



## Experimental studies of adaptive differentiation in Bahamian *Anolis* lizards

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### Abstract

Populations of the lizards *Anolis carolinensis* and *A. sagrei* were experimentally introduced onto small islands in the Bahamas. Less than 15 years after introduction, we investigated whether the populations had diverged and, if so, whether differentiation was related to island vegetational characteristics or propagule size. No effect of founding population size was evident, but differentiation of *A. sagrei* appears to have been adaptive, a direct relationship existed between how vegetationally different an experimental island was from the source island and how much the experimental population on that island had diverged morphologically. Populations of *A. carolinensis* had also diverged, but were too few for quantitative comparisons. A parallel exists between the divergence of experimental populations of *A. sagrei* and the adaptive radiation of *Anolis* lizards in the Greater Antilles; in both cases, relative hindlimb length and perch diameter are strongly correlated. This differentiation could have resulted from genetic change or environmentally-driven phenotypic plasticity. Laboratory studies on *A. sagrei* from a population in Florida indicate that hindlimb length exhibits adaptive phenotypic plasticity. Further studies are required to determine if the observed differences among the experimental populations are the result of such plasticity. Regardless of whether the differences result from plasticity, genetic change, or both, the observation that anole populations differentiate rapidly and adaptively when exposed to novel environmental conditions has important implications for understanding the adaptive radiation of Caribbean anoles.

### Introduction

Colonization of previously unoccupied areas plays an important role in evolutionary theory. Colonists often find themselves in a selective environment radically different from that which they have previously experienced (Carlquist, 1974). Further, founder populations are also usually relatively small, which may enhance the likelihood of change from either genetic restructuring or drift (Mayr, 1963; Templeton, 1980; Carson & Templeton, 1984). For these reasons, colonizing populations may be particularly likely to differentiate rapidly from their ancestral source population.

Human-mediated introductions have been regrettably common over the past several centuries.

Although unfortunate in most respects, these introductions provide the opportunity to investigate the evolutionary fate of colonizing populations. Indeed, numerous cases have been documented in which introduced populations have diverged from their ancestors, sometimes to a great extent and/or rapidly (e.g., Ashton & Zuckerman, 1951; Berry, 1964; Johnston & Selander, 1971; Baker & Moeed, 1979; Baker, 1980; Conant, 1988; St. Louis & Barlow, 1991; Johnston, 1992; Carroll & Boyd, 1992; Reznick et al., 1997).

Nonetheless, most (but not all; e.g., Reznick et al., 1997) studies of introduced populations have been opportunistic and are most useful as illustrative examples of what can happen to colonizing populations. A rigorous test of evolutionary hypotheses would require

Table 1. Islands included in the study

Island	Vegetated area (m <sup>2</sup> )	Propagule size	Year of introduction	Vegetation height (m)
Andrew	4890	5	1977	2.5
White bay	7540	10	1977	3.0
Flat rock	4800	10	1977	2.5
3 <sup>1</sup>	265	5	1977	2.0
24	1160	10	1977	1.8
11 <sup>1</sup>	4210	5	1977	2.3
13	3810	5	1977	1.5
15	1840	5	1977	2.0
16 <sup>1</sup>	1940	10	1977	2.9
18	2800	5	1977	1.1
19	3670	10	1977	2.0
209	152	5	1981	2.0
212	165	5	1981	1.82
215	89.4	5	1981	1.7

<sup>1</sup>Founding populations of five *A. carolinensis* were introduced to these islands in 1983. No males (and only one female) were found on Island three in 1991.

*Anolis sagrei* was introduced to all islands; *A. carolinensis* was introduced to three islands. Propagule size + year of introduction refers to *A. sagrei* introductions.

introductions performed in accordance with a well-designed experimental protocol, including sufficient replication.

