

Habitat use and ecological interactions of an introduced and a native species of *Anolis* lizard on Grand Cayman, with a review of the outcomes of anole introductions

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Abstract. Since its introduction ten years ago, *Anolis sagrei* has spread over much of Grand Cayman and is now more common in some habitats than the native anole, *A. conspersus*. Interspecific differences in body size, perch height, and microclimatic preference may have facilitated the colonization. Nonetheless, competition may be occurring between the species; comparisons with studies of habitat use prior to the arrival of *A. sagrei* indicate that in open habitats, where *A. sagrei* is now abundant, *A. conspersus* perches higher, but in closed habitats, where *A. sagrei* is absent, no change in perch height is evident. Review of data concerning 23 *Anolis* introductions indicates that the presence or absence of an ecologically similar native species may be an important determinant of colonization success or failure.

Key words: Invasion – Competition – Community construction – Islands – Lizards

Although community ecologists have intensely debated which factors are responsible for maintaining community structure, only recently is equivalent attention being devoted to the factors affecting the construction of communities (Drake 1990, 1991; Brooks and McLennan 1991). Several authors have suggested that in communities which arise by sequential immigration of species (such as oceanic islands), community structure is shaped by both the relatively rapid processes acting in ecological time and the slower processes acting over evolutionary time (Roughgarden et al. 1983; Rummel and Roughgarden 1983; Case 1983; Case and Sidell 1983; Grant 1986). Moreover, kinds of communities may differ in the relative importance of ecological vs. evolutionary processes, which may lead to systematic differences in community structure (Rummel and Roughgarden 1983, 1985; Schoener 1986; Taper and Case 1992a, b). For example, in “invasion-structured communities” (using the terminology of Rummel and Roughgarden [1983, 1985]), an invading species must

be pre-adapted to coexist with members of the community by sufficient differences in resource utilization or competition will result in the extinction of either the invader or one or more residents (here we focus on competition, but the concept is easily extended to other types of interactions, such as predation). By contrast, in “co-evolution-structured communities”, competition leads to evolutionary changes that may result in coexistence. Behavioral shifts have also been observed in *Anolis* (Jenssen 1973); although not explicit in the simplest models, they could be part of either scenario.

Lizards of the genus *Anolis* are ideal for analyzing community construction and faunal accumulation. Many studies (references in Losos 1990a) have documented the interactions within simple and complex communities on Caribbean islands. The extent to which these communities result from coevolutionary processes, and whether any existing simple community represents a first stage in the faunal buildups culminating in the species-rich anole communities of the Greater Antilles, is unclear (see Williams 1972; Roughgarden 1989, 1992; Losos 1992a, b).

The study of introductions of non-native species can provide valuable data relevant to understanding the dynamics of community assembly (e.g., Moulton and Pimm 1983, 1986). A great number of human-assisted anole introductions have been documented in the Caribbean region. Examination of the outcome of these events may provide an analogy useful in understanding the evolution of anole faunas in the Caribbean.

In this paper, we discuss the recent introduction of *Anolis sagrei* to Grand Cayman (114 km²), an island previously occupied solely by *A. conspersus*. *Anolis sagrei* was first detected on Grand Cayman in the western part of the island (Minton and Minton 1984); it now occurs throughout much of the island (G.C. Mayer, pers. comm.; Losos and Marks, unpubl. obs.). Below, we first discuss differences in habitat use between *A. sagrei* and *A. conspersus* and present evidence of habitat shifts by the latter in the presence of the former. We then review the history of *Anolis* introductions to assess the relative importance of ecological versus coevolutionary processes in the construction of anole communities.

Materials and methods

Habitat shift on Grand Cayman

We investigated whether *A. sagrei* and *A. conspersus* differ in body size and thermal and structural habitat on Grand Cayman. Our studies were conducted in January, 1991 in two primary locations: on the west side of the island, we worked in several localities on the southern and eastern outskirts of Georgetown; on the eastern half of the island, we worked at a site along the main southern road 7 mi east of Boddentown. In both areas, we worked in both open and closed (wooded) habitats. Body size was measured by capturing large adult males and measuring snout-vent length (svl), which is the distance from the tip of the rostrum to the anterior edge of the cloacal vent.

