1992. The Journal of Arachnology 20:179–188

NUMERICAL RESPONSE TO PREY ABUNDANCE BY *ZYGIELLA X-NOTATA* (ARANEAE, ARANEIDAE)

David A. Spiller: Department of Zoology and Center for Population Biology, University of California, Davis, California 95616 USA

ABSTRACT. To test the effect of prey abundance on the orb spider *Zygiella x-notata* I conducted two field experiments at the same site. In the first experiment, from 20 June to 9 September 1978, I augmented prey abundance in two plots interspersed within four control plots; at the end of the experiment the mean number of spiders was 2.7 times higher in prey-augmented plots than in control plots, and the difference was highly significant ($P = 0.005$). In the second experiment, from 25 June to 16 September 1979, I augmented prey abundance in one plot located in between two control plots; at the end of the experiment the number of spiders was > 3.0 times higher in the prey-augmented plot than in each control plot. Although numbers of spiders in the 1979 experiment could not be analyzed statistically because the treatment was not replicated, they support the results of the 1978 experiment. I monitored the phenology of the population at the experimental site and an unmanipulated population at a different site throughout 1978 and 1979. In both years reproduction began earlier in the experimental population than in the unmanipulated population. In 1979 I collected eggs sacs in both populations. The experimental population contained more eggs and heavier eggs than those than in the unmanipulated population. Within the experimental population, egg sacs in the prey-augmented plot contained heavier eggs than those in control plots.

Numerous comparative and experimental studies indicate that spiders often experience food shortages in nature (review in Wise 1992). However, the evidence that spider population sizes respond numerically to temporal fluctuations in prey abundance is equivocal. Some observational studies found positive correlations between abundances of spiders and their potential prey (e.g., Wingerden 1978) but others found no correlation (e.g., Greenstone 1978). Furthermore, a positive correlation could be due to both spiders and their prey responding to some other environmental factor. An experimental study in rice fields showed that spider densities increased in areas where *Drosophila* flies were released relative to control areas (Kobayashi 1975); unfortunately, problems in experimental design and presentation of statistical tests make it difficult to assess the observed response (Wise 1992). Several studies showed that spiders moved from areas with low prey abundance to areas with high prey abundance (Riechert & Gillespie 1986); this "aggregative response" (Hassell & May 1974) changes the predator's distribution, but not necessarily the predator's population size. Extensive studies of *Agelenopsis aperta* (Gertsch) demonstrated that reproductive success was related to prey availability (Riechert & Tracy 1975); however, population size was limited by suitable web sites (via territoriality), and was not influenced by prey abundance (Riechert 1981).

Several possible factors could restrict a numerical response by spiders. Riechert & Lockley (1984) suggested that the extent to which spiders respond numerically is limited by long generation times of spiders relative to their prey and by strong self limitation within spider populations. Field experiments indicate that predators may often reduce spider populations (Askenmo 1977; Gunnarsson 1983; Wise 1982; Pacala & Roughgarden 1984; Polis & McCormick 1986; Spiller & Schoener 1988). Frequently, both spiders and their predators eat some of the same types of prey (Polis et al. 1989; Spiller & Schoener 1990). Therefore, a numerical response by spiders could be impeded by spider predators responding numerically to the same prey. Wise (1992) concluded that although many field experiments have shown that food shortages limit spider growth rate and fecundity, more experiments are needed to determine whether these parameters are translated into increased population size in the next generation.

Zygiella x-notata (Clerck) is a common orb spider in coastal areas of California (Gertsch 1964; Levi 1974). In this study, to test for a numerical response by *Z. x-notata* I conducted two prey-augmentation experiments at the same site. In

Table 1.—Mean (1 SE) web radii and estimated mean web areas for different size classes of *Z. x-notata*. Mean web areas were estimated by assuming that webs were circular (which they were approximately).

Class	Body length (mm)	*n*	Web radius (cm)	Estimated mean web area (cm^2)
Hatchlings	<2.0	40	3.3 (0.1)	34
Juveniles	2.0–3.9	36	6.3 (0.2)	125
Subadults	4.0–5.9	42	8.4 (0.3)	222
Adult females	≥6.0	103	11.4 (0.3)	415

addition, I compared some life-history characteristics of the population at the experimental site to those of an unmanipulated population at a different site.

METHODS

Censusing procedures.—*Zygiella x-notata* adult females are about 6.0–8.0 mm in body length (measured from the chelicerae to the posterior end of the abdomen). Adult males are about 4.5–6.5 mm. In this study I divided the spiders into 4 age/size classes: hatchlings (< 2.0 mm), juveniles (2.0–3.9 mm), subadults (4.0–5.9 mm) and adults (≥ 6.0 mm and smaller adult males). During field censuses I counted the numbers of spiders in each class. To test my accuracy in size determination, I assigned 90 individuals to these size classes in the field, and then collected and measured them with an ocular micrometer; 83% were assigned to the correct size class.

