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Evolutionary consequences of ecological release in Caribbean *Anolis* lizards

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On the large islands of the Greater Antilles, multi-species communities of *Anolis* lizards are composed of species specialized to use particular habitats; similar sets of specialized species have evolved independently on each island. We studied species of anoles found on small Caribbean islands. Because these islands contain at most only one other species of anole, we predicted that species on these islands should not be as specialized as Greater Antillean species; rather, they might be expected to exhibit a generalized morphology and a greater breadth of habitat use. Our findings, however, do not confirm these predictions. Lesser Antillean species do not exhibit greater breadth of habitat use than Greater Antillean species, nor do they exhibit a generalized morphology. Most species are ecologically and morphologically similar to specialized trunk-crown anoles of the Greater Antilles, although some species exhibit morphologies unlike those seen in Greater Antillean species. Among descendants of specialized Greater Antillean species occurring on one- or two-species islands, most descendants of trunk-crown species have diverged relatively little, whereas several descendants of trunk-ground anoles have diverged considerably. Consequently, we propose that ancestral species in the Greater Antilles may have been trunk-crown anoles.

ADDITIONAL KEY WORDS:—adaptive radiation – lizard – phylogeny – specialization.

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INTRODUCTION

Because of their isolation, islands often are biologically depauperate. Insular plant and animal taxa often may face an environment with many available resources and few competitors or predators (Carlquist, 1974; Williamson, 1981). Evolutionary biologists have proposed two theories about the evolutionary outcome of such situations. On one hand, the availability of resources and lack of competitors may lead to 'ecological release' as organisms expand their resource use to incorporate resources they do not normally use in their ancestral environment (Lister, 1976a; Schoener, 1986). Over evolutionary time, this expansion may lead to the evolution of a generalist capable of using a broad range of resources, possibly at the cost of lack of specialization to any particular resource (Lister, 1976b). Alternatively, islands are famous for their adaptive radiations, in which a single ancestral species gives rise to a number of descendants, each specialized to a particular mode of resource use (Carlquist, 1974; Grant, 1986).

Both ecological release and adaptive radiation are well-documented in the literature and, indeed, they may not be mutually exclusive. One might suggest, for example, that ecological release is the first step in a sequence in which the original species evolves to use many resources and then, following repeated episodes of speciation, each of the descendant taxa evolves to specialize on one of these resources.

Examination of hypotheses about ecological release and adaptive radiation, and the relationship between the two, requires a group that might plausibly exhibit both phenomena and in which one might study the progression from one to the other. *Anolis* lizards on Caribbean islands provide an excellent system to examine such hypotheses. The large islands of the Caribbean document repeated and parallel cases of adaptive radiation (Williams, 1972, 1983; Losos, 1992). However, smaller islands in the Caribbean contain only 1–2 species and might be expected to represent early stages in an anole adaptive radiation (Williams, 1972). Consequently, comparison of anole faunas of larger and smaller islands may permit insight into the progression of the anole adaptive radiation.

Adaptive radiation of Caribbean Anolis

Islands in the Greater Antilles—Cuba, Hispaniola, Jamaica, and Puerto Rico (Fig. 1)—contain from seven to 40 or more species of *Anolis*, with local communities composed of as many as 10 sympatric species (Williams, 1983). Each island has experienced an evolutionary radiation in which species have adapted morphologically

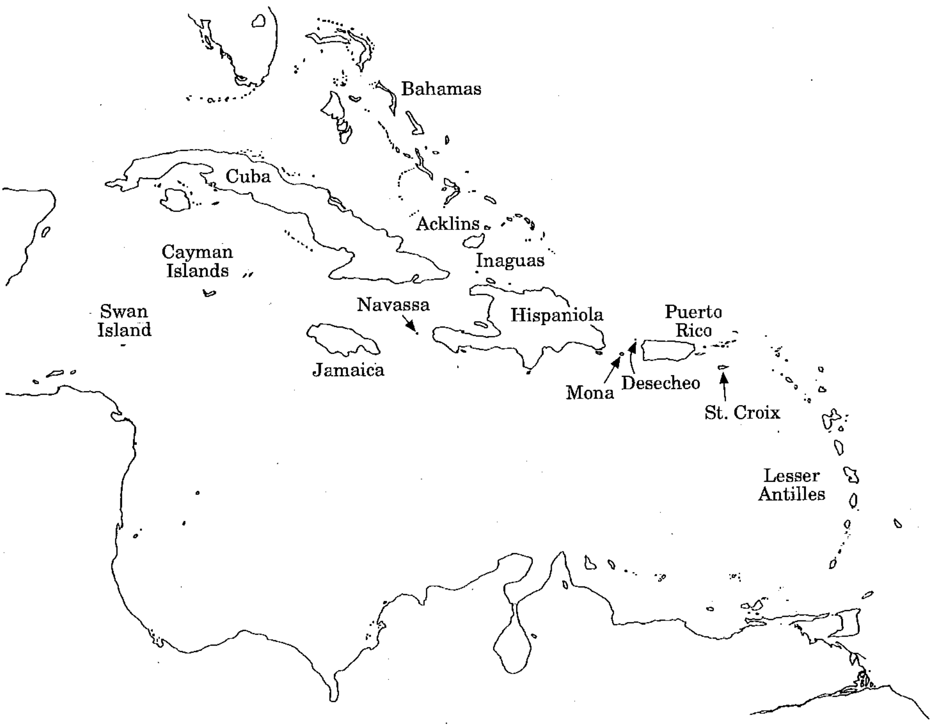

Figure 1. The Caribbean.

and behaviorally to different microhabitats. Six such 'ecomorph' classes (Rand & Williams, 1969; Williams, 1972, 1983) are recognized, each of which is named for the characteristic microhabitat of its constituent species: grass-bush, trunk, trunk-crown, trunk-ground, twig and crown-giant. Evolutionary diversification has proceeded more or less independently on each island of the Greater Antilles, producing—with several exceptions—communities containing members of each ecomorph class. Hence, strikingly similar anole communities have evolved at least four times (reviewed in Williams, 1983; Burnell & Hedges, 1990; Losos, 1994).

Phylogenetic analysis of anole community evolution on Jamaica and Puerto Rico suggested that as speciation occurred on each island, specialization to distinctive microhabitats occurred sequentially, presumably as a result of interspecific competition (Losos, 1992; see also Williams, 1972). Further, this analysis suggested that the ecomorphs were derived from an ancestral species that was intermediate in morphology and ecology and not assignable to any extant ecomorph class. The inferred morphological intermediacy of this ancestral species was interpreted to indicate that it was a 'jack-of-all-trades', specialized for no particular habitat, but capable of functioning proficiently in more habitats than its specialized extant descendants. A generalist species such as this would also be expected to be intermediate in mean habitat use and to display greater breadth of habitat use relative to the specialized ecomorphs. Although no known Greater Antillean species meets these criteria, several mainland anoles are intermediate in both morphology and habitat use (Irschick *et al.*, in press).

Two natural experiments can be used to test this hypothesis. The first involves islands in the Lesser Antilles which are inhabited by one or two species of anoles distantly related to those of the Greater Antilles. Williams (1972) proposed that these simple anole communities might be analogous to early stages in the evolution of the more complex faunas of the Greater Antilles (but see Roughgarden, 1989a; Roughgarden & Pacala, 1989). If this were the case, then one would expect anole species on these islands to be ecologically and morphologically generalized. Although quantitative data have never been presented to evaluate the degree of ecological or morphological specialization of Lesser Antillean anoles, descriptions of their habitat use, particularly for species on one-species islands, suggest that the breadth of habitat use of these species is unusually broad (Lazell, 1972).

