

University of Massachusetts Amherst

From the Selected Works of Duncan J. Irschick

1997

A comparison of evolutionary radiations in Mainland and West Indian Anolis lizards. *Ecology*

Duncan J. Irschick, *University of Massachusetts - Amherst*

L. J Vitt

P. Zani

J. B Losos



Available at: https://works.bepress.com/duncan_irschick/1/

A COMPARISON OF EVOLUTIONARY RADIATIONS IN MAINLAND AND CARIBBEAN *ANOLIS* LIZARDS

DUNCAN J. IRSCHICK,^{1,3} LAURIE J. VITT,² PETER A. ZANI,^{2,4} AND JONATHAN B. LOSOS¹

¹Department of Biology, Washington University, St. Louis, Missouri 63130-4899 USA

²Oklahoma Museum of Natural History and Department of Zoology,
University of Oklahoma, Norman, Oklahoma 73019 USA

Abstract. Comparisons between closely related radiations in different environments provide a unique window into understanding how abiotic and biotic factors shape evolutionary pathways. *Anolis* lizards have radiated extensively in the West Indies, as well as mainland Central and South America. In the Caribbean, similar communities of anole species specialized for different habitats (ecomorphs) have evolved independently on each Greater Antillean island. We examined ecological and morphological data on 49 *Anolis* species (33 Caribbean, 16 mainland) to investigate whether the same set of ecomorphs has arisen in mainland regions. More generally, we investigated whether the relationship between ecology and morphology was similar among anoles in the two regions.

Radiations in the two regions are very different. The majority of mainland anole species exhibit morphological characteristics unlike any Caribbean ecomorph. Furthermore, relationships between ecology and morphology are very different between the two sets of anole species. Among mainland anole species, toepad size is positively correlated with perch height, whereas tail length is negatively related to perch diameter. In contrast, among Caribbean anole species, both forelimb length and body mass are positively associated with perch diameter, and both tail length and hindlimb length are negatively related to perch diameter. Biomechanical considerations provide a functional basis for some of these correlations, but much variation remains to be explained. These findings demonstrate that factors that caused anole species to converge repeatedly in the West Indies are not present in mainland regions, and that environmental factors can strongly influence the shape of evolutionary radiations.

Key words: *Anolis* lizards; Caribbean Sea; ecomorphology; evolutionary radiations; mainland-island comparisons; South America.

INTRODUCTION

Comparisons of closely related clades in mainland and island habitats provide a particularly good opportunity for understanding how extrinsic factors affect evolutionary patterns. The striking differences between closely related taxa in island and mainland habitats have intrigued biologists for many years. Comparisons of island species to closely related mainland forms reveal a wide variety of differences in body size, life history characteristics, behavior, population structure, and many other features (see Carlquist 1965, 1974, Williamson 1981). In addition to focusing on particular species, many researchers have also been intrigued by differences in the extent of diversification of island and mainland clades, with most research centering on understanding the factors that cause island populations to diversify to a much greater extent than their mainland

relatives (e.g., Hawaiian *Drosophila* [Carson and Kaneshiro 1976], Darwin's finches [Lack 1947, Grant 1986]).

Many factors have been proposed to explain why particular species and clades diverge in island and mainland habitats, including fewer predators and competitors on islands, climatic differences between mainland and island areas, and the role of colonization events on the genetic structuring of island populations (Carlquist 1965, 1974, Case 1978, Williamson 1981). All of these explanations are relevant, at least in some cases. An alternative and underutilized approach, however, is to compare closely related clades that have diversified substantially in both island and mainland habitats. Just as different conditions on islands and mainlands may lead particular species to diverge, these environmental differences may also play an important role in shaping pathways of evolutionary diversification such that different evolutionary radiations arise from closely related clades occupying island and mainland habitats. Here, we show how ecomorphological patterns differ dramatically among *Anolis* lizards occurring in mainland and island habitats.

Manuscript received 5 April 1996; revised 6 December 1996; accepted 14 December 1996; final version accepted 13 January 1997.

³ Present address: Department of Biological Sciences, University of Cincinnati, Cincinnati, Ohio 45221-0006 USA.

⁴ Present address: Department of Biology, University of Oregon, Eugene, Oregon 97403 USA.

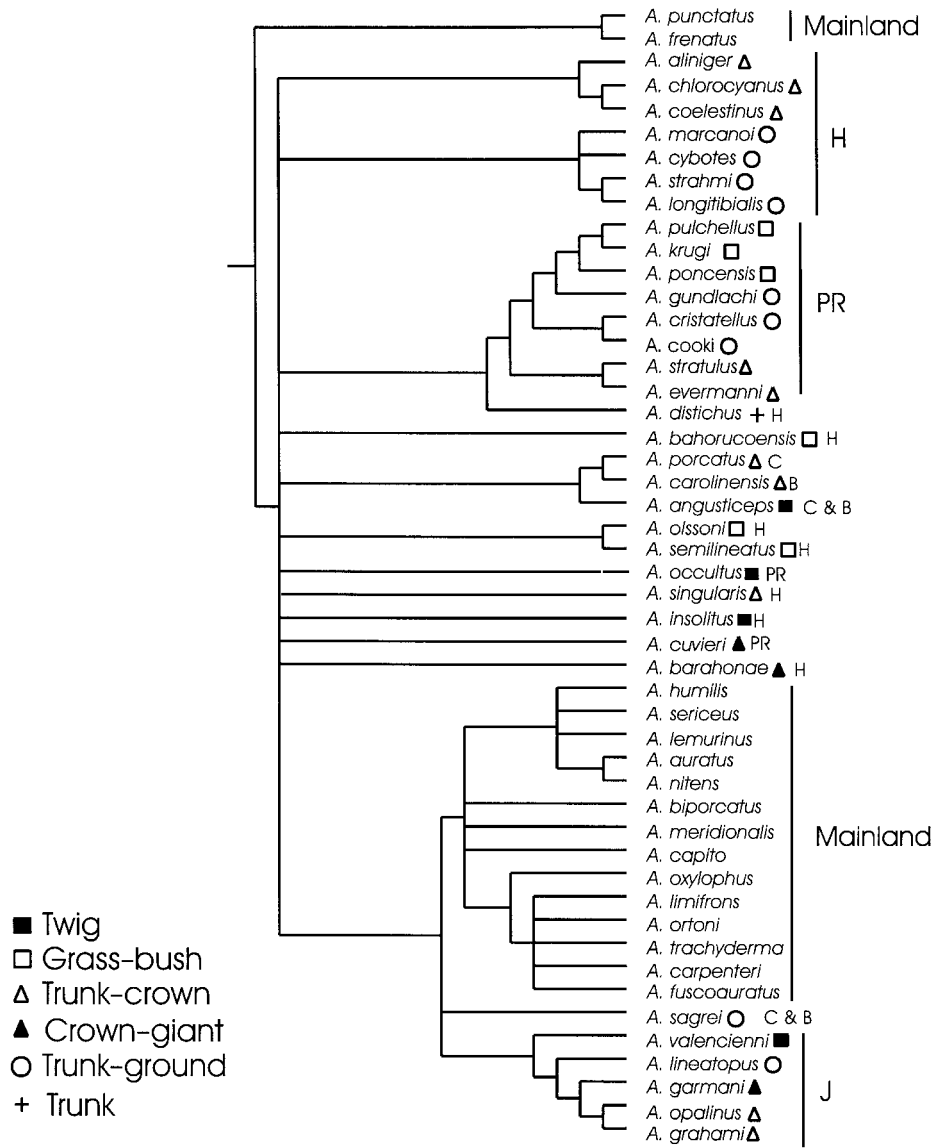


FIG. 1. A composite phylogeny among West Indian and Central and South American *Anolis* lizards. Different symbols represent different ecomorphs. H = Hispaniola, J = Jamaica, C = Cuba, PR = Puerto Rico, B = Bahamas.

Caribbean and mainland Anolis lizards

Anolis lizards provide an excellent opportunity to examine how adaptive radiations differ in island and mainland situations. *Anolis* lizards have radiated extensively in both mainland Central and South America (250+ species) and in the West Indies (138 species, Powell et al. 1996). Although higher level phylogenetic relationships of *Anolis* lizards are not currently well understood (Guyer and Savage 1986, 1992, Cannatella and de Queiroz 1989, Burnell and Hedges 1990, Hass et al. 1993), radiations in the West Indies and the mainland regions are largely independent (Fig. 1). Further, the adaptive basis of diversification in Caribbean anoles is well understood: on each of the Greater Antillean

islands of Cuba, Hispaniola, Puerto Rico, and Jamaica, *Anolis* species have radiated to produce a suite of species adapted morphologically to different microhabitats. Six “ecomorph” classes are recognized: trunk-ground, trunk-crown, grass-bush, crown-giant, twig, and trunk, named for the microhabitat they typically use (Rand and Williams 1969, Williams 1972, 1983). Ecological and morphological analyses indicate that these ecomorphs form distinguishable entities (Moermond 1979, Losos 1990a, 1992). Similar sets of ecomorphs (with some exceptions) have arisen on each Greater Antillean island, which indicates that remarkably similar anole communities have evolved at least four times within the West Indies (Williams 1983, Bur-

nell and Hedges 1990, Jackman et al., *in press*). Finally, the mechanistic basis for the relationship between morphology and ecology in Caribbean ecomorphs is well understood as a result of detailed functional and ecomorphological studies (Moermond 1979, Losos and Sinnero 1989, Losos 1990a, b, Irschick and Losos 1996, Losos and Irschick 1996).

