Variation in the magnitude of a predator's effect from small to large islands

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Should the effect of predation be stronger on small islands or on very large islands and mainlands? To make this question precise, we ask here whether the presence/absence of a particular type of predator has greater effects on given types of organisms lower down in the food web, the larger or the smaller the island. To obtain an answer, we used four studies from the same general system, subtropical islands of the Bahamas; here diurnal lizards are the predator, the direct effects are on web spiders (total density, species richness, composite diversity, dominance) and the indirect effects are on herbivory (percent leaf damage) and in part on aerial arthropods (numbers in sticky traps). In two studies, lizards were removed experimentally from enclosures on a very large island; the experiment was performed twice. In a third study, entirely unmanipulated medium-to-large islands with and without lizards were compared. In a fourth study, lizards were introduced to a set of small-to-medium islands, while two other sets, one naturally with lizards and the other naturally without lizards, served both as controls and as another comparison. Effect magnitude is measured as the ratio of the larger to smaller of the treatment means. An overwhelming tendency exists for lizards to affect spider density, species richness and composite diversity more, the smaller the island; dominance shows little difference. Herbivory is also affected on average more on small islands, but the variation in effect magnitude with island area is less. Aerial arthropods are also affected more on average on small islands, but unlike the other variables the direction of the effect can be negative or positive, and the effect is often very weak. Thus the mainly direct effects of lizards vary more in magnitude than do the mainly indirect effects of lizards. We propose two explanations for effect magnitude to be greater, the smaller the island. First, greater isolation allows less reimmigration of prey on islands, leading to a greater effect magnitude. Second, fewer kinds of predators occur, the smaller the island, implying a greater effect of removing any one kind.

Key words: Islands, Predation, Interaction magnitudes, Lizards, Spiders, Herbivory

Variació a la magnitud d'un efecte d'un depredador d'illes petites a illes grans.
L'efecte de la depredació, hauria d'esser més gran a les illes petites o a les illes molt grans i als continents? Per precisar aquesta qüestió, al present treball ens demanam si la presència/absència d'un tipus particular de depredador té efectes

més grans sobre determinats tipus d'organismes situats més abaix a la xarxa tròfica com més gran o com més petita és l'illa. Per obtenir-ne una resposta, empram quatre estudis dins el mateix sistema general, les illes subtropicals de les Bahamas; les sargantanes diürnes hi són els depredadors, els efectes directes són damunt les aranyes de tela (densitat total, riquesa d'espècies, diversitat comp ɔsta, dominància) i els efectes indirectes són sobre l'herbivoria (percentatge de fulles afectades) i en part sobre els artròpodes aeris (nombres a les trampes d'aferrament). A dos estudis, les sargantanes foren substretes experimentalment de tancats a una illa molt gran; l'experiment es va fer dues vegades. A un tercer estudi, varen esser comparades illes mitjanes a grans, sense cap manipulació, amb i sense sargantanes. A un quart estudi, varen esser introduïdes sargantanes a un conjunt d'illes petites a mitjanes, mentre que altres dos conjunts d'illots, un naturalment amb sargantanes i l'altre naturalment sense sargantanes, varen servir com a controls i com a una altra comparació. La magnitud de l'efecte es va mesurar com a la relació entre la major i la menor de les mitjanes del tractament. Es dóna una tendència aclaparadora en el sentit que com més petita és l'illa més afecten les sargantanes la densitat d'aranyes, la riquesa d'espècies i la diversitat composta; la dominància d'espècies mostra poca diferència. L'herbivoria també està afectada més de mitjana a les illes més petites, però la variació en la magnitud de l'efecte amb l'àrea insular és poca. Els artròpodes aeris també estan afectats més en promig a les illes petites, però, a diferència de les altres variables, la direcció de l'efecte pot esser positiva o negativa, i l'efecte és sovint molt feble. Per això, els efectes principalment directes de les sargantanes varien més en magnitud que els efectes principalment indirectes de les sargantanes. Proposam dues explicacions per al fet que com més petita és l'illa més gran és la magnitud de l'efecte. Primera, un aïllament més gran permet menys reimmigració de les preses, conduint a una major magnitud de l'efecte. Segona, a com més petita és l'illa, menys tipus de depredadors hi ha, cosa que implica un efecte més gran quan se'n substreu un qualsevol.

Paraules clau: Illes, Depredació, Magnitud d'interaccions, Aranyes, Herbivoria.

Introduction

How should the strength of species interactions, such as competition and predation, vary between mainlands and islands?

A number of investigators have proposed that large predators are typically absent from islands of sufficiently small area (Diamond, 1984; Belovsky, 1987; Schoener, 1989; Holt, 1993). In part this is because individual spatial requirements of large predators, which are often territorial (i.e., have more-or-less exclusive home ranges) are too great (McNab, 1963; Schoener, 1968a; Turner et al., 1969) to allow a stable population to persist there. Simple dynamical metapopulation models of food chains (Schoener et al., 1995; Holt, 1996) lead to a similar conclusion: a greater fraction of islands will have prey than predators when the latter are dependent on the former, and the fraction of species that are predators on a given island will increase with that island's area. Under such conditions, overall predation should be weaker on average, the smaller the island. Note, however, that although the effect of top predators on the next level down may be greater on larger islands by this reasoning, the level one more link farther down may thereby in fact be alleviated from their own predators, and so on seriatum in an alternating-level cascade (Hairston et al., 1960; Fretwell, 1977; Jager and Gardner, 1988).

A completely different argument is as follows. Rather than considering an entire level as the unit of interest, we can ask about the effect of particular predator species within

a predator level. The more species within a given level, the less the effect may be of removing only one of them, barring complete compensatory predation and all other things being equal. The larger the area the community occupies, the more predator species there will typically be at any level, i.e., the greater the "diffuse predation" (Hixon, 1991; Menge et al., 1994), so the effect of removing a single species of predator will be smaller there (Spiller and Schoener, 1998).

The argument for competition is similar to that for predation. The entire absence of a trophic level is argued to increase competition at the next level down (Hairston et al., 1960). Hence if a particular trophic level is more likely to be entirely or largely absent the smaller the island, the more intense should be competition there. Again, the effects alternate over succeeding levels. However, for a given level of competitors, the effect of any given one is again likely to be smaller, the more species of competitors there are (although the effect of a particular competitor, including its direction, is not always obvious in theory [Case, 1995]). Thus "diffuse competition" (MacArthur, 1972) is the analog concept to diffuse predation.

While isolation affects species composition on islands (see below), it has a more straightforward effect resulting from differences in immigration rates of prey onto islands vs onto equivalently sized sites on a mainland. Large islands may have kinds of refugia, not found on or near small islands, that allow prey locally exterminated by predators to reimmigrate relatively quickly (Spiller and Schoener, 1998). More formally, models of predation having a flow of prey into the system can be more stable, in the sense of having a single stable equilibrium point (Schoener, 1973) rather than nested cycles ("neutral stability") as in the simplest, Volterra predator-prey model (Roughgarden, 1979). Competition models whose species re-immigrate into the system are likewise relatively likely to have at least one stable equilibrium point (Schoener, 1974, 1976a).

Counter to these arguments, isolation can reduce the number of predators reaching the isolate, making it less likely that a particularly devastating one, or indeed an entire level of predators, will establish. Thus a reduced immigration of predators affects prey positively via the first of the arguments given above. Furthermore, one might argue that the area in question may have its predators exterminated also; the less the isolation, the more readily the predators will recolonize. While certainly true, the cause of the predator extermination would have to be something other than the interaction itself; for prey, the threat of extermination is ongoing by definition of the predation process. Furthermore, the immigration of predators is counterbalanced by the immigration of prey just discussed, and one might argue that the latter flow would be relatively stronger because of the higher population densities of prey compared to their predators. On the other hand, predators tend to be larger so sometimes stronger flyers and thereby better dispersers (MacArthur and Wilson, 1967), i.e., on a per-capita basis they may be more likely to immigrate.

A third characterization of islands is their greater potential exposure to physical factors such as wind and wave action, including tidal waves. This trait would seem to be exacerbated, the smaller the island (although the opposite has been argued by Cody [1966] for islands in maritime climates and out of the hurricane belt). Were physical factors chronically to hold all populations down, population densities would be low and biological interactions would be weak (Andrewartha and Birch, 1954; Wiens, 1977). In contrast, reversing the causal chain, smaller populations are more vulnerable to extinction (MacArthur and Wilson, 1967; Goel and Richter-Dyn, 1974; Terborgh and Winter, 1980; Pimm et al., 1988; Pimm, 1991; Schoener and Spiller, 1992; Hanski, 1997), so that if predation say, wiped out all individuals except those in a small number of predation refugia, physical factors could finish them off (or vice versa). This would cause predation to be more effec-

tive, the smaller the island. A similar argument can be made for interspecific competition, e.g. if a population was reduced by competition to only a small number of individuals sustainable on exclusive resources.

The above discussion shows that answers to questions about the relative effects of species interactions on islands and mainlands will depend inter alia on the precise form of the question. In this paper, we restrict the questions and the systems used to answer them to produce some precise expectations and tests. In general, we will ask, for the same kind of predator and prey, in the same geographic locale, is the effect of that kind of predator stronger on smaller or larger islands, the largest of which are effectively mainlands? Hence the predator trophic level always exists, and the expectation follows the diffuse-predation argument, as well as the principal isolation argument given above: the larger the island, the weaker the magnitude of predation. We will be looking at both the direct and indirect effects, again using the same or very similar species, so that we are effectively examining the effects on kinds of species that occur at all the sites we consider.

For about two decades we have been studying species interactions in terrestrial food webs using islands in the Bahamas as a model system. *Anolis* lizards are here major predators, eating carnivorous arthropods such as spiders, herbivorous arthropods, and detrivores such as certain dipterans (Schoener, 1968b). To investigate the direct and indirect effect of these predatory lizards, we use two complementary methods—(1) observational comparisons of the biotas on small islands with and without lizards and (2) experimental manipulations, both of lizards within field enclosures on a large island and of lizards on small islands. From this body of work we extract for this paper the relevant data from four studies—two at the same very-large-island site but during different time periods, a third on medium-to-large islands, and a fourth on very small islands. These data will be used to produce an empirical answer to the question of how the effect of a predator varies in magnitude with island area.