I censused two *Z. x-notata* populations repeatedly for over two years. The first population inhabited a group of 11 abandoned cabins located about 100 m inland from the beach at Coal Oil Point, which is approximately 2 km west of the University of California, Santa Barbara Campus. Most spiders nested underneath ledges that were 1.5 m above the ground and surrounded each cabin. I censused all individuals within 0.5 m of the ledges (total area censused was 162 m^2) about once a month from November 1977 to June 1980. The second population inhabited an assemblage of large boulders, constructed for erosion control, at the base of a cliff on the University of California, Santa Barbara Campus Beach. The assemblage was about 100 m long and 6 m wide, and was about 0.5–1.0 m above mean higher high water. The spiders built their orbs in caves formed by the boulders and caught mostly flies that bred in drift kelp on the beach. I censused all individuals within a 48 m × 6 m section of boulders about once a month from October 1977 to February 1980. The first population was unmanipulated whereas the second was prey augmented (see below).

Beginning in July 1978, I recorded the number of egg sacs and the numbers of arthropods in the spiders' webs and being consumed by the spiders in each site. For each census I computed an index of prey availability by dividing the total number of arthropods counted by the estimated total area of webs censused. I computed the total area of webs censused from the numbers of spiders with webs in each size class and the estimated mean web area of each size class. Mean web area was estimated by measuring the radii of a large sample of webs in the field (Table 1).

Prey-augmentation experiments.—On 19 June 1978, I divided the 48 m × 6 m section of boulders into six contiguous 8 m × 6 m plots, and then censused each plot. From 20 June to 9 September 1978 I augmented prey abundance in the second and fifth plots; thus, there were two treatment plots and four control plots (Fig. 1). I chose this arrangement, rather than assigning treatments randomly, to ensure that treatment plots were interspersed within control plots, as suggested by Hurlbert (1984). To augment prey abundance, I put large quantities of drift kelp at the bottom of caves within the treatment plots during the first few days of the experiment, and added smaller amounts of kelp and sea water about twice a week. I censused each plot at about 1–2 wk intervals from 25 June to 10 September 1978, and at about 2–3 wk intervals from 24 September to 10 December 1978.

On 24 June 1979, I divided the same 48 m × 6 m section of boulders into three contiguous 16 m × 6 m plots, and then censused each plot. From 25 June to 16 September 1979 I put kelp in the center plot; thus, there was one treatment in between two controls (Fig. 1). I chose this arrangement so that prey was augmented in a different location in this year than in the previous year. I censused each plot about once a month from July to December 1979.

Egg sac collections.—From 2 September to 15 October 1979 I collected all egg sacs at the unmanipulated site and all that I could find in each plot at the experimental site (I might have missed some sacs located inside crevices at the experimental site). During this time period I visited each site at least twice a week and collected each new sac produced. All the eggs from each sac were counted, dried at 60 °C for 24 hr, and weighed together. I did not analyze sacs containing hatchlings.

Analyses.—To assess whether adding kelp to the treatment plots increased prey availability during the experiment in 1978, I computed the mean index of prey availability (number of prey/m^2 web) recorded in each plot from 25 June (first census after I began adding kelp) to 10 September (one day after my last addition), and then compared the mean indices in treatment and control plots with a one-tailed *t* test. To test the overall treatment effect on *Z. x-notata* in 1978, I performed a one-tailed *t* test on total number of individuals in each plot on 10 September; in addition, I analyzed the change in total number of individuals in each plot from 19 June (the day before the experiment) to 10 September. Prey-availability indices, numbers of egg sacs and numbers of each age/size class recorded during each census are given for descriptive purposes, but they are not statistically analyzed. I present the data recorded during the 1979 experiment for descriptive purposes, but the treatment effect cannot be tested statistically because kelp was added to only one plot.

From the data on egg sacs collected in 1979, I analyzed two variables: number of eggs per sac and mean biomass per egg per sac. I treated each of the three plots in the experimental site and the unmanipulated site as four separate groups. For each variable I performed a one-way ANOVA with three contrasts. Two contrasts tested the variation among plots within the experimental site (treatment vs. control 1 + control 2; control 1 vs. control 2) and one contrast tested the variation between sites (experimental site [all plots] vs. unmanipulated site). The purpose of these tests is to describe the extent to which the variables in the areas differed, but they cannot be interpreted directly as tests of the hypothesis that the spiders are food limited.

RESULTS

Life-history observations.—The population at the unmanipulated site exhibited an annual life cycle (Fig. 2). In 1978, a cohort emerged in early spring, matured during late spring and early summer, reproduced during late summer and fall, and declined during fall and winter. The offspring produced in 1978 overwintered in egg sacs and emerged during late winter and early spring 1979. This cohort matured during late spring and early summer, reproduced during late summer and fall, and declined during fall and winter. Note that I collected 19 egg sacs from 2 September to 15 October 1979; 27 egg sacs were produced from 16 October 1979 to 15 January 1980. The offspring produced by the 1979 cohort emerged during late winter and early spring 1980 and developed later in the spring. Prey-availability indices were relatively high during winter and spring, and were relatively low during summer and fall.

