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Accepted: 23 January 1996.

Journal of Herpetology, Vol. 30, No. 2, pp. 204-210, 1996
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Dynamics of Range Expansion by Three Introduced Species of *Anolis* Lizards on Bermuda

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ABSTRACT.— Three species of *Anolis* lizards were introduced in this century to Bermuda, an archipelago formerly lacking anoles. A previous study conducted in the early 1960s indicated that *A. grahmi*, the first species introduced, rapidly expanded over almost all of the archipelago. By contrast, the other two species had only attained limited ranges by 1963. I surveyed the extent of range expansion by all three species in 1991 and studied habitat use and behavioral interactions. All three species have been able to expand their ranges into areas occupied by other species, but the rate of range expansion has been relatively slow. The species are ecologically similar, but subtle differences in habitat use exist. Behavioral interactions indicate that *A. grahmi* aggressively responds to conspecifics, displays less aggressively to *A. extremus*, and flees from the larger *A. leachi*.

Successful colonization requires not only reaching a site, but being capable of coping successfully with environmental exigencies and interacting with native predators, competitors, and parasites. Knowledge of colonization dy-

namics is crucial to understanding how communities become more diverse, but study of natural colonization is difficult due to its haphazard and unpredictable nature. The introduction of non-native species through human agency,

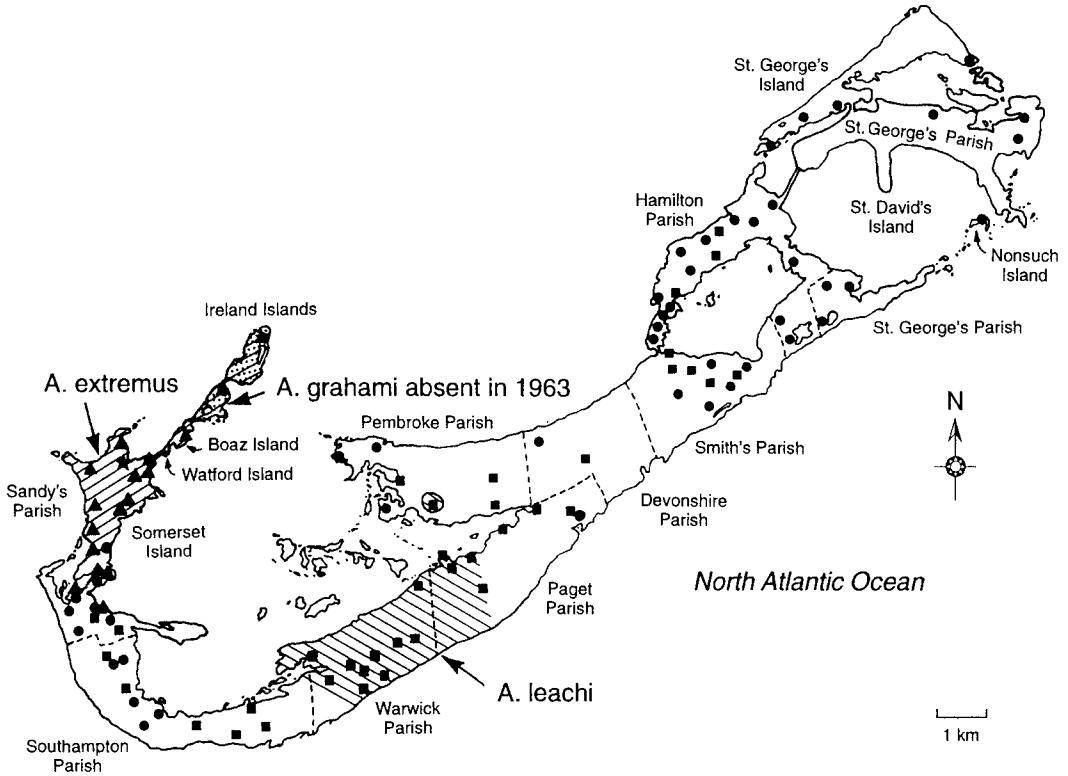


FIG. 1. Distribution of *Anolis* species in Bermuda. Circles represent localities at which only *A. grahami* was found; squares are localities at which both *A. grahami* and *A. leachi* were found; triangles are localities at which *A. grahami* and *A. extremus* were found; and the star denotes the locality (Mangrove Bay) at which all three species were found. Hatched areas represent the distribution of *A. extremus* and *A. leachi* in 1963 (Wingate, 1965). The stippled area indicates the area not occupied by *A. grahami* in 1963. This area is also hatched because *A. extremus* was present in this area at that time.

