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An experimental study of interspecific interactions between two Puerto Rican *Anolis* lizards

Abstract We analyzed the impact of interspecific interactions between two ecologically and morphologically distinct Puerto Rican lizards, *Anolis gundlachi* and *A. evermanni*, in an experimental design consisting of six 20 × 20 m plots divided into three blocks, each consisting of a pair of experimental and control plots. We removed *A. gundlachi* from experimental plots and monitored the response of *A. evermanni*. The reduction in the number of *A. gundlachi* resulted in a significant increase in the abundance of both adult and juvenile *A. evermanni*. We found no evidence for a shift in structural habitat use in *A. evermanni* in experimental plots. Two possible mechanisms, interspecific competition and intraguild predation, could explain the increase in abundance of *A. evermanni* after the removal of *A. gundlachi*. These results make clear that interactions still occur between *A. gundlachi* and *A. evermanni* even given their morphological and ecological differences.

Key words *Anolis* · Habitat partitioning · Interspecific interactions · Intraguild predation · Puerto Rico

Introduction

One of the major goals of evolutionary ecology is to understand how interactions among sympatric species affect resource partitioning. On one hand, resource partitioning may result from species behaviorally choosing to use resources so as to minimize overlap with sympatric

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species. This could result from a variety of processes, including interspecific competition, shared predators, and shared parasites (Schoener 1983; Underwood 1986; Kelt et al. 1995; Petren and Case 1996; Law et al. 1997). On the other hand, resource partitioning may be the result of evolutionary adaptation to use different resources (Schoener 1986; Winston 1995). These adaptations may include morphological, physiological, and/or behavioral traits which allow the species to use different resources. As a consequence, the pressure of sympatric species might not affect present-day resource use, although previous interactions among species may have been responsible for the evolution of their differences (i.e., "the ghost of competition past," Connell 1980).

Interspecific interactions play an important role in the distribution, abundance, and evolution of island lizards (reviewed in Case and Bolger 1991). *Anolis* lizards are the most conspicuous, abundant, and diverse diurnal vertebrates inhabiting terrestrial ecosystems on islands of the West Indies (Williams 1969, 1983). Numerous studies have described the structure of anoline communities on different West Indian islands (reviewed in Losos 1994). Interspecific competition has been invoked as the causal basis for the structural niche partitioning observed in these communities. Two basic approaches have been taken to the study of interspecific competition between anoles (reviewed in Schoener 1983; Losos 1994). The comparative approach looks at the distribution, resource use, and abundance of natural populations in different ecological situations and tries to draw inferences about the processes leading to these patterns (e.g., Schoener 1970, 1975; Jenssen 1973; Jenssen et al. 1984; Schoener and Adler 1991; Losos et al. 1993). By contrast, in experimental studies, one of the species is removed (or at least its abundance greatly lowered) and the effect on the abundance and habitat use of the other species is noted (Pacala and Roughgarden 1982, 1985; Salzburg 1984; Rummel and Roughgarden 1985; Losos and Spiller, in press).

Two main results generally ensue (reviewed in Losos 1994). First, sympatric species tend to separate them-

selves by differences in structural niche (e.g., perch diameter, perch height), and in some cases, by climatic habitat (e.g., open versus shaded habitat). Second, in the absence of one species, remaining species may increase in abundance or undergo an ecological release that is exhibited by a shift or expansion in either structural or climatic habitat, or both.

In this study, we used an experimental approach to assess whether one abundant Puerto Rican species, *Anolis gundlachi*, affects the habitat use and abundance of a second common species, *A. evermanni*. We examined these questions by removing *A. gundlachi* from experimental plots and monitoring the response of *A. evermanni*. Two sets of data were collected. First, we monitored the abundance of *A. evermanni* in the presence and absence of *A. gundlachi*. Second, we gathered structural habitat data for *A. evermanni* in the presence and absence of *A. gundlachi*. If interspecific interactions occur, we predicted that in the experimental plots where *A. gundlachi* was removed, *A. evermanni* might increase in abundance and/or show a shift in structural habitat use.