Experiments and observations

This section collects data on the direct and indirect effects of lizards from experiments and observations for a range of island areas. First, two lizard-removal experiments on a very large island ($\approx 3 \times 1$ km²), effectively a mainland, are summarized (full description in Spiller and Schoener, 1988, 1990a,b, 1994, 1998). The first experiment has lizard removal only; the second has lizard and spiders removal in a crossed design. Second, observational data are presented for lizard and no-lizard islands of medium-to-large area (112-8603 m² vegetated area). Although the data have been used in a number of studies (details of the system in Schoener and Spiller, 1992; Spiller and Schoener, 1995, 1996), the analyses given here for spiders are new. Analyses of herbivory follow previous papers (Spiller and Schoener, 1996, 1997). Third, a lizard-introduction experiment on islands of small-to-medium area (40-179 m² vegetated area) is summarized. This experiment allows comparison of a set of manipulated islands (lizard introduction) with a control set of no-lizard islands (lizards absent), as well as comparison of a set of unmanipulated, natural lizard islands with a set of unmanipulated natural no-lizard islands (the aforementioned control islands). This experiment has been described elsewhere (Schoener and Spiller, 1996, in press), but data on certain spider species-diversity-and-abundance measures are presented here for the first time.

Throughout what follows, we only report detailed statistical treatments, including P values, for results from new data compilations; these always utilize analyses of variance and covariance. When time-series data are involved, we evaluate differences in time-averages, statistically equivalent to evaluation of the between-subjects effect in a repeated-measures design in which time is the

Fig. 1. Example of enclosure used in lizard-removal experiments on the very large island, Staniel Cay.
Fig. 1. Exemple de tancat emprat als experiments de substracció de sargantanes a una illa molt gran, Staniel Cay.

repeated factor. The specific P values are not given for results tested as statistical hypotheses in previous papers; rather, we use such terms as "significant" or "significantly different" to denote P values less than 0.05. Similarly, we denote an effect "marginally significant" when $0.05 \leq P < 0.10$.

I. Very-large-island experiments.

A. <u>Experiment 1—One-way lizard removal</u>. This experiment was conducted on Staniel Cay, an island in the central Bahamas (Exumas). 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), with a few representatives of ≈ 10 species of other shrubs.

The experiment had three treatments (n = 3 for each); (1) unenclosed plots with lizards unmanipulated; (2) control enclosures with lizards; and (3) lizard-removal enclosures. Each plot and enclosure was 83.6 m^2.

Mean heights of the vegetation varied from 0.14 to 0.53 m. To take this vegetational heterogeneity into account, we stratified the plots into 3 blocks. Then one enclosure from each block was randomly assigned to have lizards removed during the experiment. Enclosure design was modified from that of Pacala et al. (1983). Wood-framed fences were built on the plot perimeters. The plots were buried 0.31 m below the ground and stood 0.93 m high, with hardware cloth (3-mm [¼ inch] mesh) attached to the sides. Polypropylene plastic was cut into 0.4-m-wide strips and mounted horizontally on top, forming a continuous 0.2-m overhang on the inside and on the outside of the fences, so that, except for the overhang, the enclosures were open on top (Fig. 1). To accomplish this construction, several thousand pounds of materials were flown in repeated trips to Staniel Cay in a small airplane.

Most lizards at the site were *Anolis sagrei*, with some *Anolis carolinensis* and *Ameiva festiva*. The biology of these species

is discussed in detail elsewhere (Schoener, 1968b; Schoener and Schoener, 1978, 1980, 1982a,b). Snout-vent lengths (mean of the largest third of all specimens collected from the 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 (N = 6). *Ameiva* were somewhat larger (precise measurements unavailable).

Initially we stocked control enclosures as needed to a level of 9 lizards (6 females and 3 males); the mean natural density at the site was 0.1 per m^2. During the experiment (May 1985-November 1988), we counted numbers of web spiders of each species at one- to three-month intervals; the spider species found at this site during this and the next experiment are listed in Tab. 1. At the same intervals we sampled aerial arthropod abundance with sticky traps; this consisted of putting out four sticky traps in each plot, then recording the number of individuals and body lengths (estimated to the nearest mm) of the arthropods caught by the traps. The traps were 22x14-cm sheets of clear plastic coated with Tanglefoot adhesive and suspended 0.25-0.50 m above the ground. Each year, we tagged leaves of sea grape and (using 5 evenly spaced areas, in each of which we tagged three undamaged leaves) measured herbivore damage (as a percent of the total leaf area) as it accumulated throughout the year. The summary measure used was the mean of the percent damage per leaf (D_L in Schoener [1988]). We distinguished three different categories of leaf damage—scars and mines (necrotic areas), holes (entirely missing areas), and galls (produced by a cecidiomyiid midge, *Ctenodactylomyia watsoni*). In the field, we observed scars produced by homopterans (Cicadellidae and Aphididae) and a hemipteran (Pentatomidae), mines produced by a lepidopteran, and holes produced by lepidopterans (Tortricidae - *Amorbia* sp. [prob *emigratella*]; Noctuidae—unidentified spp.), a coleopteran (Scarabaeidae - *Phyllophaga* sp.) and a hymenopteran (*Trachymyrmex maritimus*).

In the present paper, we simplify treatment of herbivory by lumping together all leaf-damage types; separate analyses of these types are in Spiller and Schoener (1990b, 1994, 1996).

Results of this experiment were as follows. The mean total density of web spiders was significantly higher, 3.1 times, for lizard-removal enclosures than for treatments with lizards (Tabs. 2, 3; Spiller and Schoener, 1988, 1996). Unenclosed plots and control enclosures were nearly identical, indicating that the enclosures had no effect on spider numbers; because of this, we simplify below by excluding unenclosed plots from the tables. Number of web spider species were higher in lizard-removal enclosures than in the other treatments; time averages were 1.2 times greater in removals than in control enclosures and the ratio of the former to unenclosed plots was about the same. Detailed analyses revealed that the lizard effect on spiders was caused by both predation and food competition (Spiller and Schoener, 1990a). Mean number of aerial arthropods was 1.6 times higher in unenclosed plots than in control enclosures and was 1.1 times higher in lizard-removal enclosures than in control enclosures; there was a significant enclosure effect as well as a significant lizard effect on aerial arthropods (two-tailed raw P = 0.001, 0.043, respectively). We also separated small (≤ 4 mm) and large (> 4 mm) aerial arthropods (Spiller and Schoener, 1990a). Numbers of both were greater for no-lizard than lizard enclosures (Tabs. 2, 3), but the effect ratio (larger over smaller) was substantially greater for large arthropods (1.7) than for small arthropods (1.05), and was only significant for the former (Schoener and Spiller, in press). Thus although spiders ate many of the same arthropods as did lizards, when lizards were removed increased predation by spiders did not completely compensate for the lack of lizards. Finally, lizards significantly reduced scar and mine damage and reduced hole damage as well, but not significantly (Spiller and Schoener, 1996). Interestingly, lizards significantly increased the amount of gall damage.

Taxa	I. Very-large-island site		II. Medium-to-small-islands site	III. Small-to-medium islands site
	A. First experiment	B. Second experiment		
Araneidae				
Metepeira datona	X	X	X	X
Metepeira sp.				X
Eustala cazieri	X	X	X	X
Argiope argentata	X	X	X	X
A. trifasciata				X
Eriophora ravilla	X	X	+	X
Gasteracantha cancriformis	X	X	X	
Cyclosa caroli			X	
C. walckenaeri				X
Cyrtophora sp.			X	
Tetragnathidae				
Nephila clavipes	X	X	X	
Plesiometa argyra		X	X	X
Leucauge sp.			X	
Tethragnathidae sp.				X
Uloboridae				
Uloborus trilineatus			X	X
Philoponella semiplumosa				X
Theridiidae				
Latrodectus mactans	X	X	X	
Argyrodes elevatus	X	X	X	X
A. furcatus				
Total	8	9	12	12

+ Occurs on these islands but not counted because of difficulty of detection there.

Table 1. Species of web spiders occurring at three Bahamian sites during four studies.
Taula 1. Espècies d'aranyes de xarxa presents a les tres localitats de les Bahames durant els quatre estudis.

| Variable | I. Very-large-island Experiment (Staniel Cay) | | | | II. Medium-to-large-island Observations (Exumas Region) | | III. Small-to-medium-island Experiment and Observations (Abaco Region) | | |
| | A. First experiment | | B. Second experiment | | | | | | |
	Lizard enclosures	No-lizard enclosures	Lizard enclosures	No-lizard enclosures	Lizard islands	No-lizard islands	Lizard introduction islands	Natural lizard islands	Natural no-lizard islands
1. Total spider density[a] (no./m²)	0.457	1.395	0.543	0.989	0.035	0.198	0.155	0.109	0.766
2. Number spider species (=species richness)	2.85	3.53	2.17	3.40	1.58#	2.61#	1.04	0.92	3.13
3. Spider composite diversity[b]	NC	NC	0.269[d]	0.396[d]	0.174	0.344	0.068	0.036	0.257
4. Spider dominance[b]	NC	NC	0.797[c]	0.681[c]	0.885	0.748	0.964	0.981	0.839
5. Seagrape leaf damage (percent)	1.62	3.23	0.45	1.49	0.59	1.87	NC	NC	NC
6. Buttonwood leaf damage (percent)[A]	NC	NC	NC	NC	9.0	11.7	2.0	6.7	8.9

| Variable | I. Very-large-island Experiment (Staniel Cay) | | | | II. Medium-to-large-island Observations (Exumas Region) | | III. Small-to-medium-island Experiment and Observations (Abaco Region) | | |
| | A. First experiment | | B. Second experiment | | | | | | |
	Lizard enclosures	No-lizard enclosures	Lizard enclosures	No-lizard enclosures	Lizard islands	No-lizard islands	Lizard introduction islands	Natural lizard islands	Natural no-lizard islands
7. Total number aerial arthropods (number/trap-day)[c]	3.2	3.5	3.8	3.9	NC	NC	6.5	7.9	5.5
8. Number small aerial arthropods (number/trap-day)[c]	2.9	3.1	NC	NC	NC	NC	6.4	7.9	5.4
9. Number large aerial arthropods (number/trap-day)[c]	0.23	0.38	NC	NC	NC	NC	0.10	0.04	0.06

[^] D_L measure (Schoener, 1988), green morph

[#] Back-transformed adjusted means from ANCOVAs

[a] *E. ravilla* included in Data Set I but not II because of detection difficulty on islands (it is mainly active nocturnally)

[b] Means of the individual census means for Data Set IB; means of the cumulative values (computed from frequency distributions of all the time-series data added together) for Data Sets II and III (a cumulative measure had to be used for these data sets because islands sometimes had no spiders so composite diversity and dominance could not be computed)

[c] Note that values for Data Sets IA and IB are given in Spiller and Schoener (1988, 1944) per enclosure, not per trap as in this table

[d] Cumulative measures are 0.308 and 0.461, respectively

Table 2. Effect of lizards on food-web variables: Mean values of the variables with and without lizards (NC = not calculated).
Taula 2. Efectes de les sargantanes sobre les variables de la xarxa tròfica: valors mitjans de les variables amb i sense sargantanes (NC = No calculat).

