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EFFECTS OF TOP AND INTERMEDIATE PREDATORS IN A TERRESTRIAL FOOD WEB[1]

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Abstract. To determine the effects of lizards and web spiders on species in lower trophic levels, we manipulated their abundances within large field enclosures on Staniel Cay, Bahamas, from May 1989 to March 1992. The experimental design (2 × 2 factorial) measured the separate effects of lizards and spiders and compensatory predation (lizard × spider interaction). In treatments where web spiders were unaltered, mean number of web spider individuals was 1.4 times higher in enclosures with lizards removed than in those with lizards present at natural densities. Total biomass of aerial arthropods caught in sticky traps was 1.4 times higher in treatments with web spiders removed than in treatments with web spiders unaltered. Lizards had no significant effect on aerial arthropods. Total amount of herbivore damage on sea grape leaves was 3.3 times higher in treatments with lizards removed than in treatments with lizards unaltered. Web spiders had no significant effect on leaf damage. The lizard × spider interaction was not significant in each analysis, indicating that compensatory predation was weak. Our results support a model in which the interaction between top predators (lizards) and herbivores is strong, whereas the interaction between intermediate predators (web spiders) and herbivores is weak. Consequently, the net effect of top predators on producers is positive.

Key words: compensatory predation; food web; lizards; predators; species interactions; spiders; subtropics.

INTRODUCTION

Forces controlling population and community dynamics in food webs have attracted much recent attention (e.g., Matson and Hunter 1992). Certain models predict that the effect of top predators on producers depends on the number of trophic levels in the system (Fretwell 1977, Oksanen et al. 1981); in a three-trophic-level system the effect is positive (as in Hairston et al. 1960), whereas in a four-trophic-level system (top predators, intermediate predators, herbivores, and producers) the effect is negative. These models assume that each consumer level eats only the next level down. Freshwater systems showed the predicted response when a fourth trophic level was experimentally added to a three-level system, i.e., intermediate predators decreased, herbivores increased, and producers decreased (Carpenter et al. 1987, Persson et al. 1988, Power 1990, but see McQueen et al. 1989). In terrestrial systems with both top and intermediate predators, the top predators often feed on both intermediate predators and herbivores, particularly when the top predators are vertebrates and the intermediate predators and herbivores are arthropods (Schoener 1989). This and other complex trophic interactions may be common in terrestrial systems (Polis et al. 1989, Polis 1991). Such interactions may necessitate different models in which the top predators feed on more than one trophic level.

We are studying species interactions on small islands in the Bahamas. *Anolis* lizards are often the top predators, eating both carnivorous and herbivorous arthropods (Schoener 1968, Schoener and Gorman 1968, Schoener and Schoener 1983*a*). Fig. 1 depicts the subjects and trophic links in our study system. We propose that in such a system the effect of top predators on producers may be either positive or negative, depending on the relative strengths of interactions among the upper trophic levels. In Model A the interaction between lizards and herbivorous arthropods is strong and the interaction between web spiders and herbivorous arthropods is weak; the predominant pathway from producers to top predators involves three trophic levels and the net effect of lizards on producers is positive. In Model B the interaction between lizards and herbivorous arthropods is weak and the interaction between web spiders and herbivorous arthropods is strong; here the predominant pathway involves four trophic levels and the net effect of lizards on producers is negative.

In a previous experiment numbers of web spiders were ≈3 times higher in enclosures with lizards removed than in enclosures with lizards present at natural densities (Spiller and Schoener 1988). A mechanistic analysis (Spiller and Schoener 1990*a*) revealed that the effect of lizards on spiders had both a direct component (predation) and an indirect component (food competition). Measurements of leaf damage on sea grape (*Coccoloba uvifera*) uncovered evidence for both a three-level pathway and a four-level pathway (Spiller and Schoener 1990*b*). Removing lizards both increased

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the amount of scar damage, caused by homopterans and other organisms, and decreased the amount of gall damage, caused by midges. We suggested that lizards had a direct negative effect on homopterans and an indirect positive effect on gall midges (via their negative effect on web spiders, which had a negative effect on gall midges). The lizard effect on scars supports a three-level pathway as in Model A, whereas the lizard effect on galls supports a four-level pathway as in Model B. Evidence that web spiders reduced gall midges was circumstantial, however, because the experiment was not designed to measure the impact of web spiders; only lizards were manipulated. Furthermore, lizard effects on other herbivores may have been confounded by compensatory predation by web spiders. Two other field experiments indicated that increased predation by spiders compensated for the lack of top predators (Hurd and Eisenberg 1984, Pacala and Roughgarden 1984).

In the present study we manipulated both lizards and web spiders to measure their separate effects and compensatory predation. We found that lizards reduced web spider abundance and leaf damage, but they had no significant effect on aerial arthropods caught in sticky traps. Web spiders reduced the abundance of aerial arthropods, but they had no significant effect on leaf damage. No significant evidence for compensatory predation existed. Our results support Model A in which the predominant pathway from producers to top predators involves three trophic levels. Comparisons of our present and previous experiments suggest that the effects of lizards vary temporally.

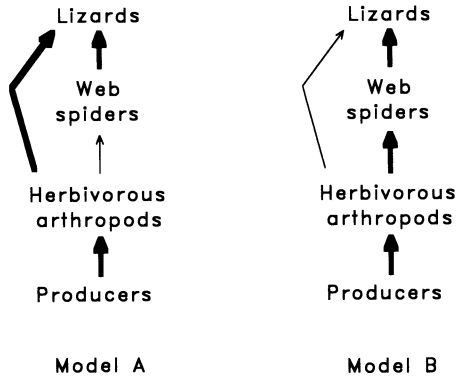

FIG. 1. Alternative models for (partial) food webs on small Bahamian islands. Arrow thicknesses are interpreted as follows. An arrow from z to y gives the effect of y on z in the absence of effects on y from other elements of the food web that connect to y (e.g., predators of y or alternative prey of y). In particular, the population size of y as directly affected by other elements of the web is not reflected in arrow thicknesses. Arrow thickness can be interpreted as a per capita effect of y on z (see Schoener 1989 for elaboration).

METHODS

Study site and manipulated species

The experiment was conducted on Staniel Cay, an island in the central Bahamas (Exumas), ≈3 × 1 km. The study site was a vegetated sandy area elevated 10–15 m above the northeastern shore. The vegetation consisted mostly of *Coccoloba uvifera* (sea grape) shrubs (0.5–1.5 m high), with a few representatives of some other shrubs.

Most lizards on the site were *Anolis sagrei,* with some *Anolis carolinensis* and *Ameiva festiva.* The biology of *Anolis* in the Bahamas is discussed in detail elsewhere (Schoener 1968, Schoener and Schoener 1978, 1982*a, b,* 1983*a, b*). Snout–vent lengths (mean of the one-third with the largest SVLs of all specimens collected from Exumas) were: *A. sagrei,* males = 54.4 mm (n = 45), females = 39.8 mm (n = 27); *A. carolinensis,* males = 60.9 mm (n = 27), females = 46.7 mm (n = 6). *Ameiva* are larger; precise data are not available.

The most abundant web spider at the site was *Metepeira datona* (body length of adult females = 2.5–5.5 mm, adult males = 2.0–4.5 mm). Two other species were fairly common, *Eustala cazieri* (adult females = 5.0–7.0 mm, adult males = 4.0–6.0 mm) and *Argiope argentata* (adult females = 18.0–26.0 mm, adult males = 3.5–5.5 mm). These three species are orb weavers (Araneidae). Rare web spider species are described elsewhere (Spiller and Schoener 1988); most are orb weavers.