Materials and methods

Field site and study species

This study was conducted at the El Verde Field Station (18°20′ N, 65°49′ W) of the Luquillo Experimental Forest (LEF) in northeastern Puerto Rico. The general topography of the area is mountainous with deeply dissected drainage and steep northeast- and southwest-facing slopes. The site lies within Holdridge's Subtropical Wet Forest life zone and the tabonuco forest type (Ewel and Whitmore 1973). The forest is dominated by *Dacryodes excelsa* (tabonuco) and *Prestoea montana* (sierra palm) and has a closed canopy at 20–25 m, many understory trees and shrubs, and only sparse vegetation on the forest floor. Mean annual precipitation is 392 cm, distributed fairly evenly over the year, although it is somewhat drier from January to April (Parrotta and Lodge 1991).

Five anoline species occur sympatrically within mature tabonuco forest at LEF: *A. cuvieri*, *A. evermanni*, *A. gundlachi*, *A. occultus*, and *A. stratulus* (Reagan 1991, 1992). Three other species, *A. cristatellus*, *A. krugi*, and *A. pulchellus*, occur in openings within the forest (Reagan 1996). Two of the most common species, *A. gundlachi* and *A. evermanni*, are the subject of this study. *A. gundlachi* is a medium-sized lizard (maximum snout-vent length [SVL]: males, 68 mm; females, 45 mm; Schwartz and Henderson 1991) with a bulky head and body, long hindlimbs and poorly developed toe-pads. It mainly uses the lower portion of tree trunks and the ground as perching and foraging sites, where its long legs are adaptive for rapid locomotion (Irschick and Losos 1998). *A. evermanni* is also a medium-sized lizard (maximum SVL: males, 70 mm; females, 45 mm; Schwartz and Henderson 1991) with a slender head and body, short legs and well-developed toe-pads; it mostly uses tree trunks 2 m or more above the ground and the crown of the vegetation as perching and foraging sites (Rand 1964; Schoener and Schoener 1971; Reagan 1996), where its well-developed toe-pads and short legs are adaptive for effective locomotion, particularly on branches of small diameter (Glossip and Losos 1997; Irschick and Losos 1998). Because both species overlap in body size, in one region of their structural habitat (the tree trunk), and in their diet (Reagan 1996), competition has been suggested as a likely outcome of their interaction (Schoener and Schoener 1971).

Removal experiment

We conducted this study from 24 June to 20 August 1994. Our six 20×20 m plots were divided into three blocks, each consisting of a pair of experimental and control plots. Each control and its paired experimental plot were separated by approximately 100 m; control 1 was located at an elevation of 390 m, whereas experimental 1 was at an elevation of 400 m; control and experimental 2 were at an elevation of 470 m; and control and experimental 3 were at an elevation of 360 m. We began removing all *A. gundlachi* from the experimental plots on 24 June. During the following 3 weeks, we removed *A. gundlachi* three times a week, but thereafter we only removed *A. gundlachi* during plot censuses. *A. gundlachi* found outside the experimental plots, but within 2 m of the perimeter of the plots, were also removed. All captured *A. gundlachi* were released elsewhere in the forest.

Our system was an open-plot design; no artificial enclosure (e.g., fences, cages) surrounded the plots. This design has two main advantages. First, installation of fences or cages may affect ecosystem functioning and alter the results of the experiment (e.g., exclusion of predators from the study area; Meserve et al. 1996). Second, one possible response after the experimental removal is an increase in abundance of the remaining species on the plot, but enclosures may prevent individuals from entering the plots from outside and thus may prevent an increase in abundance. One disadvantage of open designs is that the plots must be continually maintained to prevent the removed species from re-entering the plot and disrupting the experiment.

Eleven censuses were conducted. The first census was conducted on 24 June, with subsequent censuses beginning 13 July and continuing until 20 August at 3- to 5-day intervals. For each *A. evermanni* observed during a census, we recorded age class (i.e., juvenile or adult), perch height (at 0.5-m intervals) and diameter (in cm), and perch substrate (i.e., woody, non-woody, palm tree). For *A. gundlachi* we only recorded age class and tabulated the number of individuals inside the plot. During plot censuses, we spent approximately the same amount of searching time in each plot. No significant differences in the abundance of *A. gundlachi* existed between the control and the experimental plots at the beginning of the experiment (paired-sample *t*-test, $t = 0.13$, $P = 0.91$, $df = 2$).