By contrast, the adaptive basis of diversification in mainland *Anolis* communities has received less attention (but see Pounds 1988). A substantial body of work, however, provides compelling evidence that Caribbean and mainland anoles face very different environmental pressures (Andrews 1976, 1979, Andrews and Rand 1982, McLaughlin and Roughgarden 1989; see also Guyer 1988a, b, and Rand and Humphrey 1968). For example, the diversity of predators on anoles in mainland regions is much greater than on Greater Antillean islands (Greene 1988, Henderson and Crother 1989). In agreement with the hypothesis that predation is stronger in mainland habitats, mainland anoles suffer higher mortality rates than Caribbean species (McLaughlin and Roughgarden 1989). In the West Indies, by contrast, interspecific competition between anole species seems to be the major factor driving population differentiation (Losos 1994a; but see Schoener and Schoener [1978], Waide and Reagan [1983], and McLaughlin and Roughgarden [1989]).

The differential importance of factors such as predation and interspecific competition may play a role in shaping anole adaptive radiations in the two regions. Theoretical considerations and empirical evidence have shown that different kinds of biotic interactions strongly influence which morphological or ecological characteristics are favored by selection (Jeffries and Lawton 1984, Sih et al. 1985). For example, if mainland habitats contain a greater diversity of predators than Caribbean habitats, then we would expect certain anole behavioral or morphological characteristics present in the West Indies to be selected against in mainland habitats. Therefore, at least hypothetically, one might expect the relationship between morphology and ecology to differ between mainland and island anole radiations. On the other hand, structural habitats to which Caribbean ecomorphs have adapted also exist on the mainland, and if anoles are constrained to use and adapt to these habitats only in a certain manner, then mainland anoles may show the same ecomorphological patterns as Caribbean anoles.

We examined whether patterns of ecomorphological evolution differ among Caribbean and mainland anoles. We first asked, does a relationship between ecology and morphology exist among mainland anoles? Once we established whether such a correlation exists, we then examined whether the ecomorphological correlations are the same as among Caribbean anoles, and whether morphological types present in the West Indies also exist on the mainland.

METHODS

Determination of relationships between habitat use and morphology

Morphological data for 33 Caribbean anole species were taken from Losos (1990a, 1992; J. B. Losos, *unpublished data*) and Irschick and Losos (1996). Similar data were gathered on 16 mainland anole species. Appendix A provides a list of all species examined, sample sizes for ecological comparisons (for Caribbean anoles), as well as locality data (Table 1 provides species names and sample sizes for mainland anoles).

We followed previous studies by focusing our morphological comparisons on adult males. For each species, six morphological traits were measured: snout-vent length (SVL), body mass, number of lamellae underlying the third and fourth phalanges of the fourth toe of the hindfoot, and lengths of the forelimb, hindlimb, and tail. Length of the forelimb and hindlimb were measured as the distance from the insertion point of the limb to the longest toe of each foot. With a few exceptions, SVL, mass, hindlimb, and tail length were measured on live or freshly euthanized specimens. Because forelimb length and lamellae number were not initially measured on live mainland anoles, both variables were measured on formalin-fixed specimens. Also, because sample sizes for a few mainland anoles were small, we gathered additional data on these traits with preserved specimens.

Because measurements were taken by three different investigators (L. Vitt, D. Irschick, and J. Losos) on different kinds of specimens (J. Losos and L. Vitt measured live or freshly euthanized specimens, while D. Irschick measured preserved specimens), we attempted to correct for individual measurement error. First, a set of 24 specimens originally measured by J. Losos when alive was measured by D. Irschick when preserved. We then calculated a regression equation relating the two sets of measurements. The resulting regression equations (Appendix B) were tested on a different set of 10 lizards for which live and preserved measurements were also taken. Second, to assess differences in measurement technique between J. Losos and L. Vitt, we compared measurements taken on 13 lizards (*A. grahami*, *A. sagrei*, and *A. cristatellus*) when alive (J. Losos), and when freshly sacrificed (L. Vitt). Because the measurements of J. Losos and L. Vitt were practically identical (all mean ratios of Vitt measurements/Losos measurements were between 0.99–1.02), no corrections were made for investigator effects.

Morphological variables were \log_{10} -transformed prior to statistical analyses. Log transformation enhanced normality in all morphological variables: visualization of plots between log-transformed morphological variables showed that they exhibited linear relationships with one another (LOWESS option in SYSTAT 5.03). Mean values of each of the morphological variables were used in statistical analyses. All statistical analyses

TABLE 1. Mean morphological and ecological values for 16 mainland anole species.

Species	SVL (mm)	Body mass (g)	Tail length (mm)	Forelimb (mm)	Hindlimb (mm)	Lamellae number	Perch height (m)	Perch diameter (cm)
<i>A. frenatus</i>	135.2 (10.1, 6)	51.7 (12.6, 6)	262.2 (23.1, 6)	60.4 (4.6, 16)	106.6 (7.6, 6)	26.9 (1.1, 16)	2.6 (1.4, 11)	20.8 (10.5, 19)
<i>A. oxylophus</i>	64.8 (7.5, 39)	5.5 (1.6, 32)	104.0 (12.9, 28)	27.5 (1.4, 7)	49.2 (4.3, 32)	15.0 (0.6, 7)	0.6 (0.4, 65)	9.0 (13.8, 53)
<i>A. sericeus</i>	41.3 (3.2, 13)	1.3 (0.4, 13)	92.7 (14.8, 9)	14.2 (1.1, 12)	27.0 (2.1, 13)	15.7 (0.5, 12)
<i>A. humilis</i>	34.2 (2.8, 16)	1.0 (0.2, 16)	52.4 (6.1, 11)	14.0 (0.7, 9)	26.6 (1.9, 16)	12.7 (0.7, 9)	0.4 (0.5, 5)	110.0 (147.7, 2)
<i>A. meridionalis</i>	33.8 (6.4, 9)	0.7 (0.5, 8)	66.1 (11.1, 8)	19.4 (2.3, 6)	24.0 (4.2, 8)	13.8 (1.1, 6)
<i>A. punctatus</i>	82.9 (4.7, 11)	10.8 (3.1, 11)	192.1 (16.4, 8)	29.9 (1.8, 10)	55.8 (3.2, 11)	26.1 (1.7, 10)	4.9 (3.5, 16)	20.3 (19.3, 15)
<i>A. biporcatus</i>	90.5 (4.0, 7)	18.9 (3.1, 7)	186.8 (7.5, 5)	30.4 (4.7, 7)	57.6 (2.9, 7)	23.4 (1.3, 7)	1.4 (0.7, 5)	7.9 (3.7, 5)
<i>A. capito</i>	71.9 (9.9, 16)	8.1 (2.7, 16)	126.2 (24.0, 16)	35.4 (1.1, 6)	63.5 (9.8, 6)	15.0 (0.01, 16)	0.9 (0.9, 26)	20.1 (33.1, 19)
<i>A. ortonii</i>	43.4 (8.4, 14)	2.2 (1.0, 14)	69.9 (23.0, 5)	16.6 (2.1, 12)	28.9 (3.1, 13)	18.8 (0.7, 12)	1.2 (0.6, 7)	31.3 (22.6, 7)
<i>A. carpenteri</i>	32.5 (4.9, 4)	0.7 (0.3, 4)	59.2 (23.1, 4)	13.1 (2.1, 6)	27.2 (3.3, 3)	15.8 (1.0, 6)
<i>A. auratus</i>	45.3 (4.5, 22)	1.7 (0.4, 22)	114.7 (19.6, 12)	21.8 (1.1, 10)	30.2 (3.2, 22)	16.5 (1.0, 10)	0.4 (0.2, 15)	0.4 (0.2, 11)
<i>A. fuscoauratus</i>	42.8 (3.5, 18)	1.2 (0.2, 18)	79.8 (10.0, 16)	16.7 (1.3, 7)	31.5 (1.8, 18)	15.4 (1.0, 7)	1.0 (0.9, 62)	9.6 (22.4, 51)
<i>A. nitens</i>	56.6 (13.0, 36)	4.3 (2.7, 36)	122.2 (33.0, 35)	37.1 (2.8, 7)	50.8 (12.2, 36)	17.8 (1.3, 6)	0.5 (0.3, 13)	5.8 (8.3, 13)
<i>A. trachyderma</i>	45.6 (4.3, 18)	1.8 (0.5, 18)	90.6 (8.2, 13)	18.8 (2.4, 15)	39.9 (3.6, 18)	15.8 (0.7, 16)	1.1 (2.9, 32)	11.9 (13.8, 18)
<i>A. lemurinus</i>	48.8 (3.0, 8)	2.3 (0.4, 8)	88.1 (16.5, 7)	19.3 (2.7, 7)	38.1 (2.1, 8)	15.6 (1.0, 7)
<i>A. limifrons</i>	36.7 (2.4, 23)	0.9 (0.2, 23)	76.6 (7.2, 17)	16.1 (0.6, 4)	32.0 (1.8, 23)	15.0 (0.8, 4)	0.9 (0.4, 11)	8.2 (5.1, 11)