Habitat use was measured by slowly walking through representative habitats at each site between 8 a.m. and 4 p.m. and noting for each lizard:

- (1) *species*;
- (2) *size class*, scored as adult males, adult-female-sized lizards, or juveniles (both species show relatively great sexual dimorphism in size; following Schoener [1975], sub-adult males are combined with adult females because the categories correspond to size classes and the sex of a lizard could not always be determined from a distance; size cutoffs for juveniles may not have been exactly the same in the studies, however);
- (3) *height above the ground* (estimated to the nearest 0.25 m) for individuals above 2 m; and
- (4) *thermal microhabitat*, scored as sun, filtered sun, or shade (if the sun was not obscured by clouds).

Lizards were scored only if their initial location was observed (i.e., animals observed in flight were not included). We attempted to avoid repeated censusing in the same area so as not to resample the same individuals. Body temperature was measured by capturing lizards (generally adult males) either with a noose or by hand, and immediately inserting a quick-reading cloacal thermometer while keeping the lizard shaded. Lizards were only captured during sunny and warm periods when they had the opportunity to thermoregulate at preferred temperatures. Flight response was measured on a subset of lizards by approaching a lizard from a distance of 3–5 m at a standard pace (on average 27.5 m/min) and noting the distance at which the lizard first moved. The direction of escape (up, down, or away in a horizontal direction) was recorded for a different subset of lizards. For comparative purposes, we also report data on perch height and shade of adult male *A. sagrei* from Cayman Brac and Little Cayman (note that there are two species of anoles native to Little Cayman, and only one to Cayman Brac [though *A. maynardi* has recently been introduced to the latter]). Data were ln-transformed for all parametric statistical tests.

Several studies were conducted on the habitat use of *A. conspersus* prior to the introduction of *A. sagrei*. By comparing our data on perch height of *A. conspersus* with those reported previously, we can determine whether *A. conspersus* has experienced a shift in habitat use. We did not account for potential differences in habitat availability, which may account for shifts in perch height (Schoener 1975). However, two of the previous studies report perch height in both open and closed habitats. Because *A. sagrei* is not found in closed habitats, these data serve as a kind of control; habitat shifts would be expected only in open habitats.

The most direct comparison is between our western sites and that of Schoener (1975) at a locality near Georgetown (< 2 km from one of our main study sites). In the latter study, data were collected in an open and a wooded area in spring and early summer 1967.

Comparison to two other studies may provide less insight. First, Schoener (1967) reported data on perch height for adult and sub-adult males, adult females, and juveniles collected in April, 1966. However, these data were pooled from samples collected island-wide and no distinction was made between open and closed habitats. Schoener's (1967) data for sub-adult males and females were lumped to facilitate comparison with our data. Second, Avery (1988) collec-

ted data on the eastern half (east of the meridian 81° 08' W) of Grand Cayman in Feb–Mar, 1987, prior to the arrival of *A. sagrei*. Size/sex categories were different than those we have used such that only data for adult males are directly comparable. Data from open and closed habitats were reported separately. For several reasons, the comparison of our eastern study site to Avery's data may be difficult to interpret. First, at the time of our visit, *A. sagrei* had only recently spread to the eastern part of the island and were at relatively low abundance compared to the western study sites (G.C. Mayer, pers. comm.; Losos and Marks, unpubl.). Second, adult male *A. conspersus* at our eastern study site were small when compared to males on the western half of the island (11.6% smaller on average), to males seen at another site a short distance (< 1 km) away, and to previous reports of lizards from the eastern part of the island (Grant 1940). This observation might suggest that at our eastern site, either some event (e.g., predation, storm) had eliminated the largest individuals of the population, or that the habitat tended to select against large individuals. Perch height of these lizards seemed unusually low as well.

All previous studies presented their data in categorical form (R. Avery kindly provided us with the data used to construct his published figures). We cast our data into the same categories and compared our data to those previously reported using the Kolmogorov-Smirnov Two-sample Test (two-tailed). In cases in which the same data were used in multiple comparisons, the sequential Bonferroni technique with a table-wise alpha of 0.05 was employed to judge statistical significance (Rice 1989). Significance levels provided below are the original probability values; all remain significant when adjusted using the sequential Bonferroni method.