Statistical analyses

The effect of removing *A. gundlachi* on the abundance of *A. evermanni* was determined by comparing the abundance of *A. evermanni* on the experimental plots to its abundance on the control plots using a repeated-measures ANOVA with treatment (control or experimental) and block (block one, block two, block three) as the between-subject factors, and time (different census days) as the within subject factor (following Von Ende 1993). Reported probability values for treatment and treatment × time interactions are one-tailed because our a priori predictions were that the abundance of *A. evermanni* would increase in the absence of *A. gundlachi*, and that the differences between experimental and control plots would increase with time.

As an alternative test of the effect of the removal of *A. gundlachi* on the abundance of *A. evermanni*, we calculated the mean number of *A. evermanni* on each plot considering all censuses except the first (24 June). We then subtracted the number of *A. evermanni* seen in the original census from each of these means and analyzed the resulting values in a two-way ANOVA with block and treatment as factors. This test may be conservative because the abundance of *A. evermanni* might not increase immediately upon the removal of *A. gundlachi*, yet early censuses are given equal weight in this analysis.

To assess differences in habitat use between *A. evermanni* from the control and experimental plots, we only used data from the last census (20 August). At this time, the experiment had been going on for the longest time and thus the effects should have been greatest. We combined all the data from each of the experimental and

control plots and used the non-parametric Kolmogorov-Smirnov two-sample test to investigate whether differences existed in perch height or diameter between the *A. evermanni* from the control and experimental plots. Differences in selection of perching substrate were examined with a *G*-test of independence with Williams' correction for continuity.

We analyzed the data for adults and juveniles separately and in a combined analysis. Values given are means ± 1 SE. Statistical tests were performed with StatView (version 4.51, Abacus Concepts 1996) and SuperANOVA (version 1.11, Abacus Concepts 1989). The significance level for all tests was alpha = 0.05.

Results

In the experimental plots, the abundance of *A. gundlachi* across all age classes was significantly lower than in the control plots (repeated-measures ANOVA for treatment effect, $F_{1,18} = 14.44$, one-tailed $P = 0.03$), as was the abundance of males considered separately (repeated-measures ANOVA for treatment effect, $F_{1,18} = 17.15$, one-tailed $P = 0.03$; Fig. 1). These results indicate that our method of removing *A. gundlachi* was effective. Most of the *A. gundlachi* that emigrated into the experimental plots were females and juveniles.

Table 1 reports the results of the repeated-measures ANOVA used to evaluate the numerical response of *A. evermanni* to the removal of *A. gundlachi* from the experimental plots. There was neither a significant effect of block, nor a significant block × time interaction across all age classes. The significant treatment effect indicates that the abundance of *A. evermanni* increased in the absence of *A. gundlachi*. Furthermore, the abundance of *A. evermanni* increased significantly through time in the experimental but not in the control plots (time × treatment interaction; Fig. 2a). On the last census day, the mean abundance of *A. evermanni* in the experimental plots was three times that on the control plots. We also analyzed the data for adults and
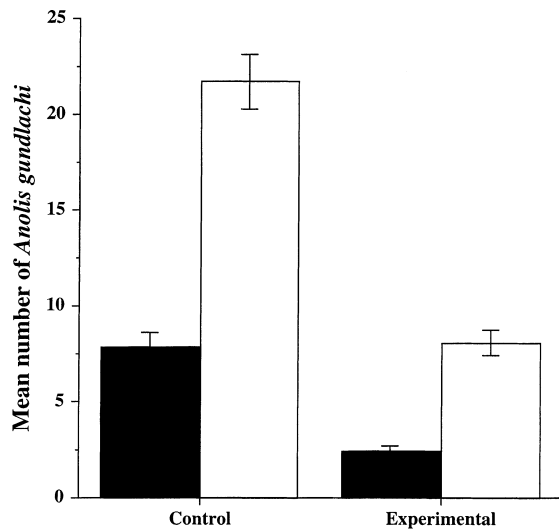

