

DIFFERENTIAL COLONIZATION SUCCESS AND ASYMMETRICAL INTERACTIONS BETWEEN TWO LIZARD SPECIES

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Abstract. Small islands in the Bahamas often do not contain *Anolis* lizards. We took an experimental approach to investigate whether absence of *A. carolinensis* and *A. sagrei* from these islands results from the inability of populations to become established and whether the presence of the other species has a negative effect on population density and probability of successful colonization. We introduced propagules of five lizards of each species, either in allopatry or sympatry, on five blocks of three islands each. Populations were censused yearly using mark–recapture methods. *Anolis sagrei* populations thrived on almost all islands, whereas within three years, many *A. carolinensis* populations had gone extinct, and most others were very small. We conclude that an inability to successfully establish populations on small islands might explain the absence of *A. carolinensis* from these islands, but not the absence of *A. sagrei*. *Anolis carolinensis* was not more likely to become extinct on islands containing *A. sagrei*, but population densities of *A. carolinensis* were lower on islands with both species (“sympatric islands”) compared to “allopatric islands.” In addition, *A. carolinensis* tended to perch higher, relative to available vegetation, on sympatric islands than they did on allopatric islands. Conversely, the presence of *A. carolinensis* had little impact on *A. sagrei* populations. However, inspection of population changes through time suggest that *A. carolinensis* may have initially had an effect on *A. sagrei*, but this effect decreased as *A. carolinensis* populations declined. The observed absence of *A. sagrei* from these islands may indicate that its dispersal abilities are limited relative to the frequency of devastating hurricanes.

Key words: *Anolis*; asymmetrical competition vs. intraguild predation; Bahamas, central; colonization success vs. interspecific competition; field experiment; habitat use; lizards; species distributions.

INTRODUCTION

Many factors potentially could explain why a species is present on some islands and not others. One factor of paramount importance is dispersal ability; many studies have documented that the distribution of populations of good dispersers is more widespread than that of poor dispersers (MacArthur and Wilson 1967, Carlquist 1974, Williamson 1981, Case and Cody 1987). Nonetheless, the ability to reach an island does not guarantee colonization success. Appropriate habitat and resources must be available, and resident species must not preclude establishment by competition or predation.

Most studies that investigate the role of colonizing ability in determining a species' distribution rely on a combination of biogeographic surveys of the focal species and potential competitors and predators, geological information on the history of a region, and natural-history observations on the species' likelihood of being able to disperse successfully (e.g., Williams 1969, Case 1975, Heaney 1986). Surprisingly few studies have

taken an experimental approach to investigate this question (e.g., Crowell 1973, Schoener and Schoener 1983a, b, Schoener and Spiller 1995). Of course, such an experimental approach would not be sensible except in the context of observed patterns of distribution, which allow appropriate hypotheses to be framed.

In this study, we utilize an experimental approach to understand the distribution of two species of *Anolis* lizards in the Bahamas. Small islands in this area often are not occupied by anoles. Our first goal is to ascertain whether this results from lack of ability of the lizards to reach these islands or lack of suitable habitat on the islands. Second, one of the species, *A. sagrei*, is more terrestrial and requires less vegetated habitat than the more arboreal *A. carolinensis* (Collette 1961, Schoener 1968, 1975). Hence, islands with vegetation high enough for *A. carolinensis* also have the lower vegetation and terrestrial surfaces necessary for *A. sagrei*, but the reverse is not true— islands with suitable habitat for *A. sagrei* do not necessarily also have suitable habitat for *A. carolinensis* (Schoener and Schoener 1983a, b). Consequently, we expect *A. sagrei*, but not *A. carolinensis*, to occur on some islands by itself. We test this hypothesis by surveying small islands in one part of the Bahamas. We then investigate whether the ab-