Review of anole introductions

Anoles have been widely transported, usually unintentionally, throughout the Caribbean and elsewhere (Williams 1977). We reviewed the literature and located 22 cases other than *A. sagrei* on Grand Cayman of anole species introduced to areas in which they were not native. This total does not include experimental introductions whose outcome was not clear, nor does it include introductions to islands or habitats in which no anoles occurred.

For each introduction, we determined whether the introduced species was ecologically similar to the resident species. In cases in which there was more than one resident species, the introduced species was compared to the most similar resident species. Whether or not two species were considered ecologically similar was determined as follows. For Greater Antillean taxa, any pair of species differing in "ecomorph" type, an indicator of structural habitat use (Williams 1983; Losos 1990a), were considered ecologically dissimilar. Further, members of the same ecomorph were considered ecologically dissimilar if they differed in thermal microclimate. In the Lesser Antilles, ecological coexistence is primarily a function of body size (Schoener 1970; Roughgarden 1992). Pairs of Lesser Antillean taxa had to differ in body size by a ratio of 1.65 to be considered dissimilar. This value corresponds to differences observed among sympatric Lesser Antillean taxa (one pair of Lesser Antillean anoles on St. Maarten differ in body size by less than 1.65, but the stability of their coexistence is unclear [Roughgarden and Pacala 1989]). The only introduction involving both Greater and Lesser Antillean taxa occurs on Bermuda. Because the invading species were from the Lesser Antilles, we used the criterion here that species must be different in body size to be judged ecologically dissimilar.

The outcome of each introduction was scored as widespread, marginal, or failed. Widespread introductions are those that have spread widely geographically: for islands, the introduction had to cover at least 50% of the total island area; for mainlands, the introduction had to have a range greater than 15 km in length. Marginal introductions refer to populations that are not geographically widespread and include some populations that are slowly increasing their range.

Results

Results of 1991 study

On Grand Cayman, adult male *A. conspersus* ($\bar{x} \pm \text{SE} = 66.0 \pm 0.89$ mm, $n = 27$) are larger than adult male *A. sagrei* ($\bar{x} = 51.1 \pm 0.57$, $n = 31$; t -test, $t = 14.8$, $P < 0.001$). Within *A. conspersus*, males tend to perch higher than female-sized lizards (hereafter referred to as "females"; Kolmogorov-Smirnov two-sample test, $D_{\max} = 0.31$, $n = 109, 193$, $P < 0.001$ [statistical analyses following Siegel and Castellan 1988]), which perch higher than juveniles ($D_{\max} = 0.25$, $n = 193, 47$, $P < 0.05$; Fig. 1). No differences exist among classes of *A. sagrei* ($P \gg 0.05$ in all comparisons). In open sites, where the species occur sympatrically, interspecific differences in microhabitat use are apparent. Both male and "female" *A. conspersus* perch higher than all classes of *A. sagrei* ($D_{\max} > 0.60$, $P < 0.005$ in all comparisons; data from western end of island). *Anolis conspersus* also tends to use more shaded perches than *A. sagrei* at these localities ($\chi^2 = 28.05$, 1 df, $P < 0.0005$; Fig. 2; males, "females", and juveniles were lumped for this comparison because no intraspecific differences were detected in either species [$P > 0.20$ in intersexual comparisons; sample sizes for juveniles were insufficient for χ^2 tests, but proportions of juveniles in the different shade categories were similar to those for males and "females"; the statistical conclusion is the same when juveniles are removed]).

The interspecific difference in thermal habitat is reflected in differences in body temperature: *A. sagrei* ($\bar{x} = 32.5 \pm 0.25$, $n = 27$) exhibits a higher mean body temperature than *A. conspersus* ($\bar{x} = 31.1 \pm 0.21$, $n = 26$; t -test, $t = 4.36$, $df = 50.4$, $P < 0.001$). These data were collected at several localities, over several days, and at different times of the day (but always collecting data for both species in all sampling periods). To investigate potential confounding factors, we also analyzed the largest data set collected at one time, a sunny morning during which we collected 13 lizards in two-hours. In this period, the species also differ

