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## ADAPTATION AND CONSTRAINT IN THE EVOLUTION OF SPECIALIZATION OF BAHAMIAN *ANOLIS* LIZARDS

JONATHAN B. LOSOS,<sup>1</sup> DUNCAN J. IRSCHICK,<sup>1</sup> AND  
THOMAS W. SCHOENER<sup>2</sup>

<sup>1</sup>Department of Biology, Campus Box 1137, Washington University, St. Louis, Missouri 63130-4899

<sup>2</sup>Section of Evolution and Ecology and Center for Population Biology, Storer Hall,  
University of California, Davis, California 95616

**Abstract.**—Interspecific interactions affect habitat use and subsequent morphological adaptation in *Anolis* lizards. We examined populations of two species of *Anolis* lizards that evolved in the species-rich communities of Cuba and are now widespread in the Bahamas. Because the species occupy islands in the Bahamas that vary in the number of lizard species present and other characteristics, we predicted that directional selection should have led to morphological differentiation. In particular, we expected that populations on one-species islands should have evolved toward a generalist morphology because of the lack of competitors. Divergence in both species has been adaptive; populations that use wider perches have longer legs. Nonetheless, these differences are relatively minor, and none of the populations appears to have differentiated from its ancestral “ecomorph” type toward a more generalized morphology. This stasis mirrors a trend observed in the radiation of Caribbean anoles, which exhibits repeated instances of evolutionary specialization, but few or no cases of reversion to a more generalized condition. The explanation for this directionality of evolution is not obvious but probably involves the tendency of specialized species to continue using and further adapting the niches for which they are specialized even as conditions change.

**Key words.**—Adaptation, *Anolis*, constraint, ecological morphology, lizard, niche, specialization.

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Biologists have long debated whether evolution is inherently directional. The modern synthesis of the 1940s rid evolutionary biology of teleological theories such as aristogenesis and orthogenesis (Romer 1949; Mayr 1988), but more biologically plausible theories have been formulated that predict an inherently directional course of evolution as a result of both intrinsic and extrinsic factors (Alberch 1980; LaBarbera 1986; Vermeij 1987; Bonner 1988; McKinney 1990).

A related topic that has received relatively little attention is the extent to which evolutionary direction can reverse (e.g., Romer 1949; Lande 1978; Blackburn 1984; Bull and Charnov 1985; Aboitiz 1990). If trends are the result of adaptive responses to changes in the environment, one might expect that, should environments revert to a previous condition, the direction of evolutionary change also would reverse course (e.g., Gibbs and Grant 1987). However, evolutionary change may proceed more easily in some directions than in others as a result of factors as disparate as developmental pathways (e.g., Alberch 1980; Maynard Smith et al. 1985; Gould 1989),

sexual selection (e.g., Lande 1981), or population dynamics (e.g., Holt and Gaines 1992), which could make adaptively based trends difficult to reverse.

To explore whether an adaptive trend can reverse direction, we studied morphological differentiation in Bahamian *Anolis* lizards. Anoles have radiated essentially independently on each of the islands of the Greater Antilles, producing faunas of seven (Jamaica) to 40 or more (Cuba, Hispaniola) species (Williams 1972, 1983). Phylogenetic analysis indicates that evolutionary radiation on these islands proceeded from an original, generalized species to species specialized to particular structural and climatic habitats (Williams 1972, 1983; Losos 1992). A wealth of data (summarized in the discussion and Losos 1994) implicates interspecific interactions, primarily competition, as the driving force behind this evolutionary specialization.

Assuming that anoles have adapted to specialized habitats as a consequence of interspecific interactions, we investigated whether, in the absence of congeners, specialized anole species would reverse evolutionary direction and be-

come more generalized. Two lines of evidence underlie this prediction. First, phylogenetic reconstruction of the anole radiation suggests that that the ancestral taxa were morphologically generalized (Losos 1992). Second, specialized Greater Antillean anoles alter and/or broaden their habitat use in communities containing few or no sympatric congeners (e.g., Laska 1970; Ruibal and Philibosian 1974; Schoener 1975; Lister 1976a). Thus, over evolutionary time, one might predict that such changes in habitat use would lead to the evolution of a generalist morphology.

Specifically, we investigated whether certain Greater Antillean anoles occurring on islands with few or no congeneric competitors reverse evolutionary direction and become more generalized. We expand on a previous test of this hypothesis (Lister 1976b) by considering a suite of morphological characters (rather than one) and by explicitly defining how to recognize evolutionary generalization.

#### *Background on the Anole Radiation*

In the Greater Antilles, anole species have specialized morphologically to distinctive structural habitats. The same set of "ecomorphs," defined on the basis of morphology, foraging and social behavior, and structural habitat use, have evolved essentially independently on each of the four Greater Antillean islands (Rand and Williams 1969; Williams 1972, 1983). Morphologically, the ecomorphs differ in lengths of the forelimb, hindlimb, and tail (all relative to body size); body shape (slender-to-stout); number of subdigital toepad lamellae; and, to a lesser extent, body size. This study involves members of two ecomorph categories. "Trunk-crown" anoles are characterized by an elongate body shape, moderately short limbs and tail, and well-developed toe pads. These species usually are found from eye level to high in a tree, either on the trunk or on branches (note that descriptions of ecomorph habitat use refer to modal values; any ecomorph may be found in any habitat at some time). "Trunk-ground" anoles usually are stocky, with long hindlimbs and tail, and poorly developed toe pads. They usually are found low on the trunk of trees where they survey the surrounding ground for food and conspecifics [behavior and ecology of ecomorphs is discussed in Williams (1983), Losos (1990a,b), and references therein; for data on Bahamian species, see Schoener (1968, 1979)].