Note: Numbers in parentheses are 1 SD (first number) and sample sizes (second number). Perch height and diameter are the ecological variables. The remaining variables are morphological and are in millimeters with the exception of body mass and lamellae number.

were carried out using SYSTAT 5.03 (Wilkinson 1990) and are two-tailed. Because each of the morphological variables increases interspecifically with body size, and because we were primarily interested in shape differences independent of size, we removed the effects of body size by regressing (least-squares regression) each variable on SVL and calculated residuals. We chose to regress variables against SVL, rather than against a composite variable (such as the first principal component from a principal component analysis [PCA]), because interpretation of residuals from regressions against SVL is more straightforward. Furthermore, SVL is highly correlated (Pearson $r = 0.98$) with PC 1 from a PCA of nonsize adjusted variables. Residuals from different morphological variables were not heteroscedastic (Hartley's F_{\max} test, $F_{\max} = 2.0$, $df = 4$, $P > 0.05$). Because Caribbean anole ecomorphs differ somewhat in body size, we also included body length (SVL that was \log_{10} transformed) in multivariate analyses. Thus, statistical analyses include both shape and size variables. Caribbean and mainland anoles do not differ significantly in body size (ANOVA, $F_{1,47} = 1.53$, $P > 0.20$).

Mean perch height and diameter data for 27 Caribbean

anole species were taken from Losos (1990a, 1992; J. B. Losos, *unpublished data*), Losos et al. (1994), Irschick and Losos (1996), and Losos and Irschick (1996) (see these references for details of how ecological data were gathered). For 12 mainland species, perch height and diameter data were gathered by L. Vitt and P. Zani from 1987 to 1995 following the same methods as outlined in the above references. To examine whether habitat use is correlated with morphology among Caribbean and mainland anoles, we performed canonical correlation analysis (CCA, see Miles and Ricklefs [1984] for a description of this technique). We also used analysis of covariance (ANCOVA) to determine if relationships between ecology and morphology differed among Caribbean and mainland anole species. Because both perch diameter and perch height tend to increase with body size among all 39 species examined (least-squares regressions, perch height, $F_{1,37} = 9.12$, $P = 0.005$; perch diameter, $F_{1,37} = 2.98$, $P = 0.09$), we removed the effects of body size from both ecological variables in the same manner as the morphological variables.

Phylogenetic analyses

Correlations among species may be statistically invalid if sister taxa tend to be similar to one another

(i.e., a phylogenetic “effect” exists [Cheverud et al. 1985, Felsenstein 1985, Gittleman and Kot 1990, Harvey and Pagel 1991, Martins and Garland 1991, Garland et al. 1992, Gittleman and Luh 1992, Losos and Miles 1994]). The fact that anole communities have converged so dramatically on different Greater Antillean islands suggests that such a phylogenetic effect does not exist, at least among Caribbean anoles. However, to evaluate whether a phylogenetic effect exists among all anoles examined in this study, we used the phylogenetic autocorrelation procedure outlined in Cheverud et al. (1985), using software originally created by T. Dow and J. Cheverud, and modified by D. Miles and A. Dunham. Simulation studies indicate that this method is effective at detecting phylogenetic effects when sample sizes (number of species) are large, as they are in this data set (Martins 1996; see also Gittleman and Luh 1992). This method examines variation in the variables of interest (e.g., morphological characteristics) in the context of a matrix of phylogenetic similarity (consisting of a matrix of distances between each taxon, with smaller distances denoting more closely related taxa) to examine whether there is significant covariation among species between the data and phylogenetic matrices. A significant positive autocorrelation coefficient indicates that closely related taxa tend to be similar. If no phylogenetic effect exists, then statistical methods incorporating phylogeny are unnecessary (Gittleman and Luh 1992, Losos and Miles 1994).

We based our autocorrelation analyses on a phylogeny (Fig. 1) which is a composite of several previous studies (Guyer and Savage 1986, 1992, Savage and Guyer 1989, Burnell and Hedges 1990, Hedges and Burnell 1990, Hass et al. 1993). As a measure of phylogenetic distance we calculated the number of nodes separating two species. This kind of phylogenetic distance assumes a model of speciation evolution, with morphological and ecological change occurring primarily at speciation. Because a large polytomy exists at the base of the tree denoting poorly understood relationships at deep levels, we considered all branches leading to that polytomy to represent 10 bifurcations. We used the number 10 to ensure that the distance between species within well-resolved clades would be less than the distances to species in other clades. Distances among species in other polytomies were set to one. Because no significant phylogenetic autocorrelation was found for any of the first four PC scores (all r^2 values < 0.16), we concluded that no phylogenetic effect was apparent, and thus used standard statistical tests on species means.

Morphological comparisons

We used the position of species in a multidimensional morphological space to determine whether a given mainland anole species belonged to one of the Caribbean ecomorph classes. Based on the first four axes

TABLE 2. Summary of canonical correlation analyses for mainland and West Indian anoles.

Canonical variate	Canonical correlation	r^2	c^2	df	P
Mainland					
1	0.96	0.92	29.83	10	0.001
2	0.91	0.83	12.52	4	0.014
West Indies					
1	0.89	0.79	48.33	10	< 0.001
2	0.70	0.49	14.69	4	0.005

of a PCA (based on a correlation matrix with all 49 species included) using size-adjusted variables and SVL, we calculated euclidean distances between all pairs of species as well as the centroid of each ecomorph class. We used these first four PC axes, because together they explain 91.7% of the variation among all species (see *Results*). For a mainland anole to be designated as a member of an ecomorph class, one of two criteria must be fulfilled. Either a mainland species must exhibit a euclidean distance to an ecomorph centroid less than the maximum value of species within that class to that centroid; or alternatively, a mainland species must exhibit a nearest-neighbor distance to an ecomorph species < 0.99 . This value of 0.99 is the mean nearest-neighbor distance of trunk-ground anoles, which is the lowest among all Caribbean ecomorph classes. We used the second criterion to allow mainland anoles that are adjacent to certain Caribbean anoles, yet just outside the ecomorph morphological space (as judged by distance to the centroid), to be included as a member of that class. In this manner, these two criteria are fairly liberal in terms of allowing a mainland anole to be designated as a Caribbean ecomorph.

RESULTS

Ecomorphological relationships

Table 1 provides mean ecological and morphological values for mainland anole species. The CCAs examining relationships between ecology and morphology were significant for both mainland and Caribbean anole species (mainland: Wilks' $\lambda = 0.014$, $F_{10,10} = 7.42$, $P < 0.0025$; West Indies: Wilks' $\lambda = 0.111$, $F_{10,40} = 8.00$, $P < 0.001$). In both mainland and Caribbean anole species, both canonical variates were significant (Table 2). Among mainland anole species, the first morphology canonical variate is correlated primarily with relative perch height, whereas morphology CV 2 is associated primarily with relative perch diameter (Table 3). Ecology CV 1 in mainland anole species exhibits high positive loadings with relative lamellae number, and is negatively correlated with relative body mass. Ecology CV 2 in mainland anole species exhibits high positive correlations with relative lamellae number and relative hindlimb length, and high negative correlations

TABLE 3. Loadings of five morphological and two ecological variables (all size-adjusted) with canonical variates for 12 mainland anole species.

Morphological variable	Ecology CV 1	Ecology CV 2
Forelimb length	-0.314 (0.09)	-0.616 (0.38)
Hindlimb length	0.151 (0.02)	0.812 (0.66)
Lamellae number	0.645 (0.42)	0.777 (0.60)
Body mass	-0.498 (0.25)	0.043 (0.002)
Tail length	0.203 (0.04)	-0.742 (0.55)
Ecological variable	Morphology CV 1	Morphology CV 2
Perch height	0.714 (0.51)	0.700 (0.49)
Perch diameter	-0.363 (0.13)	0.932 (0.86)

Note: Numbers in parentheses are proportions of variation of each variable associated with an ecological or morphological canonical variate. Correlations that are substantial (i.e., proportions > 0.35) are marked in bold.

with relative forelimb length and relative tail length (Table 3).