Experimental design

We used a 2 × 2 factorial design with the following four treatments: (1) controls with lizards and spiders unaltered (present at natural densities), (2) lizards removed and spiders unaltered, (3) spiders removed and lizards unaltered, and (4) both lizards and spiders removed. Each treatment had three replicate enclosures. Initially, the 12 enclosures were stratified into three blocks according to mean vegetation height (low, medium, and high), and each treatment was randomly assigned to an enclosure within each block. The experiment was conducted from May 1989 to March 1992.

Enclosures followed the design in Spiller and Schoener (1988), modified from Pacala et al. (1983). Briefly, each enclosure was 83.6 m^2 and consisted of wood-framed fences, with hardware cloth (3.2-mm mesh) attached to the sides. To prevent lizards from entering or leaving the enclosures, a continuous 0.4-m wide strip of plastic was mounted on top of each fence, forming 0.2-m overhangs on the inside and outside; except for the overhangs, the enclosures were open on top. Six enclosures were used in our previous experiment conducted from May 1985 to November 1988; the hardware cloth was removed from these enclosures from November 1988 to April 1989. Six new enclosures were built in April 1989. In our previous experiment, comparisons between control enclosures and unenclosed plots (both of these treatments had lizards and spiders) showed that the enclosures had no effect on web spiders or leaf damage, but they did slightly

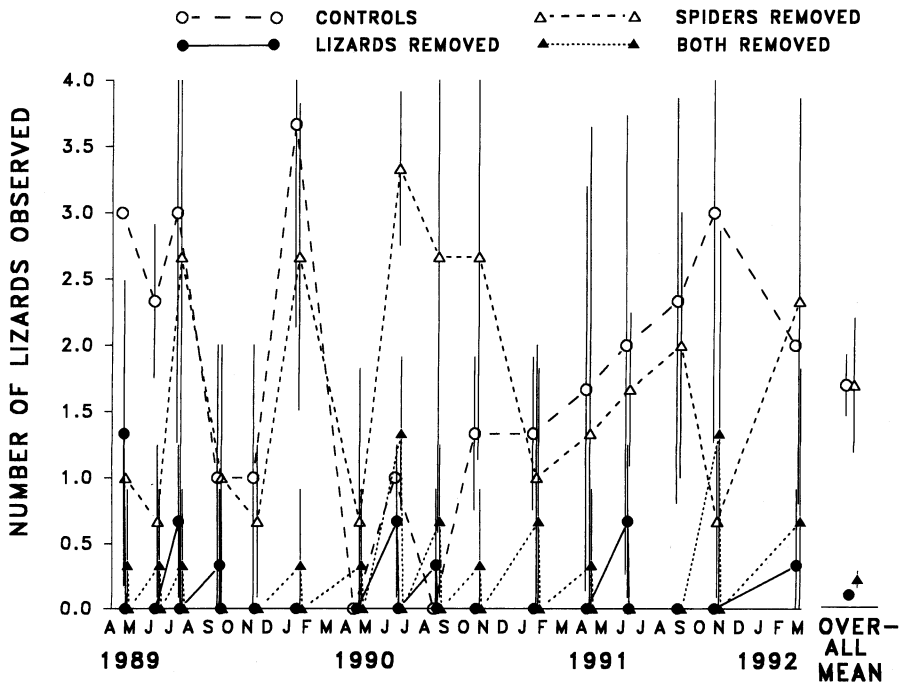

FIG. 2. Mean numbers of lizards observed in experimental enclosures. The first census was conducted before lizards and spiders were manipulated and was followed by 15 postmanipulation censuses. Error bars are ± 1 SD of the mean of the enclosures within a treatment. Overall mean is the mean of the postmanipulation values in a particular enclosure. All lizards observed were removed from the appropriate treatments during or shortly following each census; therefore, in those treatments zero values are plotted after each census and the zeros were included in overall mean calculations. These data were used only as a general assessment of the relative abundance of lizards in the different treatments (they were not used to test for species interactions).

reduce the abundance of aerial arthropods (Spiller and Schoener 1988, 1990*b*).

Species manipulations and data collection

Our major concerns were that lizard and spider densities in unaltered treatments were natural and that removals were effective. Previously, we established that mean natural lizard density at the study site was nine individuals (*A. sagrei*) per enclosure (Spiller and Schoener 1988); this density (≈0.1 individuals/m^2) is an order of magnitude lower than the maximum recorded in the Bahamas (Schoener and Schoener 1980). In May 1989 we estimated numbers of lizards in treatments 1 and 3, using standard mark–recapture methods (Schoener and Schoener 1983*c*); estimates in some enclosures, particularly the new ones, were <9 (probably due to enclosure construction), and the necessary numbers of *A. sagrei* were added so that each contained 9. No web spiders were added to enclosures. During the following week we removed all lizards observed in treatments 2 and 4 and all web spiders observed in treatments 3 and 4. Thereafter, we visited the study site at ≈1–2 mo intervals from May to late fall and at ≈3-mo intervals from late fall to May in each year. During each visit lizards and web spiders were removed from the appropriate treatments. In May 1990 and May 1991 we estimated numbers of lizards in treatments 1 and 3 (mark–recapture method); in each year, estimated numbers were <9 within a few enclosures, and the necessary numbers of lizards were added to these enclosures so that each was estimated to contain 9. During the experiment overall mean numbers of lizards and web spiders were both ≈5–10 times higher in unaltered treatments than in removal treatments (Figs. 2 and 3).

Data collection followed the general protocol of our previous experiment (Spiller and Schoener 1988). During each visit we censused web spiders in all enclosures, recording the species of each individual and the body lengths (estimated to the nearest millimetre) and orders (when possible) of arthropods in the spider's web or being consumed by the spider. The first census was conducted before lizards and spiders were manipulated and was followed by 15 postmanipulation censuses (see Fig. 3 for census dates). During the experiment, prey-consumption rate by *M. datona,* the most common web spider, was measured as follows (see also Spiller and Schoener 1990*a*). On 8 July 1991 we put numbered tags on the vegetation next to five adult females in each enclosure with spiders unaltered (treatments 1 and 2). From 8 to 15 July we observed each individual at ≈1.5-h intervals from ≈0900 to 1700 and recorded

