

PREDATION ON A COMMON ANOLIS LIZARD: CAN THE FOOD-WEB EFFECTS OF A DEVASTATING PREDATOR BE REVERSED?

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Abstract. We artificially invaded a set of small islands with the large lizard *Leiocephalus carinatus* to determine effects on food-web elements including an intermediate predator, the lizard *Anolis sagrei*; the latter was previously found to have major, mostly direct effects on web spiders, as well as detectable indirect effects on aerial arthropods (including parasitoids) and leaf damage. In addition to these food-web elements, we monitored ground-surface arthropods; they are expected to be affected directly, as well as indirectly via *A. sagrei*, by *L. carinatus*. Five islands were randomly selected for invasion while six others served as controls. In addition, four islands without *A. sagrei* were monitored to determine the natural state of the *sagrei*-free food web. We also monitored a variety of *A. sagrei*'s traits, from behavioral through physiological and demographic to morphological, to elucidate the mechanisms whereby *L. carinatus* might affect the smaller lizard and to evaluate trait-mediated as well as density-mediated effects.

Comparison of unmanipulated islands with and without *A. sagrei* showed that *A. sagrei* appeared to be affecting web-spider density and diversity, numbers of small aerial arthropods, number of large ground-surface arthropods, and two types of leaf damage, scars and mines. All effects were negative save one: Small aerial arthropods were more abundant with *A. sagrei*; this variable and parasitoid abundance were negatively related to web-spider density, implicating an indirect effect pathway from *A. sagrei* via web spiders.

Introduction of *L. carinatus* had major and immediate effects on *A. sagrei* density and perch height; effects on perch diameter, percentage hatchlings, and the width of the body-size distribution followed over time. Behavioral shifts in habitat use continued to the end of the experiment, after changes in population density had mostly leveled off. Adult-male body condition became poorer after introduction of *L. carinatus*. Among islands, percentage use of the ground was correlated negatively with percentage vegetated area of the island and positively with premanipulation relative hindlimb length. We hypothesize that longer-legged individuals do better on the ground because they are faster there. Conditional evidence for an increase in adult-male relative hindlimb length suggested that, when the ground-inhabiting *L. carinatus* was introduced, such individuals were differentially able to escape predation.

Introduction of *L. carinatus* significantly reversed *A. sagrei*'s effect on number of species and density of web spiders but had no other major effects on lower level food-web elements. Thus, a relatively short-chained (two links) effect, with a relatively strong second link (*A. sagrei* on spiders), showed the greatest indirect effect of the manipulation. Another potentially strong indirect effect, that on large ground-surface arthropods, did not occur, possibly because of compensatory (direct) predation by *L. carinatus*. Thus presence of omnivory may also be relevant to whether reversal of effects occurs. Although most *A. sagrei* effects were not reversed in the time available for the experiment, this may be typical, as natural *L. carinatus* colonizations can dwindle away to extinction over about the same time span, producing at best only short-term indirect effects. Population-density estimates from other sites and comparisons to other experimental studies suggest that, in general, predators on *Anolis* may have erratic effects in space and time.

Key words: food webs; habitat shift; herbivory; indirect effects; introduction experiments; invasion; islands; lizards; morphological shift; parasitoids; predation; spiders.

INTRODUCTION

Predators may have profound effects in ecological communities (Sih et al. 1985). Not only might their

direct effects on prey be large, but via those prey and other organisms, they may have substantial indirect effects as well, even down to the level of producers (recent reviews in Pace et al. 1999, Schmitz et al. 2000, Halaj and Wise 2001). Predators especially devastating to their prey in some communities may be less so in

Manuscript received 27 February 2001; revised 28 August 2001; accepted 3 September 2001.

others for a variety of reasons, an important one being the presence or not of predation on themselves. Because traits favoring feeding on other organisms may be different from those of predator avoidance, even a devastating predator may have its effects reversed. Hence introduction of an upper-level predator into a community having a devastating intermediate-level predator may substantially reduce the latter's effects. Several factors could prevent this. First, upper-level predators may not be effective at capturing individuals of the intermediate-level predator. In two-variable predator-prey models, reduction in the search-rate parameter can cause a severely oscillating system to stabilize at a point equilibrium; the equilibrium population size for the prey may be close to its K (review in Harrison 1995). Second, the upper-level predator may consume some of the same prey as does the intermediate-level predator, compensating for its direct reduction of the intermediate-level predator. This is an example of same-chain omnivory (Morin 1999), in which a predator feeds at multiple levels of a food-web chain (Pimm 1982). Depending upon the exact configuration, such omnivory could both reinforce or oppose the cascading effects of the upper-level predator. More commonly, opposition will occur because such predators would show intraguild predation (Polis et al. 1989), feeding at two adjacent trophic levels for functional reasons. Indeed, omnivory with its implied interspecific compensation is one reason proposed for lack of a strong "trophic cascade," whereby predators have major effects on lower trophic levels, particularly plants (Hunter and Price 1992, Strong 1992, Polis and Strong 1996). Another reason involves intraspecific compensation: when carnivores decrease herbivore population density, herbivores may compensate by increasing per capita plant consumption because of reductions in intraspecific competition, giving little or no net change in plant consumption (Schmitz 1992, 1993). A final reason is that the longer the effect chain, the less likely it is to propagate an effect under stochastic diminishment of population size or linkage strength (Schoener 1993, Abrams et al. 1996). More generally, moderately complex webs can in theory show quite variable effects (Yodzis 1988, Schmitz 1997).

While numerous field experiments have found evidence of strong top-down effects in a variety of systems (reviews in Brett and Goldman 1996, Pace et al. 1999, Schmitz et al. 2000, Halaj and Wise 2001), the discussion above suggests that perturbing the abundance of predators on other predators may not have much effect at lower levels, i.e., that trophic cascades, especially perhaps long-chained trophic cascades, may be weak. This issue has become especially intriguing for terrestrial systems, argued by some (Strong 1992, Polis and Strong 1996) to have weaker cascades than aquatic systems, a conclusion both favored (Halaj and Wise 2001) and not (Schmitz et al. 2000) in recent reviews. Clearly, more work in terrestrial systems with

food chains of varying lengths and degree of omnivory is needed to establish and clarify trends.

The preceding arguments can be made entirely on the basis of "density-mediated" effects, those acting via a change in population density (Abrams et al. 1996). It is now increasingly recognized that "trait-mediated effects," those acting via changes in behavioral, physiological, and other traits of individual organisms (Abrams 1995, Abrams et al. 1996, Peacor and Werner 2001), may also affect how perturbations are transmitted in food webs. For example, reduced prey feeding rate and/or habitat shift motivated by predator-avoidance behavior may affect which and how much food a prey consumes (Abrams 1995, Chase 1996, Beckerman et al. 1997). Monitoring of trait changes suspected to lead to such effects should increase understanding of food-web dynamics. Moreover, the nature and mechanism of trait changes can be interesting in their own right, having potential implications for behavioral and evolutionary biology (Endler 1980, McPeck 1995, Van Buskirk and McCollum 2000).

An example of an intermediate predator that can be especially devastating in its effects is the lizard *Anolis sagrei*. In both removal and introduction experiments we have found strong effects of this species on certain animals such as spiders, as well as weaker but detectable effects on other animals and on plants (e.g., Spiller and Schoener 1996, Schoener and Spiller 1999a). The effect of *A. sagrei* varies, however, with inter alia island area: In the Bahamas, the larger the island, the weaker the effect (Schoener and Spiller 1999b). One explanation is that the intensity of predation on *A. sagrei* could be a function of island area (Schoener and Spiller 1999b). A possible such predator is the larger lizard *Leiocephalus carinatus*, known to consume both *A. sagrei* and numerous kinds of arthropods (Schoener et al. 1982). Because of its commonness and similarity of habitat (*A. sagrei* is one of the more terrestrial anoles [Schoener 1968] and *L. carinatus* spends most of its time on the ground or rock surfaces [Schoener 1975]), *L. carinatus* would seem an especially suitable predator with which to examine top-down effects in a food chain one link longer than previously studied experimentally. Moreover, because *A. sagrei* and other anoles are known commonly to show habitat shift (Schoener 1975, 1977, Pacala and Roughgarden 1985, Losos 1994) and have undergone rapid morphological change when introduced to new environments (Losos et al. 1997, *in press*), this system is especially ideal for studying how trait changes may unfold and affect interactions.

We report here an experiment in which *L. carinatus* was introduced onto islands naturally having *A. sagrei*, with other such islands naturally having *A. sagrei* as controls. Concomitantly, islands naturally without *A. sagrei* were monitored to determine food-web traits in its total absence. To what extent, if at all, does introduction of the upper-level predator reverse the intermediate-level predator's effects on food-web elements

(the latter judged by comparison to islands without *A. sagrei*)? Do changes cascade down the food web with time in the anticipated manner (e.g., Yodzis 1989 on transitory effects), including the prediction that effects be more erratic, the more indirect (Schoener 1993, Abrams et al. 1996)? We also monitored trait variables of *A. sagrei*, from behavioral through demographic to morphological. To what extent do changes in these traits unfold through time as a hierarchy of levels, depending on whether the mechanisms of change are fast (behavioral), intermediate (ecological), or slow (evolutionary)? How might changes in these trait variables caused by *L. carinatus* modify the action of *A. sagrei*, changing the effect from that expected by simple removal of the latter species?

Our ultimate goals were to follow changes in food-web components on the one hand and in individual traits on the other, until the manipulated islands stabilized to a new state. Because we are interested in the importance of ecological factors in nature, we perform our experiments in the field, disturbing the natural system as little as possible: introduction of a species onto an otherwise entirely undisturbed island is perhaps the most natural of all. We hold this philosophy in part because variation in entirely natural factors, e.g., climatic conditions, may determine an effect's magnitude, a possibility we have in fact observed for *A. sagrei* on spiders (Spiller and Schoener 1995). This research strategy led to an abrupt end to our experiment. Two and one-half years after introduction, Floyd, a huge hurricane with sustained winds ~150 mph (241 km/h), swept over our study site. The associated storm surge inundated all study islands, eliminating every (hatched) lizard of both species and having massive effects on certain arthropods as well. We report results prior to that unanticipated, albeit well-defined, termination date.

HYPOTHESIZED RESULTS OF THE MANIPULATION

Expected effects of introducing the upper-level predator *L. carinatus* can be divided into those on traits of *A. sagrei* and those on food-web elements.

L. carinatus is substantially larger than *A. sagrei*, perching most commonly on the ground or rocks and using thicker branches than *A. sagrei* (Schoener 1975). Hence *A. sagrei* should respond to *L. carinatus* introduction by shifting to thinner and higher perches. Such a shift should entail morphological change; from intraspecific comparisons of geographically separated populations (Lister 1976, Losos et al. 1994) as well as interspecific comparisons (Losos 1990, Glossip and Losos 1997) we predict relatively shorter hindlimbs and more lamellae. Such differences could arise either by developmental or evolutionary mechanisms, and could occur quickly or slowly. In addition, rapid reductions in population number and per-capita food consumption should occur, were predation by *L. carinatus* effective. The latter would result from a less suitable

habitat in which to forage as well as more time spent in avoiding predation (Schoener 1971, Sih 1980, Stephens and Krebs 1986, Sih and Christensen 2001). Were morphological changes to occur, of course, the new habitat would become correspondingly more suitable.

Fewer *A. sagrei* and a possible lower per-capita consumption rate may reverberate down the food web. Previous studies have shown that an increase in *A. sagrei* affects a variety of food-web elements. A major effect is on web spiders: both density and diversity diminish (Schoener and Spiller 1996, 1999a, Spiller and Schoener 1996, 1998), although habitat shift among the spiders was not observed (Spiller and Schoener 2001). Less spectacular but nearly always present are possible effects on plants: most kinds of plant damage increase in the absence of lizards (Spiller and Schoener 1990a, 1996, Schoener and Spiller 1999a, b). Finally, aerial arthropods (mainly Diptera, but also including parasitoids) present a more varied picture: small but consistent increases in small arthropods (including parasitoids) with lizard presence have been demonstrated at the study site. At another site (Spiller and Schoener 1990b), large arthropods showed the opposite effect, but most commonly lizards have no effect on large aerial arthropods. Lizards may positively affect small arthropods (including parasitoids) via some lower level predator; while an excellent candidate is spiders, in a previous study (Schoener and Spiller 1999a) we were unable to implicate them directly. In summary, were the principal food-web effects of *L. carinatus* introduction to be via *A. sagrei*, we predict a large increase in web spiders, and small negative effects on plants and small aerial arthropods. The density-mediated effect on plants, however, may be neutralized by a trait-mediated component resulting from the expected greater arboreality of *A. sagrei*.

Additionally, *L. carinatus* is likely to have food-web effects via pathways other than through *A. sagrei*. Such effects can constitute omnivory and dampen a trophic cascade via compensation (see *Introduction*). Because of its highly terrestrial nature, we do not expect *L. carinatus* to consume many herbivorous insects, nor do we expect it to affect aerial arthropods. However, *L. carinatus* is known to consume many kinds of arthropods; indeed most of its diet consists of invertebrates rather than lizards (Schoener et al. 1982). To see if compensation occurs, we collected a type of data not included in previous studies of *A. sagrei*, ground-surface arthropods. We would expect only *A. sagrei* to affect small ground arthropods (because *L. carinatus* is larger and takes larger prey [Schoener 1967, 1968, Schoener and Gorman 1968]). However, both species should negatively affect large ground arthropods, perhaps giving no net effect of *L. carinatus* introduction on this element.

METHODS

Study site and manipulated species

The study system consisted of two types of islands, those with and those without the lizard *A. sagrei*. In general, islands of the former type average substantially larger than those without *A. sagrei*; for this study, we selected islands from the two groups to be as similar as possible in area. This resulted in 12 islands with *A. sagrei* and only 4 islands without it; even so, the former islands were somewhat larger: 137–270 m² ($\bar{X} = 191.0$) vs. 99–184 m² ($\bar{X} = 121.5$) vegetated area. All islands were covered with fairly closely spaced shrubs and trees. Vegetation height rarely exceeded 2 m. All islands were located in an $\sim 7 \times 2$ -km area, part of several “creek” waterways fanning out from Buckaroon Bay and Snake Cay, Great Abaco, Bahamas.

The manipulated lizard was *L. carinatus armouri*, a form native to the Little Bahama Bank (Schwartz and Henderson 1991). This subspecies is one of the larger representatives of the species (Schoener et al. 1982), with males here having a maximum snout–vent length of 107 mm and females having a maximum of 97 mm. By comparison, *A. sagrei* from the study islands has a maximum snout–vent length for males of 57 mm and for females of 44 mm. Where present on the study islands, *A. sagrei* was the only lizard ever recorded except for a natural colonization by *L. carinatus* (see below).

Experimental design

To select islands for introduction of *L. carinatus*, we first stratified the 12 *A. sagrei* islands into six pairs according to area, vegetation structure, and number of *A. sagrei*. Our plan was to select randomly one island from each pair, but during the year between the final pre-experimental check and commencement of the manipulation, one island was naturally colonized by *L. carinatus*. Hence we only randomized five pairs; that island paired with the naturally colonized one was added to the controls, giving an “unbalanced” design. The naturally colonized island was a year or so ahead of the artificially colonized ones and was not lumped with the latter; rather we omitted it for formal analyses. The 11 islands so classified constitute two treatments, experimental and control, for all effects including those on *A. sagrei*.