Two morphological features have been related to habitat use among the ecomorphs (e.g., Col-

lette 1961; Moody 1974; Lister 1976b; Losos 1990a,b): relative hind-limb length correlates with perch diameter and number of subdigital lamellae correlates with perch height. The ecological basis for the relationship between limb length and perch diameter is well understood (Moermond 1979; Pounds 1988; Losos 1990a,b; see below), but why species that occur higher in trees should have more lamellae is not obvious (Moermond 1979).

These previous studies of anole ecological morphology in the diverse communities of the Greater Antilles indicate that ecomorphs have specialized morphologically to particular habitats. We tested two hypotheses about the direction of intraspecific morphological differentiation among populations that should be experiencing evolutionarily reduced levels of interspecific competition: (1) interpopulational adaptation to differences in habitat use should follow the trends observed in interspecific comparisons (e.g., mean limb length and perch diameter should be correlated among populations); and (2) because the evolution of specialized morphologies (i.e., ecomorphs) was driven by the presence of many sympatric species, populations on islands with fewer sympatric species (in some cases, none) should reverse evolutionary direction and become more generalized.

#### *Study Organisms*

To test these hypotheses, we chose two widespread species of anoles, *Anolis carolinensis*, a trunk-crown anole, and *A. sagrei*, a trunk-ground anole. Both species evolved in the anole faunas of Cuba (Williams 1969), which are today complex and were likely so during their evolution as well. How long these populations have been in the Bahamas and whether all populations stem from a single invasion is not known. The Bahamas were last entirely submerged underwater in the Pliocene (Haq et al. 1987; Morgan 1989; Dowsett and Cronin 1990), which sets an upper limit on the time the populations have been differentiating.

In the Bahamas, both of these species occur in a wide variety of situations, from islands on which one or the other is the only species of anole, to islands containing three other anole species. Previous studies have shown that usually *A. carolinensis* and often *A. sagrei* shift habitat use away from the habitats of whatever species are sympatric at a site (Schoener 1975).

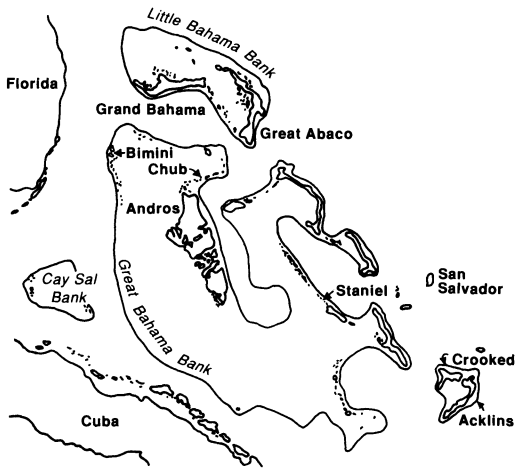


FIG. 1. Islands included in this study. North Gaulin Cay and Compass Cay are within 5.5 nautical miles of Stanial Cay. Solid lines represent the 91-m (50-fathom) contours of island banks (submerged shallow areas; figure following Olson and Pregill 1982). The bank on San Salvador is too small to appear on this map.

## MATERIALS AND METHODS

### Data Collection

In April 1992, we visited 12 Bahamian islands containing one to four species of *Anolis* (fig. 1; table 1). At each site, we collected data on perch height and diameter of adult male lizards following standard anole censusing procedures (e.g., Rand 1964, 1967; Schoener and Schoener 1971a,b; Lister 1976a; Losos 1990a); that is, only the initial position of each lizard was measured, animals moving when first seen were excluded, and censusing was restricted to periods in which the lizards had the opportunity to thermoregulate. No perch diameter was recorded for the few lizards observed on leaves. On two of the islands (Great Abaco and Grand Bahama), one or two *Anolis* species recently have been introduced, probably in the last few years (Losos et al. 1993); we sampled two sites on each of these islands, one with, the other without, an introduced species. Because of time constraints on one of these islands (Grand Bahama), habitat-use data were collected only at the site where no other species was present. At all sites, sample sizes were greater for *Anolis sagrei* ( $\bar{x} = 54.4$ , range: 7–122) than for *A. carolinensis* ( $\bar{x} = 24.4$ , range: 4–52).