Because the latter comprised only a small portion of the total leaf damage, overall damage was substantially decreased by lizards: lizard enclosures had twice as much overall damage as did no-lizard enclosures (Tabs. 2, 3).

B. Experiment 2—Two-way lizard and spider removal. This experiment was staged at the same site as was Experiment 1 and was conducted after the latter's completion (Spiller and Schoener, 1994). The expanded design (2x2 factorial) had four treatments (n = 3 for each): (1) controls with lizards and spiders unaltered (natural densities); (2) lizards removed and spiders unaltered; (3) spiders removed and lizards unaltered; and (4) both lizards and spiders removed; all treatments were conducted within enclosures. We again used three vegetation blocks of four plots each; treatments were assigned randomly within each block. Enclosure construction was identical to that in the previous experiment, but note that an additional six enclosures had to be erected. Enclosures in Treatments 1 and 2 were stocked up to a level of nine *A. sagrei* lizards apiece, the same density used in the previous experiment. We monitored the experiment at one-to three-month intervals from May 1989 to December 1994; results for aerial arthropods and leaf damage were compiled through March 1992. Methods were as in the previous experiment, except that mines and scars were measured separately (but note we again lump all damage types for purposes of the present paper).

Results of this experiment were as follows. The time average for total density of spiders was significantly higher, 1.8 times, in the treatment with only lizards removed than in the control (Fig. 2, right; Tabs. 2, 3; Spiller and Schoener, 1998). Also as in the previous experiment number of spider species was significantly higher in the treatment with only lizards removed than in the control (Fig. 2, right; Tabs. 2, 3); the effect ratio was somewhat greater—1.6 here vs 1.2 in the first experiment. In addition to number of species, we calculated (as in Spiller and Schoener, 1998)

two other measures of species diversity that incorporated relative abundances. First, we calculated *composite diversity*, the modified Simpson index (as suggested by Lande [1996]):

$$1 - \sum_{i=1}^{S} p_i^2$$

where p_i is the proportion of the total number of individuals belonging to Species i and S is the number of species. Second, we calculated *dominance*, the proportion of the total number of individuals belonging to the most abundant species, in this case *Metepeira datona*. Composite diversity was higher in no-lizard enclosures, while dominance was lower, although the second tendency was only marginally significant (Fig. 3, right; Tabs. 2, 3). Figs. 4 and 5 show how the numbers of individual spider species varied during the experiment. Numbers of aerial arthropods in the same two treatments were almost identical and not significant in the overall analysis (Spiller and Schoener, 1994) (Tabs. 2, 3). The effect of spiders on aerial arthropods was more substantial, apparently stronger than the effect of lizards. Finally, mean amounts of the major leaf-damage types—scars, mines and holes—were greater in each of the two treatments with lizards removed than in controls (Spiller and Schoener, 1994, 1996), but means with only spiders removed and controls were nearly identical. Galls were extremely rare in this experiment, and no significant effect was detected. Overall mean leaf damage (Tabs. 2, 3) was significant (Spiller and Schoener, 1994, 1996), being 3.3 times greater in lizard-removal enclosures than in enclosures with lizards. The lizard-spider interaction was not significant for either aerial arthropods or leaf damage, indicating that compensatory predation was absent or at best weak.

II. Medium-to-large-island observations.

We have been censusing spider abundances on over 100 islands in the vicinity (< 20 km) of Staniel Cay since 1981 and measu-
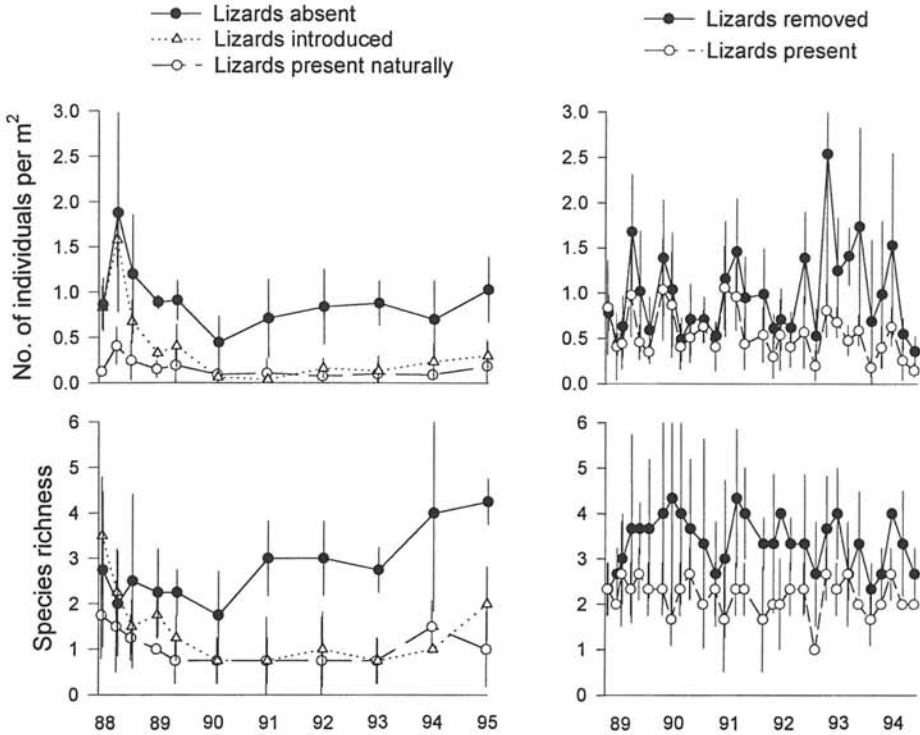
Fig. 2. Comparison of the time course of the experiment on small-to-medium islands (Abaco, Data Set III) with that of the second experiment on a very large island (Staniel, Data Set IB). Each point represents a treatment mean for a single census. Top row: total web-spider density— left, very small islands; right, very-large-island enclosures. Bottom row: total number of web-spider species (species richness)—left and right as above.

Fig. 2. Comparació del curs temporal de l'experiment sobre illes petites a mitjanes (Abaco, Conjunt de Dades III) amb el del segon experiment a una illa molt gran (Staniel, Conjunt de Dades IB). Cada punt representa una mitjana tractament per a un recompte únic. Filera de dalt: densitat d'aranyes de xarxa – esquerra, illes molt petites; dreta, tancats a illes molt grans. Filera de sota: nombres totals de les espècies d'aranyes de xarxa (riquesa d'espècies) – esquerra i dreta com a dalt.

ring leaf damage in sea grape since 1986 on all of those islands where that species occurs (11 islands with lizards, 7 islands without lizards). We (Spiller and Schoener, 1995, 1996) concentrated on that subset of those islands that included all islands ≥100 m² (vegetated area) and with maximum vegetation height ≥1 m, because most populations on poorer islands were small and ephemeral. In addition, we excluded islands with recor-

ded lizard turnover (immigration or extinction) and islands successfully colonized by spiders in a species-invasion experiment (Schoener and Spiller, 1995). With these filters, we obtained 27 islands with lizards and 24 islands without lizards; these are the islands used for the spider analyses below. As in a previous recent treatment (Spiller and Schoener, 1995), we use here the data from 1981 to March 1990, a 10-year period, to
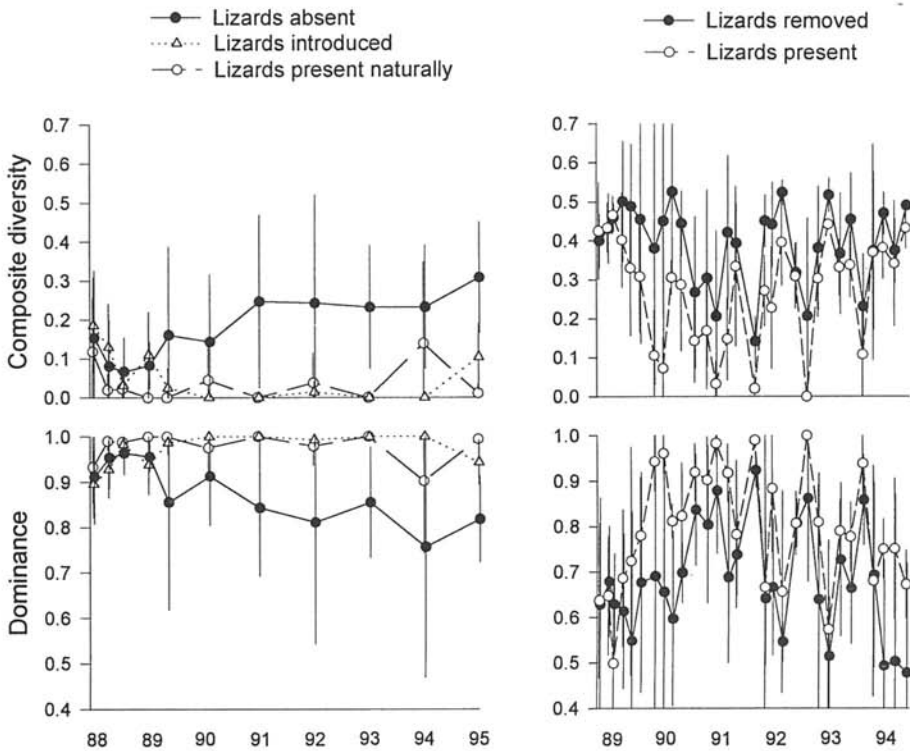
Fig. 3. Comparison of time courses of the experiment on small-to-medium islands (Abaco, Data Set III) with the second experiment on a very large island (Staniel, Data Set IB). Each point represents a treatment mean for a single census. <u>Top</u> <u>row</u>: web-spider composite diversity—<u>left</u>, very small islands; <u>right</u>, very-large-island enclosures. <u>Bottom</u> <u>row</u>: web-spider dominance—<u>left</u> and <u>right</u> as above. For Data Set III, when values could not be computed for a particular island at a particular date (because no spiders occurred there), "0" was used for composite diversity and "1" was used for dominance.