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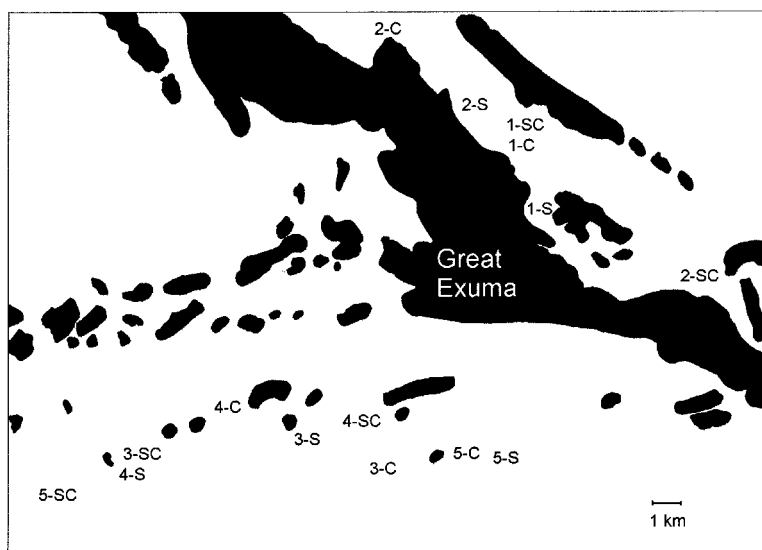


FIG. 1. Map of the study area in the central Bahamas, showing the location of each experimental island. Numbers and letters refer to blocks and treatments (see Table 1) and indicate the exact locations of the islands, which are much smaller than the surrounding islands depicted in the figure.

sence of *A. carolinensis* on these islands is due to the absence of appropriate habitat, the presence of *A. sagrei*, or both.

To distinguish between these hypotheses, we introduced *A. sagrei* and *A. carolinensis*, using treatments with each species alone and both species together, onto small islands with relatively low vegetational cover in the central Bahamas. For each species, we tested the hypothesis that its absence from these islands was due to its inability to occupy such marginal habitats. Successful introduction would indicate that their absence from these islands was due to failure to colonize them naturally. In addition, the experimental design allowed us to test whether interactions between the species had a negative impact on their colonization success and population density.

METHODS

The study was conducted on very small islands in the vicinity of Great Exuma, Bahamas (Fig. 1). Both *Anolis sagrei* and *A. carolinensis* occur on Great Exuma. *Anolis sagrei* is the more widespread species and generally occurs lower in the vegetation than *A. carolinensis*. Its long legs have been interpreted as an adaptation for locomotion on broad surfaces, such as tree trunks and the ground, whereas the shorter legs of *A. carolinensis* may be adaptive for moving on narrow surfaces, such as the twigs and branches that it frequents (Jenssen et al. 1995, Losos and Irschick 1996).

In October 1993 we surveyed 28 islands in the vicinity of Great Exuma (distance from Great Exuma 0.1–11.7 km). Most of these islands had no lizards. We selected 16 lizardless islands whose vegetation and size suggested that they might be able to support lizard populations and that were not too large for accurate

censusing (Table 1). These 16 islands were surveyed two more times, and again no lizards were found on any of the islands. The islands were grouped according to vegetation structure and locality into four blocks of four islands (Fig. 1); Block 1 had vegetation higher than the other blocks, which were about the same. Islands in each block were randomly assigned to the following four treatments: only *A. sagrei* introduced, only *A. carolinensis* introduced, both species introduced, and neither species introduced (the last treatment was a control for food-web studies, results of which will be reported elsewhere). Variation among lizard treatments was not significant for vegetated area (Analysis of variance, two-tailed, $P = 0.185$), height ($P = 0.431$) or distance to the mainland ($P = 0.548$). A propagule of five adult lizards, two males and three females, was then introduced onto each island; islands with both species received five lizards of each species. Most females were gravid at the time of introduction. On one island (Block 2, only *A. carolinensis* introduced), *A. carolinensis* went extinct in the first year. A second propagule of five lizards was introduced in 1994. This population increased in number to 12 in 1995, but went extinct in 1996. In October 1994, an additional block of islands (Block 5) was established.