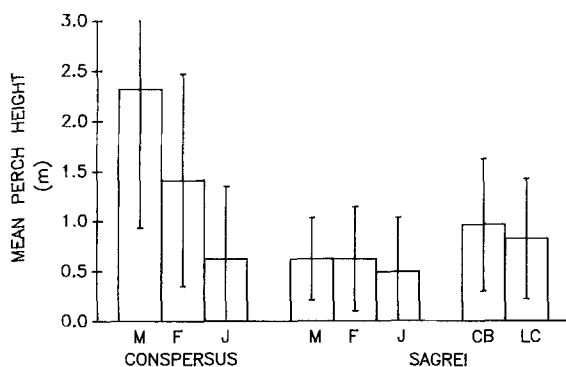


Fig. 1. Perch height of *Anolis* in the Cayman Islands (mean \pm 1 SD; see cautionary note in Table 1). Data for *A. conspersus* include all localities. Male, female, and juvenile *A. sagrei* are from Grand Cayman; values for *A. sagrei* from Cayman Brac (CB) and Little Cayman (LC) are for adult males only. Samples sizes: *A. conspersus* males – 109, females – 193, juveniles – 47; Grand Cayman *A. sagrei* males – 68, females – 48, juveniles – 11; Cayman Brac *A. sagrei* – 71; Little Cayman *A. sagrei* – 62

in body temperature (*sagrei*: $\bar{x} = 33.0 \pm 0.52$, $n = 8$; *conspersus*: $\bar{x} = 30.9 \pm 0.50$, $n = 5$; Mann-Whitney U -test, $U = 3.5$, $P < 0.02$).

Within species, male *A. conspersus* escape up more often and down less often (64% up vs 17% down, $n = 66$) than "females" (42% vs 17%, $n = 108$), and "females" escape up more and down less often than juveniles (36% vs 39%, $n = 28$) ($\chi^2 > 7.1$ [2 df] in both cases and $P < 0.05$ or better). The classes do not differ for *A. sagrei* (the same figures for males, "females" and juveniles are, respectively: 7% vs 41% [$n = 44$], 10% vs 38% [$n = 29$] and 0% vs 50% [$n = 8$]). The escape responses of the two species parallel the difference in microhabitat use: males and "females" of *A. conspersus*, which perch higher, escape by moving up more and down less often than do the same classes of *A. sagrei* ($\chi^2 > 11.8$ in all cases and $P < 0.01$ or better). Differences between the sexes in flight distance are not significant (in t -tests) for either species. Flight distance is greater for *A. sagrei* ($\bar{x} = 1.30 \pm 0.12$ m, $n = 50$) than for *A. conspersus* ($\bar{x} = 0.63 \pm 0.08$ m, $n = 50$; $t = 4.45$, 98 df, $P < 0.001$).

Comparison to previous studies on Grand Cayman

Comparison to Schoener's (1975) data provides evidence of habitat shift on the west half of Grand Cayman (Fig. 3). In open habitats, where *A. sagrei* is present, both males ($D_{\max} = 0.276$, $n = 57, 254$, $P < 0.005$) and "females" ($D_{\max} = 0.251$, $n = 60, 302$, $P < 0.005$), but not juveniles ($D_{\max} = 0.205$, $n = 8, 11$, $P \gg 0.10$), have shifted up in habitat use since the arrival of *A. sagrei* (Fig. 3a; Table 1a). In closed habitats, where *A. sagrei* does not occur, no evidence of habitat shift exists (males: $D_{\max} = 0.097$, $n = 30, 191$, $P \gg 0.10$; "females": $D_{\max} = 0.117$, $n = 45, 376$, $P \gg 0.10$; juveniles: $D_{\max} = 0.248$, $n = 8, 18$, $P \gg 0.10$; Fig. 3b; Table 1a). The island-wide comparison (Schoener 1967) also indicates that adult male *A. conspersus* uses higher perches now than before the introduction of *A. sagrei* (Kolmogorov-Smirnov two-sample test, $D_{\max} = 0.192$, $n = 109, 138$,

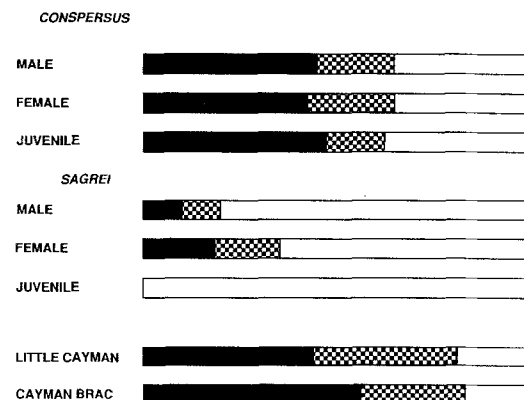


Fig. 2. Use of sun vs. shade in Cayman Island anoles. Black portion of each rectangle represents proportion of lizards of a given type observed in the shade. Similarly, the checkered portion represents lizards in filtered shade and the blank portion represents lizards in the sun. Lizards observed when the sun was obscured by clouds are not included. Data were only collected for male *A. sagrei* on Little Cayman and Cayman Brac