By contrast, morphology CV 1 in Caribbean anole species is correlated primarily with relative perch diameter, while morphology CV 2 is correlated with perch height (Table 4). Ecology CV 1 in Caribbean anole species exhibits high positive correlations with relative forelimb length and relative body mass (Table 4). Ecology CV 2 exhibits high negative correlations with relative hindlimb length and relative tail length (Table 4).

We selected ecomorphological relationships that were substantial among mainland anole species, among Caribbean anole species, or among both sets of anole species. To qualify as a significant ecomorphological relationship, both the ecological and morphological variable (e.g., relative lamellae number and relative perch height) had to have at least 35% of their variation associated with the morphological and ecological canonical variates, respectively (Tables 3 and 4). Based on this criterion, we extracted nine ecomorphological relationships that we label as “mainland” (significant among only mainland anoles), “Caribbean” (significant among only Caribbean anole species), or as “neither” (significant among neither mainland nor Caribbean anole species) (Table 5).

Only one relationship was nonsignificant among either mainland or Caribbean anole species: lamellae number vs. perch diameter. Three relationships were significant only among mainland anole species, and the remaining five relationships were significant among only Caribbean anole species. Four relationships exhibited significant heterogeneity of slopes, and in two other relationships, y intercepts were significantly different among mainland and Caribbean anole species (Table 5).

Morphological comparisons

The first four PC axes explained 91.7% of the variation among species (Table 6). The fifth and sixth axes had substantially smaller eigenvalues than the first four PC axes (0.342 and 0.160, respectively). Consequently, we only discuss variation in PC axes 1–4. Principal component 1, which explained 40.9% of the variation among species, exhibits high positive loadings for relative forelimb length, relative hindlimb length, and relative body mass. Principal component 2 exhibited high positive loadings for relative lamellae number and relative tail length, whereas PC 3 was primarily a size axis with an extremely high positive contribution from SVL. Principal component 4 exhibited no particularly large positive or negative loadings with any variable

TABLE 4. Loadings of five morphological and two ecological variables (all size adjusted) with canonical variates for 27 West Indian anole species.

Morphological variable	Ecology CV 1	Ecology CV 2
Forelimb length	0.817 (0.67)	0.482 (0.23)
Hindlimb length	0.309 (0.095)	-0.788 (0.62)
Lamellae number	0.176 (0.03)	-0.281 (0.08)
Body mass	0.781 (0.61)	0.475 (0.23)
Tail length	-0.394 (0.16)	-0.791 (0.63)
Ecological variable	Morphology CV 1	Morphology CV 2
Perch height	0.381 (0.15)	0.925 (0.86)
Perch diameter	0.946 (0.89)	-0.323 (0.10)

Note: Numbers in parentheses are proportions of variation of each variable associated with an ecological or morphological canonical variate. Correlations that are substantial (i.e., proportions > 0.35) are marked in bold.

TABLE 5. Ecomorphological relationships that differ among mainland and Caribbean anole species.

Comparison	r_{main}	r_{car}	Slopes		Intercepts	
			F	P	F	P
Mainland relationships						
Lamellae number vs. perch height	0.65*	0.24	2.43	0.128	8.10	0.007 (c)
Tail length vs. relative perch diameter	-0.76**	-0.15	0.777	0.384	0.22	0.639
Forelimb length vs. perch height	-0.59*	0.04	4.78	0.038 (c)
Caribbean relationships						
Forelimb length vs. perch diameter	0.22	0.79***	13.71	0.001 (c)
Body mass vs. perch diameter	0.51	0.76***	4.56	0.040 (c)
Hindlimb length vs. perch height	-0.21	-0.40*	0.23	0.640	0.35	0.560
Tail length vs. perch height	0.07	-0.64***	4.96	0.030 (m)
Hindlimb length vs. perch diameter	0.23	0.44*	1.11	0.298	1.38	0.250
Neither						
Lamellae number vs. perch diameter	0.07	0.08	0.21	0.649	12.70	0.001 (c)

Note: The r values are Pearson correlation coefficients between ecological and morphological variables for 12 mainland (10 df) and 27 Caribbean (25 df) anoles (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). The ‘‘Slopes’’ test is for homogeneity of slopes, while the ‘‘Intercepts’’ test examines differences in y intercepts. All ‘‘Slopes’’ tests have 1 and 35 df while ‘‘Intercepts’’ tests have 1 and 36 df. All variables are size adjusted. Significant P values (< 0.05) are marked in bold. Letters in parentheses next to significant P values indicate whether mainland (**m**) or Caribbean (**c**) anole species tended to have significantly greater slopes or intercepts.

(Table 6). Fig. 2 shows the Caribbean ecomorphs clustered in different positions of a multivariate morphological space. The majority of mainland anoles fall outside or on the periphery of the morphological spaces defined by Caribbean ecomorphs (Fig. 2).

Table 7 provides nearest-neighbor distances and distances to centroids for Caribbean ecomorph classes. In general, most of the mainland anoles exhibited high centroid and nearest-neighbor distances to Caribbean anoles, but six mainland anoles were classified as Caribbean ecomorphs (Table 8). All six mainland anoles classified as Caribbean ecomorphs had large distances to other Caribbean ecomorph centroids or other species besides the ecomorph classes to which they were assigned. By contrast, the 10 mainland anoles not classifiable as Caribbean ecomorphs exhibited large nearest-neighbor and centroid distances to all Caribbean species and centroids.

Ecological patterns among mainland anoles

We examined whether the six mainland anoles classified as Caribbean ecomorphs based on morphology

exhibited the same ecological characteristics as the ecomorphs to which they were assigned. For this comparison, we examined nonsize-adjusted perch height and diameter, because Caribbean ecomorphs have traditionally been defined based on these ecological characteristics. Caribbean ecomorphs fell into fairly discrete clusters based on relative perch height and diameter (Fig. 3), although the trunk-crown ecomorph shows substantial variability. Further, the two crown-giants and the one trunk anole fell within or on the periphery of the large trunk-crown ecological space (Fig. 3),

Ecological data were available for all mainland anoles classified morphologically as Caribbean ecomorphs except *A. sericeus*. Of these five anole species, none fell within the ecological space of the Caribbean ecomorph to which they were assigned morphologically. *Anolis frenatus* (identified by the number 1 in Fig. 3, classified as a crown-giant ecomorph) falls within the large ecological space of trunk-crown anoles, but falls somewhat near the two Caribbean crown-giant anoles. *Anolis biporcatus* (number 7, classified as a crown-

TABLE 6. Loadings from a principal components analysis of five size-removed morphological characteristics and one size variable, snout-vent length (SVL), for 33 West Indian and 16 mainland anoles.

Variable	PC 1	PC 2	PC 3	PC 4
Size	-0.001	0.004	1.000	0.013
Forelimb length	0.861	-0.091	0.004	-0.233
Hindlimb length	0.923	0.053	-0.003	0.224
Lamellae number	-0.426	0.703	0.004	-0.533
Body mass	0.719	0.025	0.008	-0.585
Tail length	0.405	0.769	-0.009	0.463
Eigenvalue	2.45	1.10	1.00	0.95
Variance explained	40.9	18.3	16.7	15.8

Note: Substantial loadings are marked in bold.