On each island, we collected ten adult males and took the following measurements (following Losos 1990a) on anesthetized individuals: snout-vent length (SVL), mass, number of subdigital lamellae under the third and fourth phalanges of

the fourth toe of the hind-foot, and length of forelimb, hind-limb, and tail. We restricted our studies to adult males because the ecomorphs have been defined primarily on the basis of males; females are generally less differentiated both morphologically and ecologically [Lister 1976b; Losos 1992; however, females tend to alter their habitat use in the presence of congeners more frequently than males (Schoener 1975) and thus might be expected to evolve in response to changing ecological conditions more readily; study of the ecological morphology of female *Anolis* is needed]. All variables increase with size in comparisons among 29 anole species and all but number of lamellae increase ontogenetically with size (Losos 1990c, unpubl. data). Based on the mechanics of running and jumping, mass and body length are the most relevant aspects of body size (Alexander 1968; Sukhanov 1968; Emerson 1985; Losos 1990c). Consequently, the score on the first axis of a principal-components analysis using only mass and SVL (ln-transformed, correlation matrix, species analyzed separately) was treated as a measure of body size (this value hereafter is referred to as size). Variables were then regressed against size and residuals considered as size-free measures of shape. In regressions involving residuals, one degree of freedom was subtracted (R. Sokal pers. comm.).

### Relationship between Habitat Use and Morphology

Mean values of size-adjusted morphological variables were used for each population. In contrast to interspecific comparisons, size correlates neither with perch diameter ( $R^2 \leq 0.01$ ) nor height ( $R^2 \leq 0.11$ ) among populations of either species; consequently, neither ecological variable was size adjusted for statistical analyses. All variables were ln transformed before analysis. Significance probabilities were one-tailed because of the existence of a priori predictions concerning the direction of relationship between morphological and habitat variables.

The results of comparative analyses that ignore phylogeny may be statistically invalid if the similarity of taxa is partially or entirely a function of how closely related they are (Felsenstein 1985; Harvey and Pagel 1991; Martins and Garland 1991). No phylogenetic information exists for these populations. However, inspection of the data reveals that geographically proximate populations (at the extreme, populations on the same island), which must be closely related, are not necessarily similar in morphology or habitat use.

To quantify this observation, we made the assumption that phylogenetic relatedness was represented by geographical proximity and used Cheverud et al.'s (1985) autocorrelation method to examine whether phenotypic similarity correlated with phylogenetic relatedness (i.e., whether a "phylogenetic effect" existed). Two analyses were conducted.

In the first, geographic distance separating populations was used as a substitute for phylogenetic relatedness. In the second, a phylogenetic tree was constructed in which geographic distance determined sister-taxon relationships with the proviso that all members of an island bank (i.e., a group of islands all on the same shallow underwater shelf) formed a monophyletic group. In this analysis, branch lengths were assigned such that sister taxa were separated by a distance of one and all members of a monophyletic group were equally distant to species outside the group. Using these criteria to construct the weighting matrix for autocorrelation analysis, no statistically significant positive phylogenetic effect was found in any of the 16 analyses (4 variables  $\times$  2 species  $\times$  2 analyses). The nonsignificance of these analyses indicates that closely related taxa are not necessarily similar in morphology, and thus phylogeny is not likely to confound statistical analyses (Gittleman and Luh 1992; Losos and Miles 1994).

As a second means of considering potential phylogenetic effects, we analyzed our data using the independent contrasts method (Felsenstein 1985; Garland et al. 1992) using the second criterion for tree construction and branch-length assignment described above. The significant results we found using nonphylogenetic regressions (reported below) turn out to be *more* significant (lower *P* value) when the contrasts method is employed. Consequently, based on reasonable hypotheses of what the phylogeny of these populations may be and on two methods of incorporating phylogenetic information into comparative analyses, we conclude that phylogeny is unlikely to have a strong confounding effect in this analysis. However, should a phylogeny be recovered for these populations, it would be worthwhile to conduct a more rigorous phylogenetic analysis (reviewed in Harvey and Pagel 1991; Losos and Miles 1994).

#### *Evolution of Generalized Morphology*

To test whether populations of *Anolis sagrei* and *A. carolinensis* have become morphologically generalized, the Bahamian populations were

TABLE 1. Populations included in this study.

Island	No. of <i>Anolis</i> species
Acklins	1 (c)
Chub Cay	4 (c, s)
Compass Cay†	3 (c, s)
Crooked	2 (c, s)
Grand Bahama‡	1 (s)
Great Abaco‡	1 (s)
North Bimini†	3 (c, s)
North Gaulin Cay§	2 (c, s)
San Salvador	2 (s)
South Andros	4 (c, s)
South Bimini	4 (c, s)
Staniel Cay	3 (c, s)

\* Letters in parentheses indicate whether *Anolis carolinensis*, *A. sagrei*, or both are present.

† *Anolis carolinensis* not studied at these localities.

‡ One or more introduced species exist at some localities of these islands (Losos et al. 1993).

§ A small island between Compass Cay and Staniel Cay in the Exuma Cays chain.

compared with a sample of 31 species of Greater Antillean *Anolis* comprising all six ecomorph types (Losos 1992, unpubl. data); this sample included a population of *A. sagrei* from Jamaica but no populations of *A. carolinensis*. Each ecomorph occupies a distinctive region of a morphological space defined on the basis of the same morphological characters measured in this study (Losos 1992). If the populations examined in this study have become more generalized, their position in the morphological space should be more centrally located and not fall within the region occupied by any of the ecomorph types. By contrast, if the populations have not become generalized, they should fall within the region of space occupied by their ancestral ecomorph type.