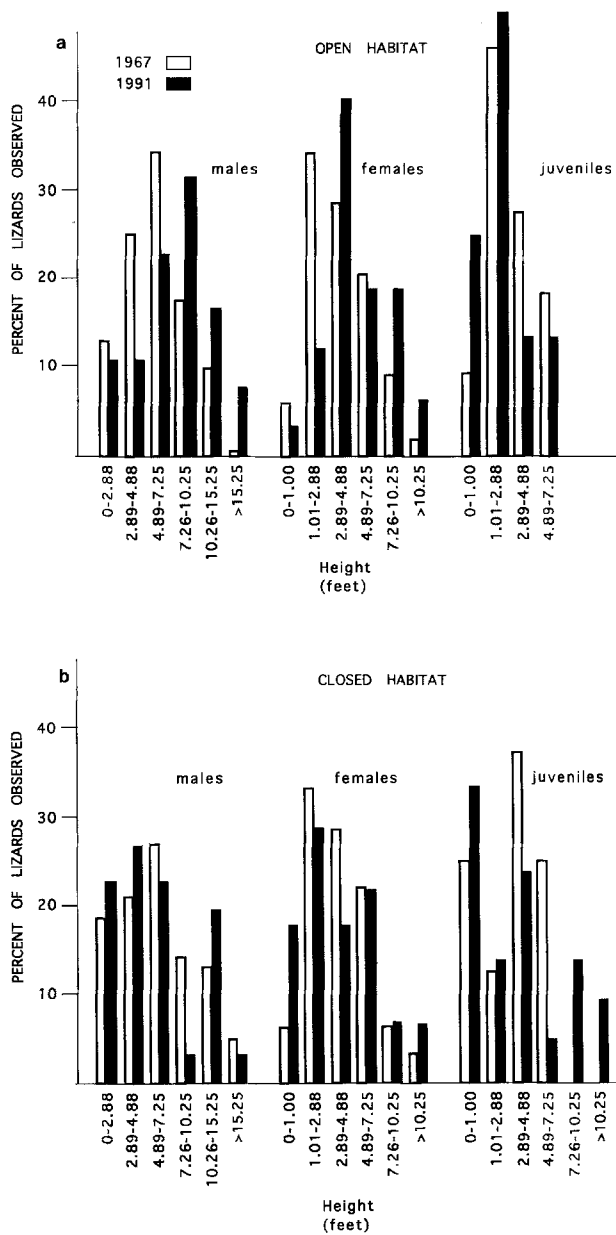


Fig. 3a,b. Comparison of perch height distributions for *A. conspersus* in 1967 and 1991. a open habitats; b closed habitats

$P < 0.025$). A similar shift is marginally significant for "females" ($D_{\max} = 0.120$, $n = 193$, 285 , $0.05 < P < 0.10$), but no shift is significant for juveniles ($D_{\max} = 0.046$, $n = 47$, 51 , $P \gg 0.10$; Table 1b). In eastern Grand Cayman, adult male *A. conspersus* exhibit an upward shift in open habitats comparable in magnitude ($D_{\max} = 0.291$; increase in mean perch height = 0.50 m) to the other comparisons (Table 1c), but the difference is not significant ($P \gg 0.10$) at this sample size ($n = 7$, 58). In closed habitats, no shift is evident ($D_{\max} = 0.067$, $n = 15$, 80 , $P \gg 0.10$).

Comparison to data from *A. sagrei* elsewhere in the Cayman Islands

Anolis sagrei males on Cayman Brac ($D_{\max} = 0.29$, $n = 68$, 71 , $P < 0.005$) and Little Cayman ($D_{\max} = 0.22$, $n = 62$, 68 ,

$P < 0.10$) use higher (marginally in one case) and shadier microhabitats ($\chi^2 > 40.0$, 2 df, $P < 0.0005$ in both cases) than their counterparts on Grand Cayman (Figs. 1 and 2).