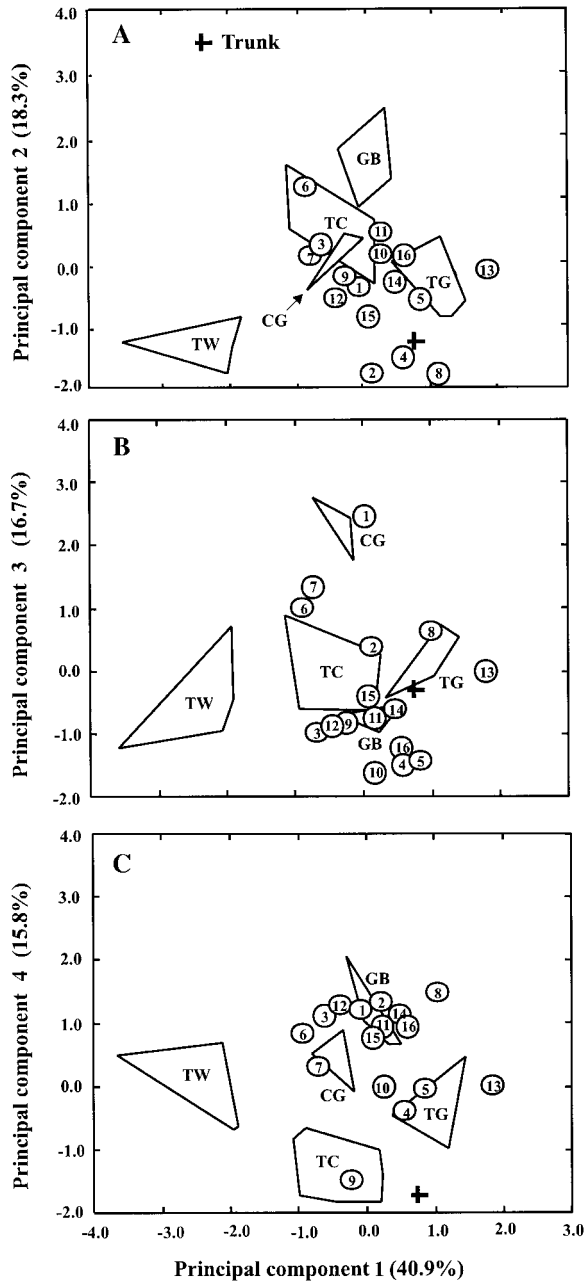


FIG. 2. (A) PC 2 (y axis) vs. PC 1 (x axis). Outlines for West Indian ecomorphs were created by connecting points such that all species within an ecomorph class were included (TG = trunk-ground, TC = trunk-crown, GB = grass-bush, TW = twig, CG = crown-giant, TR = trunk; because only one trunk anole was examined, no outlines were drawn for this ecomorph). Each point represents a species. Numbers next to mainland anoles represent the following species: (1) *Anolis frenatus*, (2) *A. oxylophus*, (3) *A. sericeus*, (4) *A. humilis*, (5) *A. meridionalis*, (6) *A. punctatus*, (7) *A. biporcatus*, (8) *A. capito*, (9) *A. ortonii*, (10) *A. carpenteri*, (11) *A. auratus*, (12) *A. fuscoauratus*, (13) *A. nitens*, (14) *A. trachyderma*, (15) *A. lemurinus*, (16) *A. limifrons*. (B) A plot of PC 1 (x axis) vs. PC 3 (y axis). (C) A plot of PC 1 (x axis) vs. PC 4 (y axis).

giant ecomorph) fell outside any Caribbean ecomorph space, and is distant from the two other Caribbean crown-giants (Fig. 3). *Anolis ortonii* (number 9, classified as a trunk-crown ecomorph) fell on the periphery of the trunk-ground ecological space, and is ecologically distant from the trunk-crown ecological space (Fig. 3). *Anolis auratus* (number 11, classified as a grass-bush ecomorph), by contrast, falls ecologically very close to the grass-bush ecomorph space (Fig. 3). Finally, *A. nitens* (number 13, classified as a trunk-ground ecomorph) fell ecologically between all Caribbean ecomorphs, and is closer to grass-bush anoles than to trunk-ground anoles (Fig. 3). On the other hand, the mainland anole *A. punctatus*, which fell squarely in the trunk-crown ecological space (Fig. 3), was morphologically closest to crown-giant anoles (Table 8).

DISCUSSION

A substantial body of research reveals that similar *Anolis* lizard communities have evolved repeatedly in the Greater Antilles (Williams 1972, 1983, Losos 1990a, Jackman et al. *in press*). This suggests some deterministic factor which appears to be shaping pathways of morphological and ecological evolution among Greater Antillean anole species. If the same factors that caused evolution to proceed in predictable directions in the Caribbean also exist in mainland Central and South America, then we would expect that the same ecomorphs present in the Greater Antilles should also exist in mainland communities. Alternatively, differences in environmental conditions faced by Caribbean and mainland anoles might result in very different ecomorphological configurations in the two regions.

Our results clearly favor the latter hypothesis. Despite using liberal criteria, only six of the 16 mainland anoles examined are morphologically similar to Caribbean ecomorphs. Of the five mainland anoles for which ecological data were available, none were similar ecologically to Caribbean classes to which they were similar morphologically. At a broader level, relationships between morphology and ecology were strikingly different for Caribbean and mainland anole species. Among Caribbean anoles, morphological variation correlated primarily with perch diameter, whereas among mainland anoles, morphology correlated primarily with perch height.

Functional bases of ecomorphological correlations

A fundamental assumption in ecomorphological studies is that relationships between ecology and morphology are functionally relevant to organisms in nature (Arnold 1986, Wainwright 1994). What are the functional bases for the ecomorphological correlations observed among mainland and Caribbean anoles?

Biomechanical and ecomorphological work, primarily on Caribbean anole species, has focused on two aspects of body shape: relative limb dimensions, and toepad characteristics (Collette 1961, Moermond 1979,

TABLE 7. Euclidean distances for 33 West Indian *Anolis* ecomorphs based on a principal components analysis of six morphological variables.

Ecomorph	<i>n</i>	Mean distance to centroid	Maximum distance to centroid	Mean nearest neighbor distance
Trunk-ground	9	0.71 ± 0.084	1.00	0.99 ± 0.072
Crown-giant	3	0.74 ± 0.093	0.83	1.28 ± 0.143
Trunk-crown	10	0.94 ± 0.088	1.45	1.36 ± 0.074
Grass-bush	6	0.72 ± 0.126	1.17	1.10 ± 0.123
Twig	4	1.22 ± 0.149	1.54	1.98 ± 0.214

Note: Means are reported ± 1 SE. (Because only one trunk anole was examined, statistics for this ecomorph are not presented.)

Pounds 1988, Losos and Sinervo 1989, Losos 1990a, c, Irschick et al. 1996, Losos and Irschick 1996, Glossip and Losos, *in press*). From this work, two functional hypotheses have been proposed linking these traits with habitat use. First, anoles using broad (relative to body size) supports should have relatively long limbs, and should move primarily by running and jumping. By contrast, anoles using relatively narrow supports should have relatively short limbs, and should move most often by walking. This hypothesis is based on the premise that anoles using narrow supports need short limbs that allow them to move slowly and position their center of gravity over the support (Cartmill 1985, Pounds 1988, Losos 1990c, Irschick and Losos 1996). On broad surfaces, anole species are not constrained to maintaining balance, and have evolved long limbs that enable them to sprint and jump effectively (Moermond 1979, Losos 1990a, c). These considerations lead to the prediction that relative perch diameter should be positively correlated with relative limb length. A second functional hypothesis is that relative number of

lamellae should be correlated with relative perch height. This hypothesis is based on the idea that anoles using relatively (i.e., compared to body size) higher perches require relatively greater clinging capabilities to effectively move around their habitats. Recent studies have shown that lamellae number is positively correlated with toepad area which, in turn, is positively

TABLE 8. Euclidean distances for 16 mainland anoles based on a morphological PCA. Ecomorph initials next to the distances are the ecomorphs to which the mainland anole is closest.

Species	Distance to closest ecomorph centroid	Smallest nearest-neighbor distance
<i>Anolis frenatus</i> †	0.896 CG	0.816 CG
<i>A. oxylophus</i>	2.442 TG	1.843 TG
<i>A. sericeus</i> †	1.470 GB	0.882 GB
<i>A. humilis</i>	1.814 TR	1.621 TC
<i>A. meridionalis</i>	1.749 TG	1.326 TG
<i>A. punctatus</i>	1.767 CG	1.556 CG
<i>A. biporcatus</i> †	1.127 CG	0.937 CG
<i>A. capito</i>	2.431 TG	1.638 TG
<i>A. ortonii</i> †	1.203 TC	0.671 TC
<i>A. carpenteri</i>	2.015 GB	1.245 TG
<i>A. auratus</i> †	1.012 GB	0.453 GB
<i>A. fuscoauratus</i>	2.140 GB	1.512 GB
<i>A. nitens</i> †	0.912 TG	0.967 TG
<i>A. trachyderma</i>	1.740 TG	1.307 GB
<i>A. lemurinus</i>	1.709 TG	1.478 TG
<i>A. limifrons</i>	1.648 GB	1.16 GB

Note: TG = trunk-ground, CG = crown-giant, TC = trunk-crown, GB = grass-bush, TW = twig, TR = trunk.
 † Mainland anole fulfills criteria as being a West Indian ecomorph.