Fig. 3. Comparació del curs temporal de l'experiment en illes petites a mitjanes (Abaco, Conjunt de Dades III) amb el segon experiment a una illa molt gran (Staniel, Conjunt de Dades IB). Cada punt representa una mitjana de tractament per a un únic recompte. <u>Filera de dalt</u>: diversitat composta d'aranyes de xarxa —<u>esquerra</u>, illes molt petites; <u>dreta</u> tancats a illes molt grans. Filera de baix: dominància d'aranyes de xarxa —<u>esquerra</u> i <u>dreta</u> com a dalt. Per al Conjunt de Dades III, quan les valors no es podien computar per a una illa particular a una data particular (perquè no hi havia aranyes), s'emprava "0" per calcular la diversitat composta i "1" per calcular la dominància.

analyze properties of spiders. From another previous recent treatment (Spiller and Schoener, 1997), we use data from 1986 (when a dynamic measure of herbivory was first employed) through 1993 to analyze leaf damage in sea grape. Additionally, we did a static measurement of leaf damage in a small species, buttonwood (*Conocarpus erectus*)

during 1984 (Schoener, 1988), which we shall also discuss in the present paper.

Web-spider censuses proceeded as follows. All webs were counted on each island, and their occupants, if any, noted as to species, size and (if possible) sex. Spiders without webs were noted but not included in the counts; few such spiders were seen. Vegetation on these islands was typically 0.5-1.5 m in height and was sparse, so that we were able to inspect visually most foliage for webs. To minimize the possibility of missing a web, we performed censuses in teams of two or three persons walking in tandem. Because of the small areas of most of the islands, it was almost always practical to census the entire island; in a few cases (Schoener and Spiller, 1992) we censused only part of the island and extrapolated, stratifying the island by vegetation type. Each annual census was conducted in late April or May. This period of time coincides with the end of the dry season, and between-year variation then is less or no greater than that at other times of the year for which we have data. This may be largely because weather is usually more severe during other times, such as winter when cold fronts destroy large numbers of spiders, or late summer to autumn, when hurricanes sweep across the Caribbean. Tab. 1 lists the web spider species found in these censuses. Of these, *M. datona* and *E. cazieri* were by far the most abundant overall; *A. argentata* and *G. cancriformis* were the two other most common species. Lizards on these islands are mostly *Anolis sagrei*; *Anolis carolinensis, Ameiva festiva* and *Leiocephalus carinatus* also occur on some of the (mostly largest) islands.

Leaf damage in sea grape is measured dynamically much as in the set of experiments just described, except that sampling techniques were necessarily somewhat different. On islands with fewer than 8 sea-grape plants, all plants were sampled. On islands with 8-20 plants, sampled plants were chosen systematically by including every other plant encountered on a circular ambit of the island.

On islands with > 20 plants, every third plant so encountered was sampled. We distinguished the same categories of damage as in the first experiment described above; galls were practically absent. Again, damage types were combined for the analysis herein.

The other species whose herbivory was measured, buttonwood, exists as more-or-less discrete morphs, silver and green, in which leaf trichomes are numerous or few, respectively (Schoener, 1987). Because only green buttonwood occurs in the comparison region (very small islands of Abaco, see III below), we only report damage for that form here. Unlike sea grape, for which damage was measured nondestructively in the field, we measured buttonwood damage by collecting leaves and analyzing them in the laboratory with a digitizer. Leaves collected for analysis were sampled by systematic selection of trees such that number of trees sampled was roughly proportional to the logarithm of buttonwood surface area on an island, with the maximum number per island being 10 trees. To sample leaves, we tossed a square haphazardly onto each tree and collected that cluster of leaves closest to the landing point; up to 9 samples per tree were thus obtained. As before, we used mean of the percent areal damage per leaf (taken over all leaves from a particular island) as our measure of herbivory.

Results for web spiders were as follows (note that previous treatments [Spiller and Schoener, 1995, 1996] are only for orb-web, not other types of web spiders; we have added the latter here—see also Tab. 1). The total number of spider individuals must be measured in some way that takes into account the several-orders-of-magnitude variation in area that the study islands show. One solution is to divide by area to obtain densities; this is a sensible procedure because a reasonable assumption, made for example in many biogeographical models (Preston, 1962; MacArthur and Wilson, 1967; Schoener, 1976b) is that number of individuals is proportional to area. A huge difference in total spider densities occurs between lizard and no-

Variable	I. Very-large-island Experiment (Staniel Cay)		II. Medium-to-large-island Observations (Exumas Region)	III. Smalll-to-medium-island Experiment and Observations (Abaco Region)	
	A. First experiment	B. Second experiment			
	No-lizard vs lizard	No-lizard vs lizard	No-lizard vs lizard	No-lizard vs lizard introduction	No-lizard vs natural lizard
1. Total Spider density (no./m²)	3.1	1.8	5.7[a]	5.0	7.0
2. Number spider species (=species richness)	1.2	1.6	1.7	3.0	3.4
3. Spider composite diversity	NC	1.5*	2.0	3.8	7.1
4. Spider dominance	NC	1.2#	1.2#	1.1#	1.2#
5. Sea-grape leaf damage (percent)	2.0	3.3	3.2	NC	NC
6. Button-wood leaf damage (percent)	NC	NC	1.3	4.4	1.3

| Variable | I. Very-large-island Experiment (Staniel Cay) | | II. Medium-to-large-island Observations (Exumas Region) | III. Smalll-to-medium-island Experiment and Observations (Abaco Region) | |
| | A. First experiment | B. Second experiment | | | |
	No-lizard vs lizard	No-lizard vs lizard	No-lizard vs lizard	No-lizard vs lizard introduction	No-lizard vs natural lizard
7. Total number aerial arthropods number/trap-day)	1.1	1.0	NC	1.2[#]	1.4[#]
8. Number small aerial arthropods (number/trap-day)	1.0	NC	NC	1.2[#]	1.4[#]
9. Number large aerial arthropods (number/trap-day)	1.7	NC	NC	1.7[#]	1.5

[†] Ratios of larger to smaller treatment value

[#] Lizard value > no-lizard value

[*] Ratios the same for cumulative measure (see text)

[a] Ratio is 4.9 for back-transformed adjusted means (see text)

Table 3. Effect of lizards on food-web variables: Effect ratios [†] (NC= not calculated).
Taula 3. Efectes de les sargantanes sobre les variables de la xarxa tròfica: taxes d'efectes (NC= No calculat).
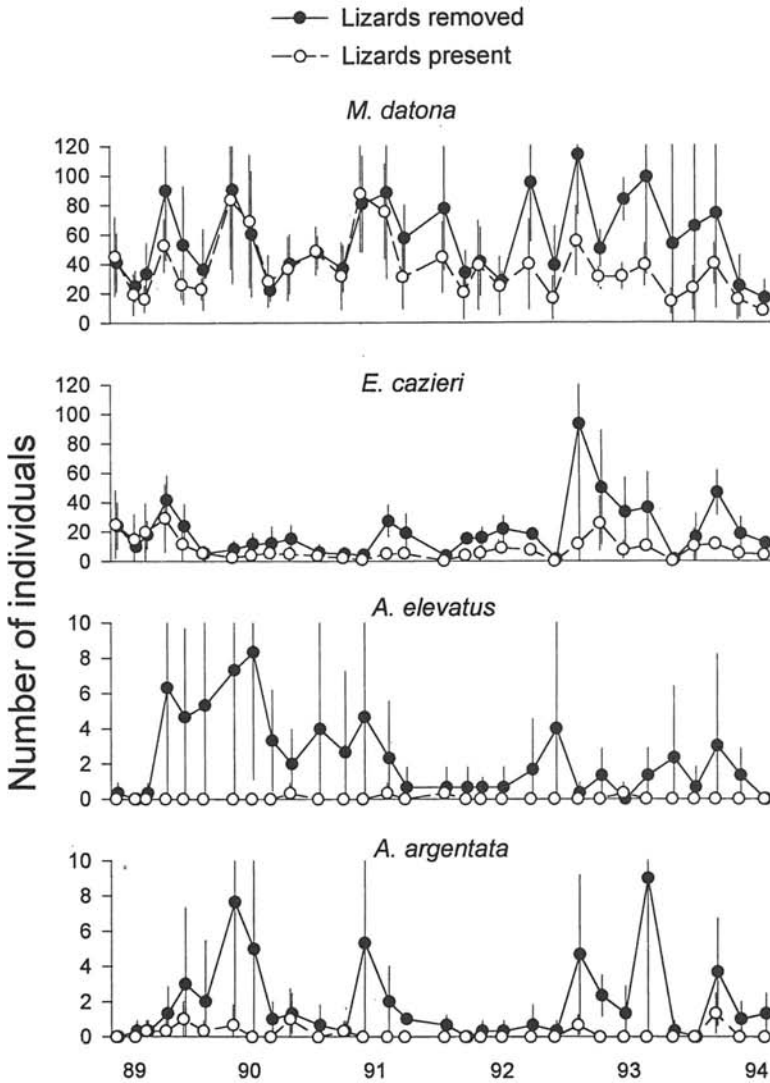
Fig. 4. Time courses of abundance for particular species from the second very-large-island experiment (Staniel, Data Set IB). Each point represents a treatment mean for a single census. Full species names given in Tab. 1. Species are excluded from Figs. 4-5 if they were so rare that fewer than five individuals were recorded in the entire data set; i.e., summed over all dates and enclosures.