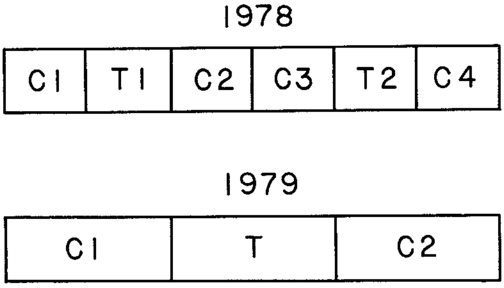

Figure 1.—Spatial design of the prey-augmentation experiments. In 1978 prey abundance was augmented in plots T1 and T2. In 1979 prey abundance was augmented in plot T (see Methods for details).

The phenology of the experimental population was more complex (Fig. 3). Hatchlings emerged in fall 1977 but they either died or emigrated during severe winter storms. (During a storm in January 1978 I observed waves breaking on the boulders; the next day no spider was present in the site.) The site was apparently recolonized in late winter and spring 1978 by juveniles and subadults. This cohort matured in late spring and early summer 1978, and some adult females reproduced in early summer. A second cohort emerged later in the summer and developed in fall 1978. Two cohorts emerged in 1979. The first emerged during late winter and early spring and matured later in the spring. Some adult females reproduced in early summer 1979. The second cohort emerged later in the summer and developed in fall 1979. Note that this cohort was relatively small because I collected all visible egg sacs within the censused area from 2 September to 15 October 1979; hatchlings that were counted during this time period emerged either from hidden sacs within the censused area or from sacs outside the censused area.

Prey-availability indices tended to be higher at the experimental site than at the unmanipu-

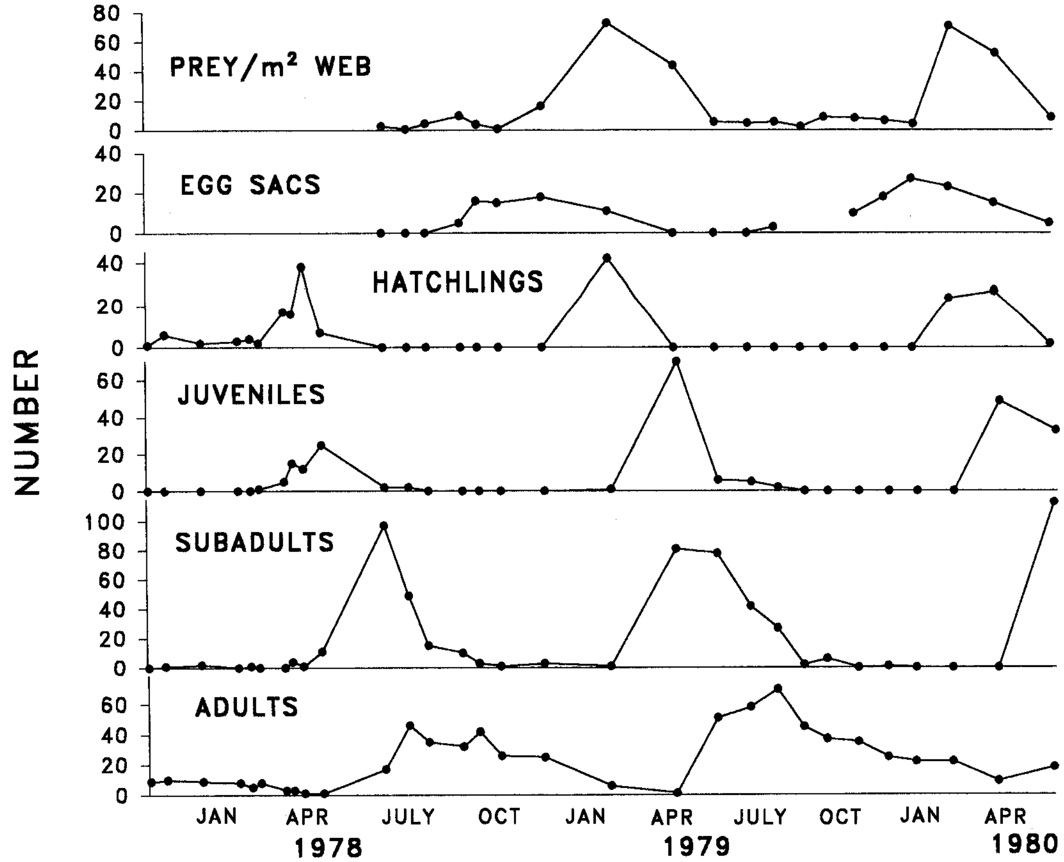

Figure 2.—Prey-availability indices (no. prey/m² web) and numbers of *Z. x-notata* in the unmanipulated site. Prey availability index and number of egg sacs were not recorded in the initial 10 censuses. Egg sacs were collected from 2 September to 15 October 1979.

lated site, particularly during the summer when kelp was added to the treatment plots. For all censuses, mean ± 1 SD of the prey-availability indices at the experimental site and the unmanipulated site were respectively, 45.8 ± 42.9 and 16.6 ± 23.1. For censuses in summer (1978 and 1979), mean ± 1 SD of indices at the experimental site and the unmanipulated site were respectively, 60.4 ± 40.7 and 3.79 ± 1.82.