We monitored all other food-web properties on both *A. sagrei* islands and an additional set of islands, the four islands naturally lacking *A. sagrei*. For these properties (see *Methods: Data collection*), there are therefore three rather than two treatments, the third treatment being islands without *A. sagrei*. The third set of islands gives us a running picture of lower level food-web properties in the same region in places without any individuals of the smaller lizard *A. sagrei*. We label each treatment as follows: (1) islands not having *A. sagrei*, (2) islands having *A. sagrei* and no manipula-

tion, and (3) islands having *A. sagrei* and *L. carinatus* introduced. Evaluation of the difference between treatments 1 and 2 as compared with the difference between treatments 2 and 3 allows the degree of reversal of *A. sagrei*'s effect, if any, to be quantitatively evaluated (see *Discussion*).

On 26 April 1997, we introduced three female and two male *L. carinatus* onto each island in treatment 3. Although mostly occurring on larger islands, *L. carinatus* in the central Bahamas naturally colonized a similarly sized (203 m²) island inhabited by *A. sagrei*, and in six years it reached a density of 0.06 individuals/m² (T. W. Schoener, *unpublished data*). This suggested that our introduction was lower, by roughly one-half to one-fourth, than the population that would eventually be attained.

L. carinatus colonists were collected from the mainland of Great Abaco, on Snake Cay immediately adjacent to the study islands (most individuals), at Marsh Harbor (~ 12 km north), or at sites between the two. Individuals were stored in large, aerated bags and in no case were held more than 16 h. Throughout the experiment, we attempted to maintain each *L. carinatus* population above the value of the initial population size, five individuals; the perturbation was in Bender et al.'s (1984) sense, a press rather than a pulse. One island, the smallest, required no supplementation, and another, the second-largest, required almost no supplementation. Table 1 shows numbers of individuals estimated; restocking was calibrated to these numbers and individual-size distributions. Eventually (after 1.5 yr), at least 5 *L. carinatus* were present on all islands, so that supplementation was no longer necessary. Maximum densities were not unusually large in comparison to the natural colonization observed at this site (island Z3, Table 1) and in the central Bahamas.

Data collection and treatment

Lizard numbers were estimated using the multiple-recapture method following Heckel and Roughgarden (1979, Fienberg 1972); in three censuses on each of three different days lizards are marked with a census-specific color of water-soluble latex paint administered long-distance with Idico spraying devices (Forestry Suppliers Incorporated, Jackson, Mississippi). No long-term ill effects on the lizards have been detected in the ~ 20 yr we have been using this method. During lizard censuses, we recorded estimated size, perch height, perch diameter, and perch substrate of each individual. Each group of three censuses was performed April 1997, July 1997, November 1997, April 1998, November 1998, and April 1999.

Raw lizard counts were converted into estimates as follows. The multivariate-contingency-table (Fienberg 1972) method fits the data to each of eight models, distinguished by which interactions (associations between the three censuses), if any, are included. The eight models are: the one with complete independence

TABLE 1. Estimated numbers of the introduced lizard *L. carinatus* on five experimental introduction islands and one natural introduction island.

Island		Vegetated area (m ²)	Estimated number						Mean of estimated number from July 1997 on
			April 1997	July 1997	Nov. 1997	April 1998	Nov. 1998	April 1999	
N1	Experimental	137.9	0	8	27	7	9	8	11.2
A18	Experimental	168.6	0	3	5	2	10	8	5.5
X10	Experimental	174.9	0	0	5	7	2	8	4.0
Z4	Experimental	216.5	0	4	14	5	11	10	8.6
Z1	Experimental	270.3	0	4	10	8	2	13	7.5
Z3	Natural	206.2	12	6	8	7	2	1	5.9†

Note: Estimates are rounded to nearest whole individual.

† Mean from April 1997 on.

of the censuses, three each with a single one of the three possible pairwise associated censuses, three each with two of the three possible pairwise associated censuses, and one with all three possible pairwise associated censuses. The simplest of the models fitting the data adequately, in the sense that the χ^2 value of the fit was less than the $\alpha = 0.05$ χ^2 value for the particular model, was selected, and the estimate that model provided used in the analysis. If no model gave a satisfactory fit, we selected that model whose χ^2 was closest to the test χ^2 . A Pascal program doing the fits was kindly provided by Joan Roughgarden. In the great majority of cases, the simplest model, that of complete independence, was adequate. Occasionally no model could be run on the data (e.g., when a number of categories equalled zero); then we took the average of the possible pairwise Lincoln estimates as the estimates to be used in the analysis. Finally, if the numbers of different individuals seen exceeded the Lincoln computational estimate, we used the former in the analysis. Note that we could not always verify that we were able to spray a particular lizard; in those cases, we counted a lizard as probably marked (0.75 individual) or possibly marked (0.25 individual).

In addition to the three censuses just discussed, each April (1997–1999) we conducted a number of actual capture sessions at the end of the study period. During those sessions, we noosed or hand-captured individuals of *A. sagrei* and recorded the following: snout–vent length, mass (only 1998–1999), hindlimb length (distance from the distal tip of digit IV to insertion of the limb in the body wall), and lamella number (expanded scales under the third and fourth phalanges of digit IV of the hindlimb) (further information on measurements in Glossip and Losos [1997] and Losos et al. [1997]). In 1997 we measured only adult males (snout–vent length >46 mm; 89 individuals in total). In 1998–1999 we measured snout–vent length and mass in all individuals of either sex whose snout–vent length exceeded 33 mm ($N = 136$ and 167 , respectively); except for the size cutoff, those individuals were captured as encountered randomly, i.e., in the proportion they were

seen to occur. Hindlimb lengths were only measured for all individuals in 1999; however, we eventually excluded females because hindlimb measurements may be very sensitive to the size of the egg(s) the female may be carrying, differentially curving the abdomen. Lamella counts were only taken for adult males except in 1999, when they were taken for all males. All measurements were made on site; individuals were returned to the capture point in less than 0.5 h.

To represent “relative hindlimb length” of *A. sagrei*, residuals were calculated using log–log regression of hindlimb length vs. snout–vent length for all islands combined and within a given yearly census. Each such regression was calculated in two ways, one using measurements from each lizard as a separate point, the second using island means (i.e., there are as many points as there are islands). The first weights islands with more lizards disproportionately, while the second has a smaller number of points. Results were qualitatively the same for the two methods, so we only report the first here. We represented “condition” of *A. sagrei* similarly, as the residuals from log–log regression of mass on snout–vent length. In addition, we analyzed condition using ANCOVA, where snout–vent length was the covariate and absolute mass was the dependent variable (both log-transformed).

Diurnal web spiders were censused as in previous studies (Schoener and Spiller 1992), recording species, body length, and web height. We attempt to find every spider with a web, a procedure that when checked provides fairly stable counts. We include in our analyses both orb-weaving (Araneidae, Uloboridae, Tetragnathidae) and non-orb-weaving (Theridiidae) species; we excluded, however, members of the Pholcidae, whose webs are typically hidden deep in holes.

To measure abundance of aerial arthropods, we put out five (the two smallest islands) or six (other islands) sticky traps. The traps were 22×14 cm sheets of clear plastic coated with Tangle-trap adhesive (The Tangle-foot Company, Grand Rapids, Michigan) on one side, suspended within openings of the vegetation 0.25–0.50 m above the ground. Traps were left out for 24 h; we

then recorded the body length (to the nearest mm) and taxon (at the ordinal level or lower) of each trapped arthropod ≥ 0.5 mm. We used a hand lens to discern hymenopteran parasitoids and other small specimens (details in Schoener et al. 1995). Data are given as numbers per trap. Both sticky-trap sessions and spider censuses were conducted during every visit, according to the same schedule as the lizard censuses.

We sampled ground arthropods by burying 7 (two islands) or 10 (other islands) test tubes (diameter 15 mm), positioning the top evenly with the ground surface; tubes were half-filled with antifreeze and were left out for 4 d (3 d were used in one session to avoid rainy weather). Data are given as number per tube per day. Tube samples were taken during every visit except July 1997; continuous rain during that time made even a 3-d session impossible.

To quantify the potential indirect effect on plants, we measured herbivory on buttonwood (*Conocarpus erectus*), one of the most common shrub species on the islands. Unlike study islands in the central Bahamas (Schoener 1987), this plant rarely produces highly pubescent leaves ("silver" buttonwood, with many trichomes) on our Abaco study islands; all leaves in this study were glabrous ("green" buttonwood, with few trichomes), which removed the potential complication of this plant defense for assessing herbivory (Spiller and Schoener 1996).

Buttonwood damage was measured from leaves picked and transferred to presses; digital photographs were taken of each leaf shortly after collection. Total leaf area and areas of various types of damage were measured with SigmaPro Image Analysis Software (SPSS Science, Chicago, Illinois). The measure of damage used, D_s (Schoener 1988), was the total area of all leaves divided into the total area of damaged portions. To select shrubs for leaf collection, we noted each shrub whose major and minor axes both exceeded 33 cm; we then ordered those shrubs around the circumference of the island (buttonwood is typically coastal) and systematically selected every 2nd-to-4th shrub, depending on island size, to obtain 6–11 focal shrubs per island, depending on the island's area. To sample leaves we tossed a square haphazardly onto each focal shrub 1–5 times, depending on shrub size, and collected that branchlet closest to a marked corner. We distinguished four types of damage. "Scars" were well-defined, usually elliptical, necrotic areas, "holes" were entirely missing areas, "mines" were serpentine, and "lines" were highly elongated, slightly raised areas. Herbivores identified from buttonwood were Lepidoptera from the families Noctuidae (*Collomena filifera* and unknown species) and Gelechiidae and a curculionid beetle (*Artipus floridanus*). In addition, using confinement trials, we showed a source of line damage to be the flea beetle *Chaetocnema brunnescens* (Chrysomelidae). To keep phenology roughly consistent, we conducted foliage-damage measurements once per year, during April.

Statistical analysis

To compare *A. sagrei* islands with and without *L. carinatus*, we performed for each response variable repeated-measures ANOVA on values using censuses beginning April 1998. To compare the two unmanipulated kinds of islands (treatments 1 and 2), we performed for each response variable repeated measures over the entire time period, including April 1997. (*P* values for single points in time are only used as descriptive indicators of when effects first appear, see *Discussion*.) Note that, for a between-subjects effect, repeated-measures analysis is equivalent to using the time average in a simple analysis. To adjust for premanipulation plot differences where appropriate, we used ANCOVA as follows. Initially, we performed a full ANCOVA with the premanipulation value on each island as the covariate. If the interaction term was not significant in the full model (slope heterogeneity rejected), we ran the model with just the covariate. If the probability value *P* for the covariate was < 0.10 , that ANCOVA was given in the results. If *P* were ≥ 0.10 (true in $\sim 50\%$ of the cases), the covariate was omitted from the analysis and an ordinary ANOVA used. When the interaction term (slope heterogeneity) was significant, we used the least-squares means test, which evaluates the difference between treatments (two *y* values) for the average value of all points on the *x*-axis. Treatment was a fixed effect. Analyses used Type III sums of squares and were executed with SAS (Littell et al. 1991).

Hypotheses concerning effects of *A. sagrei* on spider density and diversity, numbers of large arthropods, and leaf damage are directional, based on prior observations of nonexperimentally induced states and theoretical expectations; therefore, we used one-tailed *P*'s for these. We also used one-tailed *P*'s for effects of *L. carinatus* expected to occur indirectly via *A. sagrei*; from the above list, only effects on large ground-surface arthropods are excluded. A one-tailed *P* was also used for those effects on *A. sagrei* for which theoretical expectations are clear: *L. carinatus* is expected to reduce the density of this lizard, chase it off the ground and higher into trees onto perches averaging smaller diameter, eat the hatchlings preferentially, and reduce its body condition (mass relative to length). The expected effect on body size is less clear: adult males should have length and mass reduced, but classes of smaller lizards (all males, females) may not if small individuals are differentially eaten. Hence two-tailed *P*'s were used. A one-tailed *P* was used for SD of length, however, as predation is expected to reduce both ends of the *A. sagrei* size distribution. Effect direction on morphological variables (relative hindlimb length, lamella number) is also less clear, as initially lizards with the "wrong" morphology may be differentially consumed, but as they shift habitat, may then evolve or develop morphology suited to the new habitat. For morphological, as well as all other ecological variables,

TABLE 2. Natural food-web differences between islands with and without the intermediate lizard *Anolis sagrei* (treatment 1 vs. 2, time average 1997–1999).

Variable	Effect ratio	df	F	Raw P
Density all web-spider species	5.57	1, 12	9.65	0.005‡
Web-spider species (no.)	2.14	1, 12	7.45	0.009§
Small (≤ 4 mm) aerial arthropods (no.)	1.44†	1, 12	7.35	0.019§
Large (> 4 mm) aerial arthropods (no.)	1.28	1, 12	0.95	0.175
Small (≤ 4 mm) ground arthropods (no.)	1.003†	1, 12	0.80	0.388
Large (> 4 mm) ground arthropods (no.)	4.36	1, 12	3.80	0.038
Percentage leaf-hole damage	1.10	1, 12	0.08	0.391
Percentage leaf-scar damage	1.58	1, 12	7.74	0.008§
Percentage leaf-mine damage	3.91	1, 12	7.19	0.010§
Percentage leaf-line damage	1.05	1, 12	0.38	0.274

Note: Where an adjustment is indicated for a *P* value, only the most conservative of the adjustments is noted.

† *A. sagrei* islands greater.

‡ $P < 0.05$ by stepdown Bonferroni.

§ $P < 0.05$ by false-discovery rate.

|| $P < 0.10$ by false-discovery rate.

two-tailed *P*'s were used. All island-specific values except percentages were log-transformed when rendering variances more uniform (all but web height); percentages were arcsine square-root transformed. Because zero values occurred for number of large arthropods and number of parasitoids (see also Schoener and Spiller 1999a), some number had to be added before transformation; we added either the smallest possible value (one individual per trap or tube) or the smallest observed nonzero value (for density and number of species).

For tests of partly or entirely indirect effects that do not give statistical significance, we computed the power ($1 - \beta$), where β is the probability of a Type II error (Neter et al. 1996). The effect ratio was set at 2.5 times (before transformation) the value of the (highly significant) direct effect of *L. carinatus* on *A. sagrei*. Conclusions were unaltered using $2\times$, a value used to denote a "large" effect by Sih et al. (1985). Power values are used descriptively rather than inferentially (see Hoenig and Heisey 2001). We can also assess sample-size adequacy by noting the significant effects in the comparison treatment 1 vs. 2; that comparison, involving six and four islands vs. the manipulation's six and five islands, would have less power, all other things being equal.

Tablewise adjustments for multiple tests were done in two ways. The more conservative was the stepdown Bonferroni method, which is more powerful than the simple Bonferroni while maintaining strong control of the familywise error rate. The more liberal method is a step-up method that controls the false discovery rate (FDR) while not necessarily controlling the familywise error rate (SAS 1999).