Figura 4. Curs temporal de l'abundància per a espècies concretes del segon experiment a una illa molt gran (Staniel, Conjunt de Dades IB). Cada punt representa una mitjana de tractament per a un recompte únic. Els noms complets de les espècies es donen a la taula 1. Les espècies s'exclouen de les figures 4-5 si eren tan rares que només s'havien registrat menys de cinc individus en el conjunt complet de dades (és a dir, sumades en totes les dades i tancats).
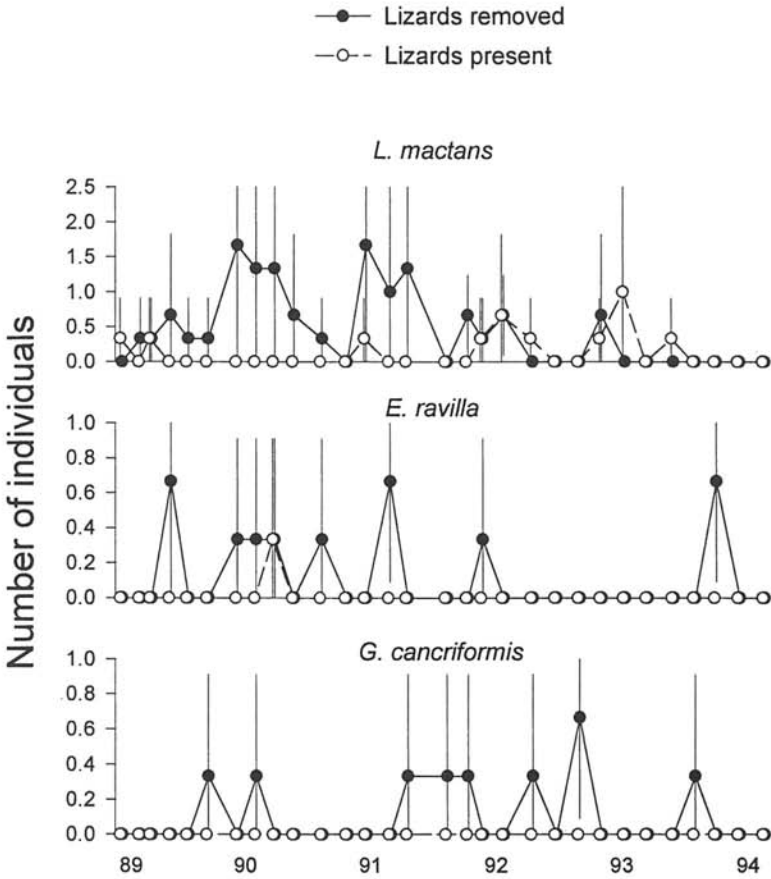
Fig. 5. More time courses of abundance for particular species from the second very-large-island experiment (Staniel, Data Set IB). Each point represents a treatment mean for a single census. Full species names given in Tab. 1.

Fig. 5. Més cursos temporals d'abundància per a espècies concretes del segon experiment a una illa molt gran (Staniel, Conjunt de Dades IB). Cada punt representa una mitjana de tractament per a un recompte únic. Els noms complets de les espècies es donen a la taula 1.

lizard islands; the latter have 5.7 times the densities as do the former (Tabs. 2, 3; see Spiller and Schoener [1995] for various statistical evaluations). Unfortunately, it is well known that the number of species is not best represented as directly proportional to area (above references), so that division by area is for that variable not justified. Alternatively, we can do covariance-type analyses, with island area as the covariate, and number of species and island area transformed appropriately. Of the two possibilities, number of species and log number of species vs log area, the latter gave the greater linearity, so we used that transformation here. The first step is to include in the model the interaction for the main effect (lizard presence and absence) with the covariate, log area. The interaction
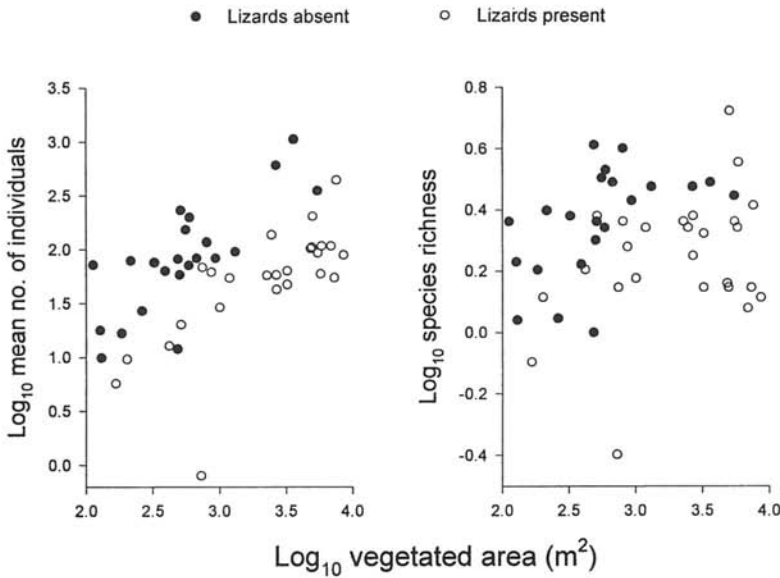
Fig. 6. <u>Left</u>. Log_{10} mean total number of spider individuals versus log_{10} island area for medium-to-small islands (Exumas, Data Set II). <u>Right</u>. Log_{10} mean number of web spider species (species richness) vs log_{10} island area for medium-to-small islands (Exumas, Data Set II). Means are averages of values from 1981 through 1990 inclusive.

Fig. 6. <u>Esquerra</u>. Log₁₀ del nombre total mitjà d'aranyes individuals versus log₁₀ de l'àrea insular per a illes mitjanes a petites (Exumas, Conjunt de Dades II). <u>Dreta</u>. Log₁₀ del nombre mitjà d'espècies d'aranyes de xarxa vs log₁₀ de l'àrea insular per a illes mitjanes a petites (Exumas, Conjunt de Dades Ii) log₁₀ de l'àrea insular per a illes mitjanes a petites (Exumas, Conjunt de Dades II). Les mitjanes són els promedis dels valors de 1981 a 1990 inclosos.

was not significant (in this analysis and all others below), indicating equality of slopes, so we then can do a "normal" ANCOVA. This analysis shows both area and the lizard effect to be significant (Tab. 4); Fig. 6 illustrates the data. From this analysis, we can calculate adjusted (= least squares) means to remove the effect of area (Tab. 2). The ratio of adjusted means, back-transformed to arithmetic values, can be computed as a measure of effect size; it is 1.7 (Tab. 3). This ANCOVA methodology can provide an alternative to the method we used above for evaluating the lizard effect and computing effect size for total spider individuals, where now we use

log number rather than density as the dependent variable. This might be especially apposite when something additional to area, e.g. some habitat measure that correlates with area, is influencing the form of the plot of number of spiders vs area. Tab. 4 shows that both the lizard and area effects are highly significant. When adjusted means are computed and back-transformed to arithmetic values, the effect ratio is 4.9, very close to the 5.7 value obtained using densities. Finally the same ANCOVA procedure for the other two variables associated with species diversity, composite diversity and dominance, shows that the area effect is not significant (Tab. 4;

Source	df	F	P
1. Log total number of spiders			
log area	1,45	51.02	5×10^{-5}*
lizards	1,45	29.85	5×10^{-5}*
2. Log number of spider species (species richness)			
log area	1,45	9.86	0.002*
lizards	1,45	12.83	4×10^{-4}*
3. Arcsine sqrt spider composite diversity			
log area	1,45	0.25	0.620
lizards	1,45	7.84	0.008
4. Arcsine sqrt spider composite diversity			
lizards	1,46	9.05	0.004
5. Arcsine sqrt spider dominance			
log area	1,45	0.27	0.609
lizards	1,45	7.95	0.007
6. Arcsine sqrt spider dominance			
lizards	1,46	9.13	0.004

* One-tailed P value: all unmarked P's two-tailed; note that we consider tests involving number of individuals and number of species (except for interactions) to have directional hypotheses because of prior theory and data; tests involving composite diversity and dominance use two-tailed P values.

Table 4. Statistical results for ANCOVAs and ANOVAs, Data Set II (Type III SS).
Taula 4. Resultats estadistics per a ANCOVAs i ANOVAs, conjunt de dades II (Tipus III SS).

see Fig. 7 for the lack of an area effect). Thus we drop area and compute significance as a simple one-way ANOVA; P values for the two are very low (Tab. 4). Effect ratios are computed directly from means of the respective island values (Tab. 2); these are 2.0 and 1.2, respectively. Despite the large variation in effect ratios, note again that the lizard effect is significant for all four variables.

The lizard effect on herbivory in the two species of plants studied is always negative (less damage with lizards) and statistically significant. Sea-grape leaf damage is 3.2 times greater in the absence than presence of lizards (Tabs. 2, 3; Spiller and Schoener, 1997). The one-time analysis of buttonwood leaf damage gave a rather small ratio of leaf damage, however, being only 1.3 (Tabs. 2, 3; Spiller and Schoener, 1996).

III. Small-to-medium islands—experimental introduction of lizards and observations from unmanipulated lizard and no-lizard islands.