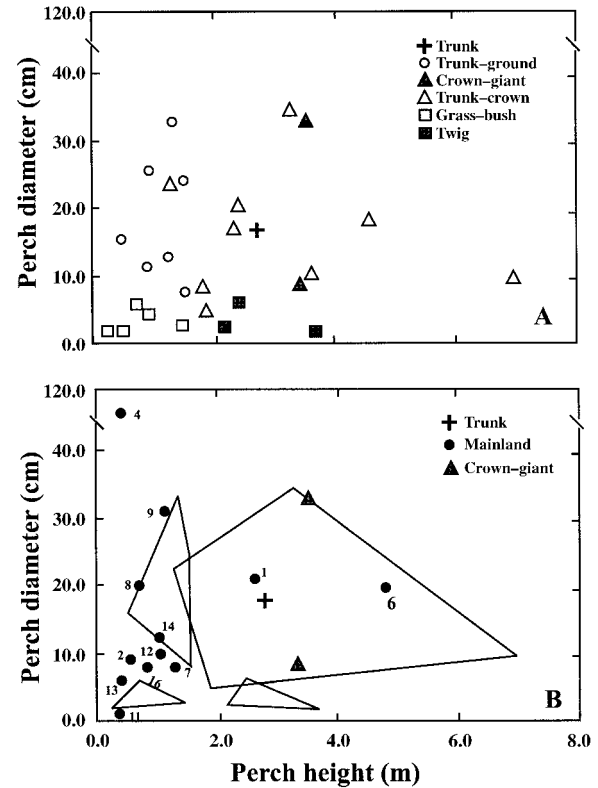


FIG. 3. (A) Mean perch diameter (y axis) vs. perch height (x axis) for 27 West Indian anoles. Each point represents a species. Different symbols represent different West Indian ecomorphs. (B) Same as Fig. 3A, but with outlines replacing West Indian anole species, and with 12 mainland anole species included. Numbers next to mainland anole species are the same as in Fig. 2A. Outlines were drawn by connecting lines between points that surround all other points in an ecomorph class. TG = trunk-ground, TC = trunk-crown, GB = grass-bush, TW = twig.

correlated with clinging ability in anoles (Irschick et al. 1996; T. Macrini, unpublished data).

An interesting finding was that the strength and direction of these two relationships vary dramatically between Caribbean and mainland anole species. Among Caribbean anole species, both hindlimb and forelimb length are positively correlated with perch diameter, in agreement with the functional model outlined above. On the other hand, among mainland anole species, neither limb measurement is significantly correlated with perch diameter. One possible reason for differences in these relationships is the absence of twig anoles among the mainland species examined (Figs. 2 and 3). Caribbean twig anoles use narrower perches than other ecomorphs, and also have relatively short hindlimbs (Irschick and Losos 1996). However, when twig anoles are excluded from analyses, forelimb length remains tightly correlated with perch diameter in Caribbean anoles (Pearson $r = 0.70$, $P < 0.001$, 23 df), but the relationship between hindlimb length and perch diameter becomes nonsignificant (Pearson $r = 0.14$, $P > 0.20$, 23 df) among Caribbean anoles. Another possibility is that too few mainland anoles were examined to detect significant relationships between limb dimensions and perch diameter. However, if this were true, we would not expect significant ecomorphological correlations among mainland anoles for other relationships as well, and this is clearly not the case.

On the other hand, the number of lamellae is positively correlated with perch height among mainland anoles, but not among the Caribbean anoles examined here. In a survey of a much greater number of Caribbean anole species ($n = 63$), Glossip and Losos (*in press*) found a weak but significant relationship between these two variables, but the correlation values in their study were not dramatically higher than among the anole species sampled here (Glossip and Losos: $r = 0.44$; in this study: $r = 0.24$). Further, in neither study did correlation values match the value observed among mainland anole species ($r = 0.65$). The reasons for the difference between correlation values among mainland and Caribbean anole species are not clear, but it is possible that the need to cling effectively is under much greater selection in mainland than in island habitats, thus leading to a tighter correlation between lamellae number and perch height among mainland anoles.

Unlike toepad and limb characteristics, the functional basis of other correlations between ecology and morphology in mainland and Caribbean anoles is poorly understood. For example, the functional basis of the strong negative relationship between relative tail length and relative perch diameter in mainland anoles (but not Caribbean anoles) offers no ready functional hypothesis. Similarly, why Caribbean anole species that perch relatively closer to the ground have relatively shorter tails is not obvious. Further biomechanical work might

elucidate the functional basis, if any, of these relationships.

Biotic and abiotic factors

Because mainland and Caribbean regions differ in numerous biotic and abiotic characteristics, we would expect these factors to play a role in influencing anole ecomorphological relationships (substantial variation in these factors also exists among the mainland sites examined [Appendix A], but we limit our discussion here to island and mainland comparisons).

Central and South American habitats contain a much greater diversity of potential anole predators than Caribbean islands (Greene 1988), which suggests that differential levels of predation pressure may be one cause of ecomorphological differences among anole species in the two regions. One means of testing whether predators are exerting a stronger influence on anole habitat use and behavior in mainland than in Caribbean sites would be to examine differences in escape behavior among mainland and Caribbean anole species. If habitat use, morphology, and behavior are correlated among mainland anoles, as they are among Caribbean anoles (Williams 1983, Losos 1990a, c), then differences in escape behavior between anole species in the two regions may lead to differences in ecomorphological relationships. While little quantitative data has been collected on this topic, anecdotal observations suggest that mainland anoles typically escape from predators in a manner very different from Caribbean anole species that use similar habitats. For example, the mainland anole *A. limifrons* uses a structural habitat similar to Caribbean trunk-ground anoles (Fig. 3), but escapes in the same manner as twig anoles by flattening its body against its substrate and hiding (Talbot 1979). The mainland anole *A. attenuatus* also differs from Caribbean ecomorphs, because although it resembles crown-giant anoles, it is slow moving, and relies on crypsis to avoid detection (Fitch et al. 1976). Finally, another aspect related to anole ecomorphology that warrants further study is whether mainland anoles exhibit a greater range of escape behaviors (i.e., "aspect diversity") as a consequence of having greater numbers of predators (Schall and Pianka 1980). An increased diversity of escape behaviors might result in a greater diversity of morphological and ecological forms in mainland regions.

Of course, mainland and Caribbean regions differ in many other characteristics that can potentially affect anole ecomorphological relationships, such as food abundance, structural habitat diversity, and rainfall patterns. How differences in such conditions between the two regions would affect ecomorphological configurations of anole species is even less clear. For example, population size in *A. limifrons*, and presumably many other mainland anole species, fluctuates greatly, possibly due to the effects of rainfall and food availability (Andrews and Wright 1994; see also Guyer 1988a, b).

These dramatic fluctuations in population size, a feature not observed in Caribbean anole populations (Schoener 1985), suggest that mainland anole populations are rarely at equilibrium, and therefore may be more influenced by abiotic factors than Caribbean anole populations.

The role of historical contingency

Recent years have seen an increased appreciation for the role that historical contingency might play in determining community structure (Ricklefs and Schluter 1993 and chapters therein; Losos 1994b). History can be an important factor due to the profound effects of historically related phenomena such as initial starting conditions, chance events, and the fact that species within one community may be more closely related to one another than to species from other communities. Could historical phenomena explain, at least in part, why mainland and Caribbean anole radiations differ so greatly? Historical contingency would be most likely to show widespread effects if mainland and Caribbean anole species form separate monophyletic groups. If this were the case, then events that occurred early in one of the clades' history might have far-reaching and long-lasting effects. Examination of Fig. 1 suggests that this scenario is conceivable. Depending on the resolution of the polytomies, anole diversity might be resolvable into only two mainland and two anole clades. If this turns out to be correct, then historical contingency may have played a role in channeling evolutionary trajectories of mainland and Caribbean anole species. Better resolution of anole phylogeny is required to more thoroughly investigate this possibility.

ACKNOWLEDGMENTS

We thank D. Frost (American Museum of Natural History), K. de Queiroz (National Museum of Natural History, Smithsonian Institution), J. Cadle (Museum of Comparative Zoology, Harvard University), and J. Mendelson (Museum of Zoology, University of Kansas) for allowing us to examine specimens; M. Leal, M. Butler, J. Cheverud, T. Case, and two anonymous reviewers for helpful comments on previous versions of the manuscript, and C. Guyer for advice. L. J. Vitt and P. A. Zani thank T. C. S. Avila-Pires (Brazil) and L. Coloma (Ecuador) for coordinating field research. For logistic support, L. J. Vitt and P. A. Zani thank the Museo de Zoología de la Pontificia Universidad Católica (QCAZ), the Museu Paraense Emílio Goeldi (MPEG), the Instituto de Pesquisas da Amazonia (INPA), the Museu de Zoologia da Universidade de São Paulo (MZUSP), and the Oklahoma Museum of Natural History (OMNH). Permits to conduct research and collect specimens in Brazil were issued by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPQ, Portaria MCT no. 170, de 28/09/94) and the Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA, no. 073/94-DIFAS). Permits to conduct research in Nicaragua were issued by the Departamento de Fauna Silvestre of Nicaragua. This research was supported by National Science Foundation grants (DEB-9200779 and DEB-9505518) to L. J. Vitt and Janalee P. Caldwell, and by NSF grant DEB-9318642 to J. B. Losos.