disastrous in case after case (e.g., Moyle et al., 1986; Drake et al., 1989), does have one positive aspect: by studying the outcome of such introductions, hypotheses concerning colonization and community diversification can be tested (Moulton and Pimm, 1983; Moulton, 1986).

One well-documented example involves the introduction of three species of the lizard genus *Anolis* to Bermuda, an archipelago having no native amphibians and only one native terrestrial reptile species, the skink *Eumeces longirostris* (Wingate, 1965). Interactions among introduced species of anoles are particularly interesting in the context of the extensive literature on community ecology and evolutionary diversification in this genus (reviewed in Losos, 1994). Interspecific competition is an important determinant of habitat use and geographic distribution among Caribbean anole species (e.g., Schoener, 1975; Pacala and Roughgarden, 1982; Salzburg, 1984) and has been implicated as the driving force behind evolutionary specialization to particular microhabitats (Williams, 1972; Losos, 1992, 1994). Thus, the extent to which

the geographic spread and habitat use of introduced anole species are affected by the presence of congeners can provide an informative test of hypotheses concerning *Anolis* community structure and evolution (Losos et al., 1993).

The history of anole introductions to Bermuda has been well-chronicled by Wingate (1965). *Anolis grahami*, native to Jamaica, was introduced to control insect pests (themselves introduced) in 1905 in Paget Parish. By 1963, it had spread throughout the island with the exception of most of the Ireland Islands at the northwestern tip of the Bermudian archipelago (Fig. 1). *Anolis leachi*, native to Antigua and Barbuda, appeared in central Bermuda around 1940 and had spread approximately 2 km to cover almost all of Warwick Parish by 1963; in addition, a small disjunct colony in Pembroke Parish also existed at that time. In 1953, *A. extremus*, from Barbados, was discovered in the Royal Dockyards on Ireland Island North and had covered that entire island, as well as Ireland Island South and Boaz island, by 1963.

On their native islands, all three species are

quite similar ecologically, being arboreal with a vertical distribution from eye-level to the crowns of trees (Rand, 1967; Schoener, 1970; Schoener and Schoener, 1971; Lazell, 1972). *Anolis leachi* is considerably larger than the other two species, which are approximately the same size (mean snout-vent length of adult males on Bermuda [Losos, unpubl.]: *A. extremus* 73.2 mm; *A. grahami*, 68.9 mm; *A. leachi* 102.3 mm). Wingate (1965) noted that *A. leachi*, which dominates *A. grahami* and forces it to shift its habitat, had spread through areas occupied by the latter species. By contrast, *A. grahami* and *A. extremus*, which might be expected to compete more intensely because of their similarity in size (Pacala and Roughgarden, 1985; Rummel and Roughgarden, 1985), were only sympatric over a small area at the time of Wingate's study. Wingate (1965) speculated that the failure of *A. grahami* to colonize most of the Ireland Island may have been due to the presence of *A. extremus*. Conversely, the limited range of *A. extremus* might be a result of the presence of *A. grahami* (Wingate, 1965; Roughgarden and Pacala, 1989).

I conducted this study to document what change in geographic distribution, if any, had occurred in the 28 yr since Wingate's analysis. In addition, I investigated whether the species, when sympatric, interacted aggressively or differed in habitat use.