Prey-augmentation experiment in 1978.—On 19 June (one day before kelp was added to treatment plots), prey-availability indices and numbers of spiders in treatment and control plots did not differ significantly (Table 2). During the experiment mean prey-availability indices were significantly higher in treatments than in controls. On 10 September mean number of spiders was 2.7 times higher in prey-augmented plots than in control plots, and the difference was highly significant. Numbers of spiders increased in all plots from 19 June to 10 September; the increase was significantly greater in treatments than in controls.

Details in Fig. 4 show that in July mean numbers of adults became higher in treatments than in controls, whereas mean numbers of smaller individuals were nearly identical in treatments and controls. In August mean numbers of egg sacs became higher in treatments than in controls. In September hatchlings emerged from the egg sacs and mean numbers of immature spiders became higher in treatments than in controls. Shortly after I stopped adding kelp to the treatments, prey-availability indices were about equal in treatments and controls, but numbers of spiders remained higher in treatments for a few months.

Prey-augmentation experiment in 1979.—On 24 June (one day before kelp was added to the treatment plot) prey-availability indices and

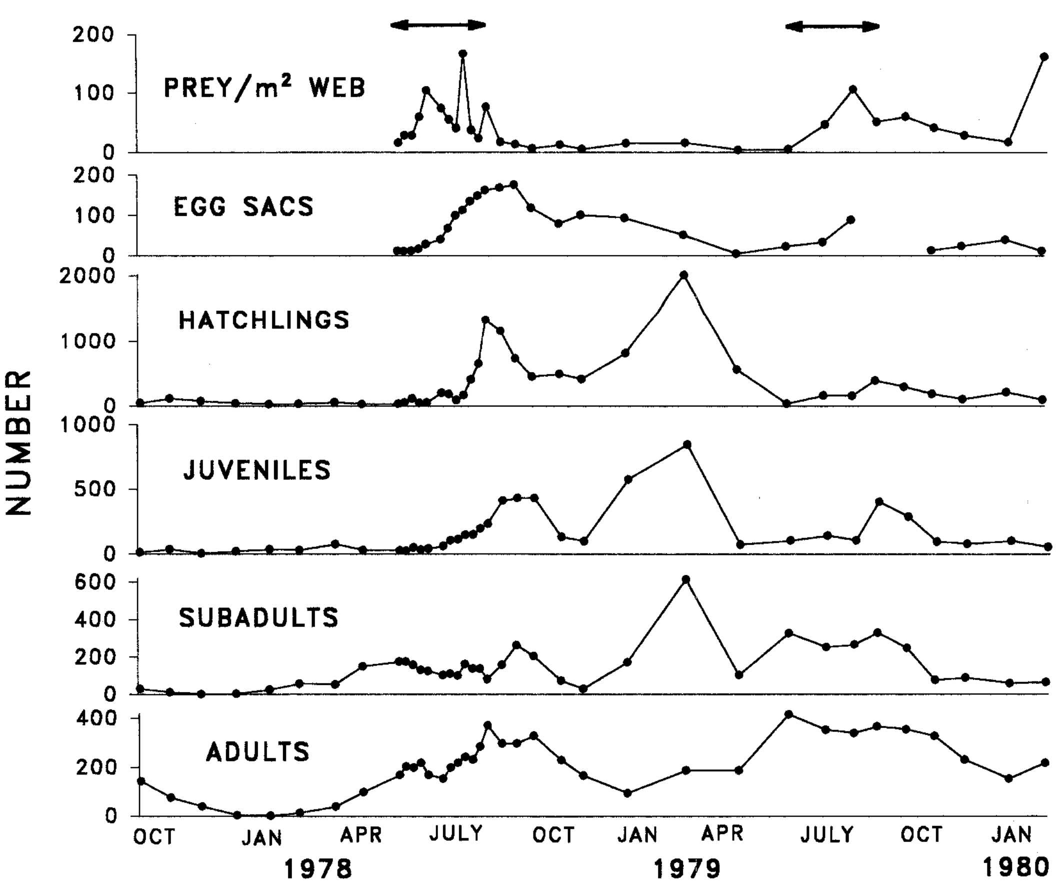

Figure 3.—Prey-availability indices (no. prey/m^2 web) and numbers of *Z. x-notata* in the experimental site. Prey-availability index and number of egg sacs were not recorded in the initial eight censuses. Egg sacs were collected from 2 September to 15 October 1979. Arrows depict time periods when kelp was added to treatment plots.