The second natural experiment involves small islands in the northern Caribbean which are inhabited by taxa derived from specialized Greater Antillean taxa. If interspecific competition is the driving force behind habitat specialization in the Greater Antilles, then, in the absence of competitors, one might expect these taxa to reverse evolutionary direction and become less specialized (Schoener, 1975; Losos, Irschick & Schoener, 1994) with concomitant increased breadth in habitat use (i.e. ecological release; see Schoener [1986] for a recent review).

We tested the prediction that *Anolis* species in simple communities are generalized relative to the specialized ecomorphs of the Greater Antilles. In the context of anole adaptive radiation, ecological generalists may be recognized by two criteria: (1) intermediate or average morphology and habitat use relative to the extremes represented by members of the specialized ecomorph classes; and (2) greater breadth in habitat use. A third criterion, that populations of generalists should be more morphologically variable, is controversial (reviewed in Schoener, 1986) and is not examined here.

MATERIAL AND METHODS

Taxa sampled

Islands in the Lesser Antilles are occupied by distantly-related anole clades, the *bimaculatus* series in the north and the *roquet* series in the south (Gorman & Atkins, 1969; Hass *et al.*, 1993). These islands are inhabited by one or two naturally occurring anole species, although as a result of human introductions, several now have three (Losos, Marks & Schoener, 1993). Of 17 one-species Lesser Antillean islands (Schoener, 1970), the resident taxa on 16 are roughly the same body size—the exception being the large-sized *A. ferreus* on Marie Galante (Fig. 2). By contrast, the anole faunas of two-species islands are made up of a large and a small species, again with one exception—the intermediate-sized *A. gingivinus* on St. Maarten. Overall, 19 species of *Anolis* occur in the Lesser Antilles; we collected data on 17 of these species, omitting *A. oculatus* (Dominica) and *A. nubilus* (Redonda).

On small islands in the vicinity of the Greater Antilles, anoles closely related to specialized Greater Antillean taxa are often found with few or no sympatric anoles. Some of these islands have never been connected to one of the large islands of the Greater Antilles. In many cases, populations on these oceanic islands, which must have originated by overwater colonization, have differentiated to the extent that they are considered separate species or subspecies; we henceforth refer to these taxa as Greater Antillean derivatives.

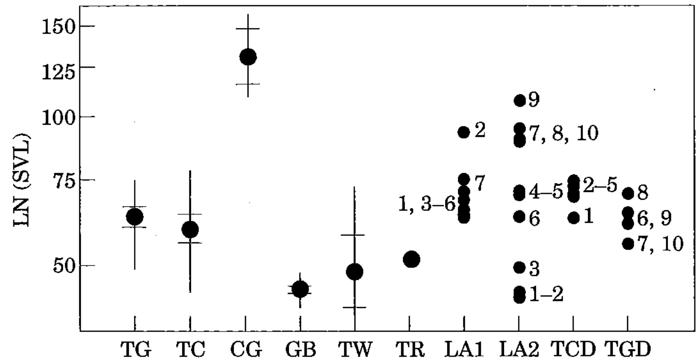

Figure 2. Body size of species in this study. For the ecomorph classes, symbols represent mean values, vertical bars represent the range in sizes and horizontal lines indicate the first standard error. Key to the numbers presented in legends to Figures 4–6. Ecomorph abbreviations: CG = crown-giant; GB = grass-bush; TC = trunk-crown; TG = trunk-ground; TR = trunk; TW = twig. Island abbreviations: LA1 = Lesser Antillean species from one-species islands; LA2 = Lesser Antillean species from two-species islands; TCD = Trunk-crown derivatives; TGD = Trunk-ground derivatives.

We studied four such taxa derived from trunk-crown species of the Greater Antilles. They are: (1) *A. conspersus* (Grand Cayman), which is closely related to *A. grahami* (Jamaica; Underwood & Williams, 1959; Hedges & Burnell, 1990); (2) *A. maynardi* (Little Cayman) and (3) *A. longiceps* (Navassa), two long-snouted relatives of *A. porcatus* (Cuba; Ruibal & Williams, 1961; Buth, Gorman & Lieb, 1980); and (4) *A. carolinensis brunneus* (southern Bahamas), a large subspecies of *A. carolinensis* which has lost the ability to change colour (Schoener, 1975). We also studied five taxa derived from trunk-ground species: (1) *A. desechensis* (Desecheo), (2) *A. monensis* (Mona), and (3) *A. scriptus* (Inagua)—all relatives of *A. cristatellus* (Puerto Rico; Heatwole, 1976; Gorman *et al.*, 1983), and two subspecies of *A. sagrei* (Cuba), (4) *A. s. nelsoni* (Swan Island) and (5) *A. s. luteosignifer* (Cayman Brac).

In addition, we include *A. acutus* (St. Croix) whose position within the *cristatellus* group is uncertain (Gorman *et al.*, 1983; Roughgarden, 1989b). Hence, although A. *acutus* occurs on a one-species island, whether it should be classified as an ecomorph derivative is uncertain.

Data collection

Morphological and ecological data for Lesser Antillean taxa were collected June–July 1992 except for *A. gingivinus*, *A. pogus*, and *A. sabanus*, for which data were collected August 1993. Collection dates for Greater Antillean derivatives were: *A. conspersus*, *A. sagrei luteosignifer* and *A. maynardi*, January 1991; and *A. carolinensis brunneus*, May 1992. Data for *A. acutus* were collected in December 1992. Morphological and ecological data for Greater Antillean taxa have been published previously (Losos, 1990a, 1992, unpubl.; Losos *et al.*, 1994; Irschick & Losos, 1996). For *A. conspersus*, which no longer occurs allopatrically on Grand Cayman due to the introduction of *A. sagrei*, we used data from habitats in which *A. sagrei* does not occur (Losos *et al.*,

TABLE 1. Greater Antillean ecomorph species included in the study.

Species	Island	Ecomorph*	Perch height C.V.**	Perch diameter C.V.**	Distance to generalist centroid
cooki	Puerto Rico	TG	41.7	96.6	0.55
cristatellus	Puerto Rico	TG	52.2	250.7	1.06
cuvieri	Puerto Rico	CG			1.58
evermanni	Puerto Rico	TC	188.0	108.2	0.88
gundlachi	Puerto Rico	TG	61.0	163.1	1.03
krugi	Puerto Rico	GB	118.3	289.8	1.15
occultus	Puerto Rico	TW			2.12
poncensis	Puerto Rico	GB	43.3	58.9	1.10
pulchellus	Puerto Rico	GB	82.4	181.9	1.23
stratulus	Puerto Rico	TC	142.0	145.5	0.83
garmani	Jamaica	CG	65.9	87.4	1.06
grahami	Jamaica	TC	81.9	149.2	1.06
lineatopus	Jamaica	TG	63.0	155.1	0.62
opalinus	Jamaica	TC	43.4	174.1	0.68
sagrei	Jamaica	TG	132.4	107.0	0.53
valencienni	Jamaica	TW	100.0	186.6	1.22
aliniger	Hispaniola	TC	67.7	92.0	0.83
bahorucoensis	Hispaniola	GB			1.25
barahonae	Hispaniola	CG			1.78
chlorocyanus	Hispaniola	TC	69.1	100.3	0.85
coelestinus	Hispaniola	TC	45.0	66.9	0.92
cybotes	Hispaniola	TG	73.1	112.0	0.94
distichus	Hispaniola	TR	85.0	53.5	1.27
insolitus	Hispaniola	TW			1.60
longitibialis	Hispaniola	TG			1.16
marcanoi	Hispaniola	TG			0.86
olssoni	Hispaniola	GB	59.2	178.0	1.81
semilineatus	Hispaniola	GB			1.82
singularis	Hispaniola	TC			1.20
strahmi	Hispaniola	TG			0.85
angusticeps[+]	Cuba	TW	50.9	128.6	1.09
carolinesis[+]	Cuba	TC	44.1	110.8	0.90
porcatus[++]	Cuba	TC			1.28

* CG = crown-giant; GB = grass-bush; TC = trunk-crown; TG = trunk-ground; TR = trunk; TW = twig.