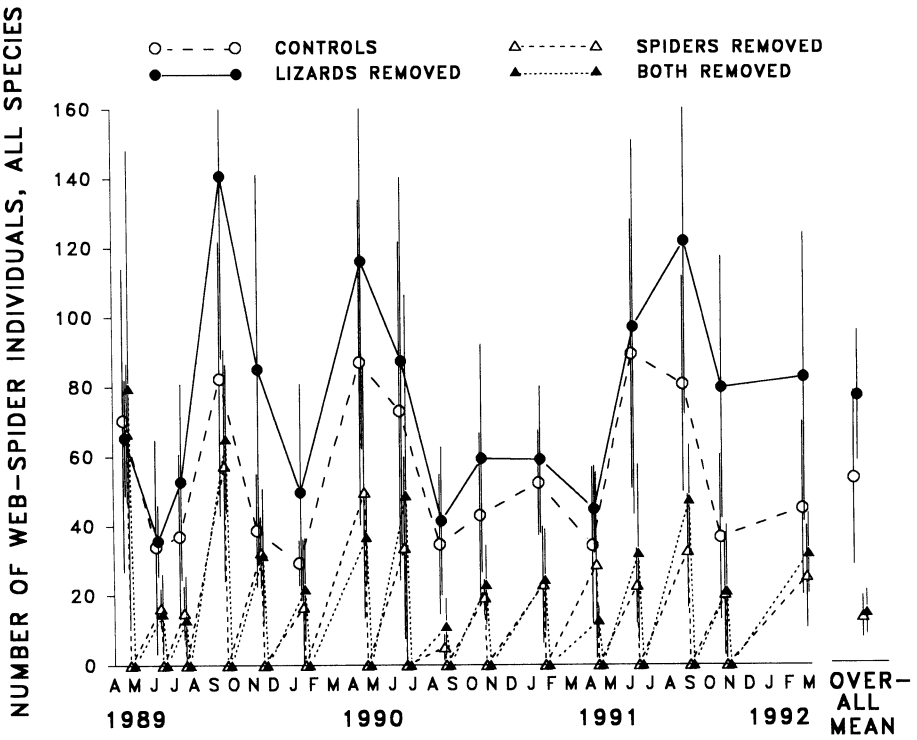

FIG. 3. Mean numbers of web spider individuals observed in experimental enclosures. The first census was conducted before lizards and spiders were manipulated and was followed by 15 postmanipulation censuses. Error bars are ± 1 SD of the mean of the enclosures within a treatment. Overall mean is the mean of the postmanipulation values in a particular enclosure. All spiders observed were removed from the appropriate treatments during or shortly following each census; therefore, in those treatments zero values are plotted after each census and the zeros were included in overall mean calculations. The data in treatments with spiders removed were used only as a general assessment of the abundance of web spiders in the different treatments (they were not used to test for species interactions).

the body lengths (estimated to the nearest millimetre) and orders (when possible) of arthropods in the spider's web or being consumed by the spider.

To measure relative abundance of aerial arthropods we put out four sticky traps in each enclosure during each visit, usually on the day following the spider census. The first set of traps was put out before species were manipulated. The traps were 22 × 14 cm sheets of clear plastic coated with Tanglefoot adhesive on one side, and were suspended within openings of the vegetation 0.25–0.50 m above the ground, with the adhesive side facing southeast (the direction of the prevailing trade winds). After 24 h we recorded the body length and order of each trapped arthropod. When weather was favorable and time permitting, the traps were left out for >1 d and arthropods were recorded and removed from each trap daily (numbers of days traps were left out during each visit are in Fig. 6). Total number of trap-days was 1536. Because of the selective properties of the traps, our measurements reflect only a subset of total arthropod abundance. We did not use other methods to sample more sedentary arthropods (e.g., sweep nets, pitfall traps) because they might have substantially disturbed the lizard and spider populations. Our traps caught no lizards and very few spiders (see Table 4, also Spiller and Schoener 1990*a*).

We measured herbivory on sea grape (as in Spiller and Schoener 1990*b*). New leaves are abundant at the beginning of the wet season (May–June). At this time in 1989, 1990, and 1991 we put numbered tags on the petioles of 15 new, undamaged leaves in each enclosure. The distribution of tagged leaves in each plot consisted of five uniformly spaced patches with three leaves per patch. Total number of leaves tagged was 540. During each visit from May to December we used a ruler to measure the maximum diameter and the diameter perpendicular to the maximum of each leaf and each damaged area on the leaf. (Because our new leaves were very tender and some leaves were quite bowed, we would have damaged leaves trying to trace them accurately; therefore, we decided to estimate areas with a ruler.) Total leaf area and damaged areas were estimated by assuming that they were elliptical. The leaves were nearly elliptical and most damaged areas were at least roughly elliptical; estimates for irregular-shaped damaged areas were crude. Rather than measuring harvested leaves in the laboratory, and thereby increasing accuracy, we decided to measure

repeatedly tagged leaves in the field. The former method can underestimate overall rates of herbivory when some leaves are entirely eaten or when heavily damaged leaves abscise before leaves with less damage (Lowman 1984); early abscission of damaged leaves occurred in our previous experiment (see also Faeth et al. 1981).

We classified several different types of leaf damage. "Scars" were well defined, usually elliptical, necrotic areas. In the field we observed scar damage produced by homopterans (aphids and leaf hoppers), although they may have also been produced by other organisms. "Mines" were serpentine areas that often developed into elliptical blotches. We have found lepidopteran larvae in the blotches. (Note that in Spiller and Schoener [1990*b*] mines were included in the scars category.) "Holes" were entirely missing areas. We observed holes produced by lepidopteran larvae (several species), an adult coleopteran (June beetle), and hymenopterans (a leafcutter ant and a leafcutter bee). "Galls" were produced by a cecidiomyiid midge (probably *Ctenodactylomyia watsoni,* identified by R. L. Gagné). "Welts" were raised areas located along the veins, apparently produced by microorganisms (E. Butler, *personal communication*). "Burns" were brown areas on the leaf edges, probably caused by physical factors (e.g., wind, salt spray). Scratch marks, obviously caused by the leaf rubbing another part of the plant, were not measured.

Analyses

To measure the effect of lizards on web spiders we compared numbers in treatment 1 (controls: both lizards and web spiders unaltered) with treatment 2 (lizards removed, web spiders unaltered). We performed separate analyses on number of individuals (all species combined) and number of species. We used a two-way ANOVA model with repeated measures on numbers during postmanipulation censuses. The two factors were blocks (low, medium, and high vegetation) and lizards (unaltered, removed). Because premanipulation numbers of individuals varied considerably we included them in the model as a covariate. To test the lizard effect we used the main (between subjects) effect, which is the same as using the mean number in each replicate as the dependent variable (Freund et al. 1986). Numbers of individuals were $\log_{10}$ transformed to stabilize variances; also, assuming that lizards reduce numbers by a constant factor and numbers of spiders vary among blocks, this transformation is appropriate for this model with no block × lizard interaction (Neter et al. 1987). Note that because we restocked treatments 1 and 3 with lizards during the experiment, the effect of spiders on numbers of lizards could not be measured.

From the observations of prey consumed by *M. datona* in treatments 1 and 2, we computed mean numbers and biomasses of prey consumed per spider per day in each enclosure. Mean rates were computed by weighting each individual rate by the number of days the spider was observed. Prey biomasses were estimated by using order-specific length–mass equations for tropical dry forest insects (Schoener 1980); biomasses of unidentified prey were estimated with the equation for all insects combined (orders of most prey were identified). Biomass consumed was computed by multiplying prey biomass by 0.66, which is the mean proportion of each prey item consumed by the funnel-web spider *Agelenopsis aperta* (Riechert and Tracy 1975). Mean rates were $\log_{10}$ transformed and analyzed with a two-way ANOVA (factors = blocks, lizards).

To analyze the effects of lizards and web spiders on numbers of arthropods in sticky traps we used a three-way ANOVA model (factors = blocks, lizards, spiders) with repeated measures on numbers caught in each enclosure each day traps were left out during postmanipulation censuses. The same model was performed on total arthropod biomasses caught in each enclosure each day; biomass of each arthropod was estimated using length–mass equations as described above. We used the main effects to test the separate effects of lizards and spiders and the lizard × spider interaction. The lizard × spider interaction tested the compensatory predation hypothesis: because spider density is higher when lizards are removed than when lizards are unaltered, the effect of spiders is stronger when lizards are removed than when lizards are unaltered, and the effect of lizards is stronger when spiders are removed than when spiders are unaltered. Of course, other mechanisms might also produce a significant lizard × spider interaction. Block × lizard and block × spider interactions were not included in the model because preliminary analyses, which included these interactions, showed that neither was significant ($P > .20$); this procedure is recommended by Winer (1971). Each repeated measure was $\log_{10}$ transformed.

For each leaf tagged in 1989, 1990, and 1991, we computed separate cumulative amounts of scar, mine, hole, and gall damage, expressed as percent of the entire leaf area. Welts and burns were not analyzed because we assume that they were not caused by herbivorous arthropods. Most of the tagged leaves were on the plants at the final census in each year (late fall). For each leaf that abscised before the final census, we used damage amounts when last measured. Percentages were arcsine transformed for statistical analysis. We analyzed the mean values of the leaves within each enclosure using a MANOVA model with repeated measures. The model had three main factors (blocks, lizards, spiders) and two repeated factors (years, damage types). The lizard × spider interaction was included in the main effects; block × lizard and block × spider interactions were not included because in preliminary analyses neither was significant, as in the analyses of aerial arthropods. We used the main effects to test the overall effects of lizards and spiders, which is the same as analyzing the sum of all damage types in all years within each enclosure.