Fig. 1 Mean number of *Anolis gundlachi* in the control and experimental plots during the duration of this study (*filled bars* males, *open bars* all lizards). *Error bars* denote ±1 SE

Table 1 Repeated-measures ANOVA for the comparison of the abundance of *Anolis evermanni* between control and experimental plots

Effect	df	MS	F	P
All lizards				
Treatment	1	301.227	10.180	0.04[a]
Block	2	109.379	3.696	0.21
Time × treatment	10	19.661	4.206	< 0.001[a]
Time × block	20	7.395	1.582	0.16
H-F epsilon = 0.743				
Adults				
Treatment	1	122.727	9.963	0.04[a]
Block	2	35.106	3.696	0.26
Time × treatment	10	7.561	1.889	0.05[a,b]
Time × block	20	2.756	0.689	0.79[b]
H-F epsilon = 1.025				
Juveniles				
Treatment	1	37.879	9.025	0.04[a]
Block	2	25.015	5.960	0.14
Time × treatment	10	4.879	3.622	< 0.001[a]
Time × block	20	3.465	2.573	0.02
H-F Epsilon = 0.947				

[a] One-tailed *P*-value
[b] *P*-value corrected for H-F epsilon greater than 1

juveniles separately. A significant increase in the abundance of adult *A. evermanni* in removal plots was observed (treatment effect), and the difference in abundance also increased significantly through time (time × treatment interaction; Table 1, Fig. 2b). The same results were obtained for juveniles (Fig. 2c), for which a significant time × block interaction was also observed.

Similarly, the two-way ANOVA of the mean abundance of *Anolis evermanni* populations revealed a significant treatment effect ($F_{1,2} = 24.6$, $P = 0.02$), which indicates that *A. evermanni* populations were larger in the experimental plots than in the controls. There was no significant block effect ($F_{2,2} = 4.24$, $P = 0.19$), indicating that the three blocks did not differ in response. Similar results were obtained for adult (treatment effect: $F_{1,2} = 110.23$, $P < 0.001$; block effect: $F_{2,2} = 7.0$, $P = 0.13$) and juvenile (treatment effect: $F_{1,2} = 11.88$, $P = 0.04$; block effect: $F_{2,2} = 10.55$, $P = 0.09$) *A. evermanni*.