** C.V. = coefficient of variation. Species with sample sizes <10 not included.

[+] Data collected in the Bahamas; *carolinensis* occurs in Florida, the Bahamas, and elsewhere in the northern Caribbean and is derived from *porcatus* on Cuba (Ruibal and Williams, 1961; Buth *et al.*, 1980).

[++] Data collected from an introduced population in the Dominican Republic.

1993). Live specimens of *A. monensis* were provided by M. Leal. Tables 1 and 2 list the taxa included in this study.

Morphological data

The following measurements were taken on live adult males: snout-vent length [SVL], hind- and forelimb length from the distal end of the longest toe to the insertion of the limb into the body wall, tail length (only on specimens with original tails), mass, and number of lamellae under the third and fourth phalanges of pedal digit IV. Data were usually collected for 10–15 individuals of each species; mean values were used in subsequent statistical analyses.

Several species (*A. longiceps*, *A. sagrei nelsoni*, *A. desechensis*, and *A. scriptus*) occur on islands from which we were unable to obtain live specimens. Fortunately, we were

TABLE 2. Lesser Antillean and Greater Antillean derivative species included in the study.

Species	Island	Sympatric congeners*	Perch height** (m)	Perch diameter** (cm)	D_k***
BIMACULATUS SERIES					
bimaculatus	St. Kitts	1	1.89±0.27 (83.2)	12.7±3.3 (142.1)	32.7
ferreus	Marie Galante	0	2.40±0.27 (34.0)	13.0±3.1 (66.6)	45.3
gingivinus+	St. Maarten	1	2.23±0.24 (74.4)	9.7±1.5 (88.5)	48.7
leachi	Antigua	1	2.97±0.42 (63.8)	15.7±2.4 (66.7)	35.1
lividus	Montserrat	0	2.01±0.21 (67.0)	7.3±1.3 (116.1)	34.8
marmoratus	Guadeloupe	0	1.67±0.13 (52.7)	9.4±1.4 (101.2)	47.1
pogus	St. Maarten	1	1.46±0.21 (96.5)	5.4±0.9 (111.5)	40.1
sabanus	Saba	0	1.88±0.42 (105.9)	10.4±2.8 (124.0)	50.7
schwartzi	St. Kitts	1	0.59±0.05 (51.0)	7.1±2.9 (152.0)	32.7
wattsi	Antigua	1	0.80±0.07 (58.9)	10.4±2.6 (161.0)	35.5
ROQUET SERIES					
aeneus	Grenada	1	1.87±0.22 (78.9)	16.7±2.6 (101.7)	43.5
extremus++	St. Lucia	0	1.60±0.29 (60.7)	9.0±1.5 (55.6)	24.4
griseus	St. Vincent	1	2.65±0.30 (55.9)	20.9±3.2 (74.9)	48.3
luciae	St. Lucia	0	1.96±0.23 (70.6)	12.6±1.7 (78.9)	38.9
richardi	Grenada	1	1.88±0.16 (55.9)	14.3±1.8 (77.2)	53.9
roquet	Martinique	0	1.81±0.18 (61.2)	9.4±1.4 (93.8)	34.1
trinitatis	St. Vincent	1	1.65±0.19 (84.0)	26.6±3.0 (80.4)	54.0
TRUNK-CROWN DESCENDANTS					
carolinensis brunneus	Acklins	0	1.68±0.22 (55.8)	2.3±0.5 (89.0)	—
conspersus+++	Grand Cayman	0	1.70±0.17 (72.4)	11.8±1.2 (71.0)	48.4
longiceps	Navassa	0	—	—	—
maynardi	Little Cayman	1	2.52±0.28 (62.2)	11.7±1.7 (79.6)	45.6
TRUNK-GROUND DESCENDANTS					
desechensis	Desecheo	0	—	—	—
monensis	Mona	0	—	—	—
sagrei luteosignifer	Cayman Brac	0	0.96±0.08 (68.7)	9.7±0.9 (68.6)	32.5
sagrei nelsoni	Swan	0	—	—	—
scriptus	Inagua	0	—	—	—
OTHER					
acutus	St. Croix	0	2.39±0.18 (52.8)	13.2±2.3 (119.3)	47.3

* Not including introduced species (see Losos *et al.* [1993] for a review).

** ±1 standard error. Coefficients of variation in parentheses.

*** Distance to the nearest perch. A single D_k value is calculated for a species; hence, no standard error or coefficient of variation exists.

+ Unlike all other large species on two-species islands, *gingivinus* is the same body size as species on one-species islands (Schoener, 1970). On St. Barthélémy and Anguilla, *gingivinus* occurs without congeners, although *pogus* occurred historically on Anguilla.

++ *extremus* is introduced on St. Lucia. It occurs naturally on Barbados, where no other anole species are found.

+++ Data for *conspersus* collected in 1991 using only sites at which *A. sagrei* did not occur (Losos *et al.*, 1993).

able to obtain well-preserved specimens of these species from the Museum of Comparative Zoology, Harvard University, and the National Museum of Natural History, Smithsonian Institution. We took the same measurements on these specimens as on live specimens. To correct for inaccuracies that may occur due to shrinkage and the position in which specimens were preserved (e.g. Lee, 1982), we took measurements on preserved specimens of other species that we previously had measured prior to preservation and then calculated the relationship for each trait between measurements on live versus preserved specimens. The resulting regression equation was used to correct measurements for preservational effects.

Ecological data

We searched for lizards in a variety of habitats on each island. For each adult male lizard observed, we recorded perch height (m), perch diameter (cm), and, except for *A. carolinensis brunneus*, distance to the nearest available perch in each of the following size categories: 0.2–1.0 cm; 1.0–1.5 cm; and >1.5 cm. For each species, we then calculated a composite nearest perch distance variable, D_k, which was the mean of the distances to each size category weighted by the proportion of lizards observed using that size category (following Pounds, 1988; Losos, 1990a). D_k, therefore, is an index of the mean distance to perches that members of a species are likely to use (e.g. distance to twigs is probably irrelevant for large species that never use twigs).

Evaluation of the status of species from simple communities

Morphological comparisons

All morphological variables examined in this study increase with body size among species of Anolis (Losos, 1990a; Losos *et al.*, 1994). To remove the effect of body size on each variable, we regressed each variable separately against svl and used the residuals in subsequent analyses. We chose to regress variables against svl, rather than against a composite variable—such as the first axis in a principal components (PC) analysis conducted on all variables—because the biological interpretation of residuals from regressions against svl is more straightforward. In any case, SVL is highly correlated with the first axis of a principal components analysis using either all of the variables (non-size adjusted) in this study ($r = 0.98$) or using only SVL and mass ($r = 0.99$; Losos *et al.*, 1994), which suggests that SVL is a reasonable proxy for overall body size. Further, morphometric analyses using residuals from regressions either on SVL or on the first axis of a principal components analysis using all variables are qualitatively almost identical (Losos & de Queiroz, unpublished).