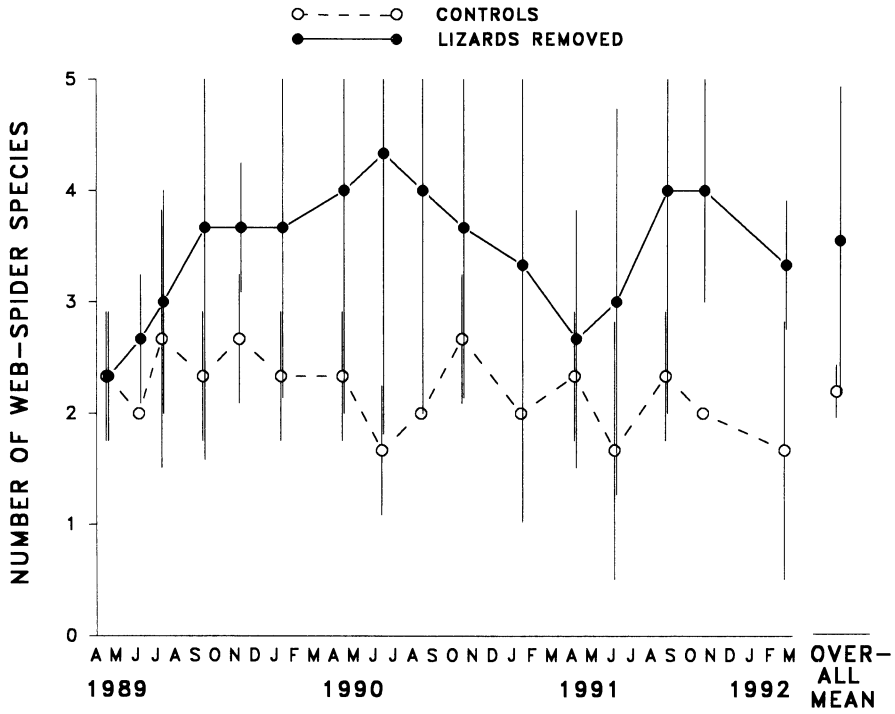

FIG. 4. Mean numbers of web spider species observed in experimental enclosures with spiders unaltered. Error bars and overall mean as in Fig. 3.

In all analyses P values reported for the separate effects of lizards and spiders are one-tailed tests; our a priori hypotheses were that lizards reduce spiders and both reduce aerial arthropods and leaf damage. All other tests are two tailed. The statistical analyses used to test a priori hypotheses are presented in four tables (Tables 1, 2, 3, and 6); each represents a separate data set. To adjust for multiple tests we performed a sequential Bonferroni test (Rice 1989) on the unadjusted P values within each table, including only those testing effects of lizards, spiders, or the lizard × spider interaction; other effects (blocks, covariates, within subjects) are given for descriptive purposes. We also performed separate analyses on variables that represented different components of the data sets; results are given in the text for descriptive purposes, but they are not intended to be formal tests.

RESULTS

Effect of lizards on web spiders

To measure the effect of lizards on web spiders we compared control enclosures (both lizards and spiders unaltered) to enclosures with only lizards removed. On the first census (May 1989), before the manipulations, mean numbers of web spider individuals were similar (Fig. 3). During fall 1989 mean numbers were ≈2 times higher in lizard-removal enclosures than in controls. The difference diminished during 1990 and the first half of 1991 but increased again during the second half of 1991. Mean of the mean numbers observed in each plot during postmanipulative censuses (overall mean) was 1.4 times higher in lizard-removal enclosures than in controls. Numbers of web spider species showed a similar trend (Fig. 4); the overall mean was 1.6 times higher in lizard-removal enclosures than in controls.

TABLE 1. Repeated-measures ANCOVA of numbers of web spider individuals and species censused from July 1989 to March 1992. The covariate (initial number) is the number on the premanipulation census (May 1989).

Effect	F	df	P†	Adj P‡
Number of individuals				
Between subjects (enclosures)				
Initial number	191.98	1, 1	.0459	
Block	42.91	2, 1	.1073	
Lizard	222.39	1, 1	.0213*	
Within subjects				
Date	3.11	14, 14	.0210	.3284
Date × lizard	0.94	14, 14	.5426	.5093
Number of species				
Between subjects				
Initial number	35.37	1, 1	.1061	
Block	12.48	2, 1	.1963	
Lizard	56.83	1, 1	.0420*	
Within subjects				
Date	1.50	14, 14	.2303	.4363
Date × lizard	1.64	14, 14	.1824	.4219

* Lizard effect is significant ($P < .05$) using the sequential Bonferroni method (two comparisons).

† Tests of initial number of block effects are two tailed; tests of lizard effect are one tailed.

‡ Significance level adjusted by the Greenhouse–Geisser epsilon method.

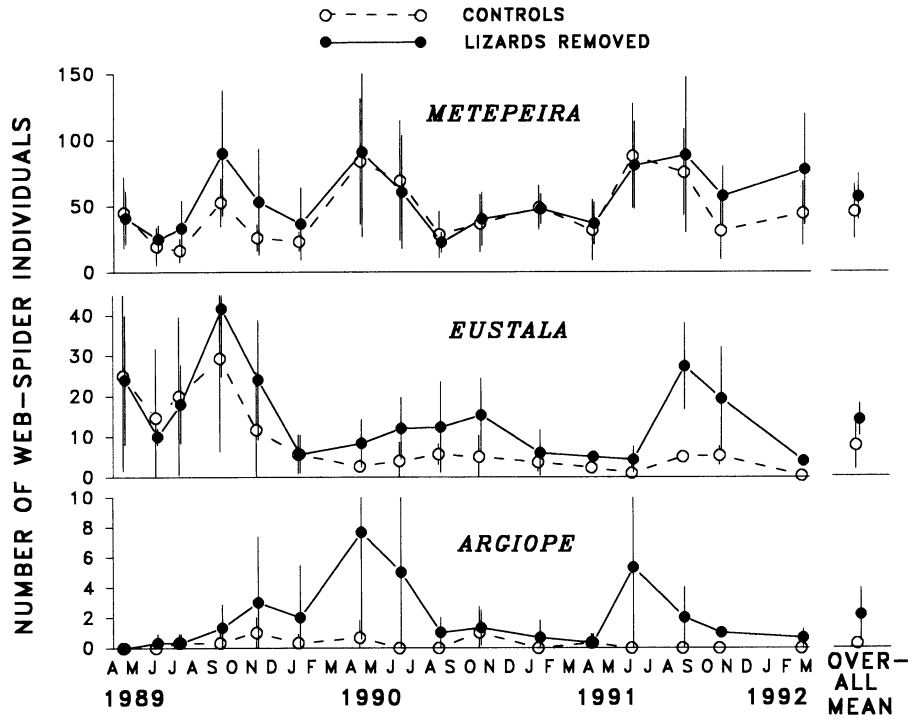

FIG. 5. Mean numbers of individuals for the three common web spider species in experimental enclosures with spiders unaltered. Error bars and overall mean as in Fig. 3.

The lizard effect was significant in separate analyses of numbers of individuals and species (Table 1). In both analyses variation among census dates was not significant when P values were adjusted by the Greenhouse–Geisser epsilon method (Freund et al. 1986), although for number of individuals the unadjusted P value was significant. No date × lizard interaction was significant.