RESULTS

Food-web differences on unmanipulated islands naturally with and without the intermediate predator A. sagrei

To determine the natural food-web effects of the intermediate predator *A. sagrei*, we compared over the

entire experimental duration islands without *A. sagrei* to islands with *A. sagrei* in their natural state, i.e., without the introduction of the large predator *L. carinatus* (treatment 1 vs. 2, April 1997–April 1999). Table 2 gives statistics for variables involved in hypotheses as well as the "effect ratio" (Schoener 1993, Spiller and Schoener 1995, Schoener and Spiller 1999a, b), defined here as the ratio of the mean of the *sagrei*-absent islands over the mean of the *sagrei*-present islands, or vice versa, whichever is larger. The log of such "response ratios" has been convincingly argued as the best measure of effect magnitude by Hedges et al. (1999; other evaluations in Osenberg et al. [1997, 1999] and Goldberg et al. [1999]). We report arithmetic ratios in the tables and text for descriptive purposes.

Islands without *A. sagrei* had more individuals and species of web spiders. Effect ratios are ~ 6 for individuals and ~ 2 for species (Fig. 1). To look for a habitat shift, we analyzed web heights of the most common species (*Eustala cazieri*) separately, rather than those of all species combined, as the species vary substantially in their typical web height. Although webs were higher with than without *A. sagrei* in both comparisons, statistical significance was marginal (unadjusted $P = 0.056$); moreover, the average vegetation height for the two types of islands differed in that high vegetation is more abundant on *A. sagrei* islands (which average larger in area). Because of the nonsignificant P and the difference in vegetation availability, we do not consider it likely that the difference in web height is caused by *A. sagrei*.

Of the arthropods other than spiders, two comparisons were significant: large ground arthropods were less abundant and small aerial arthropods more abundant in the presence of *A. sagrei* (Table 2, Fig. 2). One no-*sagrei* island had many large ground arthropods, mainly roaches; after a 3- or 4-d session, tubes were normally filled to the brim with these insects. Another no-*sagrei* island had many large arthropods as well,

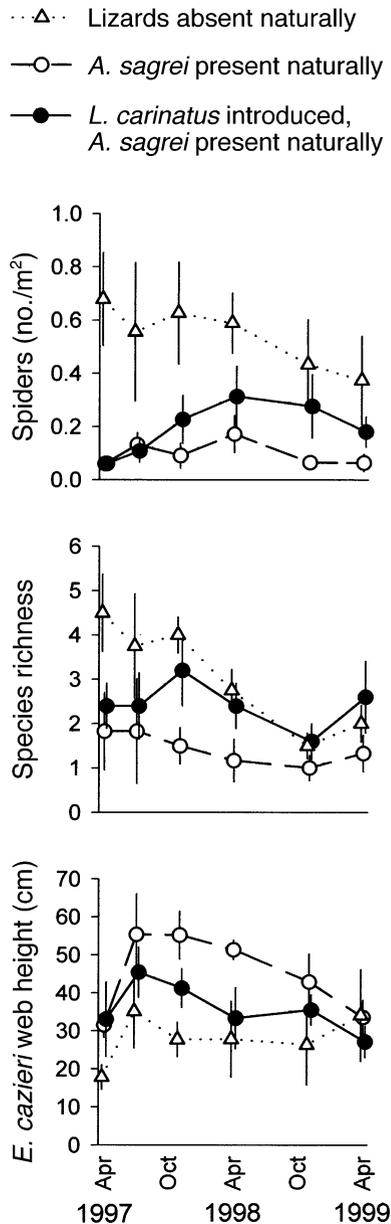


FIG. 1. Properties of web spiders: (top) density of all web-spider species combined; (middle) species richness (number of spiders) per island; (bottom) web height of the most common spider species, *Eustala cazieri*. Symbols give means ($N = 4, 6,$ and $5,$ respectively); bars represent ± 1 SD.

but large ants (*Camponotus*), were most common on this island. The two other no-*sagrei* islands had little litter (mostly bare rock) and fewer large arthropods. Despite the high interisland variation, this effect persisted throughout the experiment. Small aerial arthropods were relatively more abundant on *A. sagrei* islands at almost every census. Number of parasitoids (a small component, 8%, of small arthropods) showed little difference between treatments (Fig. 3).

Scar and mine leaf damage were greater in the ab-

sence than in the presence of *A. sagrei* (Table 2, Fig. 4), with the latter showing the greater effect (effect ratio ~ 4).

Experimentally produced effects of the larger lizard *L. carinatus* on traits of the smaller lizard *A. sagrei*

Effects of *L. carinatus* on *A. sagrei* were determined by using a repeated-measures (time average) analysis for 1998–1999 (Table 3).

Effects on *A. sagrei* density were immediate and dramatic: in only 2 mo, islands having the large predator diverged significantly away from those without it. The curves reached their maximum (arithmetic) divergence ~ 7 mo after inception (November 1997) and maintained this relative difference substantially unchanged (Fig. 5). The mean perch height of *A. sagrei* was also quickly affected, and it showed a progressive increase to the end of the experiment (Fig. 5); mean perch height in the controls, which began at almost the same value as for the experimentals, remained remarkably constant. Mean perch diameter dropped gradually; it diverged more slowly than perch height, and again the difference from controls increased over time (Fig. 5). Thus *A. sagrei* became less abundant, went higher into trees, and (perhaps in large part as a consequence) went onto perches of smaller diameters. This shifted them substantially away from the habitat of *L. carinatus*, which occurred mainly on the ground. The percentage of *A. sagrei* hatchlings (< 29 mm), while not changing as strikingly as the three variables just discussed, eventually shifted significantly toward relatively fewer hatchlings on *L. carinatus* islands. Note the huge amount of phenological variation in this variable, with highs in the mid-to-late summer (Fig. 5). Partly related to percentage hatchlings, the width (SD logs) of *A. sagrei*'s body-length distribution was less on *L. carinatus* islands than on controls. Fig. 6 gives the body lengths of all individuals from censuses beginning July 1997 (slightly earlier than the repeated-measures test period, because hatchlings are differentially abundant in July). While the major contraction was at the small-sized tail, a minor one occurred at the large-sized tail, and the middle of the distribution is decidedly more peaked for the introduction islands. This result is not included in Table 3 because it is not independent of that on percentage hatchlings, but raw $P = 0.011$.

The morphological variables obtained by capture-and-release in situ showed less overall differences between experimental and controls (Figs. 7 and 8, Table 3). Note that Table 3 gives only adult males (> 46 mm), as this class was the only one for which we had data from all years. Neither body length nor mass was significantly different. Body condition (mass relative to length) on *L. carinatus* introduction islands was significantly poorer in adult males. Using the ANCOVA method of comparing condition gave a somewhat less significant result for the mean of 1998–1999 ($P =$

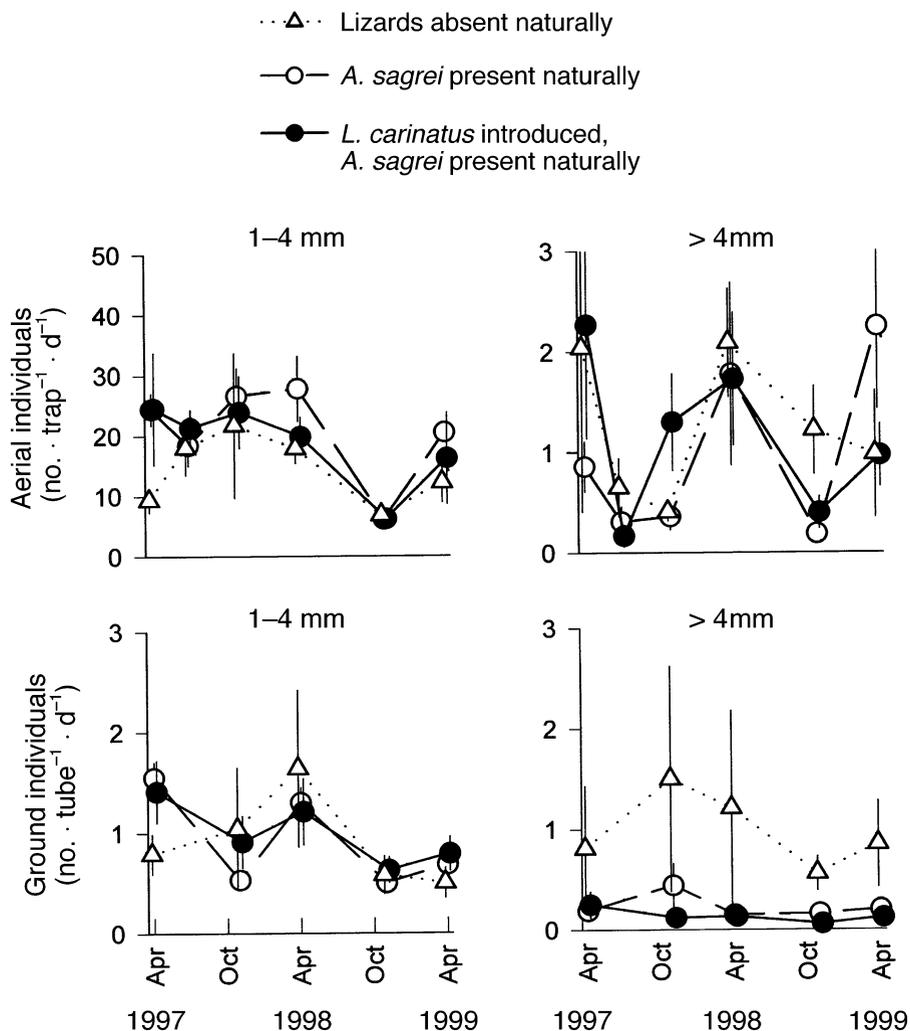


FIG. 2. Number of arthropods caught by two methods. The top row shows the number per sticky trap (each 24 h) for two body-size categories; the bottom row shows number per pitfall trap per day for the same two body-size categories. Symbols give means (*N*'s are given in Fig. 1); bars represent ± 1 SD.

0.048; Fig. 7). Other lizard classes showed no significant differences.

Results for relative hindlimb length of adult males are suggestive of an effect but are not definitive (Fig. 8). Repeated-measures analyses of 1998–1999 data show relative hindlimb length significantly larger on *L. carinatus* islands than controls (using the least-squares means test for difference at the average *x* value, since the interaction between the covariate [initial value] and treatment was significant at $\alpha = 0.05$ [see *Methods*]). However, one island (X10) had no adult males in 1999, so that island is removed from the analysis. Significance declines for individual years: raw *P* is only marginally significant, and that for only 1999 ($P = 0.078$). When X10 is removed from the 1998 data, that year's raw *P* decreases ($P = 0.028$). Moreover, the 1998 data set for X10 only has one male, so might justifiably

be considered an outlier. No difference for all males was found.

Involvement of the covariate in the adult-male-hindlimb analyses raises the question of what might underlie interisland variation in relative hindlimb length. Hypothetically, the greater the percentage time spent on broad, flat surfaces such as the ground, itself inversely correlated with percentage vegetated area, the greater the relative hindlimb length. This fits with observations that relatively longer legged lizard species are faster on the ground (Losos 1990, Bauwens et al. 1995, Bonine and Garland 1999, Irschick and Jayne 1999). Using either method of computing residuals, pre-experimental (1997) relative hindlimb length is significantly greater, the greater the (April 1997) percentage use of the ground (Fig. 9). In fact, except for one island, the correlation is nearly perfect, albeit fairly

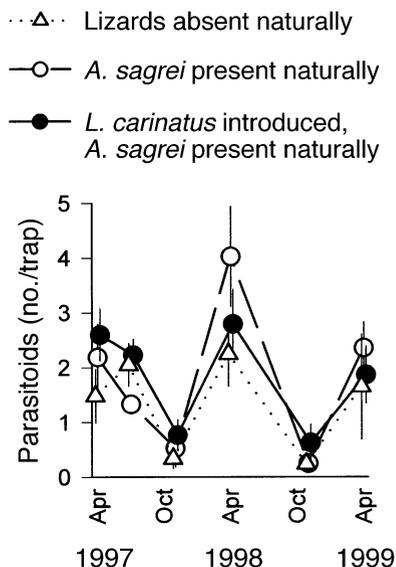


FIG. 3. Numbers of hymenopteran parasitoids caught per sticky trap (each 24 h). Symbols give means (N 's are given in Fig. 1); bars represent ± 1 SD.

nonlinear (so Spearman was computed; $r = 0.673$; $P = 0.023$). Additionally, the 1997 percentage use of the ground is negatively related to percentage vegetated area (Pearson $r = -0.657$; $P = 0.028$).

No significant difference in number of lamellae was found for adult males or all males; in fact, treatment values were nearly identical (Fig. 8).

Experimentally produced effects of the large lizard (L. carinatus) on lower level food-web components

This section summarizes the effects of *L. carinatus* introduction on food-web elements lower than *A. sagrei*, i.e., that might be affected by the latter species. Hence the effects in question are at least largely, and perhaps entirely, indirect. Recall that introduction of the large lizard had huge effects on the density and habitat of *A. sagrei*.

Numbers of web-spider individuals and species diverged toward higher values, with some time lag, upon introduction of *L. carinatus* (Fig. 1). The density of the most common spider species, *E. cazieri*, first achieved $P < 0.05$ for difference from control islands in November 1997, 7 mo after experimental inception (Fig. 10). The density of all species combined followed in April 1998, and the number of web-spider species first achieved $P < 0.05$ in November 1998. At the end of the experiment, values on the introduction islands had reached about half those on islands without *A. sagrei* (Fig. 1). Effect ratio for spider density computed from time averages from April 1998 on was 2.3, as compared to 5.6 for treatment 1 vs. 2 over the entire period. Effect ratios for spider species diversity were much closer: experimental 1.8, natural 2.1. In contrast to the other spider variables, web height of the most common spe-

cies showed no significant changes. Note that all changes are in the direction predicted from removal of *A. sagrei*, i.e., from comparing treatments 1 and 2.

No other food-web effect of introducing *L. carinatus* was statistically significant by repeated-measures tests for April 1998 on (Table 4). Effect ratios for aerial and ground-surface arthropods were overall small, ranging from 1.1 to 1.6 (Table 4, Fig. 10); the effect ratio for large ground-surface arthropods was smaller than that found in the natural comparison, but effect ratios were rather similar to natural ratios for the other three arthropod classes (Table 2). Mine damage showed a marginally significant raw P (Table 4); in fact, mine damage on *L. carinatus* islands at the last census was greater than that found on islands without *A. sagrei*. Except for mine damage, effect ratios were well below 2 (Table 4, Fig. 10). For scars and mines, the two types of damage clearly significantly different on natural islands with and without *A. sagrei*, the experimentally produced effect ratios were substantially smaller than the natural ones (scars: experimental 1.03, natural 1.6; mines: experimental 2.5, natural 3.9).

Because of the many large raw P values for food-web variables other than spiders, no P of Table 4 adjusted for multiple tests by either method was significant at $\alpha = 0.05$, even though raw P 's < 0.05 for spider density and diversity. Other tablewise comparisons might, of course, give different results.