MATERIALS AND METHODS

The current range of Bermudian anoles was investigated from 26 June–19 July 1991. I visited a large number of localities throughout Bermuda at which I searched for 5–20 min, usually continuing until ≥ 10 lizards had been discovered. Any species not seen was considered absent from a site (in several places where lizards were scarce, usually due to weather or lateness of hour, searches were discontinued before 10 lizards were found). Many sites were visited more than once, and in only one case was a species missed in the first visit subsequently discovered (the Mangrove Bay site, where one *A. leachi* was discovered at the end of a second 3+ hour visit). Sites were concentrated near the borders of the species' ranges to more accurately delimit the range boundaries. Casual observations of *extremus* and *leachi* at other localities were also recorded.

Habitat utilization data were recorded at eight sites. *Anolis grahami* was present at all eight sites. At three sites, *A. grahami* occurred alone (southern end of Somerset Railway Trail, Sandys Parish [one *extremus* found in 2½ hours of searching]; St. David's Island; Nonsuch Island), whereas it was sympatric with *A. extremus* at two sites (Mangrove Bay, Sandys Parish [one

leachi was found in approximately 7 hours]; Somerset Railway Trail, Sandys Parish [ca. 1¼ km from *grahami* only site]) and with *A. leachi* at three sites (Belmont Golf Club, Warwick Parish; Riddell's Bay Golf Club, Warwick Parish; Bermuda Botanical Garden, Paget Parish). Each site was visited once beginning after 0900 h and ending by 1545 h (Belmont Golf Club was visited twice due to low abundance of *grahami*). Visits were not made on rainy or overcast days. The sites were chosen to attempt to cover areas with similar vegetation structure. Most of the sites were mixed landscapes composed of areas containing either thick woods, isolated trees, relatively abundant low vegetation or small buildings. However, the two sites along the railway trail in Sandys Parish were somewhat different in that they were completely wooded, the trees were widely spaced so that one could walk easily amongst them, and low vegetation was relatively scarce.

At each site, the following data were recorded for each adult male observed (Rand, 1967; Schoener and Schoener, 1971): species, height, diameter of perch (not assigned to animals on the ground), and whether the individual was in the sun or shade (lizards with 25–75% of their body in the sun and the rest in shade were recorded as in filtered sunlight). To bolster sample sizes for the sun/shade analysis, localities were grouped and the filtered-sun and full-sun categories were combined. Sample sizes were lower for these analyses than for habitat analyses because no data were recorded when the sun was not out. Table 1 provides perch height and diameter data for each species at each locality.

Behavioral trials were conducted in which one lizard, attached by a dental floss noose around the waist to a 2 m pole, was moved to within 0.5–1.0 m of a resident male lizard. Behavior of the resident was observed from a distance of 2–5 m. Trials were conducted for 15 min or until the resident either attacked the intruder or fled. Because for the most part *A. leachi* and *A. extremus* expanded their ranges into area previously occupied by *A. grahami*, *A. grahami* was used as the resident in these trials. Some trials were conducted in areas in which *A. grahami* occurs alone, whereas others were held in areas in which the intruder also occurs. Because no obvious difference in the results were observed, trials were lumped for data presentation.

Data were ln-transformed prior to statistical analysis.

RESULTS

Species Distributions.—*Anolis grahami*: *A. grahami* now occupies all of the contiguous Ber-

mudian islands and some outlying islands, often at high density (Fig. 1; Nonsuch Island was the only outlying island visited as part of this study, but Wingate [1965] reported that *A. grahami* has reached others). No sites were visited at which *A. grahami* could not be found.

Anolis leachi: In the 28 yr since Wingate's census (which was also conducted during summer months), *A. leachi* has expanded into the parishes of Smith's (7.75 km from the border of its range in 1963), Hamilton (10 km), Southampton (7.25 km) and Pembroke (minimally 1.25 km from the small Pembroke enclave reported by Wingate). In addition, one *A. leachi* was discovered at the north end of Sandys Parish, 3 km from the nearest other *A. leachi* locality.

Anolis extremus: Since 1963, *A. extremus* has covered the southern third of Somerset Island and has crossed the Somerset Bridge into Southampton, a range extension of 1.25 km. Wingate (1965) noted that *A. extremus* was distributed patchily on Somerset Island, a situation which still exists, as evidenced by the several localities on that island at which only *A. grahami* was found.