TABLE 2. Mean prey-consumption rate by adult female *Metepeira datona* spiders in control and lizard-removal enclosures from 8 to 15 July 1992.

Block	Treatment	No. of prey consumed per spider per day	Biomass consumed per spider per day (μg)
Low	Controls	0.200	193
	Lizards removed	0.177	71
Medium	Controls	0.206	288
	Lizards removed	0.471	716
High	Controls	0.222	145
	Lizards removed	0.118	132

Analysis	Effect	F	df	P*
No. of prey consumed	Block	0.86	2, 2	.5391
	Lizard	0.00	1, 2	.4821
Biomass consumed	Block	2.40	2, 2	.2940
	Lizard	0.01	1, 2	.4617

* Block effect test is two tailed; that for lizard effect is one tailed.

Numbers of each common web spider species tended to be higher in lizard-removal enclosures than in controls (Fig. 5). The ratios of lizard-removal enclosures to controls in overall means for *Metepeira, Eustala,* and *Argiope* were 1.2, 1.8, and 8.0, respectively. In separate analyses (using the same model as for all species combined) the lizard effect was significant for the two most common species, *Metepeira* (P = .028) and *Eustala* (P = .032), but not for *Argiope* (P = .100). Numbers of individuals for other web spider species were very low and the lizard effect was not significant.

Numbers and biomasses of prey consumed by adult female *Metepeira* in lizard-removal enclosures and controls did not differ significantly (Table 2).

Effects of lizards and spiders on aerial arthropods

Although differences among treatments were not consistent, numbers and biomasses of arthropods caught in sticky traps tended to be higher in enclosures with spiders removed than in those with spiders unaltered (Figs. 6 and 7). Overall mean number of arthropods in the two treatments with spiders removed (spiders removed, both lizards and spiders removed) was 1.3 times higher than in the two treatments with spiders unaltered (controls, lizards removed); similarly, overall mean biomass was 1.4 times higher. P values for the overall spider effect (unadjusted for multiple comparisons) were significant in analyses of arthropod numbers and biomasses (Table 3); the sequential Bonferroni

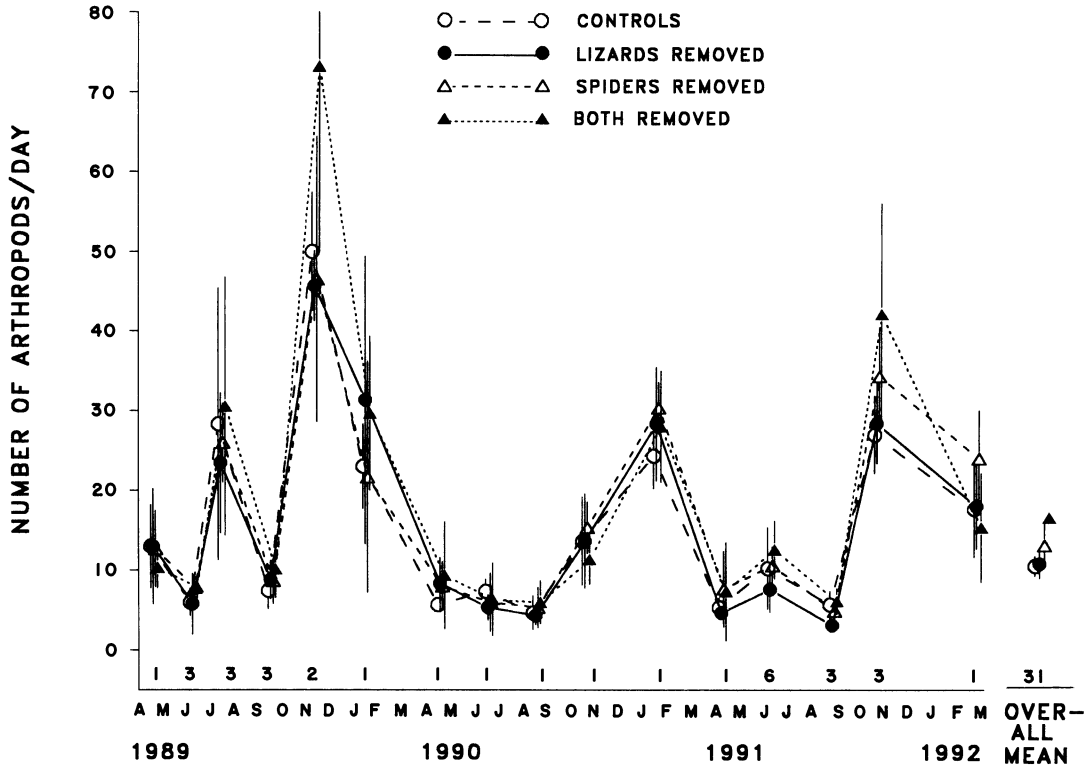

FIG. 6. Mean numbers of arthropods caught per day in aerial sticky traps in experimental enclosures. Error bars and overall mean as in Fig. 3. Numbers of days traps were left out each sampling period are above the abscissa; number above overall mean is the total.

TABLE 3. Repeated-measures ANOVA of number and biomass of arthropods in sticky traps censused from July 1989 to March 1992.

Effect	F	df	P†	Adj P‡
		Number		
Between subjects (enclosures)				
Block	0.61	2, 6	.5724	
Lizard	0.27	1, 6	.3125	
Spider	8.89	1, 6	.0129	
Lizard × spider	0.56	1, 6	.4814	
Within subjects				
Date	43.09	30, 180	.0001	.0001
Date × lizard	0.65	30, 180	.9186	.6604
Date × spider	0.90	30, 180	.6195	.4922
Date × lizard × spider	1.13	30, 180	.3108	.3685
		Biomass		
Between subjects				
Block	0.95	2, 6	.4371	
Lizard	0.49	1, 6	.2543	
Spider	16.34	1, 6	.0034*	
Lizard × spider	1.03	1, 6	.3486	
Within subjects				
Date	13.36	30, 180	.0001	.0001
Date × lizard	0.61	30, 180	.9466	.6829
Date × spider	0.81	30, 180	.7458	.5434
Date × lizard × spider	1.15	30, 180	.2828	.3568

* Spider effect is significant ($P < .05$) using the sequential Bonferroni method (six comparisons).
† Tests of block effect and lizard × spider interaction are two tailed; lizard and spider effects are one tailed.
‡ Significance level adjusted by the Greenhouse–Geisser epsilon method.