We tested this hypothesis in two ways. First, we conducted a discriminant function analysis using the aforementioned set of 31 species to investigate whether any of the Bahamian populations had diverged to such an extent that it was more similar to an ecomorph type other than its ancestral ecomorph type. The Bahamian populations of *A. carolinensis* and *A. sagrei* were not used to define the position of the ecomorphs on the canonical axes but, rather, were classified a posteriori to ecomorph type to examine whether all *A. carolinensis* populations were classified as trunk-crown anoles and all *A. sagrei* populations as trunk-ground anoles. The effect of size was removed from variables in the 31 *Anolis* species data set as described above. For this analysis, size-adjusted variables for the populations of *A. carolinensis* and *A. sagrei* were calculated using

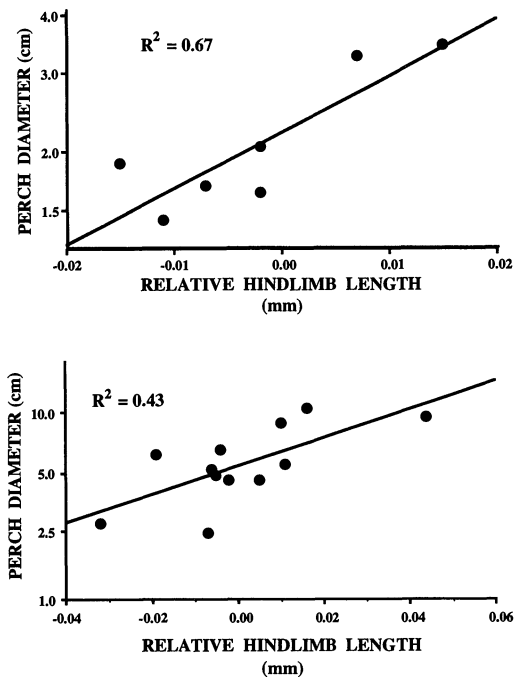


FIG. 2. Relationship between relative hind-limb length and perch diameter for Bahamian populations of (top) *Anolis carolinensis* and (bottom) *Anolis sagrei*.

the formulae for the calculation of size and residuals derived using the 31-species data set.

We then used the discriminant factor scores to plot the position of all taxa in morphological space. We visualized the positions of taxa in morphological space using a UPGMA phenogram to examine whether populations of the two species fell within the boundaries of trunk-crown and trunk-ground anoles as defined by the aforementioned 31-species data set. If Bahamian populations had evolved generalized morphology, we would expect them to lie outside of the clusters formed by the trunk-ground and trunk-crown anoles.

## RESULTS

### *Relationship between Habitat Use and Morphology*

For both species, relative hind-limb length correlates with perch diameter (*Anolis carolinensis*:  $R^2 = 0.67$ ,  $P < 0.01$ ; *Anolis sagrei*:  $R^2 = 0.43$ ,  $P < 0.01$ ; fig. 2), but no relationship exists between perch height and either number of lamellae (*A. carolinensis*:  $R^2 = 0.00$ ,  $P > 0.45$ ; *A. sagrei*:

$R^2 = 0.00$ ,  $P > 0.45$ ) or relative number of lamellae (*A. carolinensis*:  $R^2 = 0.00$ ,  $P > 0.45$ ; *A. sagrei*:  $R^2 = 0.00$ ,  $P > 0.30$ ).

### *Evolution of Generalized Morphology*

The discriminant function analysis on the 31 Greater Antillean *Anolis* species was significant (Wilks'  $\lambda = 0.001$ ,  $F = 15.57$ ;  $df = 30, 86$ ;  $P < 0.001$ ) and classified all 31 species to the correct ecomorph type. A posteriori classification of the Bahamian *A. carolinensis* and *A. sagrei* populations was similarly successful; all *A. carolinensis* populations were identified as trunk-crown anoles, and all *A. sagrei* populations were identified as trunk-ground anoles. With only two exceptions [*A. sagrei* on Crooked ( $P = 0.87$ ) and North Gaulin Cay ( $P = 0.94$ )], the probability of assignment to the correct ecomorph type was greater than 0.98. The first four canonical axes in the discriminant function analysis were significant (test of residual roots,  $P < 0.01$ ).

For all taxa (species and populations), scores on the four canonical axes were used to construct a UPGMA phenogram. Each of the six ecomorph types forms a distinct cluster containing all members of that ecomorph and no other taxa (fig. 3); all *A. sagrei* lie within the trunk-ground cluster and all *A. carolinensis* lie within the trunk-crown cluster. Indeed, differentiation among Bahamian populations of both species has been so slight that Bahamian populations occupy only a portion of the space occupied by their ancestral ecomorph type rather than being dispersed throughout that space. The Bahamian *A. sagrei* form a cluster that also includes Jamaican *A. sagrei* (one of the species in the initial 31-species data set) and *Anolis lineatopus*. The Bahamian *A. carolinensis* similarly form a cluster that also includes *Anolis porcatus*, *Anolis chlorocyanus*, and *Anolis coelestinus*.