Schoener and Schoener's (1983) experimental introduction of *Anolis* lizards in the Bahamas provides such an opportunity. In 1977 (with an additional three introductions in 1981), founding populations of *A. sagrei* were introduced onto small islands (range in vegetated area: 89–7,540 m<sup>2</sup>) near Staniel Cay, Exuma Cays, Bahamas (Table 1). Islands in 1977 were stratified by area and vegetation into pairs and then randomly assigned to receive either 5 or 10 individuals in a 2:3 sex ratio. Introductions of *A. carolinensis* (founding population size = 5) were carried out in 1983 onto three islands on which *A. sagrei* had previously been introduced. Lizards for the introductions were collected from a variety of habitats on Staniel Cay (see Schoener & Schoener (1983) for further details). The rationale for these introductions was to study the process of extinction, because islands of this size in this region did not support lizard populations naturally (Schoener & Schoener, 1983). However, on all but the smallest islands, lizard populations have persisted and on some islands thrived; some islands attained populations of hundreds of individuals (in retrospect, severe hurricanes, which periodically rav-

age these islands, may well be responsible for keeping lizards from permanent establishment on small, low-lying islands (Spiller, Losos & Schoener, 1998), which, incidentally, indicates that these introductions will have no long-term consequences).

Consequently, these introductions constitute a controlled and replicated experiment of the effect of island characteristics and founding population size on differentiation among colonizing populations. We ask the following questions:

1. Have the island populations differentiated from each other and from the source population?
2. If so, can the effect of island characteristics on direction of differentiation be predicted based on knowledge of anole adaptive radiation in the Caribbean? In particular, in comparisons both among species of Caribbean *Anolis* and among Bahamian populations of *A. carolinensis* and *A. sagrei*, relative hindlimb length and perch diameter are strongly correlated (Losos, Irschick & Schoener, 1994). Laboratory studies indicate that variation in limb length affects performance of ecologically relevant traits such as sprinting and running; field studies indicate that differences in performance ability are adaptive for the habitats that different species utilize (Irschick & Losos, 1998, 1999, and references therein). If differentiation among the experimental populations has been adaptive, we expect to find the same relationship between limb length and perch diameter here. Subdigital toe-pad dimensions are probably also related to habitat use, but the mechanistic basis for such a relationship is not clear (Glossip & Losos, 1997; Autumn et al., 2000). We include maximum toe-pad width as one of our variables.
3. If island populations differ, are these differences the results of genetic change or phenotypic plasticity?
4. Does founder population size affect the degree of differentiation? The effect of founder events on a population's ability to adapt is controversial. Sampling leads to loss of allelic diversity and decreased additive genetic variation (Wright, 1977); consequently, small populations have often been considered to have little potential for evolutionary change (Barton & Charlesworth, 1984; Barton, 1989, 1996). However, recent theoretical and empirical studies have suggested that overall genetic variation may be enhanced due to substantial increases in non-additive genetic variation and

its conversion to additive genetic variation (Lints & Bourgois 1982; Carson & Templeton 1984; Goodnight 1987; Bryant & Meffert, 1993, 1996; Cheverud & Routman, 1996; Cheverud et al., 1999).

Some of the methods and results reported here have been taken from our previous work (Losos et al., 1997, 2000). However, here we extend on our previous work by presenting new analyses on differentiation among experimental populations of *A. sagrei* and previously unpublished analyses on experimental introductions of *A. carolinensis*. In addition, we provide further details on experimental studies of plasticity within *A. sagrei*.

## Materials and methods

### Experimental introductions

The islands were visited in May 1991. Adult male lizards were captured on each island (*A. sagrei*:  $n = 1-14$ ;  $\bar{x} = 8.6$ ; *A. carolinensis*:  $n = 7-16$ ;  $\bar{x} = 11.5$ ). In addition, 41 male *A. sagrei* and 10 male *A. carolinensis* were captured at the site on Staniel Cay from which the lizards were originally captured for the introductions (no individuals from the source population were preserved at the time of the introductions because the experiment was designed to test very different hypotheses from those examined here).

The following measurements were taken on each lizard: snout-vent length (svl), mass, fore- and hindlimb length, and width of the subdigital pad on the fourth hindtoe (Losos 1990a,b; Beuttell & Losos 1997). All of the variables increase with size (Losos, 1990a & unpublished). To examine differences in body proportions (i.e., shape), the effect of size was removed in two ways. First, we used scores on the first principal components axis from a pooled within-island variance-covariance matrix (instead of the more commonly used total variance-covariance matrix) as a representation of size and used Burnaby's (1966) method to remove the effect of this composite size variable from all of the original variables. A standard principal components analysis was then conducted on the size-adjusted variables using the total variance-covariance matrix. *Anolis sagrei* populations on islands 13 and 24 could not be included in the Burnaby analysis due to low sample size; for these populations, size-adjusted variables were calculated by projecting the original ln-transformed variables onto the Burnaby size-adjusted

plane defined using the other islands. To measure the extent of morphological divergence of each experimental population from the Staniel population, we calculated Mahalanobis distances in bivariate space defined by two size-adjusted principal component axes (see Figures 1, 4). Euclidean, rather than Mahalanobis, distances were calculated for *A. sagrei* populations on islands 13 and 24 because the sample sizes did not permit the incorporation of variance-covariance matrices. For these analyses, mass was converted into linear units following the equation of Stamps et al. (1994) to make it comparable to the other measurements.

