field time there was only one instance where I saw a parasitic wasp actually pick up a spider and fly off with it.

Predation by vertebrates such as birds and lizards does not appear to contribute to high mortality rates in these spiders. All the guild members occur on shrubs and are often effectively camouflaged from predators by their cryptic coloration. There are very

few bird species in the study area and lizards were never observed on the shrubs themselves.

It is also doubtful if abiotic factors caused the decrease in population density of M. deserti at the same time both years. The heat wave which was over by the first week of June in 1981 may have reduced prey availability to the extent that starvation ensued resulting in a high mortality rate for M. deserti. However, there were no major climatic catastrophes in 1982 that could similarly account for the decrease in numbers of M. deserti in June of that year.

The most likely explanation for the decrease in female M. deserti density is that of interference competition in the form of cannibalism and intraguild predation. "Interference" is defined as any activity which either directly or indirectly limits a competitor's access to a necessary resource or requirement. In this situation, the high spider densities in the experimental plots in June of both years probably resulted in increased exploitation competition for the space resource (flowerheads). Case and Gilpin (1974) have shown that when a species is faced with a situation in which it must compete for common resources either by increasing its exploitation efficiency or else by interfering with its competitor, it often evolves in the direction of the second strategy. Thus, in this guild system, increased interactions between conspecifics and other guild members would have the effect of limiting competition because spider population densities would be maintained below available space and food levels. Similarly, Riechert (1981) has shown that interference competition in the form of intraspecific agonistic interactions produced regular

spacing among female funnel-web spiders. She posits that this kind of territorial system possibly limits population growth such that spider densities are below the carrying capacity of the environment.

This is the first replicated experimental study dealing with non-web building spiders, but other recent or ongoing experimental studies of web builders have also uncovered no evidence for major exploitative interactions between species. Wise (1979) manipulated densities of the basilica (Mecynogea lemniscata) and labyrinth (Metepeira labyrinthea) spiders and discovered that neither species affected the web placement, web-site tenacity, or egg production of the other. Cady (personal communication) in replicated removal experiments involving a community of cliff spiders has found little evidence of exploitation competition. Riechert and Cady (1983) in a study of four species of ecologically equivalent cliff spiders found no evidence of competitive release when heterospecifics were removed from experimental cliffs. They postulate that the lack of competitive release is probably the result of intraguild predation and intraspecific competitive effects.

Although there is high niche overlap along several resource dimensions, exploitative interactions appear to be minimal among this guild of ambush spiders. However, there is direct evidence for the role of interference competition in structuring the guild when resources are limiting. Both cannibalism and intraguild predation increased substantially when foraging sites and prey levels were diminished by climatic "catastrophe" in 1981.

There are numerous cases in the literature (see reviews by Fox 1975 and Polis 1981) in which cannibalism is found to be an inverse

function of the availability of alternative prey. Decreased prey availability generally triggers increased foraging time and movement changing the location of foraging stations. Each of these behaviors in turn increases the probability of inter- and intraspecific contact and the probability that a spider will be eaten by a conspecific or other guild member.

In this particular guild system three feedback loops may exist between interference competition (cannibalism and intraguild predation) and resource availability: 1) As conspecifics and other guild members are eaten the population of competitors declines and per capita food level increases; 2) As density increases, both per capita food and growth decrease (see section on Ecomorphology) producing smaller and weaker individuals that are eaten more frequently; 3) As spiders are satiated by eating conspecifics and other guild members, there is a decrease both in foraging activity and movement effectively limiting interactions among guild members.

CHAPTER 6

SUMMARY AND CONCLUSIONS

Most studies that attempt to delineate resource utilization patterns and competitive effects are done over just a single year or one season. Because they are so short the data produced may lead to incorrect conclusions with regard to community relationships. The results of this three year study are important because they point out the fact that, at least for this particular spider guild, there is a great deal of year-to-year variation in the utilization of resources. Also brought out is the fact that there are no obvious patterns in the magnitude or direction of change from year to year. Therefore, some doubt is cast upon the constancy and applicability of niche theory predictions to this spider guild.

Removal of the dominant guild member, Peucetia viridans, over a two year period did not result in competitive release for the remaining species. This result indicates that interspecific exploitation competition does not play a decisive role in the structuring of the raptorial spider guild. Rather the available evidence implicates interference competition as the mechanism by which the population density of guild members is reduced to levels such that exploitation competition is weak or absent. However, in the case of this system and all other spider guilds, there is a need for more field experiments to determine if the absence of interspecific exploitation competition is the norm and typical of spider communities in general. With reference to this raptorial spider guild, future research should

probably entail removal of each of the Misumenops species in varying combinations over an extended period of time. It would also be necessary to manipulate microhabitat and prey resources for the entire guild to see what effect resource availability has on guild structure.

Adequate testing of competition theory requires a long term approach. Any future experimentation should be done with a number of replicates over many years and at many different localities. Only then will ecologists be able to ascertain whether interspecific competition is a major proximate ecological factor in a particular type of community.

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APPENDIX

Table 1-A. Mean number of spiders per available blossom on five shrub species in experimental and control plots over a two year period. (Exp. = Experimental, Cont. = Control)

Shrub Species	Mean Number of Spiders Per Available Blossom			
	5/1/81		7/1/81	
	<u>Exp.</u>	<u>Cont.</u>	<u>Exp.</u>	<u>Cont.</u>
<u>Encelia farinosa</u>	2.97	2.25	0.04	0.06
<u>Eriogonum fasciculatum</u>	0.23	0.48	2.81	2.42
<u>Corethrogne filangifolia</u>	0.08	0.09	0.89	0.63
<u>Artemisia tridentata</u>	0.16	0.50	0.78	0.57
<u>Brassica nigra</u>	0.04	0.02	----	----
	5/1/82		7/1/82	
	<u>Exp.</u>	<u>Cont.</u>	<u>Exp.</u>	<u>Cont.</u>
<u>Encelia farinosa</u>	2.17	1.39	0.28	0.40
<u>Eriogonum fasciculatum</u>	0.11	0.51	0.15	0.20
<u>Corethrogne filangifolia</u>	0.09	0.10	0.48	0.55
<u>Artemisia tridentata</u>	0.26	0.05	1.86	0.76
<u>Brassica nigra</u>	0.03	----	0.32	0.88

VITA

Märie Turner was born in New York City, New York. She attended Mount Saint Mary's College in Los Angeles and graduated with a B.S. in biology in 1970. She then worked for two years as an accountant. In 1974 she received a secondary teaching credential from the University of California at Riverside and taught chemistry and biology at Hemet High School, California until 1977. She entered California State University at Fullerton that same year and received a Master of Arts degree in biological sciences in 1978. In the fall of 1978 she entered the doctoral program at the University of Tennessee, Knoxville and received her Doctor of Philosophy in 1983.

She is a member of Sigmi Xi, American Society of Zoologists, American Society of Arachnology and American Association for the Advancement of Science. Her interests include ethnic cooking, reading, travel and racquetball.