## DISCUSSION

A wealth of data support the conclusion that interspecific interactions (primarily competition) have driven the anole adaptive radiation. First, both observational (Jenssen 1973; Schoener 1975; Lister 1976a; Heatwole 1977; Jenssen et al. 1984; Losos et al. 1993) and experimental (Salzburg 1984; Pacala and Roughgarden 1985) comparisons indicate that anole species alter their habitat use depending on which congeners are sympatric. Second, in the absence of competitors, anoles appear to alter and/or broaden their habitat use

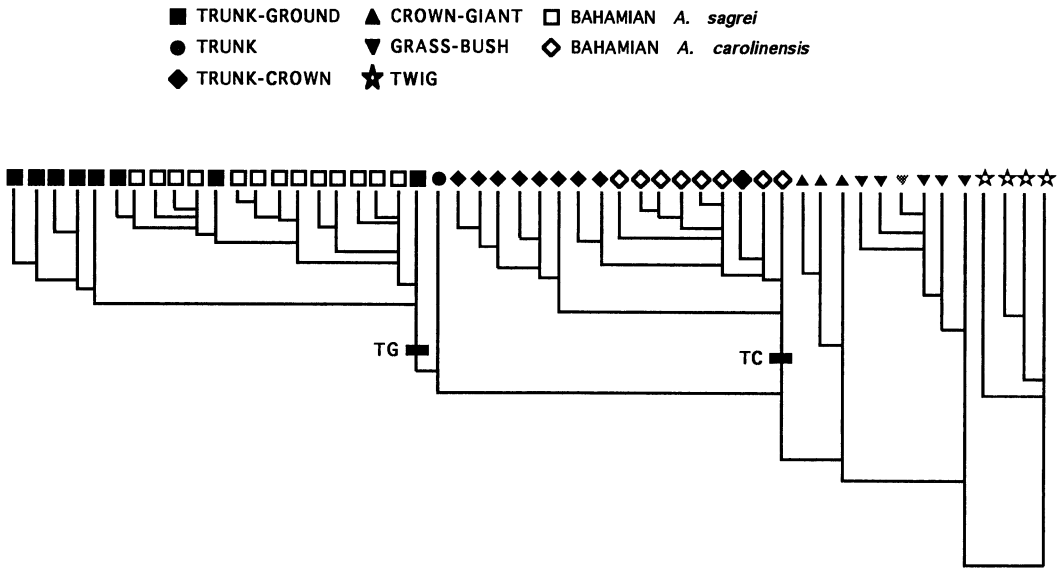


FIG. 3. Position of populations and species of *Anolis* in morphological space, as depicted by a UPGMA phenogram. The filled symbols represent the a priori sample of 31 species of *Anolis*; open symbols are the Bahamian populations of *A. sagrei* (a trunk-ground anole) and *A. carolinensis* (a trunk-crown anole). The solid bars represent the groupings of trunk-ground and trunk-crown anoles, based on the 31 species of *Anolis*. All *A. sagrei* populations fall within the predefined trunk-ground cluster and all *A. carolinensis* fall within the predefined trunk-crown cluster.

(Laska 1970; Ruibal and Philibosian 1974; Lister 1976a; Heatwole 1977). Third, on one-species islands, anoles in both the Greater and Lesser Antilles converge in body size, despite major differences in the size and habitat structure of the islands (Schoener 1969, 1970). Fourth, phylogenetic analysis of the anole radiations on Jamaica and Puerto Rico indicates that habitat partitioning and attendant morphological specialization occurred as anole communities increased in species richness (Williams 1972; Losos 1992). Taken as a whole, these observations support the conclusion that interspecific interactions led to habitat specialization in the Caribbean anole radiation (reviewed more extensively in Losos 1994).

Because the anole faunas of Bahamian islands are small, interspecific competition should be relatively reduced. Consequently, we made two predictions: (1) reduction of competition should lead to adaptive changes in morphology; and (2) these evolutionary changes should be substantial enough on some islands that populations reverse evolutionary direction and evolve a generalist morphology.

Tests of these predictions provided mixed results. Bahamian populations of both species exhibit adaptation to differences in structural habitat use, but these changes amount to adaptive fine-tuning within a specialized morphology rather than evolution of a generalist morphology. We discuss each of these results below.

#### *Adaptive Fine-Tuning*

Differentiation among Bahamian *Anolis carolinensis* and *Anolis sagrei* appears to have been adaptive (fig. 2) and parallels, at a smaller scale, adaptations that characterize the Greater Antillean anole radiation. Among Greater Antillean *Anolis*, species have adapted to differences in perch diameter by differentiating in relative limb length. The same relationship is exhibited among populations of both *A. carolinensis* and *A. sagrei* (a pilot study, in which hatchling *A. sagrei* were raised on different diameter perches for 4 mo, revealed no indication of environmental effects on relative limb length). The adaptive basis for the relationship between relative limb length and substrate diameter is well understood in ecolog-

ical, behavioral, and functional terms (Moermond 1979; Pounds 1988; Losos 1990a). On broad surfaces, relatively long legs maximize locomotor capabilities. By contrast, on narrow surfaces, quick movements are difficult and relatively shorter legs maximize agility (Losos and Sinervo 1989).