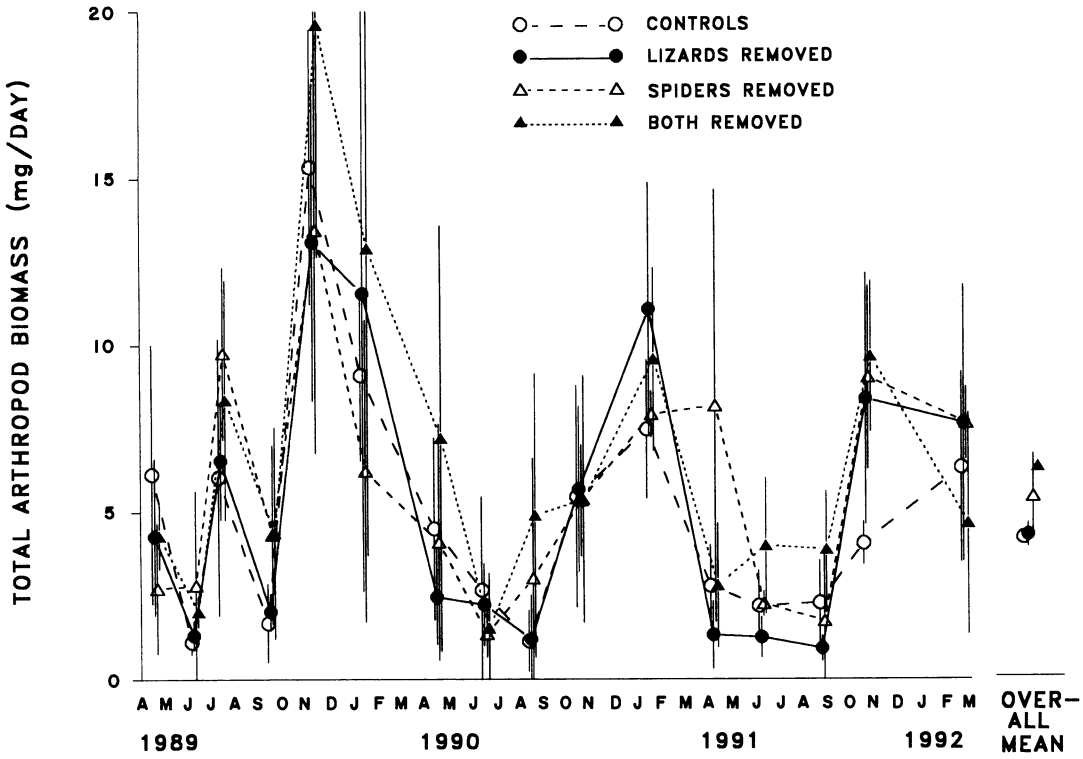

FIG. 7. Mean total biomass of arthropods caught in aerial sticky traps per day in experimental enclosures. Error bars and overall mean as in Fig. 3.

test showed that the effect was only significant in the analysis of biomasses.

Numbers and biomasses tended to be slightly higher in treatments with lizards removed than in those with lizards unaltered, but the overall lizard effect was not significant. Overall mean number of arthropods in the two treatments with lizards removed (lizards removed, both lizards and spiders removed) was only 1.1 times higher than in the two treatments with lizards unaltered (controls, spiders removed); overall mean biomass was also only 1.1 times higher.

Comparisons of individual treatments suggested that the spider effect tended to be stronger when lizards were removed than when lizards were unaltered. Overall mean number of arthropods was 1.4 times higher in the treatment with both lizards and spiders removed than in the treatment with only lizards removed, whereas it was 1.2 times higher in the treatment with only spiders removed than in controls. Overall mean biomass was 1.5 times higher in the treatment with both lizards and spiders removed than in the treatment with only lizards removed, whereas it was 1.2 times higher in the treatment with only spiders removed than in controls. Similar comparisons can be made for the lizard effect in treatments with spiders removed and unaltered. Overall mean number of arthropods was 1.2 times higher in the treatment with lizards and spiders removed than in the treatment with only spiders removed, whereas it was 1.02 times higher in the treatment with only lizards removed than in controls. However, the lizard × spider interaction was not significant in analyses of numbers and biomasses.

Variation among census dates was significant in both analyses. No date × lizard, date × spider, or date × lizard × spider interaction was significant.

Taxonomic composition of the arthropods caught by sticky traps was similar to that of the catches of web spiders. About 70% of the arthropods caught by both traps and web spiders were dipterans (Table 4). Two exceptions existed: lepidopterans were more common for traps than for web spiders and coleopterans were more common for web spiders than for traps.

To explore whether lizards and spiders affected certain types of arthropods we performed separate analyses on the total biomass caught in each enclosure for the four most common orders in sticky traps (Table 5). For Diptera, the most common order, mean biomass was 1.4 times higher in treatments with spiders removed than in those with spiders unaltered. Using the same statistical model as for all arthropods, the spider effect was significant ($P = .012$), but not the lizard effect ($P = .109$) nor the lizard × spider interaction ($P = .210$). For the other three orders no lizard effect, spider effect, or lizard × spider interaction was significant. We also divided the data into small (body length ≤ 4 mm) and large (>4 mm) arthropods (as in

TABLE 4. Percent composition of identified arthropods caught by sticky traps and web spiders in plots with spiders unaltered from May 1989 to March 1992.* n = number of arthropods in each order.

Order	Traps		Web spiders	
	n	%	n	%
Diptera†	3465	70.5	190	71.4
Hymenoptera†	697	14.2	31	11.7
Lepidoptera†	319	6.5	1	0.4
Coleoptera†	179	3.6	37	13.9
Homoptera	117	2.4	5	1.9
Psocoptera	60	1.2	0	0
Araneae	39	0.8	1	0.4
Orthoptera	20	0.4	1	0.4
Thysanoptera	7	0.1	0	0
Isoptera†	6	0.1	0	0
Hemiptera	5	0.1	0	0

* Arthropods caught by web spiders were either in their webs or being consumed by the spiders during censuses. All arthropods in traps were identified to order; 87.2% of the arthropods caught by web spiders were identified.
† Adults only.

TABLE 6. Repeated-measures MANOVA of cumulative scar, mine, hole, and gall damage on leaves tagged in 1989, 1990, and 1991.

Effect	F	df	P†
Between subjects (enclosures)			
Blocks	0.57	2, 6	.5927
Lizard	26.41	1, 6	.0011*
Spider	0.20	1, 6	.3342
Lizard × spider	1.67	1, 6	.2440
Within subjects‡			
Year	46.74	2, 5	.0006
Year × lizard	5.47	2, 5	.0551
Year × spider	0.07	2, 5	.9346
Year × lizard × spider	0.60	2, 5	.5949
Damage type	60.00	3, 4	.0009
Damage type × lizard	11.64	3, 4	.0191
Damage type × spider	0.17	3, 4	.9094
Damage type × lizard × spider	0.91	3, 4	.5101

* Lizard effect is significant ($P < .05$) using the sequential Bonferroni method (three comparisons).
† Tests of lizard and spider effects are one tailed; all other comparisons are two tailed.
‡ F ratios are from Wilks' lambda.

Spiller and Schoener 1990*a*). Using the same model again, the spider effect on biomass was significant in analyses of small arthropods ($P = .012$) and large arthropods ($P = .038$); no lizard effect or lizard × spider interaction was significant.

Effects of lizards and spiders on leaf damage

Scars, mines, and holes comprised most of the damage on sea grape leaves tagged in each year (Fig. 8). Amounts of the three common types of damage tended to be higher in treatments with lizards removed (lizards removed, both lizards and spiders removed) than in treatments with lizards unaltered (controls, spiders removed). Mean yearly total damage of all types combined was 3.3 times higher in treatments with lizards removed than in treatments with lizards unaltered; the overall lizard effect was significant (Table 6). In contrast, the overall spider effect was not significant; mean yearly total damage of all types combined in treatments with spiders removed was nearly identical to that in treatments with spiders unaltered.

The lizard × spider interaction was not significant. Comparisons of individual treatments showed no indication that the lizard effect was different when spiders were removed than when spiders were unaltered; mean yearly total damage was 3.3 times higher in the treatment with lizards and spiders removed than in the treatment with only spiders removed, and it was also 3.3 times higher in the treatment with only lizards removed than in controls. Consequently, similar comparisons showed no indication that a spider effect occurred when lizards were removed or when lizards were unaltered.

Variation among years was significant; amounts of damage were low in 1990. The year × lizard interaction was almost significant, suggesting that the lizard effect varied among years. Year × spider and year × lizard × spider interactions were not significant.

Variation among damage types was significant; gall damage was very rare. The damage type × lizard interaction was also significant, indicating that the lizard effect varied among damage types. For descriptive purposes we analyzed the amount of each damage type separately, using the same statistical model as above but without damage type as a repeated factor. Mean

TABLE 5. Total biomasses in the major arthropod orders caught by sticky traps (all censuses from July 1989 to March 1992 combined). All individuals in each order were adults. Values for each treatment are the means ± 1 SD of the three replicates.