Power calculations of the food-web variables in Table 4 not significantly affected by *L. carinatus* showed that if the effect ratio for such variables were 2.5 (approximately the observed ratio for the effect of *L. carinatus* on *A. sagrei* or on web spiders) the experiment would have probably detected a significant difference for about half of these variables; power exceeds 0.50 in four of the eight cases. Hence, the fact that all were insignificant suggests that the effect of *L. carinatus* on these variables was generally weaker than the effect on *A. sagrei* and web spiders. This conclusion is corroborated by evaluating unmanipulated islands over a similar time period: six of 10 differences between treatments 1 and 2 in the same food-web variables were significant with a smaller sample size (Table 2).

Correlations between spider density and numbers of aerial arthropods

This study allowed a test of whether web spider density is related to numbers of aerial arthropods. Because the effect may be erratic from year to year, the strongest test would be to combine data from all census periods throughout the study and to use all three treatments. A disadvantage of this approach is that the experimental treatment may be in a state of flux, with lags, so that spiders for example may have changed but aerial arthropods not yet changed, contributing to a lack of correlation. However, because there were no statistically detectable effects of the *L. carinatus* manipulation, this disadvantage is probably small. Treatment 1

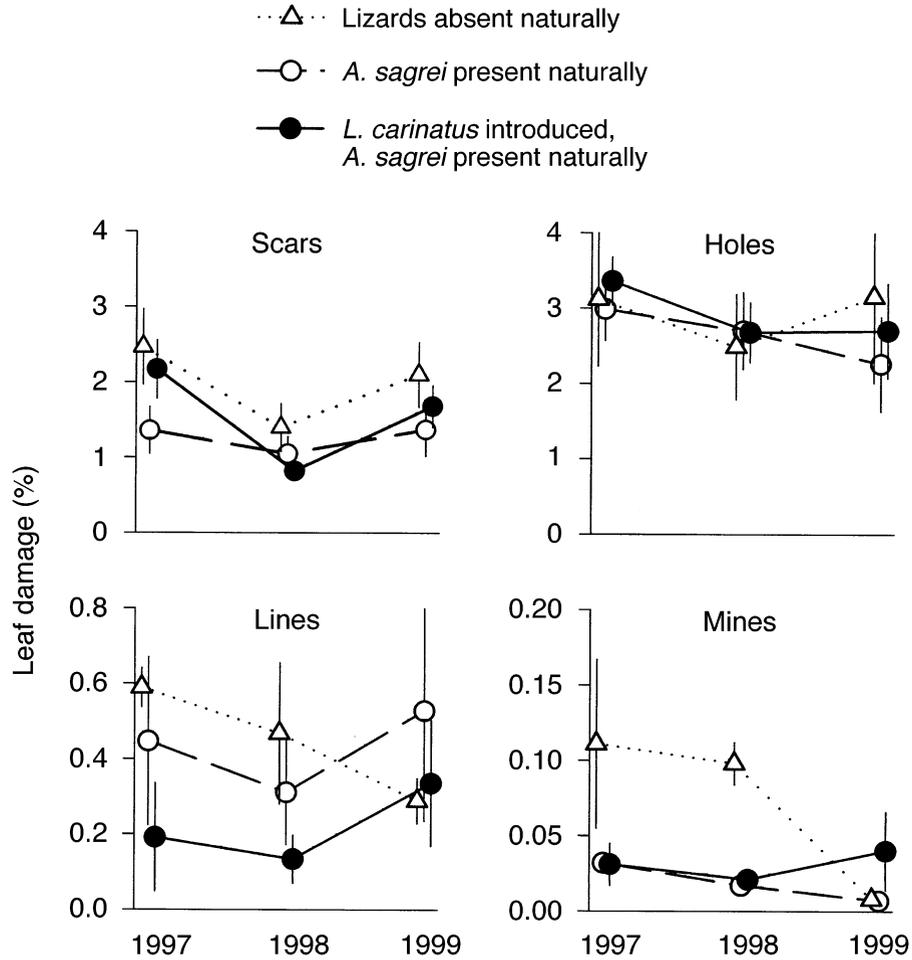


FIG. 4. Leaf damage, measured as percentage total leaf area damaged (D_s in Schoener 1988). Symbols give means (N 's are given in Fig. 1); bars represent ± 1 SD.

TABLE 3. Experimentally produced differences in traits of the lizard *A. sagrei* on islands with and without the introduced lizard *L. carinatus* (treatment 2 vs. 3, time-average 1998–1999).

Variable	df	F	P
Population density	1, 9	17.84	0.001††
Perch height†	1, 9	101.15	0.00005††
Perch diameter	1, 8‡	12.91	0.004††
Hatchlings (<29 mm; percentage)§	1, 9‡	9.91	0.007††
Adult ♂ body length†	1, 8	0.39	0.275
Adult ♂ body condition	1, 8	5.67¶	0.022‡‡
Adult ♂ relative hindlimb length†	1, 6‡	15.05#	0.008††
Adult ♂ lamella number	1, 8	0.19	0.676

Note: Where an adjustment is indicated for a P value, only the most conservative of the adjustments is noted.

† Higher with *L. carinatus*.

‡ Covariate (pre-experimental value) used.

§ Body size estimated visually (see *Methods: Data collection*).

|| Measured from captured lizards. Mass gives similar results.

¶ Also significant at $\alpha = 0.05$ for residuals computed by using island means (see *Methods: Data collection*).

Used least-squares means test because slopes significantly different (see *Methods: Statistical analysis*).

†† $P < 0.05$ by stepdown Bonferroni.

‡‡ $P < 0.05$ by false-discovery rate.

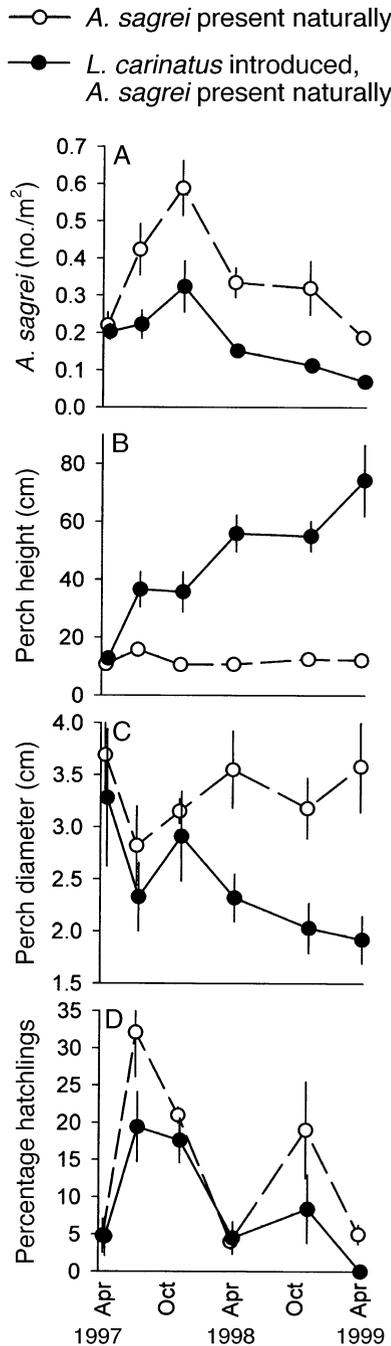


FIG. 5. Demographic and behavioral traits of the lizard *Anolis sagrei*. (A) density; (B) perch height; (C) perch diameter; (D) percentage hatchlings (<29 mm). Symbols give means (N 's are given in Fig. 1); bars represent ± 1 SD.

shows a strong negative relation between web spider density and number of small aerial arthropods (Fig. 11 top; Pearson $r = -0.99$, $P = 0.013$); the other treatments do not (treatment 2: $r = -0.52$, $P = 0.294$; treatment 3: $r = 0.28$, $P = 0.646$). An analysis of all the data confirms that slopes for the three treatments

are significantly heterogeneous ($df = 2, 9$, $F = 8.16$, $P = 0.010$).

Fig. 11 (bottom) relates parasitoid abundance to web spider density (parasitoids are completely included in small arthropods [92% are ≤ 4 mm] but most small arthropods are not parasitoids): treatment 1, $r = -0.92$ ($P = 0.084$); treatment 2, $r = -0.68$ ($P = 0.138$); treatment 3, $r = -0.47$ ($P = 0.43$). Because slope heterogeneity is not significant ($P = 0.126$), we can carry the analysis farther than for aerial arthropods. ANCOVA gives a significant slope effect ($df = 1, 11$, $F = 6.52$, $P = 0.023$) and a nonsignificant treatment effect ($df = 2, 11$, $F = 0.91$, $P = 0.429$). Thus statistically, the difference between islands for parasitoids can be ascribed to the covariate spider density alone. Removal of the treatment factor from the model gives $r = -0.68$ ($P = 0.006$).

Fate of the island naturally colonized by the large lizard L. carinatus

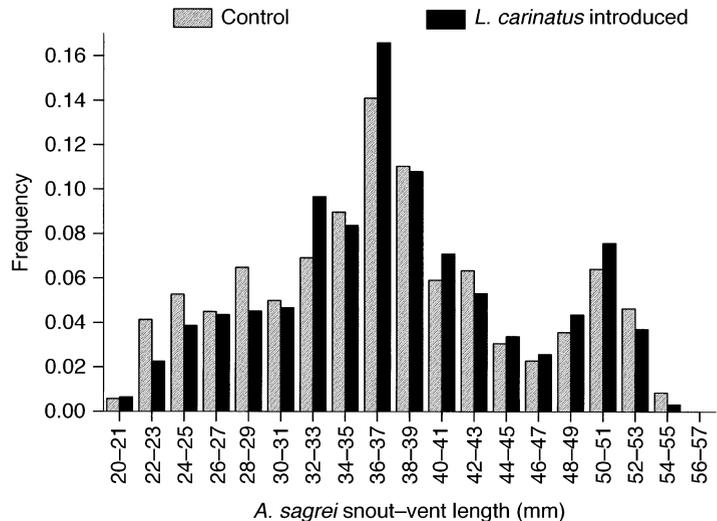
Recall that, before we were able to invade it for our experiment, Island Z3 was naturally colonized by *L. carinatus*. Fig. 12 (top) shows the estimated number of *L. carinatus* during the course of this colonization. In April 1996 no individuals were found, but by April 1997 the estimated population was already at its recorded maximum of 12 individuals (Table 1). Thereafter, the population gradually and approximately linearly decreased, until at the end it consisted of one individual. Numbers of *A. sagrei* were at first a mirror image of the *L. carinatus* plot (Fig. 12, second-from-top); the initially explosive increase in *L. carinatus* was paralleled by a sharp decrease in *A. sagrei* to about a quarter of its preinvasion value; it then recovered while *L. carinatus* remained fairly constant at 6–8 individuals. *A. sagrei* then declined again to about half of its pre-experimental value. Concurrently with changes in its numbers, *A. sagrei* rapidly increased perch height: by April 1998 (about two years after invasion) it averaged over 80 cm, >3 times higher than before invasion (Fig. 12, middle). Perch height then dropped somewhat but remained high, close to the final census mean for experimental *L. carinatus* islands (Fig. 5). Perch diameter fell correspondingly (Fig. 12, second-to-bottom panel). After *A. sagrei* populations dropped, spider numbers climbed with a lag of about one year (Fig. 12, bottom), but these were not as convincingly complementary as the experimental averages (compare Fig. 1 with Fig. 5). None of the other food-web variables on Z3 showed any obvious effect of the colonization.

DISCUSSION

Effects of A. sagrei judged by comparisons of unmanipulated islands

Fig. 10 (open circles) summarizes the effects of *A. sagrei* on the lower food-web elements. As in all pre-

FIG. 6. Frequency distribution of body (snout-vent) lengths (estimated by eye) of *A. sagrei* for islands with and without the introduced lizard *L. carinatus*. Note that both tails, but especially the left, are higher for the distribution without than with *L. carinatus*.



vious studies (Schoener and Spiller 1999b), experimental or comparative, *A. sagrei* is associated with a lowering of density and diversity of web spiders. The present density effect is quite dramatic: ratios range from a half to a whole order of magnitude. These ratios are comparable to previously determined ratios for smaller islands in the same general area (Schoener and Spiller 1996, 1999a, Table 2). The effect ratio for number of spider species is somewhat smaller, however, than that for the smaller islands, being 2.1 instead of 3.4; smaller islands may have more species at population numbers close to extinction thresholds (Goel and Richter-Dyn 1974, Pimm et al. 1988, Schoener and Spiller 1992, Rosenzweig 1995, Hanski 1999), so give a greater effect on species diversity. The mechanism of the effect of lizards on spiders was demonstrated at another site (Staniel Cay) to be a combination of predation and food competition, with the former predominating (Spiller and Schoener 1990a). A subsequent experiment at that site (Spiller and Schoener 2001) showed no tendency for interspecific spider competition to be stronger in the presence of *A. sagrei*, an effect that would have intensified the lowering of species diversity in the presence of this predator. (This kind of effect has been suggested for other organisms [Holt 1987, Mittelbach and Chesson 1987, Holt and Lawton 1994]; here, the mechanisms could have been a reduction in the spiders' food supply or spider habitat shift into more crowded conditions.) Thus lizard predation acts in a simple way on spider richness, reducing number of individuals and thereby reducing number of species; elsewhere (Schoener and Spiller 1996, Spiller and Schoener 1998), we showed that rarer species densities are affected more.

Islands with *A. sagrei* have fewer large ground-surface arthropods. Among islands without *A. sagrei*, large ground-surface arthropods show a great deal of variability, some of which must result from differences in

litter (see *Results*). As in the experimental study on smaller islands at the same site (Schoener and Spiller 1999a), small (≤ 4 mm) aerial arthropods (those caught in sticky traps) were more abundant on *A. sagrei* islands. Numbers of large aerial arthropods showed no significant differences. In studies at other sites, lizards either had no effect on small or large aerial arthropods or significantly lowered the latter (Schoener and Spiller 1999b). When the lizard effect is negative, we assume it is direct, but this cannot be so for a positive effect. In the previous study (Schoener and Spiller 1999a), we speculated that lizards affect small aerial arthropods positively by consuming some predator or predators of the latter; however, an attempt to implicate web spiders by correlational analysis failed. The present study found negative correlations of both number of small aerial arthropods and parasitoids with spider density, thereby providing the first evidence of the nature of the positive indirect effect of *A. sagrei*. Note that the overall relation bends sharply downward at some point (Fig. 11): changes in spider density have little effect when small but substantial effect when large.

In agreement with previous studies of buttonwood, islands with *A. sagrei* had less scar damage (Schoener 1988, Spiller and Schoener 1996, Schoener and Spiller 1999b). No significant differences, however, were found for holes, contrasting not only with the previous study at the same site (Schoener and Spiller 1999b), but at variance with other studies of buttonwood as well as with most studies of sea grape (*Coccoloba uvifera*) (Spiller and Schoener 1994, 1997, but see Spiller and Schoener 1990b). As in the previous experiment, however, we found no significant difference in line damage (caused by a flea beetle, see *Methods*). A fourth category of damage, mines, newly differentiated at this site for the present study, best discriminated islands with and without *A. sagrei*, but it constituted only a small amount of the total damage (note axes Fig. 4).