On the last census day, there were no significant differences in perch height selection by *A. evermanni* from experimental (2.3 ± 0.2 m, $n = 50$) and control (2.0 ± 0.1 m, $n = 15$) plots (Kolmogorov-Smirnov test, $\chi^2 = 2.33$, $P = 0.62$, $df = 2$, $n = 65$), nor were there statistical differences in perch diameter selection by anoles from experimental (4.9 ± 0.7 cm, $n = 50$) and control (7.4 ± 2.2 cm, $n = 17$) plots (Kolmogorov-Smirnov test, $\chi^2 = 2.51$, $P = 0.57$, $df = 2$, $n = 67$). We found no significant differences in vegetation substrate used as perching site between experimental and control plots (woody/non-woody/palm tree; control 6/3/8, experimental 24/5/21, G-test, $G = 1.13$, $df = 2$, $P = 0.57$).
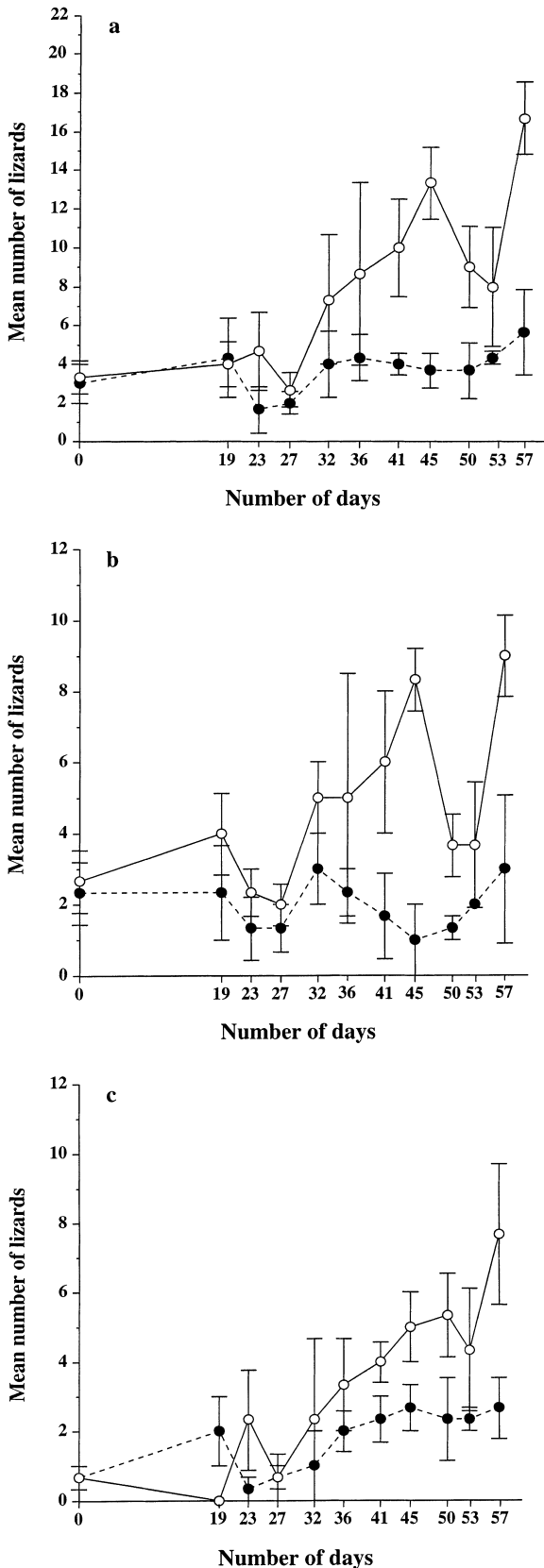
Fig. 2 Mean number of *A. evermanni* during each census in control (*filled circles*) and experimental (*open circles*) plots for all age classes (**a**), adults (**b**), and juveniles (**c**). Note the different scale for mean number of lizards on the *y*-axis of the figures. *Error bars* denote ±1 SE

Discussion

Our experiment consisted of three blocks, each containing two 20-m² plots; in one plot in each block we removed all individuals of *A. gundlachi*, whereas the other plot served as the control. Because we did not use any type of enclosure, a major concern at the outset of the experiment was whether immigration of *A. gundlachi* from outside the experimental plots would be so great as to render the experiment meaningless. Our censuses, however, indicate that lizard removal was successful: on average, *A. gundlachi* populations were reduced 64% (control 21.6 ± 1.4 lizards; experimental 8.0 ± 0.7 lizards) in the experimental plots compared to the controls. Furthermore, the number of adult male *A. gundlachi*, which are the individuals most likely to have a negative effect on *A. evermanni* (see below), were reduced to an even greater extent, 71% (control 7.7 ± 0.8 lizards; experimental 2.3 ± 0.3 lizards; Fig. 1).

The experimental reduction in the number of *A. gundlachi* had a large effect on *A. evermanni* populations. Within a relatively short time (32 days), experimental populations of *A. evermanni* were substantially greater than control populations and remained so throughout the rest of the experiment (Fig. 2a). This result is in accord with the predictions of the interspecific-interaction hypothesis. When the data are examined separately, one can see that the removal of *A. gundlachi* had a significant effect on both adult and juvenile *A. evermanni*. Figure 2 indicates that the magnitude of the effect on adults and juveniles was roughly comparable, except that the adult experimental populations were anomalously low in censuses 8 and 9. Thus, it is clear that the presence of *A. gundlachi* has a negative effect on both juvenile and adult *A. evermanni*.

Interspecific competition, the most commonly invoked hypothesis to explain patterns such as those we have observed, is certainly plausible in this case. Both species are generalized insectivores that are likely to take the same prey (Wolcott 1923; Reagan 1996). In addition to dietary overlap, interference competition, documented to occur among anoles (Jenssen et al. 1984), may also be important. For example, on two occasions during censuses of the control plots, we observed interactions between *A. gundlachi* and *A. evermanni*. One episode was between two adult females, and the other was between two young males. In both instances, behavioral displays typical of agonistic encounters (e.g., push-ups, dewlapping, lateral face-off, body compression, and tongue-bunching; Ortiz and Jenssen 1982) were performed, and on both occasions, the *A. gundlachi* prevailed and displaced the *A. evermanni* from the perching site (see also Losos 1990).