Treatment	Diptera	Hymenoptera	Lepidoptera	Coleoptera
	Biomass (mg, $\bar{X}$ ± 1 SD)			
Controls	66.2 ± 4.4	10.8 ± 2.7	18.6 ± 8.1	21.9 ± 12.3
Lizards removed	66.2 ± 7.3	13.3 ± 2.9	25.7 ± 9.0	10.2 ± 5.4
Spiders removed	80.0 ± 24.2	14.7 ± 1.5	31.7 ± 7.3	21.0 ± 14.0
Both removed	103.9 ± 8.1	14.0 ± 2.5	22.3 ± 1.8	20.6 ± 2.1

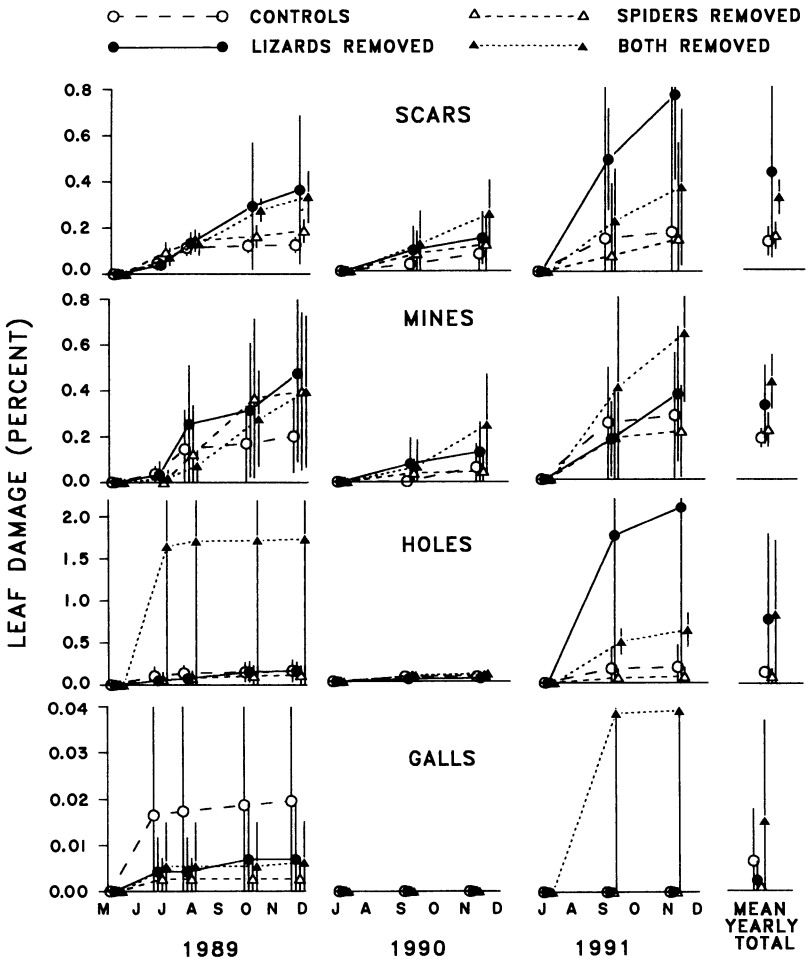

FIG. 8. Mean cumulative scar, mine, hole, and gall damage per leaf (percentage of entire leaf area) on new sea grape leaves tagged in May–June of 1989, 1990, 1991 in experimental enclosures. Each point is the mean of the mean cumulative leaf damage within each enclosure in a treatment. Error bars are ± 1 SD of the means of the enclosure means in a treatment. Mean yearly total is the mean of mean cumulative leaf damages at the end of each year in a particular enclosure.

yearly total scar damage was 2.7 times higher in treatments with lizards removed than in treatments with lizards unaltered, and the lizard effect was significant (P = .039). Mean yearly total mine damage was 1.9 times higher with lizards removed than with lizards unaltered, and the lizard effect was significant (P = .004). Mean yearly total hole damage was 7.1 times higher with lizards removed than with lizards unaltered, and the lizard effect was significant (P = .007). No spider effect or lizard × spider interaction was significant in analyses of scars, mines, and holes. No effect was significant in analysis of galls.

DISCUSSION

Lizard effects

The most direct way to evaluate whether the occurrence or the strength of a species interaction varies temporally is to repeat a field experiment on the same species at the same place but at a different time (Connell 1983). Both this experiment, conducted from 1989 to 1992, and our previous experiment, conducted from 1985 to 1988 (Spiller and Schoener 1988, 1990*a*, *b*), contained enclosures with only lizards removed and control enclosures with no species manipulated. Thus, comparison of the differences between these two treatments in our present and previous experiments represents an experiment that was repeated in the same location, evaluating the effect of lizards over a 7-yr period.

Both the present and the previous experiments demonstrated that lizards reduced numbers of web spiders, but their effect in the previous experiment was stronger. Numbers of individuals were 3.1 times higher in lizard-removal enclosures than in controls in the previous experiment, compared to 1.4 times higher in the present experiment. Lizards reduced prey consumption by adult female *Metepeira datona* in the previous experiment but not in the present experiment. In addition, in the previous experiment biomass of aerial arthropods was 1.4 times higher in lizard-removal enclosures

than in controls, whereas in the present experiment biomasses in lizard-removal enclosures and in controls were nearly identical.

We suggest that the effect of lizards on web spiders and aerial arthropods was influenced by the weather. We obtained rainfall records from 1971 to 1990 (courtesy of Department of Meteorology, Bahamas) for George Town, Exumas, the closest weather station, located ≈50 km south of our study site. During the present experiment the amounts of rainfall in 1989 and in 1990 (78.94 and 71.96 cm (original data in inches), respectively) were below the 20-yr average (1971–1990 mean ± SD = 96.5 ± 22.6 cm). Moreover, numbers of days of rainfall in 1989 and in 1990 (60 and 59 d, respectively) were the lowest recorded from 1971 to 1990 (mean ± SD = 95.0 ± 17.4 d). During our previous experiment from 1985 to 1988 the mean rainfall (88.6 cm) and the mean number of days of rainfall (87.3 d) were closer to the 20-yr averages. Thus, the effect of lizards on web spiders and aerial arthropods appears to be relatively weak in dry years. A comparative study of small islands in the vicinity of our experimental site showed that numbers of orb spiders were ≈10 times higher on islands with lizards absent than on those with lizards present in 1981 and 1982 (Schoener and Toft 1983, Toft and Schoener 1983); interestingly, annual censuses from 1981 to 1990 suggest that the lizard effect on spiders is positively correlated with rainfall (D. A. Spiller and T. W. Schoener, *unpublished manuscript*).

In the present experiment lizards reduced the amounts of scars, mines, and holes on sea grape leaves. Our observations of leaves in the study site over a 7-yr period revealed that at least some scars were caused by homopterans (aphids and leaf hoppers) and that at least some holes and probably all mines were caused by lepidopterans (several species). We found that lizards ate these taxa and other potential herbivores in our study site (Spiller and Schoener 1990*a*). Therefore, the lizard effect on leaf damage was probably caused by lizards eating herbivorous arthropods.

Contrary to the effects of lizards on web spiders and aerial arthropods, their effect on leaf damage was at least as strong in the present experiment as in the previous experiment (Spiller and Schoener 1990*b*). In the present experiment total leaf damage was 3.3 times higher in lizard-removal enclosures than in controls, whereas in the previous experiment it was 2.0 times higher. However, during the present experiment leaf damage was low in 1990 (Fig. 8), probably due to the impact of drought on herbivorous arthropod populations (Andrewartha and Birch 1954); thus, the lizard effect may have been weak, particularly for hole damage, because herbivore densities remained low even when lizards were removed.