We investigated whether Lesser Antillean species and Greater Antillean derivatives could be assigned to any of the ecomorph classes or, alternatively, whether they exhibited morphologies unlike those characterizing the Greater Antillean ecomorphs. To accomplish this goal, we conducted a principal components analysis (PCA) using the size-adjusted variables for all species; svl was also included so that the analysis included size, as well as shape, dimensions. All species—ecomorph, Lesser Antillean, and Greater Antillean derivative—were included in this analysis. We determined the centroid of each ecomorph class based on the first four PC axes (see results). For each Greater Antillean specialized species (i.e. a member of one of the ecomorph classes; see Table 1), we calculated the distance to the centroid of the ecomorph class to which it belongs. We also calculated the distances between all pairs of species within each ecomorph class. For each Lesser Antillean species or Greater Antillean derivative, we then calculated the distance to the nearest Greater Antillean specialist species and to the nearest ecomorph centroid.

We also calculated the position of a putative generalist species as the point intermediate between the ecomorph classes. The rationale for this decision is that each of the ecomorphs possesses morphologically extreme features which seem to represent habitat adaptations, such as the high number of lamellae of trunk-crown anoles or the short limbs of twig anoles (Williams, 1983; Losos, 1990a). Hence, we reasoned that a species capable of using all habitats with some proficiency most likely would have an intermediate morphology. The position of this putative generalist was determined by calculating the mean of the values for the ecomorph centroids.

To be classified as a member of an ecomorph class, a species was required to satisfy one of two criteria. Either: (1) it must fall within the multidimensional morphological space (as determined by the PCA) defined by members of that class; or (2) the euclidean distance to a member of one of the ecomorph classes must be less than 0.32, the mean nearest neighbour distance (NND) of the trunk-ground anoles, which exhibit the lowest NND of any of the ecomorph classes.

To be considered a generalist, a species must lie close to the position of the putative generalist. We used the mean distance of ecomorph species to their ecomorph centroids ($=0.51$) as the threshold; species were considered to be generalists if they occurred within a distance <0.51 to the putative generalist. Because the morphological spaces occupied by both the trunk-ground and trunk-crown anoles are large and near the position of the putative generalist, a species possibly could qualify both as an ecomorph species and as a generalist. However, none of the ecomorph species met the criterion to be considered a generalist (although *A. sagrei* and *A. cooki* are close ([Table 1]); further, only one of the species we investigated in this study qualified both as a generalist and as a member of an ecomorph class—the classification of this species must be considered ambiguous (see below).

Ecological comparisons

To be considered an ecological generalist, a species would have to display both intermediate mean habitat use and a broad range of habitat use relative to the specialized taxa of the Greater Antilles. To examine whether a species' mean habitat use was intermediate relative to that of the ecomorph species, we used a principal components analysis based on the three habitat variables described above. Because of the smaller number of variables and substantial overlap in the position of the ecomorphs in ecological space, we relied on inspection of the position of each species in a two-dimensional ecological space to determine assignment to ecomorph categories. To investigate whether Lesser Antillean and Greater Antillean descendant species have greater ecological breadth than members of the Greater Antillean ecomorph categories, we examined the coefficients of variation of perch height and diameter (D_k is a population parameter and thus has no intra-population variance).

The relationship between morphology and ecology

Among Greater Antillean anoles, morphology and ecology are related (Losos, 1990a). We investigated whether a significant relationship still exists when Lesser

TABLE 3. Loadings on Principal Components Axes for morphological analyses.

	Principal Component Axes			
Variables⁺	I	II	III	IV
ln(svl)	−0.00	−0.00	1.00	0.00
forelimb	0.92	−0.21	−0.00	0.20
hindlimb	0.95	0.13	0.00	−0.16
tail	0.46	0.82	0.00	−0.32
lamellae number	−0.36	0.52	−0.00	0.76
mass	0.79	−0.16	−0.00	0.49
Eigenvalue	2.71	1.03	1.00	0.99
% Variance	45.2	17.1	16.7	16.5

⁺ All variables except ln(svl) are residuals of regressions against svl (see text).

Antillean anoles are included in the analysis. For such comparative analyses to be statistically valid, they must be conducted in the context of the phylogenetic relationships of the taxa. To accomplish this, we used the independent contrasts method (Felsenstein, 1985; Garland, Harvey & Ives, 1992), using phylogenies for Lesser Antillean (Roughgarden & Pacala, 1989) and certain Greater Antillean taxa (Losos, 1992). The polytomy in the relationships of the *roquet* series (Roughgarden & Pacala, 1989) was resolved following Lazell (1972). Unfortunately, lack of knowledge of relationships precludes the inclusion of Hispaniolan and Cuban (except *A. sagrei*) taxa in this analysis. Furthermore, because we have no means of accurately estimating branch lengths of the phylogenetic tree either in units of time or expected variance of change, we set all branch lengths equal to one (corresponding to the speciational model of character evolution of Garland *et al.*, 1992).

Contrasts were calculated for each variable and the effect of size was removed from morphological variables by regressing contrasts for each variable against contrasts in svl. Canonical correlation analyses were conducted on these size-adjusted contrasts using Systat 5.03 (Wilkinson, 1990). Because regression analyses using independent contrasts must pass through the origin (Garland *et al.*, 1992), we omitted the constant in the canonical correlation regression equation. All variables were ln-transformed prior to all analyses.

RESULTS

Morphology

In the PCA, the first four axes accounted for 95.5% of the variation (Table 3). Examination of plots of PC axes I vs. II and I vs. IV illustrates the dispersion of the ecomorphs in morphological space (Fig. 3). PC III loads only for SVL (our proxy for body size), which is illustrated in Figure 2. Ecomorphs generally are not well differentiated by SVL, although the grass-bush anoles tend to be smaller than most members of other ecomorph categories and the crown-giants are considerably larger than all other ecomorph species (Fig. 2). Figures 3 and 4 reveal that each of the ecomorph classes occupies a unique portion of morphological space and that the position of the putative generalist lies roughly between the trunk-ground and trunk-crown anoles (Table 4, bottom).

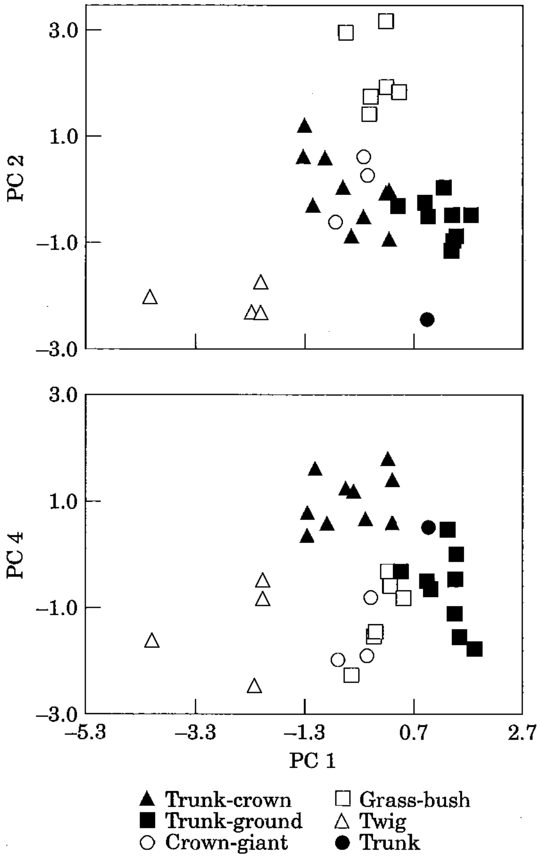

Figure 3. The position of the Greater Antillean ecomorphs in a morphological space defined by the Principal Components Analysis. PC axis III, which is not shown, loads only for body size.