Table 2.—Prey-availability indices (no. prey/m^2 web) on 19 June (one day before kelp was added to treatment plots), mean of the indices from 25 June (first census during kelp additions) to 10 September (one day after the last kelp additions) and total numbers of spiders and change in numbers (number on 10 September minus number on 19 June) in each plot during the 1978 prey-augmentation experiment. [1 one-tailed test; each test was performed on the numbers given in each column.]

	No. prey/m^2 web		Total number of spiders		
Plot	19 June	Mean of 25 June to 10 Sept.	19 June	10 Sept.	Change
Treatment 1	10.2	84.2	55	491	436
Treatment 2	11.3	108.6	63	680	617
Control 1	9.3	8.3	133	327	194
Control 2	6.0	16.4	80	182	102
Control 3	16.3	19.3	45	173	128
Control 4	64.1	57.2	37	183	143
t (*df* = 4)	0.65	3.96	0.44	4.61	6.14
P	0.553	0.008[1]	0.677	0.005[1]	0.002[1]

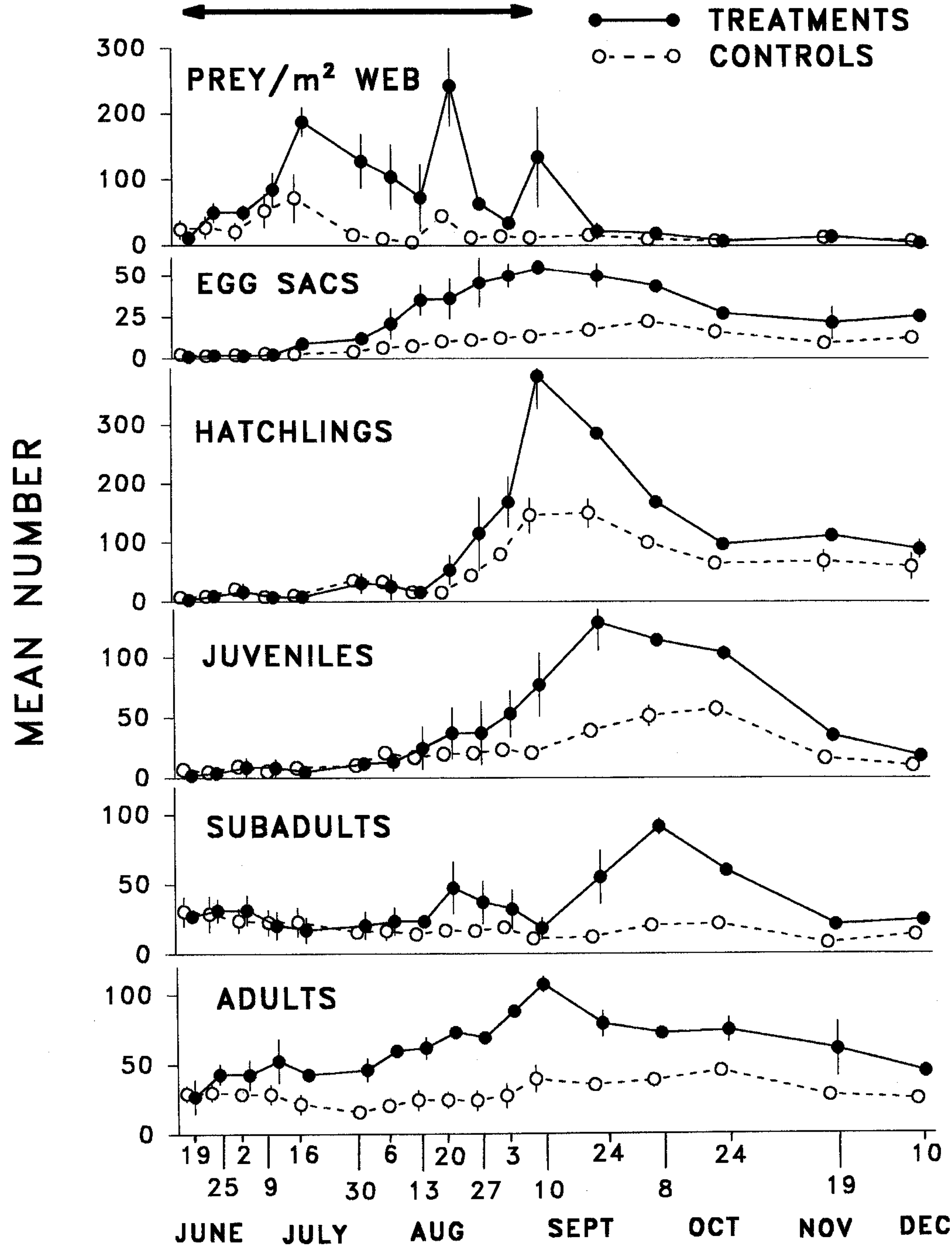

Figure 4.—Mean ± 1 SE prey-availability indices (no. prey/m² web) and numbers of *Z. x-notata* in treatment and control plots during the 1978 prey-augmentation experiment. The arrow depicts the time period when kelp was added to treatment plots.