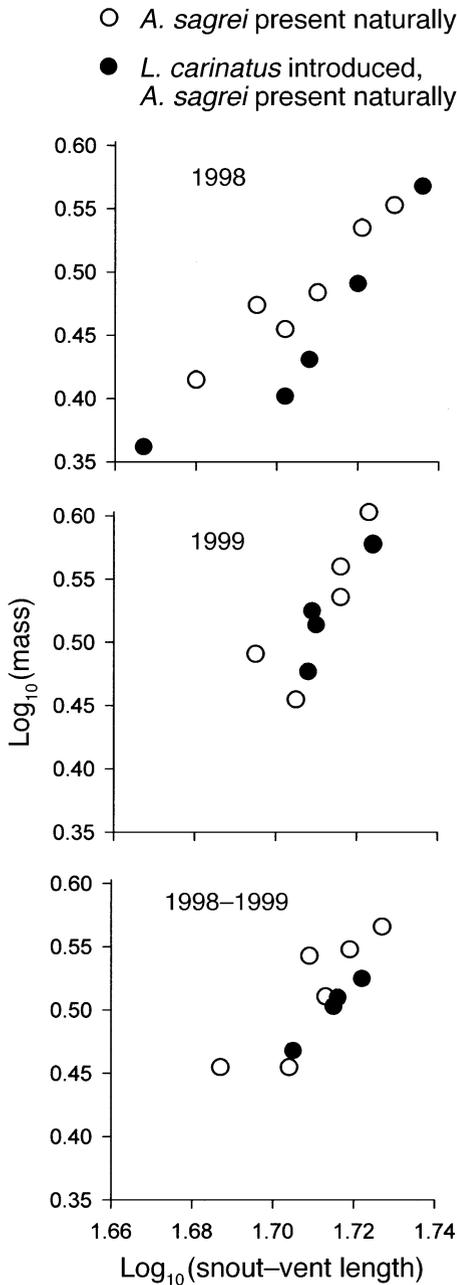


FIG. 7. Body condition of *Anolis sagrei* as represented by plots of (log) mass (measured in grams) vs. (log) snout-vent length (measured in millimeters); especially in 1998, *A. sagrei* was relatively lighter on islands invaded by the larger lizards. Note that the time average (bottom plot, giving the average of the y values for the two top plots) is equivalent to the variable tested by repeated measures.

Indeed, total damage was not very different between islands with and without *A. sagrei*.

In conclusion, the comparative portion of the study did not contradict and sometimes expanded effects of *A. sagrei* as surmised in previous studies.

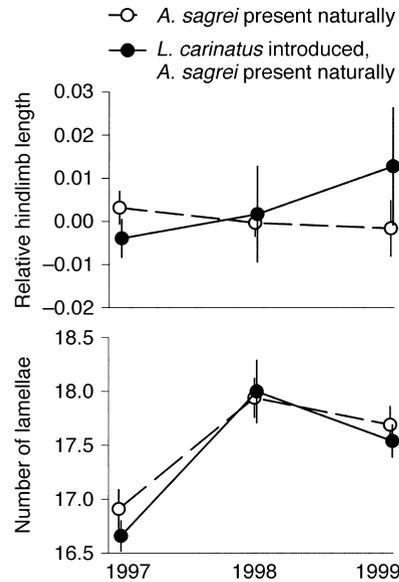


FIG. 8. Morphological traits of adult male *Anolis sagrei*. The top panel shows the relative hindlimb length (residuals [first method] of log-log regression of hindlimb length vs. snout-vent length); the greater (more positive) the value, the relatively longer legged the lizard. The bottom panel shows the number of lamellae. Symbols give means (*N*'s are given in Fig. 1); bars represent ± 1 SD.

Magnitude and speed of the food-web effects of L. carinatus experimental introduction

Previous experimental and prior and present comparative studies at the Abaco site identified many food-web effects of *A. sagrei*; were *L. carinatus* to affect substantially the smaller lizard, all present experimental effects on such components would be potentially

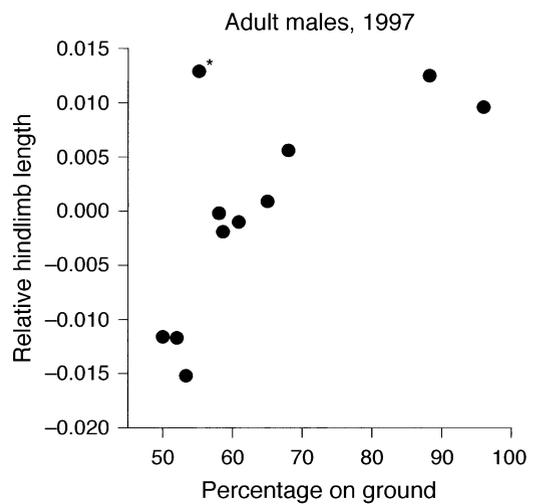


FIG. 9. Relation of relative hindlimb length of *Anolis sagrei* to percentage observed on the ground (including rocks and branches continuous with the ground). The island marked with a star symbol is well away from the otherwise tight curve.

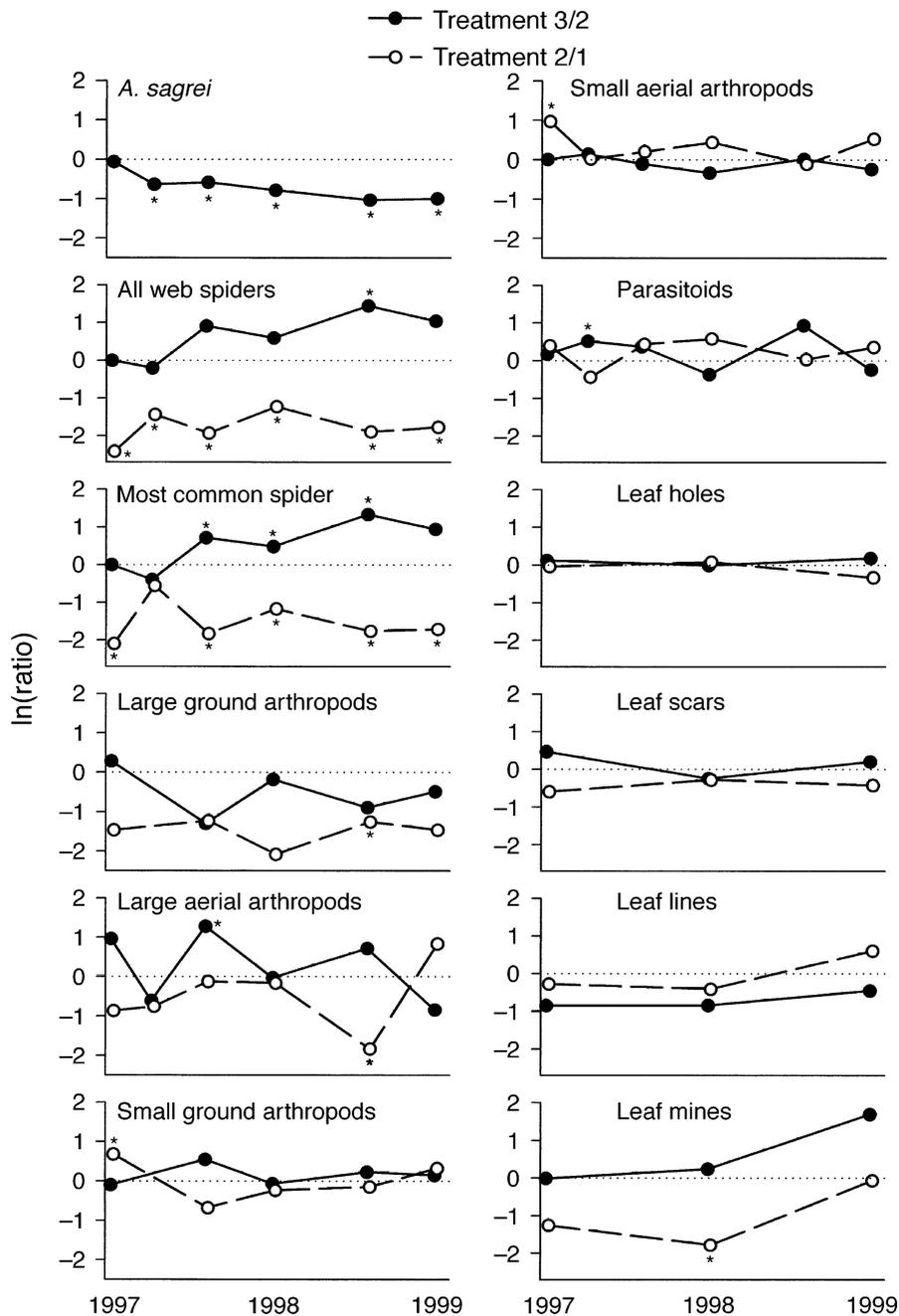


FIG. 10. Effect size over time for abundance comparisons between natural islands with (treatment 2) and without (treatment 1) *A. sagrei* (open circles), and between islands with (treatment 2) and without (treatment 3) experimental introduction of *L. carinatus* (solid circles). Asterisks indicate two-tailed $P < 0.05$ for that date; these are used for descriptive purposes (see *Methods: Statistical analysis*) and so are uncorrected for multiple comparisons. Effect size is the natural log of the ratios given at the top of the figure; these effect ratios (or their reciprocals) are used in the tables.

indirect. Table 5 lists 10 abundance-type food-web variables according to whether or not unmanipulated islands were significantly different (raw P 's) with and without *A. sagrei* (treatments 1 vs. 2); six were significantly different. If *A. sagrei* density is added, only 3 of the 11 variables showed a significant response to

the manipulation averaged over the last year (Tables 3 and 5): spider density, spider diversity, and *A. sagrei* density. The last is the only mostly directly affected variable, and direct effects are often stronger than indirect ones in both theory and nature (Schoener 1993, Menge 1995, Abrams et al. 1996). Of the potential

TABLE 4. Experimentally produced food-web differences between *A. sagrei* islands with and without the introduced lizard *L. carinatus* (treatment 2 vs. 3, time average 1998–1999).

Variable	Effect ratio	df	F	P†	Power
Density, all web-spider species	2.55	1, 11‡	4.06	0.035	
Web-spider species (no.)	1.89	1, 11‡	3.26	0.049	
Small (≤ 4 mm) aerial arthropods (no.)	1.29§	1, 12	2.47	0.142	0.826
Large (> 4 mm) aerial arthropods (no.)	1.36	1, 12	0.05	0.416	0.262
Small (≤ 4 mm) ground arthropods (no.)	1.06	1, 11‡	0.13	0.728	0.430
Large (> 4 mm) ground arthropods (no.)	1.63§	1, 11‡	0.72	0.415	0.372
Percentage leaf-hole damage	1.08	1, 11‡	0.00	0.499	0.771
Percentage leaf-scar damage	1.03	1, 12	0.10	0.380	1.000
Percentage leaf-mine damage	2.54	1, 12	2.90	0.057	<0.150
Percentage leaf-line damage	1.79§	1, 11‡	0.26	0.309	0.578

† No value significant when multiple-test adjustment made.

‡ Covariate (pre-experimental value) used.

§ Islands without *L. carinatus* have larger values.

indirect effects, none of the aerial-arthropod, ground-arthropod, or leaf-damage variables responded significantly.

The tendency for spiders to show a notable indirect effect but other variables not is related to the magnitudes of *A. sagrei*'s effects on lower level food web elements: the comparatively determined effect magnitudes are overall larger for spiders than for others (Table 2). The *A. sagrei*'s effect on spiders is in general very strong, both at this site and elsewhere (Schoener and Spiller 1999a, b). Nonetheless, effect ratios for the 1998–1999 time average were substantially lower for spider density than those obtained by comparing unmanipulated islands with and without *A. sagrei* (2.3–2.6 vs. 4.4–5.6, most common species and all species, respectively); they were somewhat lower for species diversity (1.9 vs. 2.1). Spider-density ratios were, however, very similar to the experimentally produced effect ratio of 2.5 for *L. carinatus* on *A. sagrei* density. In short, a strong indirect effect can be produced in an experimental manipulation when the direct effect of the intermediate species on the target species (*A. sagrei* on spiders in this case) is large. Other effects may have eventually become statistically significant, but they would have probably been weaker, given the small values obtained during the manipulation so far.

Summarizing, only in cases involving spiders did the *L. carinatus* introduction reverse the effects of the intermediate predator *A. sagrei*. For a given food-web variable, we can state three statistical conditions necessary for a reversal: (1) the effect of the intermediate predator must be significant in comparisons between unmanipulated islands with and without it; (2) values of the food-web variable must initially not be significantly different between the two classes of islands having the intermediate predator, those receiving the invading large predator and those not; and (3) the effect of the manipulation must be significant during the last portion, i.e., the same classes of islands as in ("2") must now show significant differences in the expected direction. Table 6 summarizes the degree to which these

conditions are met for the lower level food-web variables. Condition 1 is tested by comparing treatments 1 vs. 2 (throughout): six such comparisons were significant. Condition 2 is tested by comparing treatments 2 vs. 3 just before manipulation: no significant difference was found. Condition 3 is tested by comparing the time average of treatment 2 with that for 3 for the 1998–1999 phase: two such comparisons were significant. Thus reversibility is only shown for two variables (see Table 5); while many comparisons met the first condition, and no comparison failed the second, most failed the third. Again, this may have changed could the experiment have been continued.

We can also ask about the speed of the effect, that is when it first appears in the sense of achieving a $P < 0.05$ at a particular census date (Fig. 10). P 's (used only as a descriptive measure) are two-tailed to maintain comparability; note that degrees of freedom (except for variations from inclusion of the covariate) are the same for all comparisons. *A. sagrei* density is the only variable to change (in its eventual overall direction) at the first census after inception; it achieves $P < 0.05$ 2 mo after introduction. The three spider variables follow over the next year, with the most common spider species' density affected 7 mo after introduction, then the number of all web spider species and their density at 12 and 19 mo. Thus the indirect effect on spiders lags behind the direct one on *A. sagrei* by about a year on average. Note that the same kind of lag is apparent for the island naturally invaded by *L. carinatus* (Fig. 12). Temporal differences in first detection of direct vs. indirect effects average somewhat larger here than do those found by Menge (1997) for the marine intertidal.