All islands were visited in October of each of the subsequent 3 yr. Population sizes were usually estimated using the multiple-mark-recapture method of Heckel and Roughgarden (1979); lizards were marked with different colors on each of three subsequent days. On a few occasions, lizards were marked on only two days and the Lincoln index was used to estimate population sizes. For the sake of consistency, for the multiple-mark-recapture estimates we always used the model in which the probability of marking a lizard on

TABLE 1. Vegetated area, vegetation height and volume, and distance to the mainland (Great Exuma) for each experimental island. Treatments: C = only *Anolis carolinensis* introduced, S = only *A. sagrei* introduced, SC = both species introduced.

Treatment	Veg. area (m ²)	Mean veg. height (m)	Veg. volume (m ³)	Distance (km)
Block 1				
C	944	0.604	570	0.88
S	545	1.428	778	0.60
SC	950	0.640	608	1.05
Block 2				
C	1376	0.365	502	0.08
S	614	0.518	318	0.30
SC	1511	0.492	743	0.28
Block 3				
C	968	0.389	377	3.83
S	638	0.399	255	4.35
SC	362	0.277	100	9.95
Block 4				
C	203	0.399	81	6.65
S	475	0.315	150	10.28
SC	845	0.331	279	3.03
Block 5				
C	815	0.464	378	2.73
S	380	0.290	110	2.55
SC	644	0.314	202	11.68
Mean†				
C	861	0.444	382	2.83
S	530	0.590	322	3.62
SC	862	0.411	386	5.20

† Means of the five islands within each treatment.

one day was independent of the probability of marking it on the other days, as it is for the Lincoln index. In 32 of 36 multiple-mark-recapture cases (a case being a population estimate on an island for a given year), the independence model was not statistically rejected. In two cases, this model was rejected, but interaction models were not rejected (see Heckel and Roughgarden 1979); however, in these cases the population estimates produced by the independence and interaction models were extremely similar. In two other cases, all models were rejected.

In October 1994, we mapped the area and measured the height of the vegetation on each island as follows. Each island was approximately elliptical. A measuring tape was placed along the major axis of the island, from the beginning to the end of the vegetation. A second tape was placed perpendicular to the major axis, at 4-m intervals on larger islands and at 3-m intervals on smaller islands. The maximum height of the vegetation within a 0.5-m radius of a given point was measured along each transect, at 3-m intervals on the larger islands and at 2-m intervals on the smaller islands. Vegetated area of the entire island was estimated by connecting the outer points of the map and calculating the volume enclosed by the resulting polygon. Volume was

estimated by multiplying mean maximum vegetation height by vegetated area.

For each lizard species, we analyzed two measures of colonization success: the proportion of populations becoming extinct and the mean density of individuals. Mean density per island was computed as the average of the annual population-size estimates divided by the vegetation volume. Because these lizards are arboreal, we considered it more appropriate to use volume, rather than island area, in calculations of density; however, analyses using island area produce nearly identical results. To test the effect of interspecific interactions, we compared allopatric vs. sympatric island populations for each species; one-tailed tests were used because our a priori hypothesis was that both measurements would be higher for allopatric populations. Proportions of populations becoming extinct were compared with Fisher's exact test. Densities were compared with a two-way ANOVA with block and treatment as the main effects.

On each visit to an island, we recorded the perch height of every lizard observed that was not moving prior to detection. Mean values of all individuals observed across all years were used to compare perch height between species and between treatments within species. These analyses were conducted with analyses of covariance (ANCOVA) using mean vegetation height as a covariate.

Shortly after we conducted our censuses in October 1996, the experiment was terminated by Hurricane Lili, which extirpated lizard populations on many of the islands (Spiller et al. 1998).

RESULTS

On the 28 islands surveyed, *Anolis sagrei* was present on 8 of the islands, whereas *A. carolinensis* was found on none of the islands. The probability of achieving this difference in species' occurrences by chance is 0.002 (Fisher's exact test, one-tailed). No other lizards were observed on any of the islands.