numbers of spiders were similar in the treatment and control plots (Fig. 5). On 29 July prey-availability index and number of egg sacs were higher in the treatment than in controls but numbers of spiders remained about the same. On 25 August prey-availability index and numbers of egg sacs, hatchlings, subadults and adults were higher in the treatment than in controls. On 16 September

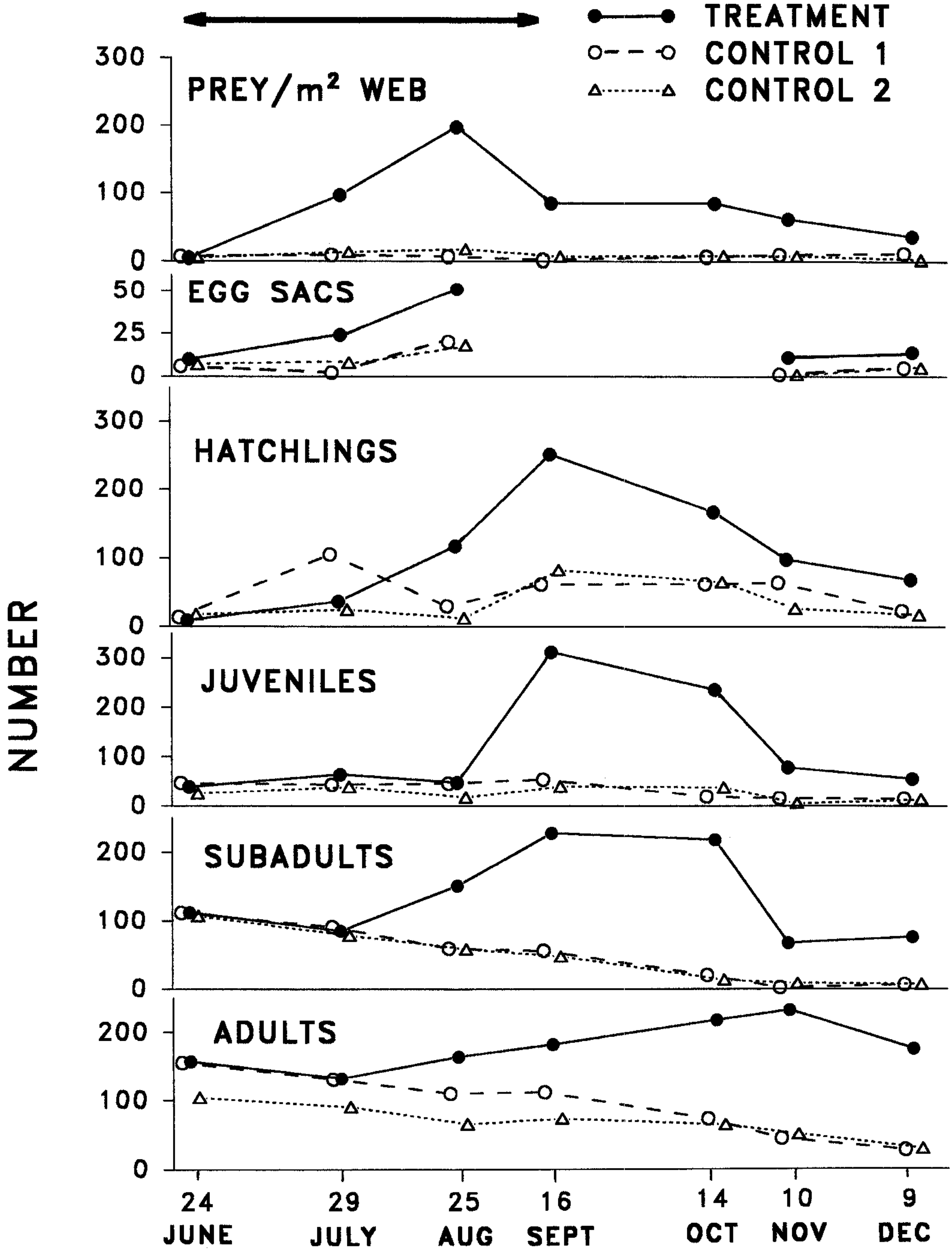

Figure 5.—Prey-availability indices (no. prey/m² web) and numbers of *Z. x-notata* in the treatment and control plots during the 1979 prey-augmentation experiment. The arrow depicts the time period when kelp was added to treatment plots. Egg sacs were collected from 2 September to 15 October.

prey-availability index and numbers of all spider classes were higher in the treatment than in controls; total number of spiders was >3.0 times higher in the treatment than in each control plot. (Note that this year egg sacs were collected from 2 September to 15 October.) Prey-availability indices and numbers of spiders remained higher in the treatment than in controls for a few months after I stopped adding kelp to the treatments.