The range extensions reported above for each species occurred in areas already occupied by another *Anolis* species. With the exception of one site in northern Sandys Parish (discussed below), no localities were visited in which all three species were found. However, in northern Southampton Parish, *A. leachi* and *A. extremus* were found at sites separated by <0.25 km. If I had sampled more intensively in this area, I might have discovered all three species occurring sympatrically.

Habitat Use.—The species generally are ecologically quite similar—they are arboreal lizards usually found around eye level on tree trunks and, less frequently, on branches. *Anolis grahami* and *A. extremus* differed in neither perch height nor perch diameter (Table 2), but *A. extremus* used the shade more frequently than *A. grahami* (92.1% vs. 64.3%; $\chi^2 = 11.79$, 1 d.f., $P < 0.005$). *Anolis leachi* and *A. grahami* also did not differ in perch height (Table 2) or use of shade (71.8% vs. 69.9%; $\chi^2 = 0.06$, 1 d.f., $P > 0.80$), but they did differ in perch diameter, with *A. leachi* occurring on larger diameter surfaces (Table 2). In the perch diameter analysis for these two species, there was also a significant locality effect, which was not apparent in any of the other analyses. In addition, use of shade by *A. grahami* did not differ between sites at which it occurred alone, co-occurred with *A. extremus*, or co-occurred with *A. leachi* ($\chi^2 = 0.89$, 2 d.f., $P > 0.60$).

Interspecific Behavioral Interactions.—The behavior of resident *A. grahami* differed depending on the identity of the intruder. Resident *Anolis grahami* attacked conspecifics in 7 of 11

TABLE 1. Habitat use (mean \pm 1 s.e.) by the three *Anolis* species on Bermuda. Localities are: 1. In and around the Belmont Golf Course grounds, Warwick Parish; 2. Nonsuch Island, St. George's Parish; 3. Bermuda Botanical Garden grounds, Paget Parish; 4. Neighborhoods near the Bermuda Marine Biological Station, St. George's Parish; 5. Somerset Railway Trail, north of Fort Scaur, Sandys Parish; 6. Southern end of Somerset Railway trail and Fort Scaur grounds, Sandys Parish; 7. Mangrove Bay neighborhoods, Sandys Parish; 8. In and around Riddell's Bay Golf Course grounds, Warwick Parish. Sample size (N) refers to perch height; sample sizes are sometimes lower for perch diameter.

Local-ity	Species	Perch height (m)	Perch diameter (cm)	N
1	<i>grahami</i>	1.4 \pm 0.2	8.4 \pm 1.9	22
1	<i>leachi</i>	1.9 \pm 0.2	13.3 \pm 1.8	51
2	<i>grahami</i>	1.9 \pm 0.2	6.8 \pm 0.6	52
3	<i>grahami</i>	1.9 \pm 0.2	15.1 \pm 2.3	41
3	<i>leachi</i>	1.9 \pm 0.3	20.1 \pm 6.2	12
4	<i>grahami</i>	1.8 \pm 0.2	8.6 \pm 1.2	55
5	<i>grahami</i>	2.2 \pm 0.3	12.4 \pm 2.0	55
5	<i>extremus</i>	2.6 \pm 0.3	12.2 \pm 1.7	30
6	<i>grahami</i>	2.0 \pm 0.2	5.3 \pm 0.6	41
7	<i>grahami</i>	2.2 \pm 0.3	10.2 \pm 1.9	27
7	<i>extremus</i>	1.6 \pm 0.2	13.7 \pm 3.2	27
8	<i>grahami</i>	1.7 \pm 0.2	8.4 \pm 2.5	27
8	<i>leachi</i>	1.9 \pm 0.2	11.6 \pm 1.5	29

trials. By contrast, when the intruder was the similar-sized *A. extremus*, the resident usually displayed (nine of 10 trials), but only attacked in two trials. When the intruder was *A. leachi*, *A. grahami* fled in all six cases.