Review of anole introductions elsewhere

A summary of anole introductions is presented in Table 2. There are only two reported cases of introduced species becoming extinct (of course, others probably failed before being noticed); both involved cases in which an ecologically similar species was already present. Seven instances exist in which an introduced species has spread widely; all occurred in the absence of an ecologically similar native species. The difference between successful and unsuccessful (= marginal + failed) introductions is significant (Fisher's Exact Test, $P < 0.005$).

Colonization success is often inversely correlated with number of species in the native community (Case 1990, 1991), but for anole introductions no obvious relationship exists (Table 2).

Discussion

Since its appearance only ten years ago, *A. sagrei* has spread rapidly to occupy most of Grand Cayman, in some places at very high densities. What factors allowed this invasion to flourish so quickly? Possibilities include ecological differences between the species before contact, i.e., pre-adaptations for coexistence, as well as differences developing after colonization in the resident or the invader or both. Kinds of differences favoring coexistence might be surmised from the more complex anole faunas of the Greater Antilles, in which three resource axes are partitioned (Schoener and Schoener 1971a, 1971b; Schoener 1977; Williams 1972): structural habitat (i.e., perch height and diameter), thermal habitat (which often reflects macrohabitat), and prey size.

Above, we presented data for the resident, *A. conspersus*, showing that a shift in structural habitat seems to have occurred after invasion. The extent to which the invader, *A. sagrei*, may have shifted subsequent to arrival on Grand Cayman might be surmised from comparisons to its probable source populations. Because of geographic proximity and commercial trade patterns, Cuba and Florida are the most likely ancestral possibilities. Cayman Brac and Little Cayman seem ruled out on morphological grounds as the source (Lee 1992). Cuban and Floridian *A. sagrei* are thermophilic and use low habitats (Collette 1961; Ruibal 1961; Salzburg 1984), just as *A. sagrei* does on Grand Cayman. Thus, major post-invasion habitat shifts by *A. sagrei* seem unlikely from these limited data.

In contrast to differences that may have developed after contact, differences that characterize the two species throughout their ranges, and thus precede sympatry on Grand Cayman, are relatively great. Preferred body temperatures suggest major thermal habitat differences, and relative limb lengths suggest major structural habitat differences (Rand 1967; Schoener and Schoener 1971a, 1971b; Lister 1976; Losos 1990a). Body-size differences, although not great, suggest some differences in prey size as

Table 1. Evidence for habitat shift by *A. conspersus* subsequent to the introduction of *A. sagrei*

		Perch height, m ($\bar{x} \pm SE$) ^a			
a) West end		Open habitat		Closed habitat	
		1967	1991	1967	1991
	Males	1.86 ± 0.06 (n = 254)	2.43 ± 0.19 (n = 57)	1.95 ± 0.09 (n = 191)	1.90 ± 0.25 (n = 30)
	Female-sized lizards	1.22 ± 0.03 (n = 302)	1.64 ± 0.13 (n = 60)	1.25 ± 0.03 (n = 376)	1.32 ± 0.19 (n = 45)
Juveniles	0.85 ± 0.26 (n = 11)	0.63 ± 0.16 (n = 8)	0.64 ± 0.16 (n = 8)	0.84 ± 0.20 (n = 18)	
b) Island-wide			1966		1991
	Males		1.49 ± 0.25 (n = 138)		2.08 ± 0.13 (n = 109)
	Female-sized lizards		0.96 ± 0.14 (n = 285)		1.27 ± 0.08 (n = 193)
	Juveniles		0.61 ± 0.31 (n = 51)		0.71 ± 0.11 (n = 47)
c) East end		Open habitat		Closed habitat	
		1987	1991	1987	1991
Males	0.88 ± 0.07 (n = 58)	1.38 ± 0.38 (n = 7)	1.43 ± 0.12 (n = 80)	1.44 ± 0.28 (n = 15)	

^a Data from 1966, 1967, and 1987 were reported in categorical form and were assigned mid-point values to calculate means and variances. We caution that data are not normally distributed, so that means and standard errors are not entirely adequate descriptions of the data