On the experimental islands, most populations increased in size in their first year (Fig. 2), but, by 1996, populations of *A. carolinensis* had become extinct on four islands, compared to no extinctions for *A. sagrei* (Fig. 2). This difference is significant using Fisher's exact test ($P = 0.043$, one-tailed because this result is in the predicted direction based on the natural occurrences of these species). One of the extinct populations of *A. carolinensis* was on an island on which *A. sagrei* was also introduced, whereas the other three were on *A. carolinensis*-only islands (Fisher's exact test, $P > 0.50$, one-tailed). In addition, by 1996, 9 out of 10 *A. sagrei* populations had more than ten individuals, whereas only two of the *A. carolinensis* populations had that many individuals (Fisher's exact test, $P = 0.0027$, one-tailed). Both of these populations of *A. carolinensis* were on islands on which *A. sagrei* was absent.

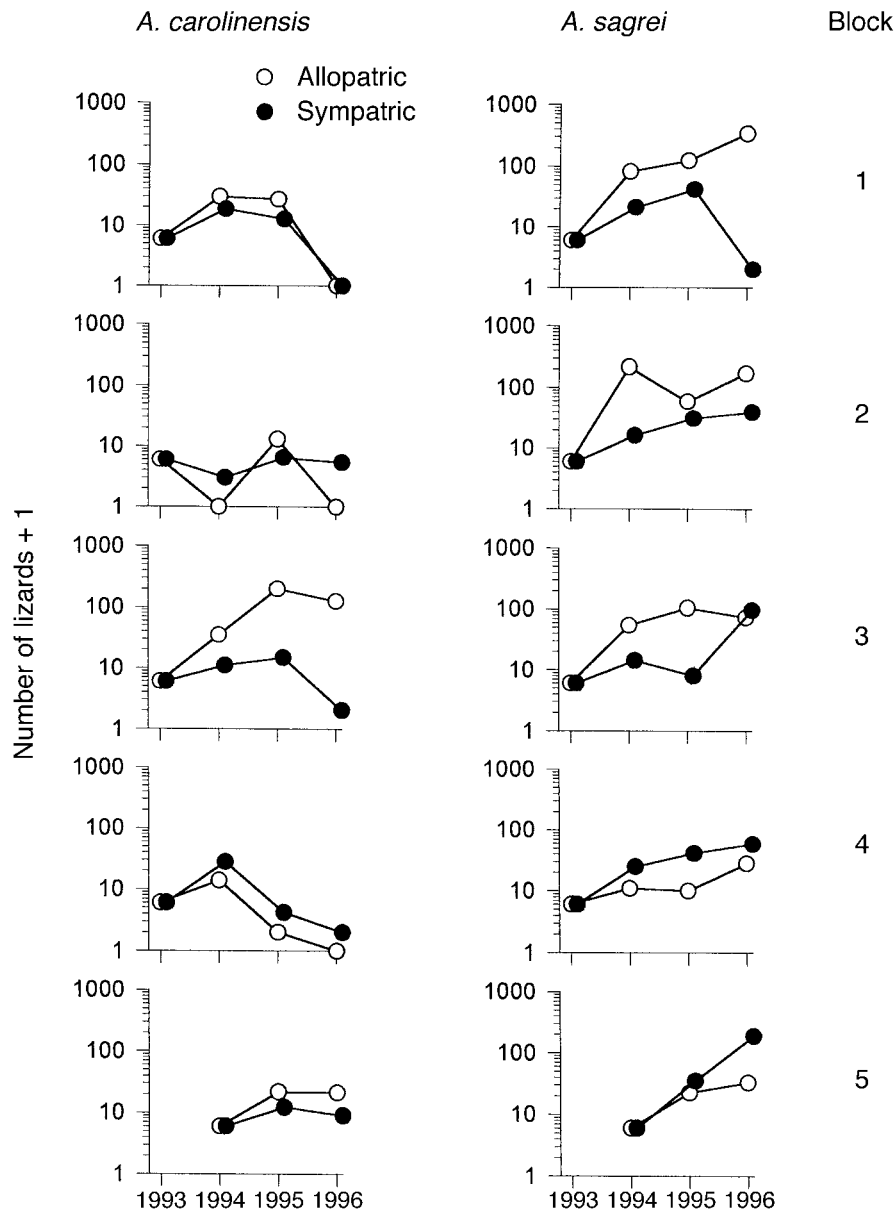


FIG. 2. Numbers of *Anolis carolinensis* and *A. sagrei* on each experimental island (note logarithmic scale on y-axis). Five lizards were introduced onto each island in blocks 1–4 in 1993 and onto each island in block 5 in 1994. In 1994, *A. carolinensis* was reintroduced onto one island (block 2, allopatric). Note that in blocks 2 and 4, although numbers are higher in the sympatric treatment, densities (number/vegetation volume) are actually lower (see Table 1).

Combining data across years, the mean density of *A. sagrei* did not differ between sympatric and allopatric populations, whereas a significant difference did exist for *A. carolinensis* density (Fig. 3, Table 2). The significant results hold for *A. carolinensis* even if Block 2 is excluded because one population was re-introduced in 1994 ($P = 0.0432$). Interesting temporal patterns emerge when the sizes of extant populations are examined. In 1994, the year following most of the introductions, the mean number of *A. sagrei* was 5 times higher for allopatric than for sympatric island populations ($P = 0.059$, one-tailed; Fig. 4). During the fol-