The study system consisted of 12 small-to-medium islands covered with fairly closely spaced shrubs and a few grasses. Height of the vegetation rarely exceeded 1.5 m and was usually substantially less. All islands were located in a 3.2 x 2.0-km area that was part of a protected "creek" waterway just south of Snake Cay, Great Abaco.

The experiment had three treatments: (1) lizards present naturally and unmanipulated; (2) lizards introduced where absent naturally and (3) lizards absent naturally and unmanipulated. Each treatment had 4 islands; to reduce initial differences between Treatments 2 and 3, all islands without lizards were first stratified into pairs similar in area and vegetation, then one from each pair was randomly assigned to Treatment 2. Note that we can compare the manipulated treatment to either of the unmanipulated treatments (the latter acting as controls), or we can compare Treatments 1 and 3; this is in fact comparing natural lizard with natural no-lizard islands. The manipulated species was again the lizard *Anolis sagrei*. This species is slightly smaller over the Little Bahama Bank, where Abaco is located, than in the Exuma region farther south: snout-vent length of males was 50.8 mm (N = 103) and that of females was 40.1 (N = 80; means of largest third, as above). On islands where it was initially present, it was the only diurnal lizard.

On 28 April 1988, we introduced 3 female and 2 male adult lizards onto each island in Treatment 2; a previous experiment (Schoener and Schoener, 1983) indicated that this propagule size was sufficient for establishment. Propagules established successfully, and populations did not become extinct for the 7-year duration of the experiment. Populations on islands having lizards naturally also showed no extinctions during that time.

Measurement of leaf-damage variables was performed at yearly intervals. Spider variables (total density of individuals, number of species, composite diversity, dominance) were measured ~4 months, 6 months and 16 months after experimental inception, as well as at all yearly intervals. Variables were computed from counts of each spider species over an entire island. The spider species found during this experiment are listed in Tab. 1. At the same intervals as for spider variables, we sampled aerial arthropod abundance with sticky traps (4-6 per island); traps were identical to those used in the very-large-island experiment and were suspended 0.25-0.50 m above the ground. Duration of trap exposure and collection of data also followed procedures outlined above for the very-large-island experiment. We measured herbivory for the commonest shrub species on the islands, buttonwood. Leaves were sampled as follows. Before the manipulation, we measured each buttonwood shrub. We then randomly selected from 4 to 11 ($\bar{x}$ = 5.7) "large" shrubs, depending on the number available (the latter ranged from 7 to 35 "large" shrubs; see Schoener and Spiller, in press, for definition of "large"). To sample leaves, we tossed a square haphazardly onto each shrub from 1 to 5 times, depending on the shrub size, and collected that branchlet or clump of branchlets closest to a marked corner. Sampling in subsequent years used the same shrubs as selected for initial sampling (except those diminishing markedly in size were excluded). A year's sample averaged 2484 leaves. Leaves were stored in plant presses and brought to the laboratory, where the total area and areas of various damage types were measured with a digitizer. We distinguished three types of leaf damage: scars, holes and lines. The first two categories are defined as above; "lines" were highly elongated, typically serpentine, slightly raised areas. Herbivores identified from buttonwood so far are Lepidoptera from the families Noctuidae (*Collomena filifera* and unknown species) and Gelechiidae, as well as a curculionid bee-
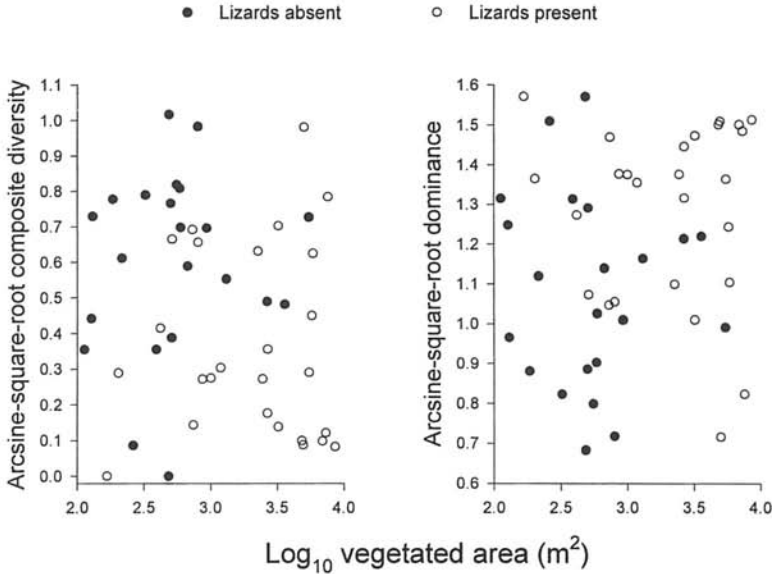
Fig. 7. <u>Left</u>. Arcsine-square-root mean composite diversity vs $\log_{10}$ island area for medium-to-small islands (Exumas, Data Set II). <u>Right</u>. Arcsine-square-root mean dominance vs $\log_{10}$ island area for medium-to-small islands (Exumas, Data Set II). Means are averages of values from 1981 through 1990 inclusive.

Fig. 7. <u>Esquerra</u>. Mitjana de l'arrel quadrada de l'arcsinus de la diversitat composta vs $\log_{10}$ de l'àrea insular per a illes mitjanes a petites (Exumas, Conjunt de Dades II). <u>Dreta</u>. Mitjana de l'arrel quadrada de l'arcsinus vs. $\log_{10}$ de l'àrea insular per a illes mitjanes a petites (Exumas, Conjunt de Dades II). Les mitjanes són els promedis de les valors de 1981 a 1990 inclusive.

tle (*Artipus floridanus*). In addition, using confinement trials we showed line damage to be produced by the flea beetle *Chaetocnema brunnescens* (Chrysomelidae). In the analyses below, we combined all damage types as above to produce the variable total leaf damage.

Results of the experiment and observations were as follows.

Before introduction, the two island classes without lizards had similar spider densities of individuals and number of spider species (Fig. 2). These values were substantially larger than those for the islands with natural lizard populations; spider density on the former was 6.7 times, and the number of species was 1.8 times, that on islands having lizards naturally. After lizard introduction, both spider density and number of species dropped precipitously, and in two years their mean values nearly coincided with values for islands having lizards naturally (Fig. 2, left). The two pairs of means remained similar throughout the five remaining years of the experiment, suggesting that a new state had been reached. The time series for composite diversity and dominance behaved rather similarly, except initial treatment values were somewhat closer, at least on an arithmetic scale (Fig. 3, left). However, as time progressed, a fairly clear divergence of the introduction-island mean from the no-lizard-island

mean occurred, and the two classes of lizard islands showed quite similar values (lower composite diversity, higher dominance) during the final five years. Because of the similarity of these two lizard classes—introduction and lizards present naturally—we combine the two for statistical evaluation. For all four variables, the difference between these two classes combined and the no-lizard class (Tab. 2) is highly significant (for time averages, P = two-tailed, P = 0.015 and P = 0.018, for composite diversity and dominance, respectively; see Schoener and Spiller [1996] for the first two variables). Figs. 8 and 9 show how the numbers of individual spider species varied during the experiment.

To present effect ratios, we make two comparisons for each variable: natural lizard vs natural no-lizard, and introduction vs natural no-lizard (Tab. 3). This is because in some cases the two ratios are very different. For the first comparison, which includes non-manipulated islands only, ratios for both spider density and composite diversity are both very high: 7.0 and 7.1, respectively. The ratio for spider species number was 3.4, whereas that for dominance was 1.2. Ratios using introduction islands in place of islands having lizards naturally were generally smaller, being 5.0, 3.0, 3.8 and 1.1, respectively.   By tracking individual species (see below, Figs. 8 and 9), we were able to document in detail the devastating effect of lizard introduction. The proportion of species becoming extinct was 12.6 times higher on lizard-introduction islands than on islands without lizards. Locally common and rare species were both reduced by the introduction of lizards, but nearly all of the latter became permanently extinct.

The lizard effect on spiders is mainly a direct one (Spiller and Schoener, 1990a). The lizard effect on the other variables in this experiment is indirect; patterns were weaker and more variable. Lizards reduced leaf damage of buttonwood, but an overshoot occurred on introduction islands; herbivory there during the middle years of the experiment was less than that on islands having

lizards naturally (Tab. 2). This difference is reflected in the effect ratios: that using the natural lizard and no-lizard islands is small, being 1.3, whereas that using introduction and no-lizard islands is substantially larger, being 4.4 (Tab. 3; P's for time averages of the two comparisons are mostly very small [Schoener and Spiller, in press]). Curiously, the lizard effect on aerial arthropods, when one occurred, was opposite in direction to that in the experiments on a very large island (Tab. 2). Lizards significantly increased the number of small (≤4 mm) arthropods but had no significant effect on large arthropods (Schoener and Spiller, in press); note that most arthropods were small. Effect ratios were always small, and in the case of large arthropods inconsistent in direction among the two comparisons (Tab. 3).