Hence, comparisons between our present and previous experiments and among years in the present experiment suggest that the effects of lizards on other species in the community vary temporally. We propose that much of this variability may be linked to varying weather conditions. Such interactions between abiotic and biotic factors are probably common (Connell 1975, Menge and Sutherland 1976, Peterson and Black 1988, Dunson and Travis 1991).

Web spider effects

The present experiment demonstrated that web spiders reduced biomass of arthropods caught in sticky traps. Diptera, the most common order caught in traps, was the only order reduced significantly. Diptera was also the most common order caught by web spiders during this experiment (Table 4) and during our previous experiment (Spiller and Schoener 1990*a*), indicating that the mechanism responsible for the spider effect was direct predation. We found no evidence that web spiders reduced leaf damage, probably because herbivorous arthropods (e.g., Homoptera and Lepidoptera) comprised a small fraction of prey caught by web spiders (Table 4, Spiller and Schoener 1990*a*). Our previous experiment suggested that web spiders reduced gall midges, which are dipterans, but midges may have been too rare in this experiment to detect a spider effect.

In our previous study we found that the type of enclosures used in this experiment reduced aerial arthropods (Spiller and Schoener 1988); numbers and biomasses in sticky traps were 1.5 times higher in unenclosed plots than in control enclosures (lizards and spiders were unaltered in both treatments). Were the impact of spiders inversely density dependent (stronger at low prey density), the spider effect might have been slightly exaggerated within enclosures. However, differences between enclosures with and without spiders removed appeared to be about the same during censuses when aerial arthropod abundances were high and low (Figs. 6 and 7), suggesting that the spider effect was density independent. On the other hand, because the enclosures were open on top and most arthropods could pass through the hardware cloth (3.2 mm mesh), movements of aerial arthropods from enclosures with spiders removed to enclosures with spiders unaltered may have diluted the spider effect.

Experimental evidence that web spiders alone reduce insect abundance is rare, although other studies demonstrated that insect populations were reduced by cursorial spiders or the entire spider complex (Oraze and Grigarick 1989, Riechert and Bishop 1990, review in Wise 1993). Smith (1983) and Spiller (1984*a, b*) showed that orb spiders competed for food, providing some evidence that they reduced prey abundance. However, other studies found little or no evidence of food competition in web spiders (reviews in Wise 1984, 1993). In this study, the overall spider effect on aerial arthropods was significant, but the effect was not apparent on each sampling date. This inconsistency may have been due to sampling error, or the spider effect may

have varied temporally. We note for future studies that in our study extensive sampling (1536 trap-days) was performed, and this may be necessary in general to assess the overall effect of web spiders.

Compensatory predation

When compensatory predation occurs, the effects of lizards and spiders are different when each is alone than when they are together. Given that lizards reduced web spiders and web spiders reduced aerial arthropods, one would expect the effect of web spiders on aerial arthropods to be stronger without lizards than with lizards. Comparisons of overall means show that the spider effect (spiders removed vs. spiders unaltered) tended to be greater when lizards were removed than when lizards were unaltered (Figs. 6 and 7). However, no lizard × spider interaction (the statistical test of the hypothesis) was significant in analyses of aerial arthropods. Perhaps, were the lizard effect on web spiders stronger, as in our previous experiment, the interaction would have been significant. The lizard × spider interaction was also not significant in the analysis of leaf damage, but this interaction is less plausible as we found no evidence in this experiment that web spiders affected leaf damage.

In a similar field experiment, Pacala and Roughgarden (1984) showed that numbers of web spiders were 20–30 times higher in enclosures with lizards removed than in control enclosures. In addition, numbers of insects caught in sticky traps placed on the ground were 2–3 times higher, but numbers caught in aerial traps were 25% lower in lizard removals than in controls. They concluded that lizards had a direct negative effect on web spiders and ground insects, whereas they had an indirect positive effect on aerial insects via decreased predation by web spiders. We note that the lizard effect on spiders was much stronger in their experiment than in either of our experiments.

Pacala and Roughgarden's (1984) experiment revealed that the direct negative effects of lizards on web spiders and ground insects were stronger than the hypothesized indirect positive effect of lizards on aerial insects. In our previous experiment, abundances of web spiders and aerial arthropods were higher in lizard-removal enclosures than in controls, suggesting that the direct negative effect of lizards on aerial arthropods was stronger than an indirect positive effect via web spiders. The present experiment uncovered evidence for two direct effects, the impact of lizards on web spiders and the impact of web spiders on aerial arthropods, but no significant evidence of compensatory predation, which requires the indirect effect pathway. Thus, Pacala and Roughgarden's (1984) experiment and our experiments indicate that direct effects are generally stronger than indirect effects in this type of terrestrial system. Stronger direct than indirect effects are consistent with certain theory and the majority of data from other studies (Schoener, *in press*).

Food web dynamics

In this experiment leaf damage was significantly reduced by lizards but not by web spiders, supporting Model A (Fig. 1). Model A was also supported by our comparative study of buttonwood leaf damage on small islands with and without lizards (Schoener 1988) and by total leaf damage in our previous experiment (Spiller and Schoener 1990*b*). Aerial arthropod abundance was reduced by web spiders but not by lizards, which is opposite to their respective effects on leaf damage. We suggest that most aerial arthropods caught in our sticky traps were not herbivores; many may be detritivores. Hence, interactions in a detritus-based food web may be quite different from a producer-based web. However, the effect of removing lizards on total leaf damage (3.3-fold increase) was greater than the effect of removing web spiders on total biomass of aerial arthropods (1.4-fold increase), suggesting that lizards had a greater impact on the entire community than did web spiders. On two occasions during our previous experiment numbers of web spiders decreased substantially in censuses following storms (Spiller and Schoener 1988). We suggest that abiotic factors may reduce web spider populations periodically and thereby reduce the impact of web spiders on the community.

Another terrestrial experiment that measured the effect of insectivorous vertebrates on producers showed that birds had a positive effect on understory plants in a Swedish forest (Atlegrim 1989). Although this study did not measure the effect of birds on spiders or other invertebrate predators, other experimental studies demonstrated that birds reduced spider densities in Swedish forests (Askenmo et al. 1977, Gunnarsson 1983). Hence, community-level effects of birds in this terrestrial system appear to be similar to the effects of lizards in our system.

In our system containing top and intermediate predators, the net impact of top predators on producers was positive. In contrast, certain experiments in freshwater systems with top and intermediate predators showed that the net impact of top predators on producers was negative (Carpenter et al. 1987, Persson et al. 1988, Power 1990). A major difference between our terrestrial system and the experiments in freshwater pelagic systems is that the size difference between top predators and herbivores is greater in the latter (adult piscivorous fish vs. herbivorous zooplankton) than in the former (lizards vs. herbivorous arthropods). Consequently, except during early juvenile stages, piscivorous fish do not eat herbivores, and the interaction between top predators and herbivores is weak, as in Model B. Thus, body-size relationships between predators and prey may influence the main pathways in food webs (Pimm 1982, Stein et al. 1988, Lawton 1989, Schoener 1989). Furthermore, in the freshwater experiments intermediate predators ate primarily herbivores, whereas in our experiment intermediate predators ate mostly other types

of prey. In our experiment, because some herbivores were relatively sessile they were more likely to be caught by lizards than by web spiders. These include homopterans and larval lepidopterans; note that adult lepidopterans have removable scales on the exoskeleton that enable them to escape spider webs (Eisner et al. 1964). Thus, other factors that affect the vulnerability of herbivores to different predators can also be important (Power et al. 1992).

In conclusion, we propose that the effect of top predators on producers is determined, in part, by the relative strengths of interactions among the upper trophic levels.

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