lowing two years, numbers of sympatric *A. sagrei* increased and began to converge with numbers of allopatric *A. sagrei*. By contrast, mean numbers of allopatric and sympatric *A. carolinensis* were about the same in 1994, but steadily diverged over the next two years so that in 1996, the mean of the allopatric populations was 20 times higher than that of sympatric populations ($P = 0.018$, one-tailed, extinct populations excluded). Hence, from 1994 to 1996, sympatric *A. sagrei* increased while sympatric *A. carolinensis* decreased. On the sympatric islands where both species were extant in 1996, the mean number of *A. sagrei* was

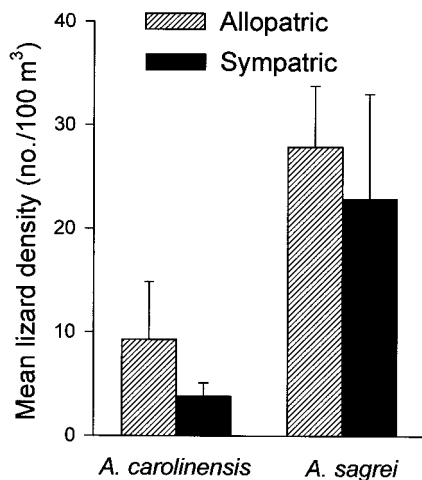


FIG. 3. Mean (and 1 SE) of the mean density per island for *Anolis carolinensis* and *A. sagrei* within each treatment. Mean density per island is the average of the post-introduction annual densities.

26 times higher than the mean number of *A. carolinensis* (paired *t* test, $P = 0.007$, two-tailed). Similarly, the mean density of *A. sagrei* for the experiment as a whole was significantly higher than for *A. carolinensis* ($t = 3.34$, $P < 0.0036$, two-tailed).

A. carolinensis perched higher than did *A. sagrei* (Fig. 5; ANCOVA, difference in intercepts, $P < 0.0005$, one-tailed; test of slope heterogeneity, $P = 0.41$, two-tailed). Sympatric populations of *A. carolinensis* tended to perch higher than did allopatric populations (ANCOVA, difference in intercepts, $P = 0.089$, one-tailed; Fig. 5); however, because this difference was only apparent on islands with low vegetation (test of slope heterogeneity, $P = 0.056$, two-tailed), the test of intercepts should be taken with caution. No effect of *A. carolinensis* on perch height of *A. sagrei* was apparent (ANCOVA, test of slope heterogeneity, $P = 0.64$, two-tailed; difference in intercepts, $P = 0.14$; one-tailed).