Among the Lesser Antillean taxa, all species on one-species islands belong to the trunk-crown ecomorph category (Fig. 4) except *A. ferreus*, which differs in its large size (Fig. 2), but is, nonetheless, closer to the trunk-crown anoles than it is to any of the other ecomorphs or to the putative generalist (Table 4). *Anolis lividus*, which lies slightly outside the trunk-crown boundary, qualifies as a trunk-crown anole by its proximity to *A. grahami* (euclidean distance = 0.19; Table 4). By contrast, anoles on two-species islands in the Lesser Antilles are more varied morphologically (Fig. 5). Only one species is categorized as a member of a particular ecomorph class: *A. trinitatis* is a trunk-crown anole. In addition, *A. griseus* lies very near the crown-giant space. The other seven species, however, are not particularly close to any of the ecomorph classes (the large size of *A. bimaculatus* and *A. leachi* distinguishes them from trunk-crown anoles); two of them, *A. aeneus* and *A. gingivinus*, qualify as generalists (Table 4).

All of the ecomorph derivatives descended from trunk-crown anoles were classified as trunk-crown anoles (Table 4, Fig. 6) with one exception: *A. carolinensis brunneus* does not fall within trunk-crown morphospace and is closer to the putative generalist than it is to any of the ecomorph centroids, although it is too distant to qualify as

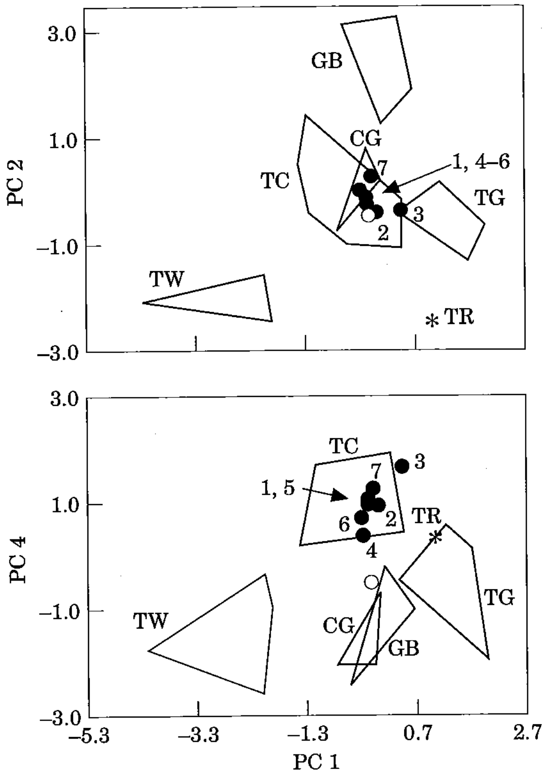

Figure 4. The position of Lesser Antillean species from one-species islands in morphological space. Outlines correspond to the space occupied by the ecomorphs in Fig. 3. Open circle is the position of a hypothetical generalist species. 1. *A. extremus*; 2. *A. ferreus*; 3. *A. lividus*; 4. *A. luciae*; 5. *A. marmoratus*; 6. *A. roquet*; 7. *A. sabanus*.

a generalist. In contrast, several of the trunk-ground descendants have diverged greatly from their ancestral ecomorph type (Fig. 6). The most extreme case is *A. desechensis*, which almost qualifies as a trunk-crown anole based on its distance from the trunk-crown species *A. grahami* (Table 4). In addition, *A. scriptus* and *A. sagrei nelsoni* qualify as generalists. *Anolis monensis* also qualifies as a generalist, but its proximity to the trunk-ground *A. sagrei* qualifies it as a trunk-ground anole as well; this is the only species which meets the criteria for both an ecomorph class and the generalist category. The remaining trunk-ground derivative, *A. sagrei luteosignifer*, lies within the trunk-ground morphological space. Sister-taxa comparisons support our classifications of these species; all species classified as generalists and *A. carolinensis brunneus* lie closer to the generalist than the ecomorph species from which they were derived (compare values in Tables 1 and 4).

Anolis acutus is classified as a generalist. Among the ecomorph species, it is most similar to the trunk-crown anoles.

Habitat use

Figure 7 reveals that the ecomorphs can be fairly well differentiated on the basis of the first two axes of a principal components analysis (Table 5), with the exception

TABLE 4. Euclidean distances based on morphology

Species	Distance to nearest neighbours		Distance to nearest ecomorph centroid		Distance to generalist centroid	Morphological classification+
BIMACULATUS GROUP						
bimaculatus	TC	0.49	TC	0.81	1.29	—
ferreus	TC	0.56	TC	0.82	0.96	—
gingivinus	TG	0.34	TG	0.55	0.35	GEN
leachi	TC	0.69	TC	0.76	1.14	—
lividus	TC	0.19	TC	0.54	1.02	TC
marmoratus	TC	0.32	TC	0.23	0.69	TC
pogus	GB	0.47	GB	0.68	1.06	—
sabanus	TC	0.27	TC	0.24	0.88	TC
schwartzi	TC	0.52	TC	0.73	1.02	—
wattsi	TG	0.49	TC	0.74	0.64	—
ROQUET GROUP						
aeneus	TC	0.66	TC	0.65	0.32	GEN
extremus	TC	0.24	TC	0.25	0.75	TC
griseus	CG	0.35	CG	0.67	1.19	—
luciae	TC	0.42	TC	0.50	0.59	TC
richardi	CG	0.51	CG	0.79	0.95	—
roquet	TC	0.28	TC	0.34	0.66	TC
trinitatis	TC	0.30	TC	0.49	0.65	TC
TRUNK-CROWN DERIVATIVES						
carolinensis brunneus	TC	0.53	TC	0.90	0.79	—
conspersus	TC	0.25	TC	0.46	1.02	TC
longiceps	TC	0.18	TC	0.97	1.31	TC
maynardi	TC	0.21	TC	0.68	0.86	TC
TRUNK-GROUND DERIVATIVES						
desechensis	TC	0.33	TC	0.59	1.07	—
monensis	TG	0.25	TG	0.54	0.50	TG/GEN
sagrei luteosignifer	TG	0.27	TG	0.74	0.88	TG
sagrei nelsoni	TG	0.46	TG	0.62	0.42	GEN
scriptus	TG	0.45	TG	0.67	0.24	GEN
OTHER						
acutus	TC	0.57	TC	0.53	0.39	GEN
ECOMORPH CENTROIDS++						
crown-giant (0.43 ± 0.09)	CG	0.29	TG	1.67	1.44	
grass-bush (0.44 ± 0.08)	GB	0.26	TC	1.47	1.35	
trunk	TR	—	TG	1.06	1.27	
trunk-crown (0.56 ± 0.06)	TC	0.37	TG	1.22	0.76	
trunk-ground (0.43 ± 0.06)	TG	0.20	TR	1.06	0.72	
twig (0.68 ± 0.09)	TW	0.48	TC	1.70	1.40	

+ Based on criteria outlined in Materials & Methods. Species not classified to as a generalist or a member of any ecomorph class are indicated by (—).