Large aerial arthropods first became more abundant on *L. carinatus* islands in November 1999, 7 mo after inception. The direction of this result is that expected were *A. sagrei* to link *L. carinatus* and large aerial arthropods. The result appears at the same time as the effect on the density of the most common spider species, and it has the same number of links (two). How-

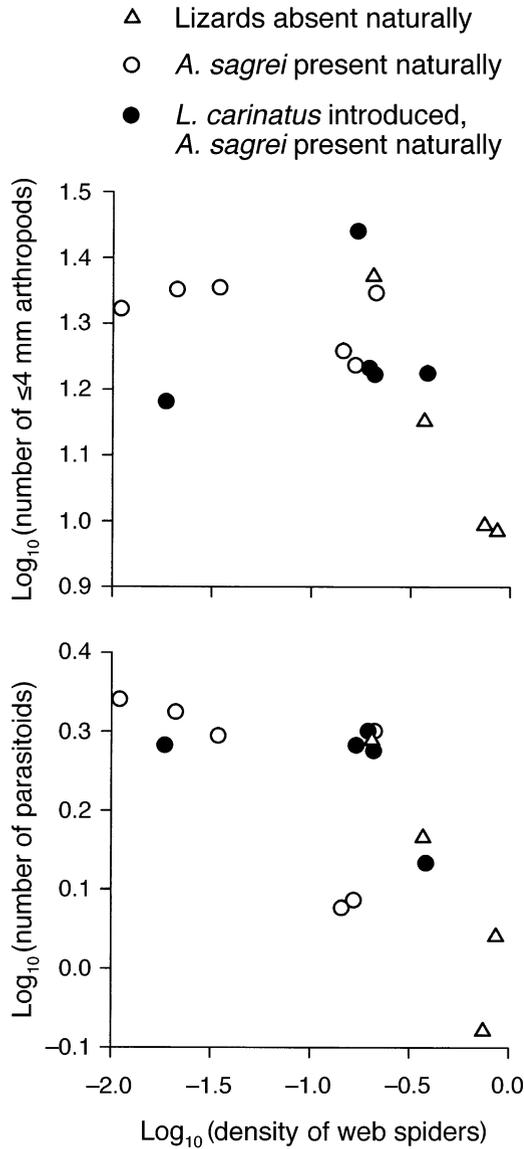


FIG. 11. The top panel shows a log-log plot of mean number of small (≤ 4 mm) arthropods per sticky trap (measured per day) vs. mean density of web spiders (number per square meter), 1997–1999 inclusive. Each point represents a separate island. The bottom panel shows a log-log plot of mean number of parasitoids per sticky trap (measured per day) vs. mean density of web spiders (number per square meter), 1997–1999 inclusive. Each point represents a separate island.

ever, the tendency did not remain, so time-average significance was not achieved (Table 4). The number of parasitoids also changed as if it were a two-link effect; this change, however, occurred only 2 mo after inception and eventually was reversed so should probably be discounted. In any event, Fig. 10 shows that (hypothetically) one-link effects (lizards) appear first, two-link effects (spiders, large aerial arthropods) appear next, and that three-link effects (small arthropods, leaf

damage) never appear. Thus despite the foreshortened experiment, the effect of the manipulation can be seen rather precisely to proceed down the food web over time.

Geometry of the food web

Fig. 13 gives a hypothetical food web for the system discussed here, based on a combination of experimental results and natural-history observations. When there was no evidence to the contrary, we parsimoniously assumed the smallest number of links (e.g., Fretwell 1977) consistent with the data.

To what extent do species appear to show single-

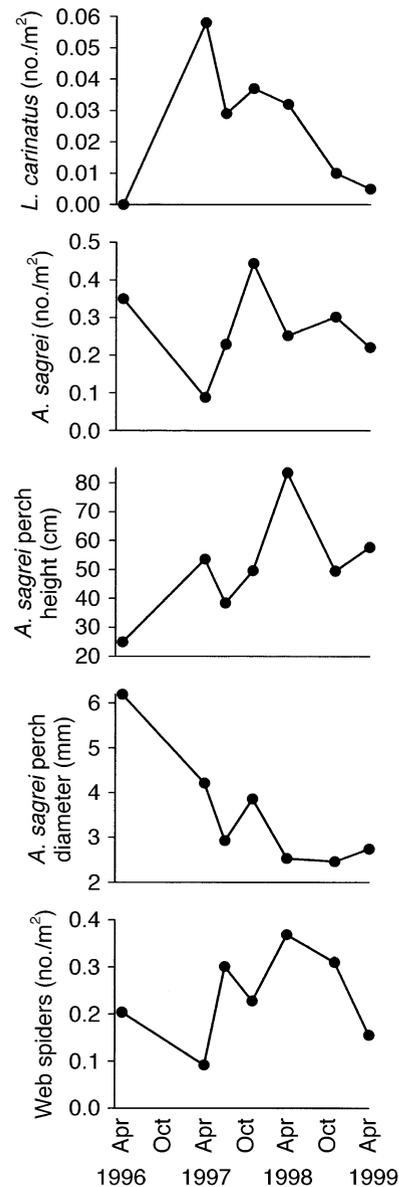


FIG. 12. History of the single island Z3, colonized naturally by *Leiocephalus carinatus* sometime between April 1996 and April 1997.

TABLE 5. Degree to which food-web effects of *A. sagrei* have been reversed by predation from *L. carinatus*.

Variable	Difference with and without <i>A. sagrei</i> †‡		Difference at start§	Difference at end (1998–1999)	
	Effect ratio	<i>P</i>		Effect ratio	<i>P</i>
Density all web-spider species†	5.57	0.005	0.546	2.55	0.035
Web-spider species (no.)†	2.14	0.009	0.417	1.89	0.049
Large (>4 mm) ground arthropods (no.)	4.36	0.038	0.888	1.63	0.415
Percentage leaf-mine damage	3.91	0.010	0.720	2.54	0.057
Percentage leaf-scar damage	1.58	0.008	0.123	1.03	0.380
Small (≤4 mm) aerial arthropods (no.)	1.44	0.019	0.559	1.29	0.142
Large (>4 mm) aerial arthropods (no.)	1.28	0.175	0.417	1.36	0.416
Percentage leaf-line damage	1.05	0.274	0.358	1.79	0.309
Percentage leaf-hole damage	1.10	0.391	0.588	1.08	0.499
Small (≤4 mm) ground arthropods (no.)	1.003	0.388	0.536	1.06	0.728

† Variables for which reversal is statistically documented (see *Discussion: Magnitude and speed of the food-web effects*).

‡ Treatment 1 vs. 2 (see Table 2).

§ Treatment 2 vs. 3.

|| Treatment 2 vs. 3 (see Table 4).

chain omnivory or intraguild predation, i.e., feed at several trophic levels? It is consistent with effect directions that *L. carinatus* affects all elements except large ground-surface arthropods via the intermediate lizard *A. sagrei*. Large ground-surface arthropods showed a strong comparative effect of *A. sagrei* (Tables 2 and 3) yet no sign of even the beginnings of a positive effect of the *L. carinatus* manipulation; indeed, numbers on introduction islands averaged ~60% controls (Fig. 2). Because *L. carinatus* is a large lizard that perches mostly near the ground, we might expect it to compensate for its reduction of *A. sagrei* by substituting for the latter as a predator of large ground-surface arthropods. In contrast, web spiders, some of which are large but which are mostly out of *L. carinatus*'s reach, show a positive effect of the latter.

Another place where the web in Fig. 13 shows omnivory is nearer the base, with respect to *A. sagrei*'s effect on aerial arthropods and plants. Although we could not demonstrate the full cascade (i.e., from *L. carinatus* on) here, previous experiments and observations (Spiller and Schoener 1996, Schoener and Spiller 1999b) show that the effect of *A. sagrei* on overall undamaged leaf surface is positive. Thus a major three-link pathway should extend from *L. carinatus* to plants, as the large predator affects *A. sagrei* greatly. However, complicating the main effect of *A. sagrei* on plants may be an extra link in the chain from *A. sagrei* to plants via small aerial arthropods. Were it operative, *A. sagrei* would have a negative, not positive effect on plants via that pathway. Indeed, the previous experiment at this site (Schoener and Spiller 1999a), which manipulated *A. sagrei*, showed an initially positive effect of *A. sagrei* on line damage, the latter produced at least in part by a small flea beetle that could conceivably be captured in spider webs or by other arthropod predators depressed by *A. sagrei*. While not occurring in the present study, the effect may be erratic

over time, kicking in and out so as to give little net tendency. Also in a previous study on sea grape, we found a significantly positive effect of *A. sagrei* on gall damage (Spiller and Schoener 1990b), produced by a midge. But its abundance fluctuated greatly, nearly disappearing in some years and frustrating our attempt to implicate the pathway experimentally (Spiller and Schoener 1994).

In conclusion, the *L. carinatus* food web has one and probably two reticulate portions complicating top-down effects. In addition to arguments (Yodzis 1988, Schoener 1993, Menge 1995, 1997, Abrams et al. 1996, *Introduction*) concerning the strength and timing of indirect effects as a function of their length (number of links), multiple pathways between two elements causing opposing effect directions may also result in effects being erratic and weak (Yodzis 1988, Schoener 1993, Schmitz 1997).

TABLE 6. Progression of effects on *A. sagrei*: time at which the first experimentally produced effect occurred, using two-tailed *P* at $\alpha = 0.05$ (treatment 2 vs. 3).

Variable	Time
Population density	July 1997
Perch height	July 1997
Perch diameter	April 1998
% hatchlings (<29 mm)	April 1999
sd log length all individuals	never
Adult ♂ body length	never
Adult ♂ body mass	never
Adult ♂ body condition	April 1998
Adult ♂ relative hindlimb length	never
Adult ♂ lamella number	never
All ♂ body length	April 1998
All ♂ body mass	April 1998
All ♂ body condition	never
♀ body length	never
♀ body mass	never
♀ body condition	never

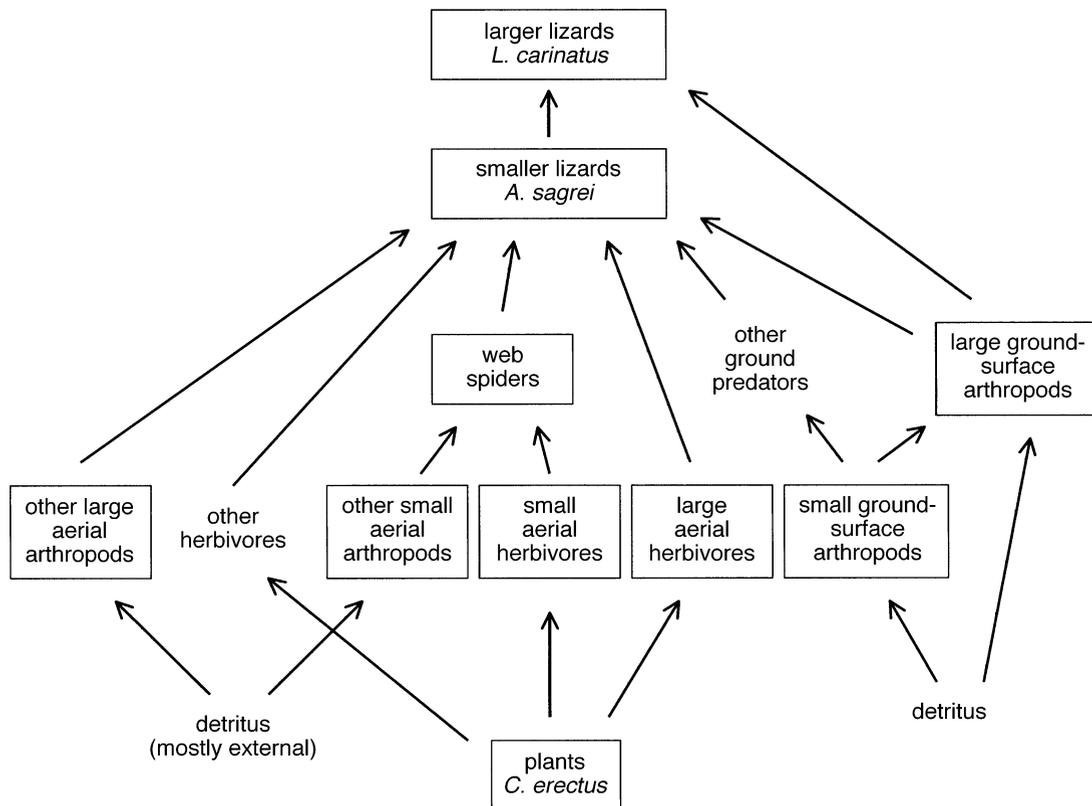


FIG. 13. Partial food web for the study islands. Components in rectangles were monitored in this study. Arrows indicate direct consumption. The web is a “working hypothesis” (see *Discussion: Geometry*).

Magnitude and speed of the effects of L. carinatus introduction on traits of the smaller lizard A. sagrei

Experimental introduction of the large lizard *L. carinatus* had immediate effects on *A. sagrei*: two months after inception (July 1997), the density of *A. sagrei* went from near parity to about half the control mean. Presumably, this resulted mainly from direct mortality, although emigration is possible, as it has been produced experimentally in *A. sagrei* placed on very small islands (Schoener and Schoener 1983). Change in relative perch height was rather surprisingly even more dramatic; while controls maintained the same value, *A. sagrei* moved substantially higher on introduction islands (Fig. 5). Thus a major habitat shift took place concomitantly with a major (relative) reduction in population size. This is in contrast to another predator-induced habitat shift, that of grasshoppers in the experiments of Beckerman et al. (1997). Whether using “risk” spiders (individuals modified so they were unable to consume prey) or unmodified predatory spiders, grasshoppers lost ~25% of their energy intake as a result of a dietary/habitat shift in their food; no significant population-density differences with the two kinds of predators were detectable, so that mortality was from factors other than direct predation.

Despite the shift upward, *A. sagrei* had $P > 0.05$ for

perch diameter at the July 1997 census (Fig. 5). It is as if individuals ascended trees but mostly stayed on or near the main trunk rather than went to the outer branches. However, as mean perch height continued to shift upward (which it did continuously and almost linearly to the end of the experiment), perch-diameter differences broadened; $P < 0.05$ first in April 1998, a year after inception. Diameter effects, like those of perch height, increased until the end. In contrast, difference in density of *A. sagrei* leveled off after July 1997 (Fig. 5). Perhaps the habitat shift was for a while effective in preventing further substantial losses to the *A. sagrei* population via predation from *L. carinatus*.

Differences in demographic traits other than population size lagged somewhat behind behavioral traits in time of first appearance. Percentage hatchlings (snout-vent < 29 mm) is very phenologically variable, peaking during late summer/early fall (Fig. 5). *A. sagrei* apparently has seasonal reproduction at the study site. Both Lee et al.’s (1989) and Licht and Gorman’s (1970) data from Florida, the same latitude as the northern Bahamas, showed a reduced reproductive state in the fall. The few Bahamian specimens available to Licht and Gorman (from south of our study site) showed complete testicular regression in October and substantial reversal by April–June. Thus a treatment effect is

somewhat masked by the large natural variation in reproduction already taking place. Nonetheless, $P < 0.05$ was finally achieved in April 1999 (Table 6). Partly related to the change in the proportion of hatchlings, the width (SD) of the length distribution estimated from sight records for the entire population (smaller lizards could not be sexed visually) also diminished, but more subtly: while the 1998–1999 timed average was different (raw $P = 0.011$), no individual census gave $P < 0.05$. As Fig. 6 suggests, the reduction in size breadth is due to a relative reduction of the largest as well as the smallest individuals.

This result is only partially supported by measurements of captured individuals, measurements that were more precise yet of smaller samples. Only the class “all males” (≥ 34 mm, so not including hatchlings) gave $P < 0.05$ (for a size reduction) in any census (April 1998; Table 6), and overall time averages were not significantly different for either male class. Theoretical expectations for percentage hatchlings and overall size distributions may not be the same. Clearly, a tiny hatchling is an easy mouthful for the large *L. carinatus*, whose head size is not that different from its entire snout–vent length. Thus direct predation can account for the foreshortening of the left tail of the size distribution. But the expected net effect on the largest sizes is less clear. Males might increase in boldness as they grow and therefore be more conspicuous and ultimately vulnerable. Alternatively, their greater size may imply the opposite, allowing “escape in size” from predation, and if this were the only factor, larger lizards should predominate. Indirect effects on size may also operate. If energy intake were curtailed, perhaps because of an increased awkwardness in feeding on the thin, high twigs of their new habitat (Losos and Sinervo 1989), then individuals may grow to smaller sizes than in the absence of the large predator. On the other hand, prey may tend to increase size under non-selective predation via an indirect effect on their food supply (Abrams and Rowe 1996).