Collation and interpretation

Data from the experiments just described are now used to determine whether the effect of lizards on spiders, which is largely a direct result of predation, is stronger on small or large islands. To accomplish this, we arrange the data in the tables according to island area, from the largest to the smallest. Tab. 2 gives the raw data, and Tab. 3, which we shall concentrate on, gives the effect ratios—larger over smaller of the two treatment means being compared; the greater the ratio, the greater is the effect. Note that these ratios are mostly computed from data with no obvious temporal trend, rather than from data whose values are changing systematically through time; for experimental data, this generally entails computing the time-average over the latter portion of the experiment; for observational data, the entire time period is used to compute time-averages. An exception is buttonwood leaf damage in Data Set III, for which there is an overshoot lasting several years on introduction islands (see below); final values here are about the same, being all low, for all three treatments. So far as conclu-
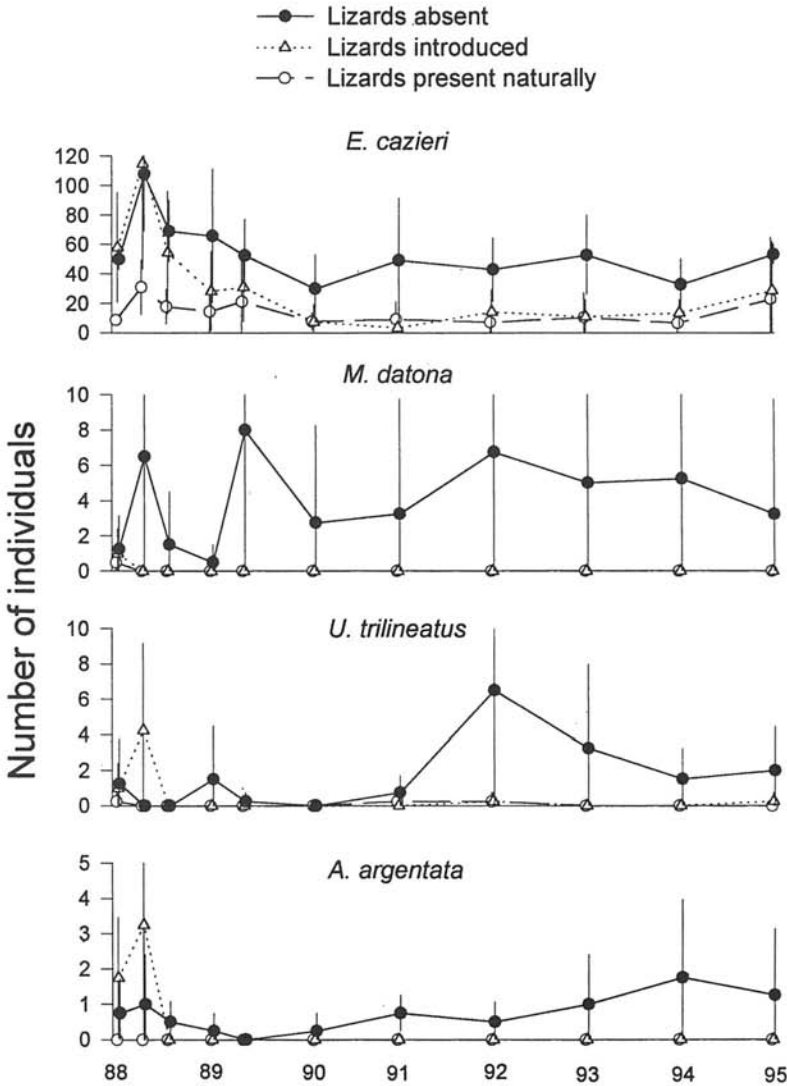
Fig. 8. Time courses of abundance for particular species from the small-to-medium-island experiment (Abaco, Data Set III). Each point represents a treatment mean for a single census. Full species names given in Tab. 1. Species are excluded from Figs. 8-9 if they were so rare that fewer than five individuals were recorded in the entire data set, i.e., summed over all dates and islands.

Figura 8. Cursos temporals de l'abundància d'espècies concretes de l'experiment en illes peti-tes a mitjanes (Abaco, Conjunt de Dades III). Cada punt representa una mitjana de tractament per a un únic recompte. Els noms complets de les espècies es donen a la taula 1. Les espècies s'exclouen de les figures 8-9 si eren tan rares que només s'havien registrat menys de cinc indi-vidus en el conjunt complet de dades (és a dir, sumades totes les dates i tancats).
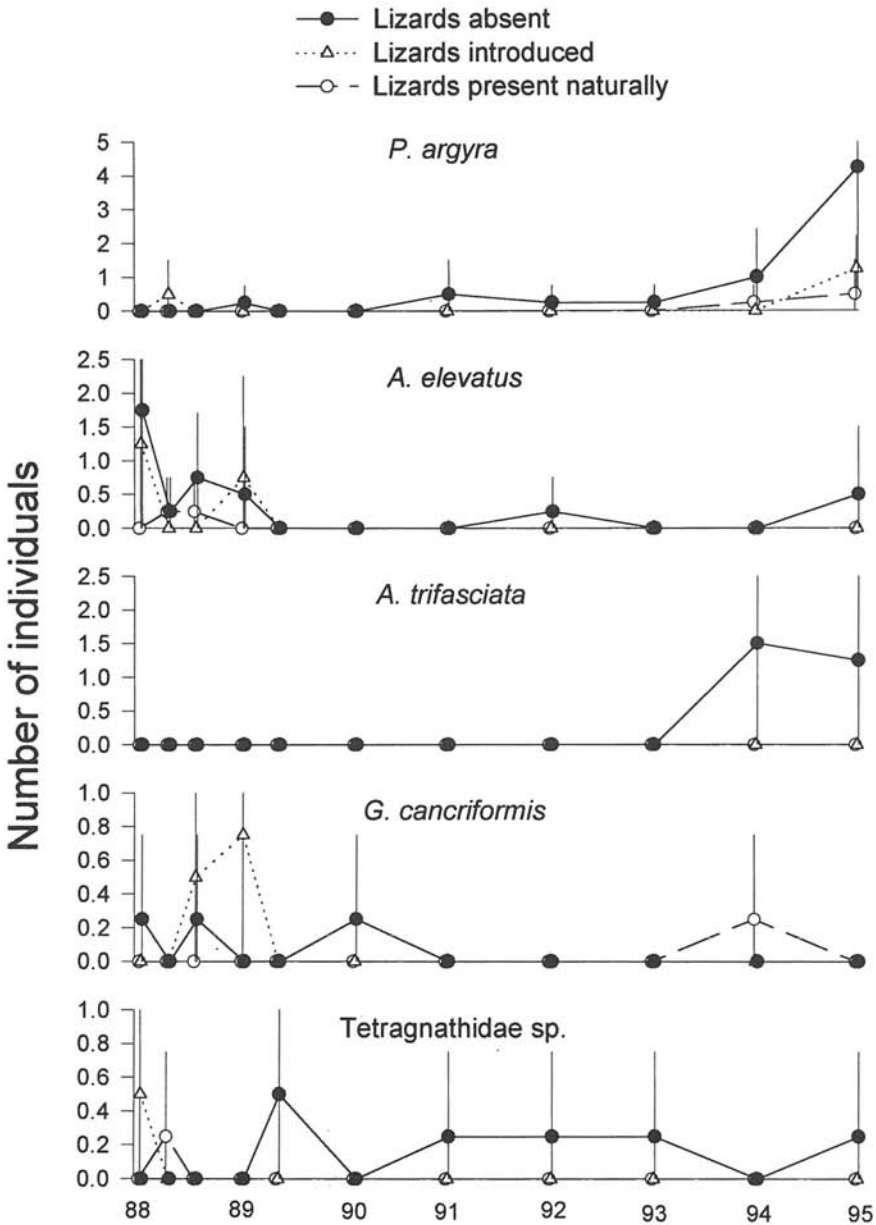
Fig. 9. More time courses of abundance for particular species from the small-to-medium-island experiment (Abaco, Data Set III). Each point represents a treatment mean for a single census. Full species names given in Tab. 1.

Fig. 9. Més cursos temporals de l'abundància per a espècies concretes de l'experiment a les illes petites a mitjanes (Abaco, Conjunt de Dades III). Cada punt representa una mitjana de tractament per a un únic recompte. Els noms complets de les espècies es donen a la taula 1.

sions concerning spatial differences in comparison of direct vs indirect effects, using a long-term average for these data, which we do, is conservative. Also be aware that ratios are best compared among the same kind of data (i.e., like quantities). Thus ratios of composite diversities or dominances may not be expected to vary the same way as ratios of densities or numbers of species. Ratios of adjusted means from ANCOVAs may also vary differently from those using raw data; however, note that in the single instance for which we computed ratios both ways (total spider density, Data Set II), the two ratios were very close (see above). Finally, note that Tab. 5 gives the rankings of ratios, as well as separate rankings of mean values of the variables for lizard and no-lizard treatments; this will be helpful in following the discussion below.

The negative effect of lizards on the density of all spiders combined shows a near monotonic increase from very large to very small islands (Tabs. 2, 3, Row 1). Effect ratios increase from 1.8 to 7.0; only the comparison of introduction to no lizard islands (III), whose ratio is 5.0, is slightly out of order, being less than the 5.7 ratio attained from observations on medium-to-large islands (but notice an alternate way of computing the latter gives 4.9, which places it back in order). Note from Tab. 5 that there is somewhat of a tendency for data sets with greater densities to have lower ratios: thus the two very-large-island experiments (I) have greater densities than the two island sites; however, within that set (compare IA to IB) and within the non-main-island sites (compare II to III) the tendency is reversed for no-lizard data and reversed in the latter for lizard data. To the extent that the tendency exists, it is the opposite of that found for temporal variation of islands of the Exumas site (Data Set II) over a 10-yr period (Spiller and Schoener, 1995); in the latter, the higher the density, the higher the ratio. In both studies, densities of lizard and no-lizard treatments at the same site or time tend to co-vary, i.e., they rise or fall together

(Tab. 5); here, only the two very-large-island experiments are out of order.

Species richness (number of spider species) shows the same tendency as does spider density: the smaller the island, the greater the lizard effect, which is here to reduce species number (Tabs. 2,3, Row 2). The tendency is here perfectly monotonic. Ratios show less variation (1.2-3.4) than those for densities. The mean number of species again shows a tendency to be higher, the smaller the ratio, i.e., to be higher for data sets with larger islands: the rank is exactly the same for no-lizard treatments as for spider densities. The species tendency for lizard treatments is more monotonic than the same tendency for spider densities; in fact species number ranks exactly inversely with effect ratio. It follows that lizard and no-lizard treatments do not co-vary perfectly, but they tend to do so. Finally, note that the total number of species found during the appropriate time period at each site is similar from one data set to another (Tab. 1).

Composite diversity was computed for three, rather than four data sets, so trends are somewhat less well evaluated. Nonetheless, the same results occur: lizards reduce composite diversity, and the smaller the island, the greater the effect ratio (Tabs. 2, 3, Row 3). Actual values increase monotonically with decreasing ratio (and thereby increasing island size); ratios range from 1.5 to 7.1; lizard and no-lizard treatments co-vary perfectly. Note, of course, that composite diversity is not independent of species richness, so this and the previous (and the subsequent) comparisons are not independent.