Egg sacs collected in 1979.—Within the ex-

Table 3.—Mean (1 SE) number of eggs and mean biomass per egg in *Z. x-notata* sacs collected from 2 September to 15 October 1979. Prey was augmented in the treatment plot at the experimental site. [[1] one-tailed test.]

Site	Plot	*n*	No. of eggs/sac	Mean biomass (mg)/egg/sac
Experimental				
	Treatment	27	74.1 (3.6)	0.163 (0.004)
	Control 1	13	66.7 (6.0)	0.146 (0.006)
	Control 2	6	63.7 (8.8)	0.145 (0.003)
Unmanipulated		19	51.5 (2.9)	0.130 (0.005)

ANOVA:	*df*	SS	*F*	*P*
Number of eggs				
Treatment vs. Controls 1 + 2	1	814.6	2.45	0.0612[1]
Control 1 vs. Control 2	1	37.6	0.11	0.7377
Experimental vs. Unmanipulated	1	3299.9	9.93	0.0013[1]
Error	61	20 261.5		
Mean biomass/egg				
Treatment vs. Controls 1 + 2	1	0.00303	7.30	0.0044[1]
Control 1 vs. Control 2	1	0.00000	0.00	0.9544
Experimental vs. Unmanipulated	1	0.00561	13.53	0.0003[1]
Error	61	0.02529		

perimental site mean biomass per egg was significantly greater in the treatment than in control plots (Table 3). Numbers of eggs per sac tended to be higher in the treatment than in control plots, but the difference was not significant at the 0.05 level. Numbers of eggs and mean biomasses per egg in the two control plots were very similar. Number of eggs and mean biomass per egg were significantly greater in the experimental site than in the unmanipulated site.

DISCUSSION

Phenologies of unmanipulated and experimental populations differed considerably. The unmanipulated population reproduced during late summer and fall, and the next generation emerged during late winter and early spring in the following year. The experimental population began to reproduce in early summer, and some of the next generation emerged later in the same season. In addition, egg sacs produced in the experimental population contained more eggs and heavier eggs than those produced in the unmanipulated population.

Field experiments on other web spiders showed that growth rates or fecundities were influenced by food supply (Wise 1975, 1979; Spiller 1984; Spiller & Schoener 1990). My indices of prey availability during summer 1978 and summer 1979 were much higher at the experimental site than at the unmanipulated site. This suggests that the differences between populations in life-history characteristics were influenced by higher prey abundance at the experimental site. However, this interpretation should be taken with caution for two reasons. First, differences between sites in physical factors (e.g., temperature) might have influenced life-history characteristics. Second, my indices of prey availability did not take into account the size of individual prey; therefore, were prey sizes larger at the unmanipulated site than at the experimental site, comparisons between sites could be misleading.

Within the experimental population, egg sacs in the treatment plot contained heavier eggs than those in controls. Although this difference was statistically significant, the analysis does not demonstrate that it was caused by prey abundance because in 1979 the treatment was not replicated (Hurlbert 1984). Hence, comparisons among plots within the experimental population are subject to the same caveats as the comparison between populations. However, the fact that the treatment plot was in between the two control plots, and egg biomasses in control 1 and control 2 were nearly identical, provides compelling evidence that prey abundance influenced egg biomasses. Number of eggs per sac tended to be higher in the treatment plot than in the controls but the difference was not significant at the 0.05 level. Possibly, the number of eggs that a reproductive female produces in a sac is determined before the biomass of each egg. Therefore, if an adult female moved from a control plot to the treatment plot after number of eggs was determined, the increased food supply might have increased egg biomass but not number of eggs.

The prey-augmentation experiment in 1978 demonstrated that *Z. x-notata* responded numerically to prey abundance. During July and August numbers of adults became higher in treatments than in controls. Three different mechanisms could have produced this result: 1. adults moved from control plots to treatment plots, 2. adult survivorship was higher in treatments than in controls, or 3. developmental rate of immatures was higher in treatments than in controls. Because marked individuals were not followed during the experiment I cannot assess the importance of these possible mechanisms. Following the increase in adults, numbers of egg sacs became higher in treatments than in controls; subsequently, the numerical response became more pronounced when the second generation emerged in September. During the 1979 experiment numbers of spiders became substantially higher in the treatment plot than in control plots. I could not statistically analyze the results of this experiment because the treatment was not replicated in 1979. However, the data support the overall results of the 1978 experiment.

Rypstra's (1983) enclosure experiments showed that food abundance influenced densities of several web-spider species; interestingly, some solitary species exhibited some degree of coloniality when prey abundance was high (Rypstra 1986). Although *Z. x-notata* is typically solitary, other studies found that individuals were attracted to conspecific silk, and that some individuals reduced their web sizes in response to crowding (Leborgne & Pasquet 1987a, 1987b). In this study, *Z. x-notata* webs were occasionally attached to one another in treatment plots when prey availability was high. Such behavior might have facilitated the numerical response by *Z. x-notata*.