Another possible mechanism that may explain the increase in abundance of juvenile *A. evermanni* in the experimental plots is intraguild predation (Polis et al. 1989). Several anoline species have been reported to eat other anoles (e.g., Reagan 1992, 1996; Dial and

Roughgarden 1994), and it is very likely that adult *A. gundlachi*, particularly males, would eat juvenile *A. evermanni*. Consequently, intraguild predation could potentially explain the difference in abundance of juveniles in experimental versus control plots. Juvenile *A. evermanni* were rare on all plots early in the experiment (Fig. 2c), and although their number increased in all plots throughout the experiment, the increase was markedly greater in the experimental plots. However, because morphological constraints of their feeding apparatus limit anoles to eat prey of considerably smaller body size than their own (Schoener and Gorman 1968), intraguild predation cannot explain an effect of adult *A. gundlachi* on adult *A. evermanni*.

Two related hypotheses, the shared predator (Holt and Lawton 1994) and shared parasite (Schall 1992; Schall and Vogt 1993) hypotheses, seem less plausible in this case. These hypotheses suggest that species partition habitats to avoid predators or parasites that are attracted to the other species. Given that our plots were relatively small, it seems likely that predators or parasites that are attracted to *A. gundlachi* would still occur in the experimental plots because *A. gundlachi* was present in high numbers a short distance away. Hence, the interspecific competition and intraguild predation hypotheses, both of which rely on direct effects of *A. gundlachi* on *A. evermanni*, seem more likely to be responsible for observed patterns.

We found no evidence of a shift in structural habitat use by *A. evermanni* in the experimental plots. Given that *A. gundlachi* generally occurs within 2 m of the ground, whereas *A. evermanni* is usually observed at 2 m or above (Reagan 1992, 1996; Dial and Roughgarden 1994), we expected that the removal of *A. gundlachi* might have led to a shift in the mean perch height of *A. evermanni*. However, no difference in any aspect of structural habitat use of *A. evermanni* was observed between the experimental and control plots. Nonetheless, the observed increase in the abundance of *A. evermanni* might actually reflect a shift in perch height. *A. evermanni* is fairly generalized in its habitat use (Rand 1964; Schoener and Schoener 1971; Reagan 1996) and, even in the presence of *A. gundlachi*, sometimes occurs within 2 m of the ground. Because our censuses were conducted at ground level and *A. evermanni* may occur at high densities in the canopy (Dial and Roughgarden 1994), the increased number of *A. evermanni* that we detected in the experimental plots may have resulted from an increased tendency of *A. evermanni* to move down from the canopy, thus becoming detectable at approximately the same height as the *A. evermanni* in the control plots. Without simultaneously monitoring lizard abundance at the ground and canopy levels, this question cannot be answered. Of course, both habitat shift and immigration into the plots may have contributed to the increase in abundance of *A. evermanni*. Regardless of the mechanism that led to the increase in abundance of *A. evermanni* in the experimental plots, our study demonstrates that, in the absence of *A. gundlachi*, the abundance of *A. evermanni* increases significantly in the ecological space normally used by *A. gundlachi* (i.e., the lower part of the tree trunk).

Sympatric species of anoles in the Greater Antilles usually differ in structural habitat and exhibit morphological differences that have evolved as a result of adaptation to these differences in habitat use (Williams 1983). Interspecific competition has been invoked as the driving force leading to the evolution of these morphological differences (Losos 1994). Given that these anoline species have evolved specializations to use different parts of the habitat, one might question whether they are still interacting or, alternatively, whether the differences in habitat use are so great that the species no longer interact. Our results make clear that interactions do still occur between such species, even given their morphological and ecological differences. The rapid response by *A. evermanni* to the absence of *A. gundlachi* suggests a rather strong ongoing interaction between the two species. Hence, "the ghost of competition past" may be a present-day specter as well. However, further work is required to sort out the relative contribution of competition versus that of intraguild predation in regulating abundances of populations of Greater Antillean *Anolis*.

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