LITERATURE CITED

- Andrews, R. M. 1976. Growth rate in island and mainland anoline lizards. *Copeia* 1976:477–482.
- . 1979. Evolution of life histories: a comparison of *Anolis* lizards from matched island and mainland habitats. *Breviora* 454:1–51.
- Andrews, R. M., and A. S. Rand. 1982. Seasonal breeding and long-term fluctuations in the lizard *Anolis limifrons*. Pages 405–412 in E. G. Leigh, Jr., and A. S. Rand, editors. *The ecology of a tropical forest: seasonal rhythms and long-term changes*. Smithsonian Institution Press, Washington, D.C., USA.
- Andrews, R. M., and J. S. Wright. 1994. Long-term population fluctuations of a tropical lizard: a test of causality. Pages 267–286 in L. J. Vitt and E. R. Pianka, editors. *Lizard ecology: historical and experimental perspectives*. Princeton University Press, Princeton, New Jersey, USA.
- Arnold, S. J. 1986. Laboratory and field approaches to the study of adaptation. Pages 157–179 in M. E. Feder and G. V. Lauder, editors. *Predator-prey relationships: perspectives and approaches from the study of lower vertebrates*. University of Chicago Press, Chicago, Illinois, USA.
- Burnell, K. L., and S. B. Hedges. 1990. Relationships of Caribbean *Anolis* (Sauria: Iguanidae): an approach using slow-evolving protein loci. *Caribbean Journal of Science* 26:7–30.
- Canatella, D. C., and K. de Queiroz. 1989. Phylogenetic systematics of the anoles: is a new taxonomy warranted? *Systematic Zoology* 38:57–69.
- Carlquist, S. 1965. *Island life*. Natural History Press, Garden City, New York, USA.
- . 1974. *Island biology*. Columbia University Press, New York, New York, USA.
- Carson, H. L., and K. Y. Kaneshiro. 1976. *Drosophila* of Hawaii: systematics and ecological genetics. *Annual Review of Ecology and Systematics* 7:311–345.
- Cartmill, M. 1985. Climbing. Pages 73–88 in M. Hildebrand, D. M. Bramble, K. F. Liem, and D. B. Wake, editors. *Functional vertebrate morphology*. Belknap, Cambridge, Massachusetts, USA.
- Case, T. J. 1978. A general explanation for insular body size trends in terrestrial vertebrates. *Ecology* 59:1–18.
- Cheverud, J. M., M. M. Dow, and W. Leutenegger. 1985. The quantitative assessment of phylogenetic constraints in comparative analyses: sexual dimorphism in body weight in primates. *Evolution* 39:1335–1351.
- Collette, B. B. 1961. Correlations between ecology and morphology in anoline lizards from Havana, Cuba and Southern Florida. *Bulletin of the Museum of Comparative Zoology* 5:137–162.
- Felsenstein, J. 1985. Phylogenies and the comparative method. *American Naturalist* 125:1–15.
- Fitch, H. S., A. F. Echelle, and A. A. Echelle. 1976. Field observations on rare or little-known mainland anoles. *University of Kansas Science Bulletin* 51:91–128.
- Garland, T., Jr., P. H. Harvey, and A. R. Ives. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. *Systematic Biology* 41:18–32.
- Gittleman, J. L., and M. Kot. 1990. Adaptation: statistics and a null model for estimating phylogenetic effects. *Systematic Zoology* 39:227–241.
- Gittleman, J. L., and H. K. Luh. 1992. On comparing comparative methods. *Annual Review of Ecology and Systematics* 23:383–404.
- Glossip, D., and J. B. Losos. *In press*. Ecological correlates of subdigital lamellae in anoles. *Herpetologica*.
- Grant, P. R. 1986. *Ecology and evolution of Darwin's Finches*. Princeton University Press, Princeton, New Jersey, USA.

- Greene, H. W. 1988. Species richness in tropical predators. Pages 259–280 in F. Alameda and C. M. Pringle, editors. Tropical rainforests: diversity and conservation. California Academy of Sciences, San Francisco, California, USA.
- Guyer, C. 1988a. Food supplementation in a tropical mainland anole, *Norops humilis*: demographic effects. *Ecology* **69**:350–361.
- . 1988b. Food supplementation in a tropical mainland anole, *Norops humilis*: effects on individuals. *Ecology* **69**:362–369.
- Guyer, C., and J. M. Savage. 1986. Cladistic relationships among anoles (Sauria: Iguanidae). *Systematic Zoology* **35**:509–531.
- Guyer, C., and J. M. Savage. 1992. Anole systematics revisited. *Systematic Biology* **41**:89–110.
- Harvey, P. H., and M. D. Pagel. 1991. The comparative method in evolutionary biology. Oxford University Press, Oxford, UK.
- Hass, C. A., S. B. Hedges, and L. R. Maxson. 1993. Molecular insights into the relationships and biogeography of Caribbean anoline lizards. *Biochemical Systematics and Ecology* **21**:97–114.
- Hedges, S. B., and K. L. Burnell. 1990. The Jamaican radiation of *Anolis*: an analysis of relationships and biogeography using sequential electrophoresis. *Systematic Zoology* **26**:7–30.
- Henderson, R. W., and B. I. Crother. 1989. Biogeographic patterns of predation in West Indian colubrid snakes. Pages 479–518 in C. A. Woods, editor. Biogeography of the West Indies: past, present, and future. Sandhill Crane Press, Gainesville, Florida, USA.
- Irschick, D. J., C. Austin, R. Fisher, K. Petren, J. B. Losos, and O. Ellers. 1996. A comparative analysis of clinging ability among pad-bearing lizards. *Biological Journal of the Linnean Society* **59**:21–35.
- Irschick, D. J., and J. B. Losos. 1996. Morphology, ecology, and behavior of the twig anole, *Anolis angusticeps*. Pages 291–301 in R. Powell and R. W. Henderson, editors. Contributions to Caribbean herpetology: a tribute to Albert Schwartz. Society for the Study of Amphibians and Reptiles (SSAR) Contributions in Herpetology. Volume 12. SSAR, Ithaca, New York, USA.
- Jackman, T. R., A. Larson, and J. B. Losos. *In press*. Phylogenetic studies of convergent faunal evolution in Caribbean *Anolis* lizards. In *Molecular evolution and adaptive radiation*. Cambridge University Press, Cambridge, UK.
- Jeffries, M. J., and J. H. Lawton. 1984. Enemy-free space and the structure of ecological communities. *Biological Journal of the Linnean Society* **23**:269–286.
- Lack, D. 1947. Darwin's finches. Cambridge University Press, Cambridge, UK.
- Losos, J. B. 1990a. Ecomorphology, performance capability, and scaling of Caribbean *Anolis* lizards: an evolutionary analysis. *Ecological Monographs* **60**:369–388.
- . 1990b. The evolution of form and function: morphology and locomotor performance in Caribbean *Anolis* lizards. *Evolution* **44**:1189–1203.
- . 1990c. Concordant evolution of locomotor behavior, display rate, and morphology in *Anolis* lizards. *Animal Behavior* **39**:879–890.
- . 1992. The evolution of convergent structure in Caribbean *Anolis* communities. *Systematic Biology* **41**:403–420.
- . 1994a. Integrative approaches to evolutionary ecology: *Anolis* lizards as model systems. *Annual Review of Ecology and Systematics* **25**:467–493.
- . 1994b. Historical contingency and lizard community ecology. Pages 319–333 in L. J. Vitt and E. R. Pianka, editors. Lizard ecology: historical and experimental perspectives. Princeton University Press, Princeton, New Jersey, USA.
- Losos, J. B., and D. J. Irschick. 1996. Escape behavior in Caribbean *Anolis* lizards: laboratory-based predictions and field tests. *Animal Behavior* **51**:593–602.
- Losos, J. B., D. J. Irschick, and T. W. Schoener. 1994. Adaptation and constraint in the evolution of specialization of Bahamian *Anolis* lizards. *Evolution* **48**:1786–1798.
- Losos, J. B., and D. B. Miles. 1994. Adaptation, constraint, and the comparative method. Pages 60–98 in P. C. Wainwright and S. M. Reilly, editors. Ecological morphology. University of Chicago Press, Chicago, Illinois, USA.
- Losos, J. B., and B. Sinervo. 1989. The effect of morphology and perch diameter on sprint performance of *Anolis* lizards. *Journal of Experimental Biology* **145**:23–30.
- Martins, E. P. 1996. Phylogenies, spatial autoregression, and the comparative method: a computer simulation test. *Evolution* **50**:1750–1765.
- Martins, E. P., and T. Garland, Jr. 1991. Phylogenetic analyses of the correlated evolution of continuous characters: a simulation study. *Evolution* **45**:534–557.
- McLaughlin, J. F., and J. Roughgarden. 1989. Avian predation on *Anolis* lizards in the northeastern Caribbean: an interisland contrast. *Ecology* **70**:617–628.
- Miles, D. B., and R. E. Ricklefs. 1984. The correlation between ecology and morphology in deciduous forest passerine birds. *Ecology* **65**:1629–1640.
- Moermond, T. C. 1979. Habitat constraints on the behavior, morphology, and community structure of *Anolis* lizards. *Ecology* **60**:152–164.
- Pounds, J. A. 1988. Ecomorphology, locomotion, and microhabitat structure: patterns in a tropical mainland *Anolis* community. *Ecological Monographs* **58**:299–320.
- Powell, R., R. W. Henderson, K. Adler, and H. A. Dundee. 1996. An annotated checklist of Caribbean amphibians and reptiles. Pages 51–93 in R. Powell and R. W. Henderson, editors. Contributions to Caribbean herpetology: a tribute to Albert Schwartz. Society for the Study of Amphibians and Reptiles (SSAR) Contributions in Herpetology Volume 12. SSAR, Ithaca, New York, USA.
- Rand, A. S., and S. S. Humphrey. 1968. Interspecific competition in the tropical rain forest: ecological distribution among lizards at Belem, Paraguay. *Proceedings of the United States National Museum* **125**:1–17.
- Rand, A. S., and E. E. Williams. 1969. The anoles of La Palma: aspects of their ecological relationships. *Breviora* **327**:1–19.
- Ricklefs, R. E., and D. Schluter. 1993. Species diversity in ecological communities: historical and geographic perspectives. University of Chicago Press, Chicago, Illinois, USA.
- Savage, J., and C. Guyer. 1989. Infrageneric classification and species composition of the anole genera, *Anolis*, *Ctenonotus*, *Dactyloa*, *Norops*, and *Semiurus* (Sauria: Iguanidae). *Amphibia-Reptilia* **10**:105–116.
- Schall, J., and E. R. Pianka. 1980. Evolution of escape behavior. *American Naturalist* **115**:551–566.
- Schoener, T. W. 1985. Are lizard populations unusually constant through time? *American Naturalist* **126**:633–641.
- Schoener, T. W., and A. Schoener. 1978. Inverse relation of survival of lizards with island size and avifaunal richness. *Nature* **274**:685–687.
- Sih, A., P. Crowley, M. McPeck, J. Petranka, and K. Strohmeier. 1985. Predation, competition, and prey communities. *Annual Review of Ecology and Systematics* **16**:269–311.
- Talbot, J. J. 1979. Time budget, niche overlap, inter- and intraspecific aggression in *Anolis humilis* and *A. limifrons* from Costa Rica. *Copeia* **1979**:472–481.
- Vitt, L. J., and G. R. Colli. 1994. Geographical ecology of