DISCUSSION

Very small islands in the central Bahamas frequently do not naturally harbor lizard populations. Their small size and sparse vegetation suggests that these islands often may be incapable of supporting a viable lizard population. In a survey of 521 islands throughout the Bahamas, most of which were larger than the islands included in this study, Schoener and Schoener (1983a) quantified this impression, determining that both island area and vegetation profiles are important in predicting lizard island occupancy.

Our experimental results, however, do not support the hypothesis that lizard populations cannot survive on islands naturally lacking lizards, at least for *Anolis sagrei*. Unoccupied small vegetated islands are capable of supporting thriving populations of *A. sagrei*, a result

TABLE 2. Analysis of variance of mean post-introduction lizard density (no./100 m³) for *Anolis carolinensis* and *A. sagrei* on each experimental island (based on the data in Fig. 3.).

Species	Effect	df	MS	F	P†
<i>A. carolinensis</i>	Block	4	0.5229	26.48	0.0039
	Treatment	1	0.1700	8.61	0.0214
	Error	4	0.0197		
<i>A. sagrei</i>	Block	4	0.1535	0.72	0.6208
	Treatment	1	0.1724	0.81	0.2096
	Error	4	0.2130		

† Treatment effect is a one-tailed test; block effect is two-tailed.

also discovered elsewhere in the Bahamas (Schoener and Schoener 1983c, Schoener and Spiller 1996). Three years after five lizards were introduced, populations on 9 of the 10 islands had increased to at least 25 individuals; several populations numbered well over 100 lizards.

Consequently, we conclude that the absence of *A. sagrei* from these islands must result from failure to reach these islands, rather than lack of suitable conditions. Given that all islands on the Great Bahama Bank were united due to lower sea levels 8000–10 000 yr ago, forming an island comparable in size to Cuba (Carew and Mylroie 1995), and that the habitat on these

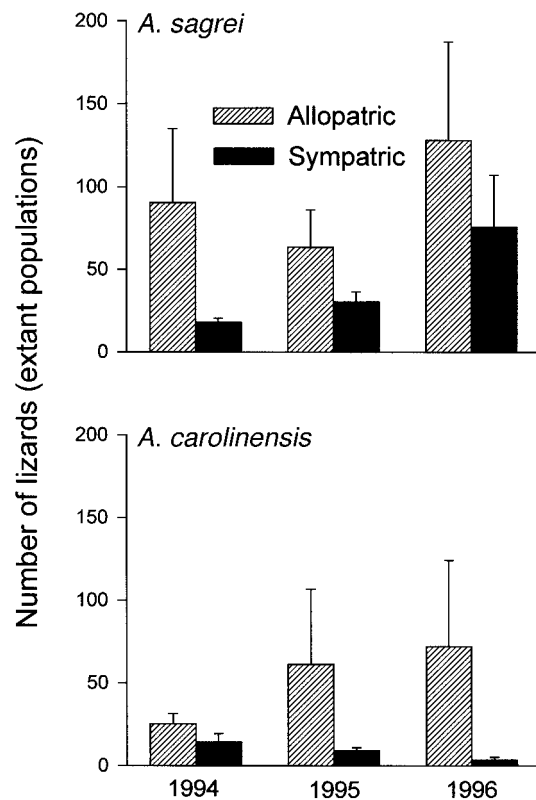
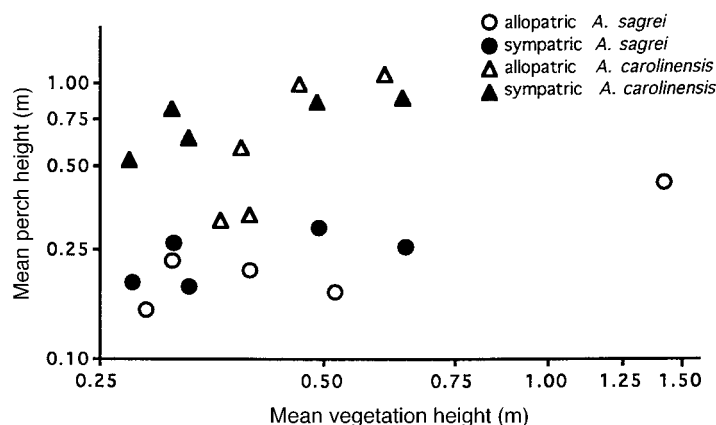


FIG. 4. Number (mean and 1 SE) of *Anolis carolinensis* and *A. sagrei* within each treatment. Islands on which a population went extinct are not included in the calculations.