++ Distances are from the ecomorph centroid to the nearest species and nearest other centroid. Numbers in parentheses are the mean distances (± 1 s.e.) of members of an ecomorph class to the centroid for that ecomorph. Because the data include only one trunk anole, no mean NND exists.

that the trunk-crown and crown-giant anoles overlap considerably and the single trunk anole (*A. distichus*) falls within the trunk-crown anole polygon. Most Lesser Antillean taxa lie in or adjacent to the space defined by trunk-crown anoles, with the exception of *A. extremus* and the three small species from two-species islands in the northern Lesser Antilles (members of the *wattsi* species group), all of which lie in or adjacent to the grass-bush and trunk-ground portions of ecological space (Figs

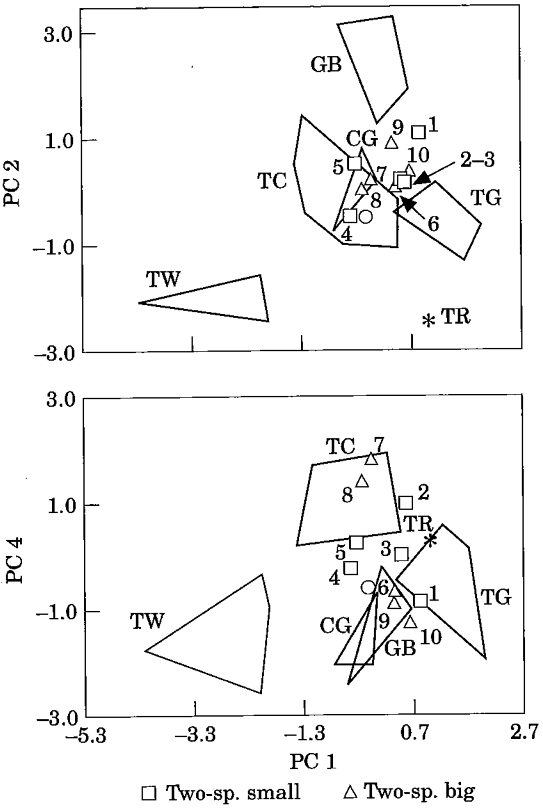

Figure 5. The position of Lesser Antillean species from two-species islands in morphological space. 1 = *A. pogus*; 2 = *A. schwartzi*; 3 = *A. wattsi*; 4 = *A. aeneus*; 5 = *A. trinitatis*; 6 = *A. gingivinus*; 7 = *A. bimaculatus*; 8 = *A. leachi*; 9 = *A. griseus*; 10 = *A. richardi*.

8, 9). The similarity of *A. extremus* to grass-bush anoles is due to the combination of relatively low distance to nearest perch and small perch diameter, which may have been an artifact of the locality on St. Lucia at which the data were collected. *Anolis extremus* introduced to Bermuda display habitat use typical for trunk-crown anoles (Losos, 1996; we did not study *A. extremus* in Barbados where it occurs naturally).

We had complete habitat use data for only three of the Greater Antillean derivative species. Both trunk-crown derivatives lie within the trunk-crown space (Fig. 10). In addition, perch height and diameter data for *A. carolinensis brunneus* (Losos *et al.*, 1994) indicate that it is similar to trunk-crown anoles as well (Table 3). The only trunk-ground derivative for which we have ecological data is *A. sagrei luteosignifer*, which appears to be a trunk-ground anole ecologically (Fig. 10).

Anolis acutus also displays habitat use similar to that of trunk-crown anoles.

In terms of breadth of habitat use, Lesser Antillean anoles did not have broader ranges than Greater Antillean ecomorphs for either perch height ($t = -0.57$, 36 df, $P > 0.50$, one-tailed) or perch diameter ($t = -1.21$, $P > 0.50$); if anything, Lesser Antillean species have narrower ranges (Fig. 11). These results did not change appreciably if only species from one-species Lesser Antillean islands were used. Similarly, no difference was found between Greater Antillean ecomorphs and their

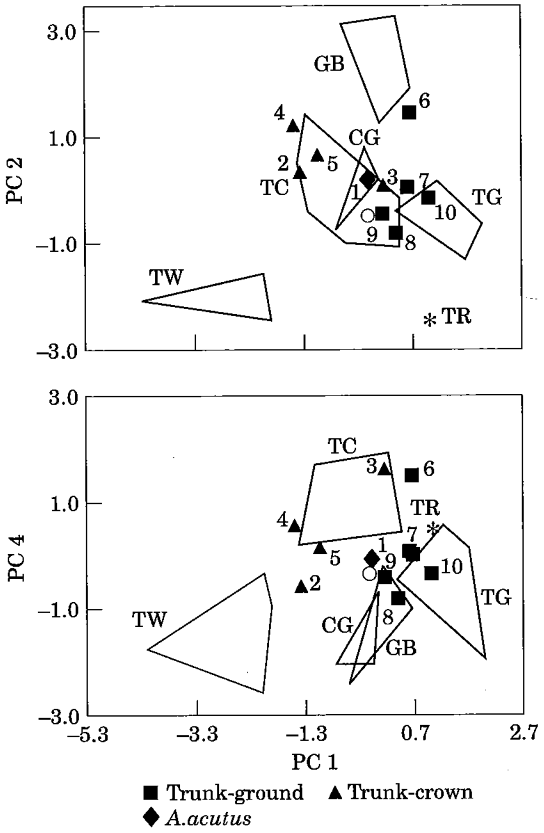

Figure 6. The position of Greater Antillean derivative species and *A. acutus* in morphological space. 1 = *A. acutus*; 2 = *A. carolinensis brunneus*; 3 = *A. conspersus*; 4 = *A. longiceps*; 5 = *A. maynardi*; 6 = *A. desechensis*; 7 = *A. monensis*; 8 = *A. sagrei nelsoni*; 9 = *A. scriptus*; 10 = *A. sagrei luteosignifer*.

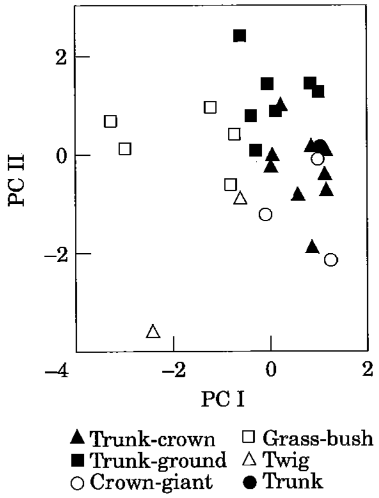

Figure 7. Habitat use of Greater Antillean ecomorphs.

TABLE 5. Loadings on Principal Components Axes for ecological analyses

Variables[+]	Principal Component Axes I	 II
Perch height	0.67	−0.73
Perch diameter	0.83	0.43
Nearest perch	0.90	0.14
Eigenvalue	1.96	0.74
% Variance	65.3	24.7

[+] All variables ln-transformed.

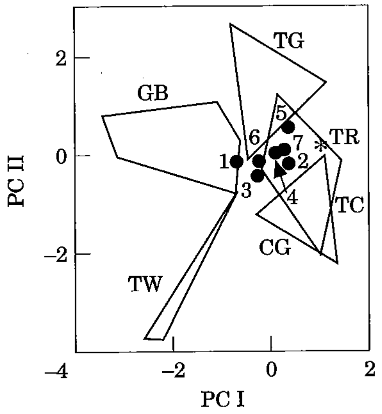

Figure 8. Habitat use of Lesser Antillean species on one-species islands. Outlines correspond to the space occupied by the ecomorphs in Fig. 7. Species numbered as in Fig. 4.

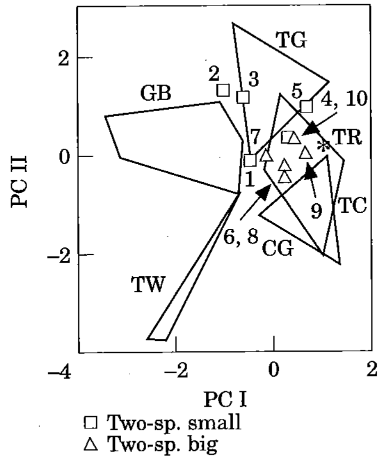

Figure 9. Habitat use of Lesser Antillean species on two-species islands. Outlines correspond to the space occupied by the ecomorphs in Fig. 7. Species numbered as in Fig. 5.