If overall size is reduced because of low feeding intake, this should also reduce condition, i.e., mass relative to length. To test for this, we ran log–log regressions on the two variables and calculated residuals. Only results for adult males were significant (Table 3); the first $P < 0.05$ appeared a year after manipulation (Table 6, Fig. 7). Hence an effect on lizards via their energy intake (or less likely their energy expenditure) is implicated.

Perhaps least expected to change over our time span are the morphological traits, relative hindlimb length and number of lamellae. While the latter showed no significant effects, we were surprised that relative hindlimb length did show a significant time-average difference (Table 3), albeit only for the first method of computing residuals and only when X10 (with one adult male in 1998 and none in 1999) was excluded. The plot (Fig. 8) shows that relative hindlimb length was

initially lower on experimentals than controls, but it became gradually higher. The change is perhaps visually not as much as expected for statistical significance, but note the latter was achieved using a covariate (1997 value on each island), and that on average 1997 values were lower on control islands than islands to be invaded. This initial difference was itself probably not random, but rather was due to what appears to be an adaptation to differences in time spent on the ground, the latter to some extent related to percentage vegetated area of the island (*Results*). Specifically, populations on islands whose members used the ground more frequently had significantly longer relative hindlimbs (Fig. 9). This startling discovery fits well with what we know about lizard movement: the greater the relative hindlimb length, the more rapidly lizards can move on the ground, both intraspecifically and interspecifically (Losos 1990, Garland and Losos 1994, Kohlsdorf et al. 2001). If we accept that there was a change toward relatively longer legs on introduction islands, an inevitable hypothesis is that it resulted from selection (mortality) against short-legged, slower lizards, because *L. carinatus* is rarely found away from the ground and must catch nearly all of its prey there.

While the results just reviewed are consistent, a priori we expected that relative hindlimb length would become smaller, not larger, on introduction islands! We reasoned that this change would follow the habitat shift onto perches of smaller diameter (and away from the ground, whose surface should functionally be equivalent to a very large-diametered horizontal branch). Indeed, in another study we found that *A. sagrei* experimentally introduced onto small islands with scrubby vegetation than their island of origin came to have relatively shorter hindlimbs, the more so the scrubby the vegetation (Losos et al. 1997). We interpreted these differences as resulting from smaller perch diameters on scrubby islands and later (Losos et al. 2000) were able to reproduce them by raising lizards in artificial environments varying in perch diameter. Moreover, the experimentally produced differences paralleled in both magnitude and direction those found between populations of *A. sagrei* throughout the Bahamas (Losos et al. 1994), although between-species differences are much larger (Williams 1983, Losos et al. 2000). Perhaps differences in hindlimb length of lizards in the present experiment would have shifted toward the other direction as time went on, but its abrupt termination prevented us from knowing.

Despite that termination, we were still able to get a partial picture of the progression of trait changes with time according to the likely mechanism—behavioral, physiological, demographic, and developmental/evolutionary. Table 6 shows that behavioral traits were first to appear, although one demographic variable, population density, also became different very early. Another demographic variable, percentage hatchlings, appeared later. Those morphological variables that showed an effect, and

most had not by the end of the experiment, appeared about midway through the experiment (although most were unable to be measured earlier). Of these, body condition is much more likely to result from physiological than evolutionary or even developmental mechanisms, so changes here are expected to be short term. Body size (length, mass) is a combination of physiological, demographic, and perhaps developmental/evolutionary mechanisms, so short-term changes are not unexpected. In contrast, changes in relative limb length may be long term if evolutionary, but they could be short term under severe initial differential mortality or major developmental effects (e.g., Losos et al. 2000). Because statistical conclusions for this variable depend on the method of computing residuals and whether an outlier is excluded or not, the existence of this change is presently best viewed as ambiguous.

Presence and absence of habitat shift as a result of changes in predator abundance

This experiment produced a striking contrast in the degree to which changes in the predatory regime caused behavioral changes favoring prey escape. In the lizard *A. sagrei*, the introduction of a large predator caused a major shift upward and onto thinner perches. Although interspecific competition has been shown or suggested to cause such habitat shift in other *Anolis* (Jenssen 1973, Schoener 1975, Pacala and Roughgarden 1985, Losos 1994) and may be partially operative here, the initial rapid population drop and differential loss of hatchlings implicates predation as the primary mechanism. The effect of predation likely involved more than just the differential mortality of individuals that behaved "incorrectly," because it continued after differences in population density had stabilized. Very probably, individual *A. sagrei* lizards were learning how to avoid the large predatory lizards as time went on. In contrast to *A. sagrei*, the most common spider species *E. cazieri* showed little tendency to alter its habitat (web height) as the abundance and positioning of a principal predator, *A. sagrei*, changed. A previous experiment (Spiller and Schoener 2001) in which *A. sagrei* was directly manipulated also failed to produce a habitat shift in *E. cazieri*. Overall, the difference between the invertebrate and vertebrate is striking, and relative cognitive abilities may provide an explanation.

A consequence of the habitat shift in *A. sagrei* going on well after population differences leveled off is that this predator may change how it affects prey even after its own density stabilizes, i.e., the additional effect then becomes "trait-mediated" (Abrams 1995, Beckerman et al. 1997) rather than "density-mediated." Here, the increasingly greater arboreality of *A. sagrei* may have resulted in more web spiders being consumed per predator individual; this could compensate for *A. sagrei*'s population drop. Then treatment differences in spider abundance should decrease after differences in their predators' abundance stabilized. We have no way to test this except by data inspection, but the tendency

exists, both in plots of treatment means (Fig. 2) and in the plot of the naturally colonized island Z3 (Fig. 12). A similar argument could be made for why the introduction produced no change in foliage damage: per capita consumption of folivores may have increased because of the habitat shift.

General impact of Anolis lizards on food webs

Do the major effects of *L. carinatus* on *A. sagrei* found here suggest that effects of *sagrei* or other *Anolis* are likely to be small in complex communities, which likely have numerous predators? Since the greater portion of land mass occupied by *Anolis* species is probably in this category, even in the Caribbean, the question is significant. The best way to find out is to do experiments in the complex communities, such as on the large islands of the Greater Antilles or in Central America. Only one experiment so far, however, has determined the effect of *Anolis* removal on lower food-web elements at a very-large-island site, that of Dial and Roughgarden (1995) in Puerto Rico. Quite astonishingly, virtually the same set of food-web effects obtained for *A. sagrei* in simpler communities appeared in this more complex one. Lizards had strong negative effects on large arthropods; orb spiders were substantially affected, among others; small arthropods were more abundant with lizards but differences were not significant. Leaf damage was significantly greater in the lizard-removal "plots" than in controls. In view of this similarity, one might ask if there is something about predators of *Anolis* that make them ineffective in general as agents of control or even of substantial influence?

A suitable place to begin exploring this question is at the site of the present experiment, where major predatory effects upon *Anolis* were produced. The arena consisted of rather small islands, but still of an area at which the manipulated predator, *L. carinatus*, sometimes colonizes naturally. Such natural colonizations are obviously somewhat rare, or else not enough *Leiocephalus*-free islands would have been available to do the experiment. Colonizations may also not typically be long-lasting: the one observed on Z3 was on its way out, having one individual at the last census before the hurricane drowned everything. Our attempts to establish *L. carinatus* suggest an even shorter persistence time of colonizing populations. Rather than simulate colonizations, with replicated successes and failures, however, our goal was to simulate a substantial (but natural) level of *L. carinatus*. Thus persistence of *L. carinatus* on some islands was artificially enhanced. In a sense, the hurricane's abrupt termination of our experiment may have contributed to its naturalness, in that its time span may have been that of a typical *L. carinatus* colonization episode. Hence that *L. carinatus* may not have had time to extend its effects over the entire breadth of the food web, i.e., to small aerial arthropods and plants, but only had detectable effects

over short numbers of links, may be natural. Put another way, large predators that cannot maintain colonizing populations on small pieces of land will only show direct and shorter chained indirect effects when substantial time is needed for the longer chained indirect effects to appear.

But most of the land mass on which the two lizards occur consists of islands larger than the study islands. In addition to island size, however, *L. carinatus* may also be limited by habitat. This large ectotherm prefers open, rocky areas, and it is rare where *A. sagrei* occurs, even on the main island of Great Abaco where *A. sagrei* densities can be huge (Schoener 1975, Schoener and Schoener 1980; T. W. Schoener, unpublished data). Thus the influence of *L. carinatus* may be marginal, literally as well as figuratively, on the main island, mainly influencing *A. sagrei* at the edges of the latter's most abundantly occupied habitat. Experimental removals of *L. carinatus* along a gradient of its occurrence would be quite interesting.

Many kinds of organisms other than lizards can eat *Anolis*, e.g., birds (Adolph and Roughgarden 1983, McLaughlin and Roughgarden 1989, Roughgarden 1995), snakes (Henderson 1984, Henderson et al. 1987, Henderson and Crother 1989), and rats (T. W. Schoener, personal observation). Are any of those likely to reverse food-web effects of *Anolis*? Elsewhere in the Bahamas, *Anolis* lizards had greater mortality rates on two large islands, Great Abaco and Andros, than on the smaller island of Bimini (Schoener and Schoener 1978, 1980); the former have double the list of resident land birds, including some potential predators of *Anolis*. The weakening of *Anolis*'s food-web effects with increasing island size is inferential evidence that predators of *Anolis* may be involved, although there are other explanations: compensation by other predators of the prey of anoles and more refugia for those prey on larger islands (Spiller and Schoener 1998, Schoener and Spiller 1999b). Moreover, the results of Dial and Roughgarden in Puerto Rico, despite the panoply of potential predators, were at least qualitatively similar to ours. Possibly very large predators are more often than not patchy and erratic in their influence, so that intermediate predators are the more encompassing and reliable in their effects.

Conclusion: can the effects of a devastating predator be reversed by the introduction of a yet-higher predator?

This experiment investigated whether introduction of a large predator, *L. carinatus*, could reverse the effects, some major, of the intermediate predator, *A. sagrei*. The answer depended upon how strong the effects of the intermediate predator were, how indirect (in numbers of links) the effects were, and the degree of omnivory of the large predator. One component, web spiders, affected strongly and (mostly) directly by the intermediate predator, had those effects substantially

reversed. Another component, large ground arthropods, are eaten both by the large predator as well as by the intermediate predator; the apparent compensation caused no significant effect on that component. Other food-web components, weakly and/or more indirectly affected by the intermediate predator, were not significantly affected during the time available for the manipulation. Were the experiment not to have been interrupted, they might have been, but if actual colonization episodes of the large predator are of the time scale of the present experiment, they will not be much affected under natural conditions. The large predator was extremely effective in suppressing the intermediate predator, affecting the latter's population size quickly as well as its behavior both quickly and continuously to the end of the experiment. Hatchlings were differentially reduced, and body condition, among other variables, was reduced as well. For some islands, we had to reintroduce some individuals of the large predator 1–3 times; thus behaviorally *L. carinatus* was equipped to suppress the effects of the intermediate predator, but it was unable to build to a steady state on all islands without this artificial help. Large predators in general may be maintained only with difficulty in small areas at stable population sizes (Schoener 1989), even on a main island if habitat patchiness is involved. Indeed, this may follow from the very nature of a top predator, marginally viable in any given place and perhaps sustained through metapopulational migration (e.g., Hastings 1972, 1978, Hanski 1999). For such a system, a theory of transitory states is more appropriate than equilibrium theory, but such theory is presently far less developed (Yodzis 1989). In short, the possibly erratic distribution of large predators in space and time may be a general factor contributing to their inadequacy in reversing completely the effects of intermediate predators. More study, both empirical and theoretical, of this general proposition is needed.

ACKNOWLEDGMENTS

We thank NSF for support and the reviewers and editor for very helpful comments.

LITERATURE CITED

- Abrams, P. A. 1995. Implications of dynamically variable traits for identifying, classifying, and measuring indirect effects in ecological communities. *American Naturalist* **146**:112–134.
- Abrams, P. A., B. A. Menge, G. G. Mittelbach, D. A. Spiller, and P. Yodzis. 1996. The role of indirect effects in food webs. Pages 371–395 in G. A. Polis and K. O. Winemiller, editors. *Food webs: integration of pattern and dynamics*. Chapman and Hall, New York, New York, USA.
- Abrams, P. A., and L. Rowe. 1996. The effects of predation on the age and size of maturity of prey. *Evolution* **50**:1052–1061.
- Adolph, S., and J. Roughgarden. 1983. Foraging by passerine birds and *Anolis* lizards on St. Eustatius, Lesser Antilles: implications for interclass competition and predation. *Oecologia* **56**:313–317.
- Bauwens, D., T. Garland, Jr., A. M. Castilla, and R. Van Damme. 1995. Evolution of sprint speed in lacertid lizards:

- morphological, physiological and behavioral covariation. *Evolution* **49**:848–863.
- Beckerman, A. P., M. Uriarte, and O. J. Schmitz. 1997. Experimental evidence for a behavior-mediated trophic cascade in a terrestrial food chain. *Proceedings of the National Academy of Sciences (USA)* **94**:10735–10738.
- Bender, E. A., T. J. Case, and M. E. Gilpin. 1984. Perturbation experiments in community ecology: theory and practice. *Ecology* **65**:1–13.
- Bonine, K. E., and T. Garland. 1999. Sprint performance of phrynosomatid lizards, measured on a high-speed treadmill, correlates with hindlimb length. *Journal of the Zoological Society of London* **248**:255–265.
- Brett, M. T., and C. R. Goldman. 1996. A meta-analysis of the freshwater trophic cascade. *Proceedings of the National Academy of Sciences (USA)* **93**:7723–7726.
- Chase, J. M. 1996. Abiotic controls of trophic cascades in a simple grassland food chain. *Oikos* **77**:495–506.
- Dial, R., and J. Roughgarden. 1995. Experimental removal of insectivores from rain forest canopy: direct and indirect effects. *Ecology* **76**:1821–1834.
- Endler, J. A. 1980. Natural selection on color patterns in *Poecilia reticulata*. *Evolution* **34**:76–91.
- Fienberg, S. E. 1972. The multiple-recapture census. *Biometrika* **45**:591–603.
- Fretwell, S. D. 1977. Food chain dynamics: the central theory of ecology? *Oikos* **50**:291–301.
- Garland, T., Jr., and J. B. Losos. 1994. Ecological morphology of locomotor performance in squamate reptiles. Pages 240–302 in P. C. Wainwright and S. Reilly, editors. *Ecological morphology: integrative organismal biology*. University of Chicago Press, Chicago, Illinois, USA.
- Glossip, D., and J. B. Losos. 1997. Ecological correlates of number of subdigital lamellae in anoles. *Herpetologica* **53**:192–199.
- Goel, N. S., and N. Richter-Dyn. 1974. *Stochastic models in biology*. Academic Press, New York, New York, USA.
- Goldberg, D. E., T. Rajaniemi, J. Gurevitch, and A. Stewart-Oaten. 1999. Empirical approaches to quantifying interaction intensity: competition and facilitation along productivity gradients. *Ecology* **80**:1118–1131.
- Halaj, J., and D. H. Wise. 2001. Terrestrial trophic cascades: how much do they trickle? *American Naturalist* **157**:262–281.
- Hanski, I. 1999. *Metapopulation ecology*. Oxford University Press, Oxford, UK.
- Harrison, G. W. 1995. Comparing predator–prey models to Luckinbill's experiment with *Didinium* and *Paramecium*. *Ecology* **76**:357–374.
- Hastings, A. 1972. Spatial heterogeneity and the stability of predator–prey systems. *Theoretical Population Biology* **12**:37–48.
- Hastings, A. 1978. Spatial heterogeneity and the stability of predator–prey systems: predation-mediated coexistence. *Theoretical Population Biology* **14**:380–395.
- Heckel, D. G., and J. Roughgarden. 1979. A technique for estimating the size of lizard populations. *Ecology* **60**:966–975.
- Hedges, L. V., J. Gurevitch, and P. Curtis. 1999. The meta-analysis of response ratios in experimental ecology. *Ecology* **80**:1150–1156.
- Henderson, R. W. 1984. The diets of Hispaniolan colubrid snakes. I. Introduction and prey genera. *Oecologia* **62**:234–239.
- Henderson, R. W., and B. I. Crother. 1989. Biogeographic patterns of predation in West Indian colubrid snakes. Pages 479–517 in C. A. Woods, editor. *Biogeography of the West Indies: past, present and future*. Sandhill Crane Press, Gainesville, Florida, USA.
- Henderson, R. W., A. Schwartz, and T. A. Noeske-Hallin. 1987. Food habits of three colubrid tree snakes (genus *Uromacer*) on Hispaniola. *Herpetologica* **43**:241–248.
- Hoening, J. M., and M. Heisey. 2001. The abuse of powers: the pervasive fallacy of power calculations for data analysis. *American Statistician* **55**:19–24.
- Holt, R. D. 1987. Prey communities in patchy environments. *Oikos* **50**:276–290.
- Holt, R. D., and J. H. Lawton. 1994. The ecological consequences of shared natural enemies. *Annual Review of Ecology and Systematics* **25**:495–520.
- Hunter, M. D., and P. W. Price. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* **72**:724–732.
- Irschick, D. J., and B. C. Jayne. 1999. Comparative three-dimensional kinematics of the hindlimb for high-speed bipedal and quadrupedal locomotion of lizards. *Journal of Experimental Biology* **202**:1047–1065.
- Jenssen, T. 1973. Shift in the structural habitat of *Anolis opalinus* due to congeneric competition. *Ecology* **54**:863–869.
- Kohlsdorf, T., T. Garland, Jr., and C. A. Navas. 2001. Limb and tail length in relation to substrate usage in *Tropidurus* lizards. *Journal of Morphology* **248**:151–164.
- Lee, J. C., D. Clayton, S. Eisenstein, and H. Perez. 1989. The reproductive cycle of *Anolis sagrei* in southern Florida. *Copeia* 1989:930–937.
- Licht, P., and G. C. Gorman. 1970. Reproductive and fat cycles in Caribbean *Anolis* lizards. University of California Publications in Zoology **95**:1–52.
- Lister, B. C. 1976. The nature of niche expansion in West Indian *Anolis* lizards II: evolutionary components. *Evolution* **30**:677–692.
- Littell, R. C., R. J. Freund, and P. C. Spector. 1991. SAS system for linear models. SAS Institute, Cary, North Carolina, USA.
- Losos, J. B. 1990. Ecomorphology, performance capability, and scaling of West Indian *Anolis* lizards: an evolutionary analysis. *Ecological Monographs* **60**:369–388.
- Losos, J. B. 1994. Integrative approaches to evolutionary ecology: *Anolis* lizards as model systems. *Annual Review of Ecology and Systematics* **25**:467–493.
- Losos, J. B., D. A. Creer, D. Glossip, R. Goellner, A. Hampton, G. Roberts, N. Haskell, P. Taylor, and J. Ettlting. 2000. Evolutionary implications of phenotypic plasticity in the hindlimb of the lizard *Anolis sagrei*. *Evolution* **54**:301–305.
- Losos, J. B., D. J. Irschick, and T. W. Schoener. 1994. Adaptation and constraint in the evolution of specialization of Bahamian *Anolis* lizards. *Evolution* **48**:1786–1798.
- Losos, J. B., T. W. Schoener, K. I. Warheit, and D. Creer. *In press*. Experimental studies of adaptive differentiation in *Anolis* lizards. *Genetica*.
- Losos, J. B., and B. Sinervo. 1989. The effects of morphology and perch diameter on sprint performance in *Anolis* lizards. *Journal of Experimental Biology* **145**:23–30.
- Losos, J. B., K. I. Warheit, and T. W. Schoener. 1997. Adaptive differentiation following experimental island colonization in *Anolis* lizards. *Nature* **387**:70–73.
- McLaughlin, J. F., and J. Roughgarden. 1989. Avian predation on *Anolis* lizards in the northeastern Caribbean: an inter-island contrast. *Ecology* **70**:617–628.
- McPeck, M. A. 1995. Morphological evolution mediated by behavior in the damselflies of two communities. *Evolution* **49**:749–769.
- Menge, B. A. 1995. Indirect effects in marine rocky intertidal interaction webs: patterns and importance. *Ecological Monographs* **65**:21–74.
- Menge, B. A. 1997. Detection of direct versus indirect effects: were experiments long enough? *American Naturalist* **149**:802–823.

- Mittelbach, G. G., and P. L. Chesson. 1987. Predation risk: indirect effects in fish populations. Pages 315–332 in C. W. Kerfoot and A. Sih, editors. *Predation: direct and indirect impacts on aquatic communities*. University Press of New England, Hanover, New Hampshire, USA.
- Morin, P. J. 1999. *Community ecology*. Blackwell, Oxford, UK.
- Neter, J. M., H. Kutner, C. J. Nachsheim, and W. Wasserman. 1996. *Applied linear statistical models*. WCB McGraw-Hill, New York, New York, USA.
- Osenberg, C. W., O. Sarnelle, and S. D. Cooper. 1997. Effect size in ecological experiments: the application of biological models in meta-analysis. *American Naturalist* **150**:798–812.
- Osenberg, C. W., O. Sarnelle, S. D. Cooper, and R. D. Holt. 1999. Resolving ecological questions through meta-analysis: goals, metrics, and models. *Ecology* **80**:1105–1119.
- Pacala, S. W., and J. Roughgarden. 1985. Population experiments with the *Anolis* lizards of St. Maarten and St. Eustatius. *Ecology* **66**:129–141.
- Pace, M. L., J. J. Cole, S. R. Carpenter, and J. F. Kitchell. 1999. Trophic cascades revealed in diverse ecosystems. *Trends in Ecology and Evolution* **14**:483–488.
- Peacor, S. D., and E. E. Werner. 2001. The contribution of trait-mediated indirect effects to the net effects of a predator. *Proceedings of the National Academy of Sciences (USA)* **98**:3904–3908.
- Pimm, S. L. 1982. *Food webs*. Chapman and Hall, London, UK.
- Pimm, S. L., H. L. Jones, and J. Diamond. 1988. On the risk of extinction. *American Naturalist* **132**:757–785.
- Polis, G. A., C. A. Myers, and R. D. Holt. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annual Review of Ecology and Systematics* **20**:297–330.
- Polis, G. A., and D. R. Strong. 1996. Food web complexity and community dynamics. *American Naturalist* **147**:813–846.
- Rosenzweig, M. L. 1995. *Species diversity in space and time*. Cambridge University Press, Cambridge, UK.
- Roughgarden, J. 1995. *Anolis lizards of the Caribbean*. Oxford University Press, New York, New York, USA.
- SAS. 1999. SAS Online Doc, version 8. SAS Institute, Cary, North Carolina, USA.
- Schmitz, O. J. 1992. Exploitation in model food webs with mechanistic consumer-resource dynamics. *Theoretical Population Biology* **41**:161–183.
- Schmitz, O. J. 1993. Trophic exploitation in grassland food webs: simple models and a field experiment. *Oecologia* **93**:327–335.
- Schmitz, O. J. 1997. Press perturbations and the predictability of ecological interactions in a food web. *Ecology* **78**:55–69.
- Schmitz, O. J., P. A. Hamback, and A. P. Beckerman. 2000. Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. *American Naturalist* **155**:141–153.
- Schoener, T. W. 1967. The ecological significance of sexual dimorphism in size in the lizard *Anolis conspersus*. *Science* **155**:474–477.
- Schoener, T. W. 1968. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. *Ecology* **49**:704–726.
- Schoener, T. W. 1971. Theory of feeding strategies. *Annual Review of Ecology and Systematics* **2**:369–404.
- Schoener, T. W. 1975. Presence and absence of habitat shift in some widespread lizard species. *Ecological Monographs* **45**:233–258.
- Schoener, T. W. 1977. Competition and the niche. Pages 35–136 in C. Gans and D. Tinkle, editors. *Biology of the Reptilia*. Volume 7, Chapter 2. Academic Press, London, UK.
- Schoener, T. W. 1987. Leaf pubescence in buttonwood: community variation in a putative defense against defoliation. *Proceedings of the National Academy of Sciences (USA)* **84**:7992–7995.
- Schoener, T. W. 1988. Leaf damage in island buttonwood, *Conocarpus erectus*: correlations with pubescence, island area, isolation and the distribution of major carnivores. *Oikos* **53**:253–266.
- Schoener, T. W. 1989. Food webs from the small to the large. *Ecology* **70**:1559–1589.
- Schoener, T. W. 1993. On the relative importance of direct versus indirect effects in ecological communities. Pages 365–411 in H. Kawanabe, J. E. Cohen, and K. Iwasaki, editors. *Mutualism and community organization: behavioral, theoretical and food web approaches*. Oxford University Press, Oxford, UK.
- Schoener, T. W., and G. C. Gorman. 1968. Some niche differences among three species of Lesser Antillean anoles. *Ecology* **49**:819–830.
- Schoener, T. W., and A. Schoener. 1978. Inverse relation of survival of lizards with island size and avifaunal richness. *Nature* **274**:365–381.
- Schoener, T. W., and A. Schoener. 1980. Densities, sex ratios, and population structure in four species of Bahamian *Anolis* lizards. *Journal of Animal Ecology* **49**:19–53.
- Schoener, T. W., and A. Schoener. 1983. On the voluntary departure of lizards from very small islands. Pages 491–498 in A. G. J. Rhodin and K. Miyata, editors. *Advances in herpetology and evolutionary biology*. Harvard University Press, Cambridge, Massachusetts, USA.
- Schoener, T. W., J. B. Slade, and C. H. Stinson. 1982. Diet and sexual dimorphism in the very catholic lizard genus *Leiocephalus* of the Bahamas. *Oecologia* **53**:160–169.
- Schoener, T. W., and D. A. Spiller. 1992. Is extinction rate related to temporal variability in population size? An empirical answer for orb spiders. *American Naturalist* **139**:1176–1207.
- Schoener, T. W., and D. A. Spiller. 1996. Devastation of prey diversity by experimentally introduced predators in the field. *Nature* **381**:691–694.
- Schoener, T. W., and D. A. Spiller. 1999a. Indirect effects in an experimentally staged invasion by a major predator. *American Naturalist* **153**:347–358.
- Schoener, T. W., and D. A. Spiller. 1999b. Variation in the magnitude of a predator's effect from small to large islands. Pages 35–66 in *Monografies de la societat d'història natural de les balears 6: Ecologia de les illes*. Gràfiques Miramar, S. A., Palma, Spain.
- Schoener, T. W., D. A. Spiller, and L. W. Morrison. 1995. Variation in the hymenopteran parasitoid fraction on Bahamian islands. *Acta Oecologica* **16**:103–121.
- Schwartz, A., and R. W. Henderson. 1991. *Amphibians and reptiles of the West Indies*. University of Florida Press, Gainesville, Florida, USA.
- Sih, A. 1980. Optimal behavior: can foragers balance two conflicting demands? *Science* **210**:1041–1043.
- Sih, A., and B. Christensen. 2001. Optimal diet theory: when does it work, and when does it fail? *Animal Behavior* **61**:379–390.
- Sih, A., P. Crowley, M. McPeck, J. Petranka, and K. Strohmeier. 1985. Predation, competition, and prey communities: a review of field experiments. *Annual Review of Ecology and Systematics* **16**:269–311.
- Spiller, D. A., and T. W. Schoener. 1990a. A terrestrial field experiment showing impact of eliminating top predators on foliage damage. *Nature* **347**:469–472.
- Spiller, D. A., and T. W. Schoener. 1990b. Lizards reduce food consumption by spiders: mechanisms and consequences. *Oecologia* **83**:150–161.
- Spiller, D. A., and T. W. Schoener. 1994. Effects of top and

- intermediate predators in a terrestrial food web. *Ecology* **75**:182–196.
- Spiller, D. A., and T. W. Schoener. 1995. Long-term variation in effect of lizards on spider density is linked to rainfall. *Oecologia* **103**:133–139.
- Spiller, D. A., and T. W. Schoener. 1996. Food web dynamics on some small subtropical islands: effects of top and intermediate predators. Pages 160–169 in G. A. Polis and K. O. Winemiller, editors. *Food webs: integration of pattern and dynamics*. Chapman and Hall, New York, New York, USA.
- Spiller, D. A., and T. W. Schoener. 1997. Folivory on islands with and without insectivorous lizards: an eight-year study. *Oikos* **78**:15–22.
- Spiller, D. A., and T. W. Schoener. 1998. Lizards reduce spider species richness by excluding rare species. *Ecology* **79**:503–516.
- Spiller, D. A., and T. W. Schoener. 2001. An experimental test for predator-mediated interactions among spider species. *Ecology* **82**:1560–1570.
- Stephens, D. W., and J. R. Krebs. 1986. *Foraging theory*. Princeton University Press, Princeton, New Jersey, USA.
- Strong, D. R. 1992. Are trophic cascades all wet? The redundant differentiation in trophic architecture of high diversity ecosystems. *Ecology* **73**:747–754.
- Van Buskirk, J., and S. A. McCollum. 2000. Functional mechanisms of an inducible defense in tadpoles: morphology and behavior influence mortality risk from predation. *Journal of Evolutionary Biology* **13**:336–347.
- Williams, E. E. 1983. Ecomorphs, faunas, island size, and diverse end points in island radiations of *Anolis*. Pages 326–370 in R. B. Huey, E. R. Pianka, and T. W. Schoener, editors. *Lizard ecology: studies of a model organism*. Harvard University Press, Cambridge, Massachusetts, USA.
- Yodzis, P. 1988. The indeterminacy of ecological interactions as perceived through perturbation experiments. *Ecology* **69**:508–515.
- Yodzis, P. 1989. *Introduction to theoretical ecology*. Harper and Row, New York, New York, USA.