Unlike Greater Antillean anoles, however, no relationship between perch height and number of lamellae is revealed in either species. Lister (1976b) did find such a relationship for seven populations of *A. sagrei* scattered throughout the Caribbean (see also Moody 1974), but we fail to confirm his finding with a larger data set. Our results are also not significant even if we incorporate data for several of the most morphologically extreme non-Bahamian populations (Cayman Brac, Little Cayman, and Swan Island) included in Lister's study [incorporating data from Losos et al. (1993) and Lister (1976b); see the Appendix]. Furthermore, interspecific relationships between number of lamellae and perch height are complicated because both variables correlate with body size; with the effect of size removed, the relationship can be considerably weaker (see Appendix table, row 3). Based on these conflicting results, all one can conclude is that further work is necessary to understand whether and how variation in number of lamellae is an adaptive response to perch height in *Anolis*.

#### *Constraints on the Direction of Evolutionary Change*

Because competition from other species presumably led to resource partitioning and the evolution of morphological specialization, we predicted that, with the number of competing species reduced, selection would favor the evolution of more generalized traits. In contrast to our prediction, morphological differentiation among Bahamian populations of *A. carolinensis* and *A. sagrei*, although adaptive, has been relatively insignificant in the context of the adaptive radiation of Caribbean anoles, amounting to microevolutionary fine-tuning: none of the populations appears to have diverged from its ancestral ecomorph type (contra the conclusions of Lister 1976b). The failure of these populations to exhibit more substantial evolutionary change is particularly notable because some of the populations occur on islands with no or only one sympatric congener. Several nonmutually exclu-

sive hypotheses may explain this lack of evolutionary reversal.

#### *Have the Populations Been Isolated Too Recently for Substantial Differentiation to Occur?*

One possible explanation for the limited degree of evolutionary change is that populations have not been isolated for a sufficiently long period of time for divergence to occur. Lack of sufficient time is a difficult hypothesis to disprove. No data exist on divergence times of these populations. Certainly some populations, such as those on the Great Bahama Bank, were isolated from each other only recently (within the past 10,000 yr) as rising sea levels fragmented large landmasses into many smaller islands (Lighty et al. 1979; Sheridan et al. 1988; see fig. 1). However, each of the Bahamian banks has been geologically isolated since the late Cretaceous (Sheridan et al. 1988), which indicates that interbank isolation was not compromised during periods of lower sea levels. An upper limit for the length of time Bahamian populations have been differentiating is set by the length of time anoles could have resided in the Bahamas. Most, but not all, of the Bahamas has been periodically submerged, most recently 120,000 yr ago. However, the last time the Bahamas were entirely submerged was approximately 3 mya in the Pliocene (Haq et al. 1987; Morgan 1989; Dowsett and Cronin 1990).

Even if Bahamian populations are relatively recent in origin, we argue that ample time has elapsed for substantial morphological differentiation among these populations. We base this argument on both general and specific grounds.

First, many cases are known of rapid morphological evolution over the course of hundreds or thousands of years when populations encounter novel or depauperate ecological conditions (e.g., Mayr 1963, chap. 18; Johnston and Selander 1971; Baker and Moeed 1979; Baker 1980, 1992; Conant 1988; St. Louis and Barlow 1991; Wayne et al. 1991; Carroll and Boyd 1992; Schluter and McPhail 1992, 1993; Williams 1992, chap. 9.1). Furthermore, Malhotra and Thorpe (1991) have demonstrated that strong selection can operate on anole populations and have suggested that novel ecological circumstances cause the selection (Katti [1992] and Lawton and McArdle [1992], however, differ in this interpretation).

Second, comparisons among Bahamian *Anolis*

populations indicate that they have diverged significantly in a variety of morphological characters. Our analyses demonstrate that the populations have diverged adaptively in response to differences in habitat use (fig. 2). In addition, substantial divergence has occurred in a variety of other characters, including scalation, head shape, body and dewlap coloration, and body size (Oliver 1948; Schwartz and Henderson 1991). Indeed, Bahamian populations of *A. carolinensis* included in this study have differentiated to the extent that they have been classified as three subspecies that are distinct enough to be considered separate species by some authors (e.g., Schoener 1975; Schwartz and Henderson 1991). Although most of these characters have not been well quantified, the data in Oliver (1948) indicate that the magnitude of difference in head dimensions among Bahamian subspecies of *A. carolinensis* approaches the degree of differentiation in limb dimensions and number of lamellae of the Greater Antillean ecomorphs (Losos unpubl. data). Geographic variation also exists among Bahamian *A. sagrei* in some of these characters (Schoener 1969, 1975; Lee 1992; Losos, unpubl.), although all are considered one subspecies. Hence, we conclude that at least some Bahamian populations of these species have been isolated long enough for substantial differentiation to occur. The failure of these populations to break out of their ancestral ecomorph mold is thus unlikely to be simply a result of insufficient time (but see below). Nonetheless, a precise chronology, as well as a phylogeny, for these populations would prove informative.