FIG. 5. Mean *Anolis* perch height vs. mean vegetation height for all islands. Each perch height point represents the mean of all individuals over all years.



islands is suitable, it may seem puzzling that *A. sagrei* does not occur on these islands. However, low-lying islands are particularly vulnerable to scouring by hurricanes, which can extirpate a lizard population on an island, as happened to some of our populations in 1996 (Spiller et al. 1998). Our survey indicates that, even though islands of the size included in this study can support populations of *A. sagrei*, relatively few do. Consequently, the absence of this species from these islands indicates that its dispersal abilities are limited relative to the frequency of devastating hurricanes. Schoener and Schoener (1983a, b) also concluded that dispersal ability plays a role in the distribution of Bahamian anoles.

In contrast to *A. sagrei*, *A. carolinensis* did not thrive on most of the experimental islands. Three years after their establishment, four populations had perished and another four were barely hanging on. Only one island exhibited a population explosion comparable to that seen on a number of the *A. sagrei* islands. The extinction of three allopatric populations indicates that many sparsely vegetated islands are not suitable for *A. carolinensis*. Thus, the experimental results are consistent with Schoener and Schoener's (1983a) finding that *A. sagrei* occurs on islands with much lower vegetation than islands on which *A. carolinensis* occurs. Given that *A. carolinensis* is incapable of persisting on many of these islands, we cannot draw any conclusions about the dispersal capabilities of this species because even if a propagule reached one of these islands, it most likely would not survive for long.

The data also suggest that interspecific interactions may play a role in the distribution of *A. carolinensis*. Populations sympatric with *A. sagrei* had lower densities than surviving allopatric populations. Although only one sympatric *A. carolinensis* population went extinct, by 1996 the other four sympatric populations were all at risk of extinction; no sympatric population had more than 8 individuals, whereas the extant allopatric populations contained 20 and 124 individuals. In addition, and in agreement with a comparative study

across many islands (Schoener 1975), *A. carolinensis* tended to perch lower in allopatry than when it was sympatric with *A. sagrei*. Our data also suggest the possibility that *A. carolinensis* had a negative effect on *A. sagrei* density, but this effect disappeared as *A. carolinensis* populations declined (Fig. 4).

Despite the extensive evidence for competition among anole species (reviewed in Losos [1994]), including both experimental and observational data, this is the first experimental study to document population-level responses to the presence of congeners; previous experimental (e.g., Pacala and Roughgarden 1982, 1985, Salzburg 1984) and comparative (e.g., Jenssen 1973, Schoener 1975) studies have documented effects on individuals (e.g., changes in perch position, growth rate). Although competition, either interference or exploitative, is a plausible mechanism for this effect, interspecific predation of adults on juveniles (i.e., intra-guild predation), which has been documented among anoles (reviewed in G. Gerber, *unpublished manuscript*), is also possible (Polis et al. 1989); our data cannot distinguish between these two hypotheses.

Given that our experimental islands contain habitat that is more suitable for *A. sagrei* than it is for *A. carolinensis*, the asymmetry in the interspecific interactions is not surprising. *Anolis carolinensis* might be at a competitive disadvantage or more vulnerable to predation, or both, because it is forced on these islands to use habitats to which it is not well adapted. Repetition of these experiments on larger islands containing habitat more typical of that normally used by *A. carolinensis* would allow a test of the hypothesis that the extent and asymmetry of interspecific interactions is a function of island size and vegetation structure. More generally, these experiments indicate that the distributional pattern of these species results from differences in adaptation to conditions on small islands: *A. carolinensis* cannot survive on many of these islands; even where it can survive, the presence of the better adapted *A. sagrei* may drive it toward extinction.

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