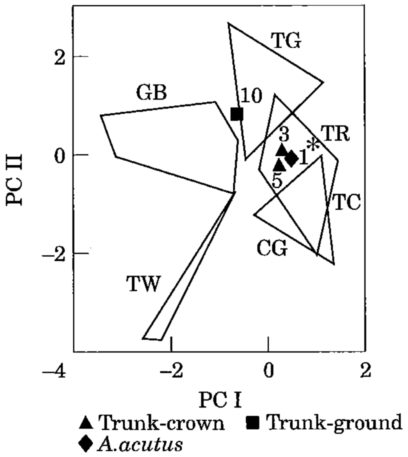

Figure 10. Habitat use of Greater Antillean derivative species and *A. acutus*. Outlines correspond to the space occupied by the ecomorphs in Fig. 7. Species numbered as in Fig. 6.

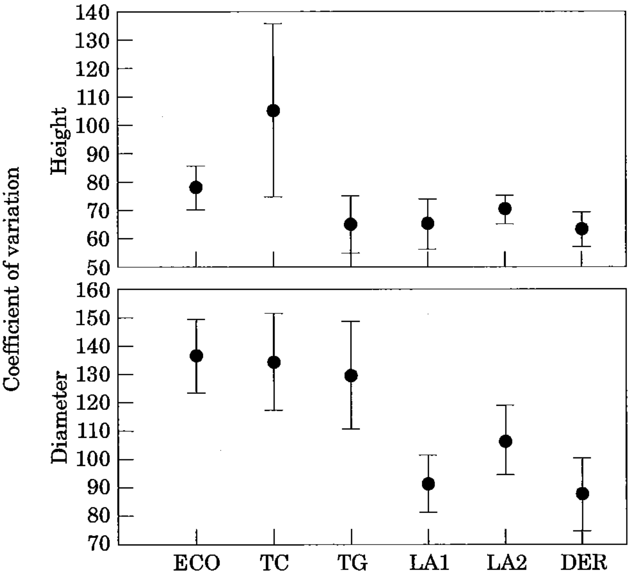

Figure 11. Coefficients of variation for perch height and diameter. Eco = all ecomorph species; TC = trunk-crown species; TG = trunk-ground species; LA1 = Lesser Antillean species from one-species islands; LA2 = Lesser Antillean species from two-species islands; DER = Greater Antillean derivative species.

derivatives (height: $t = -0.75$, 21 df, $P > 0.50$; diameter: $t = -2.05$, $P > 0.50$; Fig. 11); these results also do not change if the comparison is limited to only trunk-ground and trunk-crown anoles, rather than to all ecomorph species.

The relationship between species' position in morphological and ecological space was marginally significant (canonical correlation = 0.67; Wilks' $\lambda = 0.38$, $F_{18,74} = 1.70$, $P < 0.06$). Examination of the loadings on the canonical axes indicates that the

TABLE 6. Loadings on canonical correlation axes

Variables[+]	Canonical Axis I
svl	0.64
hindlimb	0.41
forelimb	0.66
mass	0.21
lamellae number	−0.25
tail	−0.19
perch height	0.46
perch diameter	0.78
distance to nearest perch	0.52

[+] Based on an independent contrasts analysis. All morphological variables except svl are residuals of the contrasts for each variable regressed against contrasts in svl (see text).

variables contributing most strongly to this relationship were body size, relative limb length, and perch diameter (Table 6).

DISCUSSION

Are anoles in simple communities generalists?

We tested the hypothesis that species of *Anolis* in relatively simple communities are ecologically and morphologically generalized in comparison with their relatives in more complex communities by examining two types of simple communities. First, we examined islands in the Lesser Antilles, where no more than two species have been able to evolve on or colonize an island, perhaps due to the small size of the islands (reviewed in Rand, 1969). If these communities represent an early stage in anole community evolution (Williams, 1972), the species inhabiting them should be less specialized than species in more complex communities. Second, we looked at anole communities on small islands that have been colonized by specialized species from the Greater Antilles. Assuming that interspecific competition is the driving force behind specialization, we predicted that these species should reverse evolutionary direction and become less specialized in the absence of competitors (Lister, 1976b; Losos *et al.*, 1994).

Lesser Antillean species

Previous research has indicated that morphology and ecology are strongly correlated among Greater Antillean anoles (Moermond, 1979a; Losos, 1990a). Here, we have documented that this correlation continues to hold when Lesser Antillean taxa are added to the analysis. This correlation indicates that if Lesser Antillean taxa are ecological generalists, then they should also be morphologically generalized.

Our data do not indicate, however, that the Lesser Antillean anoles are generalists. With one exception, all taxa on one-species islands qualify morphologically as trunk-crown anoles (the exception, *A. ferreus*, is also similar to trunk-crown anoles). Ecologically, these species are also similar to trunk-crown anoles (although their central position in ecological space space also renders many of them similar to a hypothetical generalist [Fig. 8]). The two Lesser Antillean species not included in this study are also from one-species islands. Unfortunately, little is known about their structural habitat use and morphology (see Lazell, 1962; Gorman & Stamm, 1975; Malhotra & Thorpe, 1997a, b). By contrast, the majority of taxa on two-species islands do not fit neatly into any of the ecomorph categories, but most are similar to the more arboreal ecomorphs, either the trunk-crown or crown giant anoles. The data also provide no suggestion that Lesser Antillean species exhibit greater ecological breadth than the specialized species of the Greater Antilles. Thus, although two species (*A. aeneus* and *A. gingivinus*) meet one of the criteria (morphological intermediacy) to be considered generalist species, the 15 other species do not meet either of the criteria.

Greater Antillean derivatives

A previous study (Losos *et al.*, 1994) found that Bahamian populations of *A. carolinensis* and *A. sagrei* had diverged little from their ancestral ecomorph types even though some populations occurred on islands with one or no sympatric anoles. Consequently, this previous analysis suggested that habitat specialization in anoles was a unidirectional process; interspecific competition could lead to its evolution, but the removal of competitors did not lead to reversal in evolutionary direction.

The more extensive examination of this hypothesis reported here contradicts the earlier findings. Our analysis of descendants of trunk-ground and trunk-crown anoles that now inhabit simple communities indicates that specialized species can evolve a more generalized condition in simple communities; further, the data suggest the possibility that this evolutionary generalization occurs more commonly in descendants of trunk-ground anoles than in descendants of trunk-crown anoles, although samples are small: only one trunk-crown derivative was not classified as a trunk-crown anole, whereas, four of the five trunk-ground descendants had diverged away from their ancestral trunk-ground morphology. Indeed, one of these (*A. desechensis*) is more similar to trunk-crown than trunk-ground anoles.

The only trunk-crown descendant not classified as a trunk-crown anole is the Bahamian *A. carolinensis brunneus.* The discrepancy in classification of this species between this study and that of Losos *et al.* (1994), which classified this taxon as a trunk-crown anole, results from differences in analytical techniques. Losos *et al.* used discriminant function analysis and UPGMA clustering, whereas this study relies on direct examination of euclidean distances and position in multivariate morphological space. Discriminant function analysis can be misleading in a study such as this because it forces all taxa to be classified into an existing category. Even if a taxon is distinct from all of the categories, it can be classified with high probability to one of them, if it is more similar to that category than to any other (Klecka, 1980). A similar problem occurs in UPGMA analyses, which also can be misleading because they are constrained to represent relationships as simple nested hierarchies and thus often fail to capture important aspects of complex multidimensional similarity (Sneath & Sokal, 1973; de Queiroz & Good, 1997). For these reasons, we prefer to use criteria that do not force taxa into existing categories and which were chosen specifically for their relevance to ecomorphological classifications.