DISCUSSION

Anolis grahami was introduced to Bermuda in 1905. In less than 60 yr (by 1963), it had almost entirely covered the archipelago. *Anolis leachi* and *A. extremus* have now been on Bermuda for almost that long (minimally 56 and 43 yr, respectively [Wingate, 1965]), but their expansion has been considerably less rapid: *A. leachi* now covers approximately half of the archipelago and *A. extremus* is still restricted to a relatively small area in northwestern Bermuda. Comparison of the rate of spread of the three species is complicated by human agency. Wingate (1965, pp. 213) noted that "because *Anolis* [*grahami*] was a novelty in Bermuda, the dispersion was aided by various people who caught lizards in the central parishes for release in gardens at either end of the island."

Similarly, *A. leachi* may have been transported around the island either intentionally, as Wingate described for *A. grahami*, or unintentionally by thriving Bermudian horticultural

TABLE 2. Two-way analyses of variance for differences in habitat use at sympatric species localities. Unpublished multivariate analyses of variance provided similar results.

	Sum of squares	d.f.	Mean square	F-Ratio	P
a) <i>A. grahami</i> - <i>A. extremus</i>					
i) Perch Height					
Species	0.014	1	0.014	0.020	0.888
Locality	1.460	1	1.460	2.156	0.145
Species × Locality	2.275	1	2.275	3.359	0.069
Error	77.218	114	0.677		
ii) Perch Diameter					
Species	0.770	1	0.770	1.034	0.312
Locality	0.906	1	0.906	1.216	0.273
Species × Locality	0.407	1	0.407	0.547	0.461
Error	78.199	105	0.745		
b) <i>A. grahami</i> - <i>A. leachi</i>					
i) Perch Height					
Species	1.348	1	1.348	2.710	0.102
Locality	1.334	2	0.667	1.341	0.264
Species × Locality	0.710	2	0.355	0.714	0.491
Error	87.571	176	0.498		
ii) Perch Diameter					
Species	4.433	1	4.433	4.922	0.028
Locality	6.695	2	3.347	3.717	0.026
Species × Locality	1.657	2	0.829	0.920	0.401
Error	139.585	155	0.901		

businesses, as several Bermudians suggested to me. In support of the former possibility, Mr. R. Winchell of the Bermuda Aquarium informed me (pers. comm.) that *A. leachi* had been introduced intentionally onto the aquarium grounds in northern Smith's Parish. With regard to the possibility that nurseries were transporting lizards along with the plants they sell, one nursery operator I spoke with said she had never seen lizards transported on nursery deliveries because the lizards always abandoned the plants as they were loaded onto vehicles; still, eggs could easily be translocated in this manner. Certainly, the isolated populations of *A. leachi* in Pembroke Parish originally reported by Wingate (1965; but no longer isolated from the main *A. leachi* population; Fig. 1) and in Sandy's Parish (this study) suggest that humans may have played a role in their dispersal.

Regardless of the mechanism by which these species have expanded their range, these findings suggest two important conclusions concerning anole community structure. First, as Wingate (1965) noted, the presence of *A. grahami* may have inhibited the spread of the two subsequently introduced species. This result would not be surprising given the similarity of the three species in habitat use (Wingate, 1965; Schoener, 1970; this study) and diet (Simmonds, 1958; Wingate, 1965). Thus, whereas *A. grahami* was able to expand into areas unoccupied by

competitors, the two subsequently introduced species were forced to expand into areas already occupied by a potentially competing species. Indeed, compelling evidence exists that interspecific competition is an important factor structuring anole communities in general (Losos, 1994). Of course, other factors may have contributed to the interspecific differences in rate of range expansion, including the loss of tree cover in the 1940s, after *A. grahami* was already widely distributed (Wingate, 1965), or differences in predation pressure, human transport (discussed above), or susceptibility to cold weather (see Wingate, 1965).