Table 2. Success of introductions to anole-inhabited localities

Island	Introduced species	Resident species ^a	Ecologically similar ^b	Result ^b	References
Anguillita	<i>pogus</i>	<i>gingivinus</i> (1)	yes	Failed	1
Bermuda	<i>leachi</i>	<i>grahami</i> (1)	no	Widespread	2
Bermuda	<i>extremus</i>	<i>grahami</i> (1)	yes	Marginal	2
Cayman Brac	<i>maynardi</i>	<i>sagrei</i> (1)	no	Marginal	3
Florida	<i>distichus</i> ^c	<i>carolinensis</i> (1–2)	no	Widespread	4
Florida	<i>sagrei</i>	<i>carolinensis</i> (1–2)	no	Widespread	4
Florida	<i>equestris</i>	<i>carolinensis</i> (2–3)	no	Widespread	4
Florida	<i>conspersus</i>	<i>carolinensis</i> (1)	yes	Failed	5
Florida	<i>cybotes</i> ^c	<i>sagrei</i> (2–3)	yes	Marginal	4
Florida	<i>cratellus</i>	<i>sagrei</i> (2–3)	yes	Marginal	4
Florida	<i>garmani</i>	<i>equestris</i> (3–4)	yes	Marginal	4
Grand Bahama	<i>carolinensis</i>	<i>sagrei</i> (1–2)	no	Marginal ^d	3
Grand Bahama	<i>distichus</i>	<i>sagrei</i> (1–2)	no	Widespread	3
Grand Cayman	<i>sagrei</i>	<i>conspersus</i> (1)	no	Widespread	6
Great Abaco	<i>distichus</i>	<i>sagrei</i> (1)	no	Marginal	7
Hispaniola	<i>cratellus</i>	<i>cybotes</i> (4)	yes	Marginal	8
Hispaniola	<i>porcatus</i>	<i>chlorocyanus</i> (4)	yes	Marginal	9
Jamaica	<i>sagrei</i>	<i>lineatopus</i> (5)	no	Widespread	10
Louisiana	<i>sagrei</i>	<i>carolinensis</i> (1)	no	Marginal	11
St. Lucia	<i>wattsi</i>	<i>luciae</i> (1–2)	yes	Marginal ^e	12
St. Lucia	<i>extremus</i>	<i>luciae</i> (1–2)	yes	Marginal	13
St. Maarten	<i>bimaculatus</i>	<i>gingivinus</i> (2)	yes	Marginal	14
Trinidad	<i>aeneus</i>	<i>trinitatis</i> ^f (2)	yes	Marginal	15

References 1. Roughgarden et al. 1984; 2. Wingate 1965; 3. Losos, unpubl. (voucher specimens deposited in the Museum of Comparative Zoology, Harvard University); 4. Wilson and Porras 1983; 5. King and Krakauer 1966; 6. This study; 7. Schoener, unpubl.; 8. Fitch et al. 1989; 9. Powell et al. 1990; 10. Williams 1969; 11. Thomas et al. 1990, R.A. Thomas, pers. comm.; 12. Corke 1987, pers. comm.; 13. Gorman 1976; 14. Powell et al. 1992; 15. Gorman et al. 1971; Gorman and Boos 1972

^a Number in parentheses is the total number of *Anolis* species in the local community at the time of invasion. In some cases of multiple introductions, uncertainty exists concerning this number, so a range of numbers is given

^b Defined in text

^c A previous introduction of *A. cybotes* and *A. distichus ignigularis* (King and Krakauer 1966) appears to have failed (Wilson and Porras 1983), though it is unclear whether the latter may have been replaced by other subspecies of *A. distichus* now in Miami

^d Based on 1.5 days of fieldwork on Grand Bahama in 1992, *A. carolinensis* does not appear to be widespread (Losos, unpubl. data)

^e Contrary to Gorman (1976), *A. wattsi* is common in some localities and has expanded its range on St. Lucia (Corke 1987; pers. comm.; Losos and de Queiroz, unpubl.)

^f Although no historical documentation exists, both taxa appear to have been introduced (Gorman et al. 1971). The species are found in pure enclaves, and *A. aeneus* appears to be expanding at the expense of *A. trinitatis* (Gorman and Boos 1972)

Table 3. Summary of successes and failures of *Anolis* introductions

	Widespread	Marginal	Failed
Ecologically similar	0	10	2
Ecologically different	7	4	0

well (data [including *A. sagrei* and *A. conspersus*] in Schoener 1967, 1968; Schoener and Gorman 1968; Roughgarden 1974; but see Floyd and Jenssen 1983). Consequently, differences that developed before rather than after invasion seem to have played the larger role in allowing the thoroughly established coexistence we now observe.