Ecological data are scarce for these taxa, but seem to agree with the findings based on morphology. Among trunk-ground derivatives, two of the morphologically-generalized taxa, *A. scriptus* (Laska, 1970) and *A. sagrei nelsoni* (Lister, 1976a), appear to be generalized in structural habitat use. The situation is less clear for other trunk-ground derivatives; published reports are contradictory on whether *A. monensis* (Gorman & Stamm, 1975; Lister, 1976a) or *A. sagrei luteosignifer* (Lister, 1976a; this study) are more ecologically generalized than their relatives from larger islands with more complex faunas. Among trunk-crown descendants, the literature also suggests that *A. conspersus* has unusually broad habitat use (Lister, 1976a), but our data did not indicate that its habitat use, nor that of *A. carolinensis brunneus* or *A. maynardi*, is any broader than that of trunk-crown anoles in the Greater Antilles.

Considering the data as a whole, we conclude, in agreement with Lister (1976b), that specialized anoles, particularly trunk-ground ecomorphs, are capable of reversing evolutionary direction and becoming either more generalized or specialized to use a different microhabitat. However, more research would allow us to be less tentative regarding this conclusion—ecological data on *A. desechensis* would be especially interesting.

In addition, we should point out that our investigation of habitat use has centered on use of the structural habitat (e.g. perch dimensions), because these are the features partitioned among sympatric ecomorph species. However, examination of other habitat variables might prove interesting. In particular, some Greater Antillean derivatives (e.g., *A. conspersus* [Losos *et al.*, 1993]) and Lesser Antillean species (e.g., *A. marmoratus*, *A. oculatus* [Lazell, 1962, 1972; Malhotra & Thorpe, 1991, 1994]) use a wide variety of different habitat types (e.g., arid scrub, rainforest for the latter two species), whereas other species are more restricted in use of habitat types (Lazell, 1972; Roughgarden *et al.*, 1983). Greater Antillean ecomorph species also vary in the breadth of habitat type use (e.g. Schoener & Schoener, 1971a, b), so it is not clear whether any overall trend exists; a more detailed examination would prove worthwhile.

An alternative hypothesis

Although several species that we examined met our criteria to be considered generalists, most did not. Our failure to find generalists in most simple anole communities leads us to question the hypothesis that species occupying the complex anole communities of the Greater Antilles are descended from generalized ancestral species. As an alternative, we suggest that anole communities may have evolved from specialized ancestral species, in particular, from trunk-crown anoles.

We base this new hypothesis on the results of our examination of simple communities in the Lesser and Greater Antilles. In the Lesser Antilles, most species do not appear to be generalists; rather, they are similar to the trunk-crown anoles of the Greater Antilles. This is particularly true of all taxa occupying one-species islands, the species which would have been predicted most likely to be generalized.

The data on Greater Antillean derivative species also indicates that anoles in simple communities are likely to be trunk-crown anoles. Whereas trunk-crown anoles generally maintain their ancestral morphology and ecology when they colonize empty islands, trunk-ground anoles frequently become more arboreal and evolve morphologically to become more like trunk-crown anoles. These observations could be interpreted as indicating that natural selection favours the evolution and maintenance of a trunk-crown morphology in simple anole communities. On the other hand, the finding that three Greater Antillean derivatives—one trunk-crown and two trunk-ground descendants—are morphologically similar to a putative generalist could be taken as evidence that a generalist is favoured in such communities. This latter explanation, however, would not account either for the evolution toward trunk-crown morphology in the trunk-ground derivative *A. desechensis* or the observation that trunk-ground derivatives appear to be more likely than trunk-crown derivatives to evolve away from their ancestral morphology. Further, the putative generalist is itself somewhat intermediate between trunk-ground and trunk-crown anoles in morphological space (Figs 4–6) and thus proximity of the trunk-ground derivatives to the putative generalist also indicates that they have evolved to become more similar to trunk-crown anoles.

Two other lines of evidence lend credence to the hypothesis that ancestral species were trunk-crown anoles. Among the ecomorph classes, trunk-crown anoles are ecologically the most flexible in that they use a wide variety of structural habitats (e.g. Collette, 1961; Moermond, 1979b; Losos, 1990b; Jenssen, Greenberg & Hovde, 1995) and hence might be most likely to evolve in simple anole communities. In addition, two fossil anoles preserved in amber from Miocene deposits in the Dominican Republic appear indistinguishable from trunk-crown anoles (Rieppel, 1980; de Queiroz, Chu & Losos, in prep.), which indicates, if nothing else, that trunk-crown anoles have been around for a long time.

Re-evaluation of the phylogenetic basis for inferring that ancestral species were generalists

The hypothesis that the ancestral species in the Greater Antilles were trunk-crown anoles is contradicted by phylogenetic reconstructions of the Jamaican and Puerto Rican radiations, which suggest that this ancestor was a generalist (Losos, 1992). Several factors, however, could result in incorrect reconstructions of ancestral morphologies. One possibility is that the phylogenies used in these analyses are incorrect. The phylogenies of the Jamaican and Puerto Rican anoles are based on earlier studies (e.g. Underwood & Williams, 1959; Williams, 1972; Gorman *et al.*, 1983; Hedges & Burnell, 1990). In recent years, however, methods of phylogenetic analysis have increased dramatically in sophistication (reviewed by Swofford *et al.*, 1996). Using some of these newer methods, our preliminary reanalyses of published data, as well as preliminary analyses of newly collected DNA sequence data (D.J. Irschick, pers. comm.), have revealed that previous phylogenetic hypotheses may not be correct.

An additional potential difficulty is that the Puerto Rican radiation is not monophyletic, but rather is composed of three distinct phylogenetic units (Guyer & Savage, 1986; Williams, 1989; and references therein): *A. cuvieri*, the Puerto Rican crown giant; *A. occultus*, the Puerto Rican twig anole; and the *cristatellus* group containing the other nine Puerto Rican species. Due to lack of information on phylogeny of the entire genus, the Puerto Rican species were treated as monophyletic for purposes of ancestor reconstruction, which potentially could lead to mistaken reconstructions of ancestral nodes. We hope that current DNA sequencing efforts in our and other laboratories will soon clarify *Anolis* relationships and allow re-examination of these questions.

Another possible difficulty concerns the underlying assumptions of the methods used to infer ancestral character states. Previous reconstruction of anole community evolution (Losos, 1992) relied on parsimony methods to infer ancestral community structure. Parsimony is likely to yield correct estimates of ancestral character states when rates of character evolution are low relative to rates of speciation (Maddison & Maddison, 1992). To the extent that these assumptions are not met, the inferences drawn from parsimony reconstructions may be incorrect. Unfortunately, no method exists to evaluate whether rates of character evolution conform to the assumptions of parsimony (Maddison & Maddison, 1992; Losos & Miles, 1994). Nonetheless, high levels of homoplasy would seem to indicate that rates of evolution have been high, particularly when homoplasy is estimated using parsimony methods, which minimize homoplasy. Thus, as a rule of thumb, the greater the homoplasy inferred from character reconstructions using parsimony, the less confidence one may have in the accuracy of such reconstructions. Because convergence in the characters used to define the anole ecomorphs is widespread, levels of homoplasy in these characters would seem to be relatively high. Whether this level of homoplasy is so great as to render ancestral reconstructions based on parsimony uninformative is unknown.

CONCLUSIONS

Previous workers have suggested that anoles in simple communities may be analogous to early stages in the Greater Antillean anole radiations (e.g. Williams, 1972). Our data, however, indicate that species occupying these simple communities are dissimilar to those postulated to have occurred early in anole radiation. We must conclude either that previous theories about how the anole radiation proceeded are incorrect or that simple extant communities are not analogous to the first steps in anole diversification.

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