- a neotropical lizard: *Ameiva ameiva* (Teiidae) in Brazil. Canadian Journal of Zoology **72**:1986–2008.
- Vitt, L. J., and P. A. Zani. 1996a. Ecology of the South American lizard *Norops chrysolepis* (Polychrotidae). Copeia 1996:56–68.
- Vitt, L. J., and P. A. Zani. 1996b. Ecology of the elusive tropical lizard *Tropidurus* (= *Uracentron*) *flaviceps* (Tropiduridae) in lowland rainforest of Ecuador. Herpetologica **52**:121–132.
- Vitt, L. J., and P. A. Zani. 1996c. Organization of a taxonomically diverse lizard assemblage in Amazonian Ecuador. Canadian Journal of Zoology **74**:1313–1335.
- Vitt, L. J., P. A. Zani, and R. D. Durtsche. 1995. Ecology of the lizard *Norops oxylophus* (Polychrotidae) in lowland forest of southeastern Nicaragua. Canadian Journal of Zoology **73**:1918–1927.
- Waide, R. B., and D. P. Reagan. 1983. Competition between Caribbean anoles and birds. American Naturalist **121**:133–138.
- Wainwright, P. 1994. Functional morphology as a tool in ecological research. Pages 42–59 in P. C. Wainwright and S. M. Reilly, editors. Ecological morphology. University of Chicago Press, Chicago, Illinois, USA.
- Williams, E. E. 1972. The origin of faunas. Evolution of lizard congeners in a complex island fauna: a trial analysis. Evolutionary Biology **6**:47–89.
- . 1983. Ecomorphs, faunas, island size, and diverse end points in island radiations of *Anolis*. Pages 326–370 in R. B. Huey, E. R. Pianka, and T. W. Schoener, editors. Lizard ecology: studies of a model organism. Harvard University Press, Cambridge, Massachusetts, USA.
- Williamson, M. 1981. Island populations. Oxford University Press, Oxford, UK.
- Wilkinson, L. 1990. SYSTAT 5.03: the system for statistics. SYSTAT, Evanston, Illinois, USA.

APPENDIX A

Sample sizes for Caribbean anoles and locality data for both Caribbean and mainland anoles. For Caribbean anoles, numbers in parentheses are sample sizes for ecological data. See Losos (1990a, 1992) for sample sizes for morphological data for Caribbean anoles. JA = Jamaica, PR = Puerto Rico, H = Hispaniola, BAH = Bahamas. Numbers next to mainland anoles correspond to the following localities where ecological data were gathered: (1) lowland rain forest near the Rio Curuá-Una at Agropecuaria Treviso LTDA, 101 km S and 18 km E of Santarém, Pará, Brazil (3°9' S, 54°50' W); (2) lowland forest 30 km NW Caracará, Roraima, Brazil (2°0' N, 62°50' W); (3) the Estación Biología de la Universidad Católica near the Río Cuyabeno in Sucumbíos Province, Ecuador (0°0' latitude, 76°10' W); (4) undisturbed lowland Caribbean rain forest north of the Río San Juan in Río San Juan Province, Nicaragua (11°3' N, 85°40' W); (5) Barro Colorado island, Panama. A general description of areas 1–4 appear elsewhere (Vitt and Colli 1994, Vitt et al. 1995, Vitt and Zani 1996a, b, 1997).

Anolis sagrei—Trunk-ground, JA (18); *A. lineatopus*—Trunk-ground, JA (18); *A. cooki*—Trunk-ground, PR (15); *A. cristatellus*—Trunk-ground, PR (28); *A. gundlachi*—

Trunk-ground, PR (28); *A. cybotes*—Trunk-ground, HISP (71); *A. longitibialis*—Trunk-ground, HISP; *A. marcanoi*—Trunk-ground, HISP (14); *A. strahmi*—Trunk-ground, HISP; *A. grahami*—Trunk-crown, JA (18); *A. opalinus*—Trunk-crown, JA (18); *A. evermanni*—Trunk-crown, PR (28); *A. stratulus*—Trunk-crown, PR (28); *A. chlorocyanus*—Trunk-crown, HISP (86); *A. aliniger*—Trunk-crown, HISP (36); *A. coelestinus*—Trunk-crown, HISP (40); *A. singularis*—Trunk-crown, HISP; *A. porcatus*—Trunk-crown, HISP (11); *A. carolinensis*—Trunk-crown, BAH (172); *A. pulchellus*—Grass-bush, PR (28); *A. poncensis*—Grass-bush, PR (18); *A. krugi*—Grass-bush, PR (28); *A. olssoni*—Grass-bush, HISP (46); *A. semilineatus*—Grass-bush, HISP; *A. bahorucoensis*—Grass-bush, HISP (5); *A. distichus*—Trunk, HISP (44); *A. brevirostris*—Trunk, HISP; *A. valencienni*—Twig, JA (15); *A. occultus*—Twig, PR; *A. insolitus*—Twig, HISP (4); *A. angusticeps*—Twig, BAH (16); *A. cuvieri*—Crown-giant, PR (5); *A. garmani*—Crown-giant, JA (18); *A. baharonae*—Crown-giant, HISP; *A. frenatus*—5; *A. oxylophus*—4; *A. humilis*—4; *A. punctatus*—1, 3; *A. biporcatus*—4; *A. capito*—4; *A. ortonii*—1, 3; *A. auratus*—2; *A. fuscoauratus* 1, 3; *A. nitens*—1, 3; *A. trachyderma*—1, 3; *A. limifrons*—4.

APPENDIX B

Linear (least-squares) regression equations expressing relationships between preserved and live *Anolis* lizards, and ratios of “corrected” preserved specimens divided by “real” specimens. Twenty-five lizards from 10 *Anolis* species were used for comparing preserved vs. live measurements (six *A. richardi*, five *A. extremus*, three *A. leachi*, three *A. luciae*, three *A. watsi*, one *A. pulchellus*, one *A. krugi*, one *A. cristatellus*, one *A. lividus*, and one *A. roquet*). Equations are in the form $y = mx + b$ (m = slope, b = y intercept). SVL: live

= 0.96(preserved) + 0.884; body mass: live = 0.84(preserved) - 0.062; tail length: live = 0.96(preserved) + 2.950; forelimb length: live = 0.91(preserved) - 0.186; hindlimb length: live = 0.96(preserved) + 2.13. Ten lizards that were originally measured when alive were also measured when preserved, and then had the above regression equations applied to test the equations. Mean (± 1 SE) ratios of corrected preserved values/real live values are: SVL: 1.000 + 0.004; body mass: 1.005 \pm 0.040; tail length: 0.993 \pm 0.005; forelimb length: 1.013 \pm 0.009; hindlimb length: 1.011 \pm 0.006.