Second, colonizing species can become established and expand their range in the presence of ecologically similar resident species. This finding is important because theories of competition-induced coevolutionary change (e.g., character displacement) require as their first stage that similar species exist in sympatry. Some theoretical treatments predict that two ecologically similar species cannot coexist long enough for evolutionary change because one species is likely to become extinct (reviewed in Taper and Case, 1992). However, the case of *A. extremus* and *A. grahami* indicates that species similar in both ecology and body size can not only coexist, but also can expand their ranges into areas occupied by the other species (*A. grahami* into the Ireland Islands, *A. extremus* into Sandys and

Southampton Parish). Knowledgeable Bermudian naturalists had informed me where to look to find these species sympatrically; thus, these records probably represent real range expansions rather than aberrant or seasonal occurrences.

Although ecologically similar, the species are not identical; ecological differences between the species may be sufficient for coexistence. *Anolis leachi* is considerably larger than the other two species and thus can take prey too large to be consumed by the other species (Wingate, 1965; a relationship between body size and prey size is common in anoles [e.g., Schoener and Gorman, 1968; Roughgarden, 1974]). In sympatry, *A. leachi* is behaviorally dominant to *A. grahami* (Wingate [1965] and above) and forces it to use more peripheral perches that are too small for *A. leachi*. Although vegetational differences precluded investigation of whether *A. grahami* shifts its habitat use in the presence of *A. leachi*, Schoener's (1975) analysis, which corrected for differences in habitat availability among sites, found such a shift. Consequently, the coexistence of these two species may result both from differences in prey utilization and in the ability of the behaviorally subordinate *A. grahami* to use habitats unavailable to *A. leachi*.

Anolis extremus and *A. grahami* are similarly sized and utilize similar prey (Wingate, 1965). They differ in their use of thermal microhabitat: *A. extremus* prefers cooler areas and is more often found in the shade relative to the more heliophilic *A. grahami* (Wingate, 1965; Schoener, 1970; this study). These preferences are so extreme that the occupation of a particular perch will change from one species to the other during the course of the day as the perch's insulation changes from sun-to-shade or vice-versa (Schoener, 1970; Losos, unpubl.). This study failed to find a difference between the two species in perch height or diameter, but Schoener's previous study (1970) found slight differences in perch diameter and height (*A. grahami* on higher and thinner perches). Consequently, I conclude that *A. grahami* and *A. extremus* are similar enough ecologically to compete for resources, and thus slow their range expansions, but are not so similar as to preclude coexistence. A review of 23 anole introductions in the Caribbean indicates that this is a common outcome of anole introductions (Losos et al., 1993).

Conclusions.—The study of introduced species can provide insight into the assembly of multi-species communities. *Anolis* has experienced independent evolutionary radiations on each of the islands in the Greater Antilles (Williams, 1972). One model of this radiation posits that: (1) ecologically similar species come into sympatry; (2) competitive pressures force them to

utilize distinctive microhabitats; (3) subsequent evolutionary adaptation to these niches leads to the evolution of specialized morphologies and physiologies; and (4) repeated instances of this specialization produce communities containing a suite of specialist species (Williams, 1972, 1983; Losos, 1992, 1994). Anole introductions in Bermuda thus re-create the conditions of the first stage of this hypothesis when ecologically similar species come into contact. The results reported here indicate that such species can coexist and even expand their range. Investigation of the next step in the hypothesis—adaptation to particular microhabitats—would provide a valuable test of the anole adaptive radiation hypothesis.

Acknowledgments.—For permission to work on their property, I thank Mrs. Fay Watlington, Mr. David Wingate (Superintendent, Nonsuch Island), The Bermuda Marine Biological Station, Bermuda Botanical Garden, Belmont Golf Club, and Riddell's Bay Golf Club. For assistance, advice, information, and comments on previous versions of this manuscript, I thank D. Wingate, S. DeSilva, T. Schoener, R. Henderson, L. Wilson, R. Winchell, and an anonymous reviewer. Field work was ably assisted by C. Losos, J. Losos, D. Silverman, and S. C. Baxter. Permission to conduct this research was kindly granted by N. Burnie, Department of Agriculture, Fisheries, and Parks, Bermuda. This research was funded by a grant from the National Geographic Society and by the Center for Population Biology, University of California, Davis.

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Accepted: 23 January 1996.