Several authors have suggested that the homogenizing influence of gene flow could prevent significant evolutionary divergence except at speciation events, when gene flow ceases (e.g., Stanley 1979; Futuyma 1987). We can provide no data on gene flow among the populations included in this study, but we expect it to be minimal because of the distances separating most of these islands. Furthermore, even populations on closely situated islands are not necessarily morphologically similar (Losos et al. unpubl. data). Regardless, gene flow certainly has not been strong enough to prevent divergence in the wide variety of characters discussed above.

#### *Potential Causes for the Lack of Evolutionary Reversal*

The idea that evolution proceeds from generalists to specialists much more frequently than

the reverse is widespread in evolutionary biology, but with few good examples (see Futuyma and Moreno 1988; Sanderson 1993; Siddall et al. 1993). Why the secondary evolution of a generalist morphology occurs less frequently than evolution away from that morphology in anoles is not clear. We now discuss several potential avenues of explanation worthy of further investigation.

One possible explanation is that anoles tend to resist major evolutionary change. Wake et al. (1983) argued that evolutionary adaptation should be thought of more as a process of persistence in a successful mode rather than continual fine-tuning or optimization to changing environmental conditions. Indeed, one explanation for stasis is that organisms are proficient in seeking out their preferred habitat and, when the environment changes, organisms simply follow their preferred habitat, increasing or decreasing in abundance or shifting geographic range concomitantly (Charlesworth et al. 1982; Eldredge 1989; Pease et al. 1989; see also Holt [1987] and Rosenzweig [1989] on the evolutionary significance of habitat selection).

Other scenarios can also lead to predictions of niche conservatism. For example, in Holt and Gaines' (1992) models, most individuals occur within the fundamental niche of a population. Consequently, in some circumstances, a mutation that increases fitness within that niche will be more strongly selected than one that increases fitness outside of the fundamental niche. As a result, selection will favor enhanced specialization within the fundamental niche rather than increased adaptation to regions not already included within it.

In the case of anoles, these arguments suggest that populations, once specialized to a particular habitat, would not readily evolve as long as that habitat exists. Behavior and phenotype (e.g., morphology, physiology, etc.) would be mutually reinforcing, as organisms choose to live in the habitat to which they already are specialized. Evolutionary change typically would be expected only when the preferred habitat (e.g., vegetation type) largely disappears or when it becomes less favorable because of the appearance (via invasion or speciation) of new competitors, predators, or parasites (extinction is another possibility in such instances; Pease et al. 1989). None of this is to argue that the evolution of generalization from specialization is impossible; rather, in theory it would be expected to take very long in

comparison with the evolution of specialization from generalization.

If this line of reasoning is correct, then the lack of evolutionary reversal in Bahamian anoles may not be surprising. The Bahamas contain abundant trunk-ground and trunk-crown habitats, but are faunistically depauperate. *Anolis carolinensis* and *A. sagrei*, which evolved in the complex fauna of Cuba, probably have not received a "push" to alter their habitat use by other taxa. As noted, Bahamian islands have few lizard competitors; moreover, except for the larger islands, they also have few lizard predators (Schoener and Schoener 1978, 1982, 1983; Henderson and Crother 1989; incidentally, for this reason we consider it unlikely that specialization is maintained by predation-driven stabilizing selection). Consequently, this explanation would predict that Bahamian anoles would continue to use the same habitats as their ancestors and thus would not exhibit much morphological evolution.

More generally, one would only expect major evolutionary change among Greater Antillean anoles when new species are added to island faunas, as may occur through speciation or colonization. This prediction might seem to be contradicted by observations that some anoles do change their habitat use as a function of which of an island's species are absent at a particular locality (see references above), but these shifts may represent relatively small and graded changes rather than quantum alterations in how the lizards interact with their environment. Certainly, all of the Bahamian populations we studied exhibited habitat use and locomotor behavior consistent with their ancestral ecomorph type (Schoener 1975; Losos, unpubl. data). Moreover, it is interesting to note that a common morphological response in *Anolis* lizards (and perhaps vertebrates generally; e.g., Robinson and Wilson 1994) to changes in the number of sympatric competitors is to evolve differences in overall body size (Schoener 1969, 1970). At least in anoles, such changes in body size generally reflect changes in prey size rather than changes in habitat use and associated behavior (Williams 1972; Losos 1990a); anoles usually adapt to differences in habitat use by changes in shape and proportions than in body size (Losos 1990a). Thus, the specialized anoles of the Greater Antilles may not alter habitat use in a fundamental way in response to reductions in the number of sympatric competitors. More detailed studies of anole behavior, functional morphology, and fitness

in different habitats are necessary to evaluate this explanation for the absence of evolutionary reversal.