An important factor that accounted for the numerical response by *Z. x-notata* was the emergence of a second generation in the same year. Many spider species have obligatory annual life cycles, and would probably not exhibit such a marked numerical response within a season (Riechert & Lockley 1984). Thus, the extent to which spiders respond numerically may depend on the behavior and phenology of the species.

ACKNOWLEDGMENTS

I wish to thank Joseph H. Connell for his encouragement and support. I thank M. Fawcett and N. Spiller for field assistance, H. Levi for identifying specimens, and L. Bishop, M. Greenstone, T. Schoener, and D. Wise for comments. I was supported by NSF grant BSR90-20052 while preparing the manuscript.

LITERATURE CITED

Askenmo, C., A. von Broemssen, J. Eckman & C. Jansson. 1977. Impact of some wintering birds on spider abundance in spruce. Oikos, 28:90–94.

Gertsch, W. J. 1964. The spider genus *Zygiella* in North America (Araneae: Argiopidae). American Mus. Novit., 2188:1–21.

Greenstone, M. H. 1978. The numerical response to prey availability of *Pardosa ramulosa* (McCook) (Araneae: Lycosidae) and its relationship to the role of spiders in the balance of nature. Symp. Zool. Soc. London, 42:183–193.

Gunnarsson, B. 1983. Winter mortality of spruce-living spiders: effect of spider interactions and bird predation. Oikos, 40:226–233.

Hassell, M. P. & R. M. May. 1974. Aggregation of predators and insect parasites and its effect on stability. J. Anim. Ecol., 43:567–594.

Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecol. Monogr., 54:187–211.

Kobayashi, S. 1975. The effect of *Drosophila* release on the spider population in a paddy field. Appl. Ent. Zool., 10:268–274.

Leborgne R. & A. Pasquet. 1987a. Influence of conspecific silk-structures on the choice of a web-site by the spider *Zygiella x-notata* (Clerck). Revue Arachnol., 7:85–90.

Leborgne R. & A. Pasquet. 1987b. Influences of aggregative behavior on space occupation in the spider *Zygiella x-notata* (Clerck). Behav. Ecol. Sociobiol., 20:203–208.

Levi, H. W. 1974. The orb-weaver genus *Zygiella* (Araneae: Araneidae). Bull. Mus. Comp. Zool., 146: 267–290.

Pacala, S. & J. Roughgarden. 1984. Control of arthropod abundance by *Anolis* lizards on St. Eustatius (Neth. Antilles). Oecologia, 64:160–162.

Polis, G. A. & S. J. McCormick. 1986. Scorpions, spiders and solpugids: predation and competition among distantly related taxa. Oecologia, 71:111–116.

Polis, G. A., C. A. Myers & R. D. Holt. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. Annu. Rev. Ecol. Syst., 20:297–330.

Riechert, S. E. 1981. The consequences of being territorial: spiders, a case study. American Nat., 117: 871–892.

Riechert, S. E. & R. G. Gillespie. 1986. Habitat choice and utilization in web-building spiders. Pp. 23-48, *In* Spiders: Webs, Behavior, and Evolution. (W. A. Shear, ed.) Stanford Univ. Press, Stanford, California.

Riechert, S. E. & T. Lockley. 1984. Spiders as biological control agents. Annu. Rev. Entomol., 29: 299–320.

Riechert, S. E. & C. R. Tracy. 1975. Thermal balance and prey availability: bases for a model relating website characteristics to spider reproductive success. Ecology, 56:265–284.

Rypstra, A. L. 1983. The importance of food and space in limiting web-spider densities: a test using field enclosures. Oecologia, 59:312–316.

Rypstra, A.L. 1986. High prey abundance and a reduction in cannibalism: the first step to sociality in spiders (Arachnida). J. Arachnol., 14:193–200.

Spiller, D. A. 1984. Competition between two spider species: experimental field study. Ecology, 65:909–919.

Spiller, D. A. & T. W. Schoener. 1988. An experimental study of the effect of lizards on web-spider communities. Ecol. Monogr., 58:57–77.

Spiller, D. A. & T. W. Schoener. 1990. Lizards reduce food consumption by spiders: mechanisms and consequences. Oecologia, 83:150–161.

Wingerden, W. K. R. E. van. 1978. Population dynamics of *Erigone arctica* (White) (Araneae, Linyphiidae) II. Symp. Zool. Soc. London, 42:195–202.

Wise, D. H. 1975. Food limitation of the spider *Linyphia marginata*: experimental field studies. Ecology, 56:637–646.

Wise, D. H. 1979. Effects of experimental increase in prey abundance upon female reproductive rates of two orb-weaving spider species. Oecologia, 41: 289–300.

Wise, D. H. 1982. Predation by a commensal spider, *Argyrodes trigonum*, upon its host: an experimental study. J. Arachnol., 10:111–116.

Wise, D. H. 1992. Spiders in Ecological Webs. Cambridge Univ. Press. Cambridge, UK.

Manuscript received 8 June 1992, revised 23 October 1992.