Six other introduced *Anolis* species have become geographically widespread, and in each case, as in Grand Cayman, resident species were not ecologically similar to the introduced species. By contrast, no introduced species has been able to expand to a significant extent in the presence of a similar species. In a similar vein, both documented instances of failure of an introduction involved ecologically similar species. In addition, on Trinidad, where two ecologically similar species were introduced, *A. aeneus* appears to be pushing the (ironically designated) *A. trinitatis* toward extinction (Gorman et al. 1971; Gorman and Boos 1972).

Nonetheless, more surprising is the number of introduced species – ten – able to avoid extinction despite the presence of an ecologically similar resident species. In at least one instance (*A. cristatellus* in Hispaniola), the species are parapatric, but in most other cases, the species are apparently sympatric (this, however, requires more careful study). In the latter introductions, selection pressure may strongly favor the evolution of ecological differences that permit coexistence. In one case, ecological shifts have been documented in resident *A. sagrei* in Florida in response to the introduction of *A. cristatellus* (Salzburg 1984). Whether evolutionary change occurs in this, or other, introductions should be worth studying.

No cases exist in which an introduced species perished in the presence of an ecologically dissimilar species. Nonetheless, competitive interactions may be substantial between such species. For example, in Bermuda, the presence of *A. leachi* apparently causes *A. grahami* to perch substantially lower (Wingate 1965; Schoener 1975). Similarly, competition-driven habitat shifts might result from the interaction between *A. carolinensis* and *A. sagrei* in Florida (Collette 1961; this interaction has little published documentation). On Grand Cayman, the situation is clear-cut: even though *A. sagrei* and *A. conspersus* were initially ecologically dissimilar and *A. sagrei* has easily spread over much of the island, competitive pressures appear to be enhancing the ecological segregation between the species. Over time, one might expect shifts in structural and climatic habitat to lead to morphological and physiological change; the precise documentation of these introductions and the periodic collection of specimens are needed to test this hypothesis.

We might speculate about why *A. sagrei* is historically absent from Grand Cayman. The overwater dispersal

ability of *A. sagrei* cannot be doubted given its occupation of isolated Caribbean islands and small portions of the Central American mainland (Williams 1969). Given this ability and the fact that *A. sagrei* has reached Cayman Brac and Little Cayman, a mere 112 km from Grand Cayman, it is indeed surprising that *A. sagrei* had not previously colonized Grand Cayman. In 1969, Williams suggested that the presence of *A. conspersus* prevented the establishment of *A. sagrei*. The success of *A. sagrei* subsequent to William's hypothesis may be accounted for in several ways. First, the presence of *A. conspersus* may have reduced the probability of an *A. sagrei* introduction succeeding (e.g., MacArthur 1972), albeit not to extremely low values. Second, propagules introduced by humans may be larger than natural propagules, which would make the success of an introduction more likely (Goel and Richter-Dyn 1974). Third, anthropogenic habitat alterations may have paved the way for the spread of *A. sagrei*, much as Williams (1969) suggested for Jamaica. *Anolis sagrei* was never observed in the closed forest on Grand Cayman, which has substantially diminished in area in this century (Proctor 1984). An admittedly *ad hoc* explanation of the failure of *A. sagrei* from Cayman Brac and Little Cayman to colonize Grand Cayman is that the *A. sagrei* on those islands, which tend to perch higher and in shadier microclimates than *A. sagrei* on Grand Cayman, are similar in structural and thermal habitat to *A. conspersus* (Figs. 1 and 2); their propagules may have been competitively exterminated because of great initial ecological similarity.

In conclusion, for the *Anolis* studied so far, initial differences between the species rather than those developing after contact may be more important in determining the outcome of invasions. Nonetheless, establishment of introduced populations in sympatry with residents sets the stage for coevolutionary processes to affect community structure as well. Further study of introductions may help us understand the important ecological and evolutionary factors in the build-up of the diverse and complex anole assemblages of Greater Antilles.

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