#### *Macroevolutionary Perspectives*

Although the cause of the lack of secondary evolution of generalists must remain speculative at this point, it is interesting to note that a similar pattern is seen in macroevolutionary trends in Caribbean anoles. Phylogenetic analysis of both the Greater and Lesser Antillean anole radiations documents repeated patterns of the evolution of specialization, to particular habitats in the Greater Antilles and to particular prey sizes in the Lesser Antilles, but little or no evidence of reversion from a specialized to a more generalized condition (Williams 1972; Losos 1990d, 1992). Consequently, the patterns we have documented for intraspecific evolution within Bahamian anoles appear to extend to macroevolutionary differentiation and radiation.

#### CONCLUSIONS

Previous discussions of evolutionary irreversibility have focused primarily on the inability to regain lost structures (sometimes termed "Dollo's Law"; see Gould 1970). In a more general discussion, Bull and Charnov (1985, p. 1153) emphasized that irreversibility results "from the constraints imposed at the levels of selection, inheritance, and phenotypic variation." Anole specialization occurs via continuous characters that are generally variable and heritable; consequently, the constraints may exist at the level of selection. We have suggested two possible explanations for selective constraints. Whether an inherent bias in the direction of selection exists and/or whether habitat selection by specialist species causes stabilizing selection for specialist morphologies can be determined only by experimental investigation.

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## APPENDIX

*The Relationship between Number of Lamellae and Perch Height*

Among 29 species of *Anolis* (Losos unpubl. data), both number of lamellae and perch height are correlated with body size, but when the effect of size is removed, the relationship between residual number of lamellae and residual perch height is not significant (table A1, row 3). Consequently, one might suggest that the interspecific correlation between perch height and number of lamellae is an artifact of the correlation between both variables and size. However, when size is removed from both variables for Lister's (1976b) sample of 14 populations from nine species of trunk-

crown and trunk-ground anoles, the relationship still exists (table A1, row 4); this is also true for his sample of *Anolis sagrei* alone (table A1, row 1). Furthermore, when only trunk-crown and trunk-ground anoles from the interspecific sample of 29 species (Losos unpubl. data) are considered, a relationship between size-adjusted number of lamellae and size-adjusted perch height does exist (table A1, row 5). Finally, for the populations of *Anolis carolinensis* and *A. sagrei* in this study, neither number of lamellae nor perch height correlates with size (see text), even in a data set expanded to include some non-Bahamian taxa (table A1, row 2). If the variables are adjusted for size nonetheless, still no relationship exists.

TABLE A1. Relationship between number of lamellae and perch height.

Group	Comparison*			
	Lamellae no. vs. perch height	Lamellae no. vs. size	Perch height vs. size	Relative lamellae no. vs. relative perch height†
1. <i>Anolis sagrei</i> ‡				
Lister 1976b	$r^2 = 0.72$	$r^2 = 0.48$	$r^2 = 0.43$	$r^2 = 0.43$
$N = 7$	$P < 0.025$	$P < 0.025$	$P < 0.05$	$P < 0.05$
2. <i>Anolis sagrei</i> §				
Losos et al. unpubl. data	$r^2 = 0.00$	$r^2 = 0.02$	$r^2 = 0.00$	$r^2 = 0.00$
$N = 16$	$P > 0.15$	$P > 0.10$	$P > 0.40$	$P > 0.35$
3. Greater Antillean Anoles  #				
Losos et al. unpubl. data	$r^2 = 0.24$	$r^2 = 0.51$	$r^2 = 0.19$	$r^2 = 0.04$
$N = 29$	$P < 0.0025$	$P < 0.0005$	$P < 0.005$	$P > 0.075$
4. Greater Antillean trunk-crown and trunk-ground Anoles‡:**				
Lister 1976b	$r^2 = 0.69$	$r^2 = 0.22$	$r^2 = 0.16$	$r^2 = 0.61$
$N = 14$	$P < 0.0005$	$P < 0.03$	$P < 0.05$	$P < 0.005$
5. Greater Antillean trunk-crown and trunk-ground Anoles  #;††				
Losos et al. unpubl. data	$r^2 = 0.14$	$r^2 = 0.10$	$r^2 = 0.00$	$r^2 = 0.22$
$N = 15$	$P < 0.05$	$P > 0.05$	$P > 0.35$	$P < 0.025$

\* All probability values unadjusted for multiple comparisons.

† Relative number of lamellae and relative perch height are the residuals from regressions against size. For the sake of uniformity, we compute these residuals regardless of whether the variables are significantly related to size.

‡ Jaw length used as a measure of body size for the Lister (1976b) data because no other suitable measure was reported by Lister (1976).

§ Data are *sagrei* populations reported in this paper plus three other populations of *sagrei* which Lister (1976b) reported to have high numbers of lamellae (Cayman Brac, Little Cayman, and Swan Island). Data for these three islands from Losos et al. (1993) except that Swan Island data were taken from Lister (1976b). Because no size data were presented by Lister (1976b), the Swan Island population was included only in the number of lamellae versus perch height analysis. Estimating body size for this population and including it in the analyses does not substantially change the results.

|| Size was calculated as in this paper for comparisons #2, #3, and #5; no size estimate was possible for Swan Island.

# Data from Losos (1990, unpubl. data). Perch height data were unavailable for four species.

\*\* This comparison includes the seven populations of *sagrei* (#1) plus single populations of seven other species.

†† A subset of #3.