Although lizards increase dominance, that variable shows virtually no variation at all in effect ratio—three values equal 1.2 and the fourth is 1.1(Tabs. 2, 3, Row 4). This is despite variation among data sets in absolute values of dominance: no-lizard treatments have values ranging from 0.681 to 0.839, and they decrease monotonically from small to large islands; lizard treatments have values ranging from 0.797 to 0.981, and they also decrease monotonically from small to large

Variable	Ranking of Ratios (smaller to larger)	Ranking of Mean Values (larger to smaller)	
		Lizard	No-lizard
1. Total spider density	IB	IB	IA
	IA	IA	IB
	II	III	III
	III[a]	II	II
2. Number of spider species	IA	IA	IA
	IB	IB	IB
	II	II	III
	III	III	II
3. Spider composite diversity	IB	IB	IB
	II	II	II
	III	III	III
4. Spider dominance	≅†	III	III
		II	II
		IB	IB
5. Sea-grape leaf damage	IA	IA	IA
	II	II	II
	IB	IB	IB
6. Buttonwood leaf damage	II	II	II
	III	III	III
7. Total number aerial arthropods	IB	III	III
	IA	IB	IB
	III	IA	IA

† "≅" signifies that ratios are about the same
[a] For Data Set III, the average of the two ratios is used

Table 5. Rankings of data sets by magnitude of the effect ratio and magnitudes of the mean values for the major variables used in this study. Ratios are ranked from smaller to larger while mean values are ranked from larger to smaller. Hence *(1) When ratios and mean values show the same order of data sets, a perfect inverse co-variation occurs, and (2) When mean values for lizard and for no-lizard treatments show the same order of data sets, a perfect direct co-variation occurs.* Roman numerals refer to data sets in Tabs. 2, 3.
Taula 5. Ordenacions de conjunts de dades segons la magnitud de la taxa de l'efecte i les magnituds dels valors mitjans per a les variables principals emprades en aquest estudi. Les taxes s'ordenen de menor a major, mentre que les valors mitjans s'ordenen de major a menor. Per això, (1) quan les taxes i valors mitjans presenten la mateixa ordenació de conjunts de dades, hi ha una covariació inversa perfecta, i (2) quan els valors mitjans per als tractaments amb sargantanes i sense sargantanes presenten la mateixa ordenació de conjunts de dades, hi ha una covariació perfecta. *Els números romans es refereixen als conjunts de dades de les taules 2 i 3.*

islands. Thus all values are rather large, but the tendency reaches its extreme on the very small islands of the Abaco experiment (III), where monocultures of *Eustala cazieri* are common (recall that dominance for this data set had to be computed from cumulative data—see above).

Very interestingly, the indirect effects of lizards, on leaf damage and (in part) on aerial arthropods, show similar but substantially weaker trends in effect ratio from small to large islands than the direct effect.

Leaf damage of sea grape can be compared for two sites, one of which has two experiments (IA, IB, II; Tabs. 2, 3, Row 5). Effect ratios increase from the average of the two very-large-island data sets to the medium-to-large-islands data set. However, values only vary from 2.0 to 3.3, and one of the ratios for the very large island is slightly greater than that for the medium-to-large islands (3.3 vs 3.2, respectively). Magnitude of damage increases with decreasing ratio, and the lizard and no-lizard treatments co-vary perfectly.

Leaf damage of buttonwood has only two data sets to compare (II and III; Tabs. 2, 3, Row 6). Within one of these sets, however (Abaco experiment, III), we can look at two ratios, that for natural lizard to natural no-lizard islands and that for lizard-introduction to natural no-lizard islands. The former comparison (which is entirely observational) gives the same ratio as that for the medium-to-large islands (II), being 1.3. However, as described above, introduction islands showed an overshoot of the lizard effect, i.e., leaf damage there became significantly smaller than on either of the other treatment classes, including natural lizard islands. The effect ratio here is 4.4, substantially higher than the 1.3 for medium-to-large islands. As before, when comparing data sets actual values of damage rank inversely with the ratios, and lizard and no-lizard treatments co-vary perfectly.

Total number of aerial arthropods can be compared for three data sets, two from the very large island and one from small-to-medium islands (IA, IB, III). First, we must note that the effect of lizards on aerial arthropods is not the same from one site to the next: lizards decrease aerial arthropods on the very large island but increase them on the small-to-medium islands. The first effect is likely to be direct, or mostly so, but the second must be indirect. In any case, effect ratios are very small, being 1.0 or 1.1 for the negative lizard effect and 1.2 or 1.4 for the positive lizard effect. While ratios are greater for the small-to-medium islands, the effect reversal should be noted. While lizard and no-lizard treatment values (Tab. 2) co-vary perfectly, effect ratios show no regular relationship to those values (Tab. 5). Results for small arthropods alone are similar (most arthropods are small), but those for large arthropods show equal or nearly equal effect ratios on small-to-medium islands and a very large island (IA, III, Tabs. 2, 3, Rows 9, 10).

In summary of the main trend, there is an overwhelming tendency for the lizard effect to be stronger, the smaller the island, and it is especially evident for certain direct effects, such as those on spider density, spider species richness and spider composite diversity. This fairly complete survey of our data thus agrees with the more limited comparisons—all between the two experimental data sets IB and III—reported by Spiller and Schoener (1998). In the latter treatment, we gave two reasons why the tendency might be so.

First, we suggested that the lizard effect should be stronger on islands rather than mainlands because the experimental units were more isolated in the former. Because the plots are relatively close to one another on the very large islands, dispersal of spiders from removal to control treatments may have diluted the lizard effect. Perhaps more importantly, the heterogenous landscape on the very large island may have contained habitats suitable for web spiders but not lizards, which would be natural refugia for rare species and sources of immigration for enclosures. Such

refugia may not exist at all on small islands, and sources having such refugia would be much more distant. Indeed, nearly all species that become extinct on the lizard-introduction islands of the small-to-medium-island experiment did not recolonize for the remainder of the experiment. This can be seen from the species-by-species time series given in Figs. 8 and 9; note the open triangles. In contrast, in the lizard plots of the very-large-island experiment most species becoming extinct later recolonized. This can be seen for the corresponding species-by-species time series of Figs. 4 and 5; note the open circles. Note also that lizards have been shown experimentally to have a huge effect on the likelihood of successful spider colonization (Schoener and Spiller, 1995). Finally, on medum-to-large-lizard islands, where we census the entire island (and not just plots within the island), some refugia may exist, and these would be averaged into the island-wide spider density, skewing its value toward that expected for a no-lizard island.

A second reason why islands may show a stronger lizard effect the smaller they are involves diffuse predation, i.e., predation by a number of different predator species (Hixon, 1991; Menge et al., 1994). The argument is that the more kinds of predators, the more likely that removal of any one of them will fail to have a major effect because another predator or other predators will slow down the expected increase of the prey. Other vertebrates that may eat spiders (e.g. birds) were present on the very large island (and often observed within or near the experimental plots), but they were very infrequently observed on the very small islands and somewhat less infrequently observed on the medium-to-large islands. It is likely that invertebrate predators of spiders, e.g. hymenopterans, also are more abundant the larger the island (e.g. Schoener et al., 1995). Hence the impact of lizards on spiders may have been weaker, the larger the island, because predation was more diffuse, the larger the island. Actual predation on the lizards them-

selves, expected to be highest on the very large island, would further weaken the lizard effect, i.e., soften the consequences of removing the predator. Somewhat at variance with this general hypothesis is that the magnitude of the effect of lizards on spiders we found on the very large island was similar to that found by Dial and Roughgarden (1995) in a Puerto Rican rain forest, despite the latter's greater complexity. This suggests that the relation of degree of diffuse predation to the strength of the lizard effect may level off over large to very large island sizes.

Finally, the hypothesis that smaller islands are more physically disturbed, therefore have lower population densities which imply weaker species interactions, is clearly contradicted by our data. Probably this is because the reproductive rate of lizards is so high that invading predators multiply rapidly, as has been shown in other lizard introduction experiments (Schoener and Schoener, 1983; Losos and Spiller, in press) and has indeed happened in the introduction experiment discussed here. The data are, however, consistent with the opposing hypothesis given in the introduction: predators reduce populations to such sizes that they are more likely to be "finished off" by physical factors, or vice versa (indeed, additive density-independent mortality factors act effectively to reduce the intrinsic rate of increase, r, which means that removal of one of them leads to a greater effect ratio when the others are present than when they are not). We have no direct evidence of such a mechanism, but we do find that the rarer species are those becoming extinct most readily (Schoener and Spiller, 1996; Spiller and Schoener, 1998).

A secondary result of our comparisons is that the difference between large and small islands in effect ratio is smaller for indirect than direct effects. If indirect effects in general are small, then this would be expected, because all ratios would tend to be small, hence similar. In fact, arguments exist for indirect effects being smaller than direct effects overall (Schoener, 1993; Abrams et

al., 1996), and this has been found to varying degrees, both in our studies (Spiller and Schoener, 1994; Schoener and Spiller, in press) and in other studies (Schoener, 1993; Menge, 1995). However, while indirect effects might tend to be smaller than direct effects, the difference in effect ratios could be the same for large and small islands. Clearly, the explanation of this secondary result should it be real—and more corroborative evidence is needed—awaits additional theoretical work.

In conclusion, when the precise question is asked, does removal of a given type of predator affect prey more on a small or on a large island, the answer is resoundingly more on the former. Different precise forms of the general question concerning the relative strengths of ecological interactions on small vs large islands may have different answers. Ours, however, has important implications for the kinds of sites that would be especially sensitive to the effects of an introduced predator. In particular, isolated sites such as islands will be affected more than equivalently sized sites on a mainland, and the smaller the island, the greater the impact. Likewise, fragmentation of mainland habitats into small isolated sites would particularly affect their vulnerability to an invading predator. Thus our results may provide a preview of impending environmental devastation yet at the same time confer some causal understanding that helps point the way toward prevention and even cure.

Acknowledgments

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