In the second method for removing the effects of size, we estimated size using only svl and mass. Scores on the first axis of a principal components axis including just these two variables were considered to represent size (following Losos et al., 1994). Each variable was then regressed against size and residuals were used in subsequent analyses. Because these two methods give qualitatively identical results, we report only the results of the first method.

Habitat use was measured by recording the height and perch diameter for each male lizard observed (*A. sagrei*:  $n = 7-57$ ,  $\bar{x} = 26.7$ ; *A. carolinensis*:  $n = 16-23$ ,  $\bar{x} = 19.5$ ); individuals moving when first observed were not included and measurements were taken throughout the day from 900 to 1630 (following standard protocol (e.g., Rand, 1964; Losos, 1990b)). Maximum vegetation height on each island was used as a measure of vegetational differences among islands (on islands of similar size elsewhere in the central Bahamas, maximum vegetation height is related to a variety of other measures of vegetation structure (Losos et al., 1997)). Population size of *A. sagrei* is strongly related to island area among a subset of nine experimental islands (Spearman Rank correlations in 1985–1987 are 0.95, 0.95, and 0.93 (Schoener, unpublished data)). Because we do not have population size estimates for all islands, we used island area as a surrogate variable.

We used linear regression to investigate if a relationship exists between mean size-adjusted hindlimb length and mean perch height among *A. sagrei* populations. To account for among-island differences in the accuracy of our estimates of island means resulting from unequal sample sizes and variances, we conducted weighted least squares and correlation analyses using weighted sums of squares and products for relative hindlimb length and perch diameter (see Neter et al., 1985 for brief description of methods). The squared deviation from means of both relative

hindlimb length and perch diameter and their cross product for each island population was weighted using the reciprocal of an estimate of the expected variance of each island's bivariate mean (means for relative hindlimb length and perch diameter). We used the reciprocal of the expected variance because greater weight would therefore be given to those populations with smaller variances (Neter et al., 1985). That is, the correlation analyses resulting from this type of weighting would emphasize more those islands with less variability about their means. The expected variance of the bivariate mean was estimated as the geometric mean of the variances of the relative hindlimb length (variance divided by sample size for relative hindlimb length) and perch diameter mean (variance divided by sample size for perch diameter) for each island (F.J. Rohlf, pers. comm.). The weighted square deviations and cross products were summed to produce weighted sums of squares and cross products for relative hindlimb length and perch diameter and these quantities were used to generate the correlation coefficient (see Sokal & Rohlf, 1995).

To examine further whether the significant relationship between relative hindlimb length and perch diameter could have resulted from a random process, we employed two types of randomization procedures, the second of which takes into account intra-island variation.

First, we conducted a randomization test for the correlation. Here, we randomly ordered the means for the relative hindlimb length from each of the islands creating random pairs of mean relative hindlimb length and perch diameter and conducted a correlation analysis on this new data set (see Manly, 1991; Sokal & Rohlf, 1995 for more detailed discussion of the randomization test as it is applied to regression-type analyses). We repeated this procedure 500 times to produce a frequency distribution of  $r$ -values. If the significant relationship described is a result of a random process and relative hindlimb length is not related to perch diameter, any random pairing of relative hindlimb length and perch diameter would have a high probability of producing an  $r$ -value equal to or greater than the value we obtained ( $r = 0.59$ ).

As an alternative approach to account for intra-island variation, we conducted a bootstrap analysis. To calculate mean relative hindlimb length and perch diameter for each population, we randomly selected with replacement the appropriate sample size of values for each island from the distribution of values for that island. For each new data set, we calculated a

correlation coefficient using linear regression as with the original data set. We repeated this procedure 500 times, thereby producing a distribution of correlation coefficients.

#### *Laboratory studies of phenotypic plasticity*

Two experiments were conducted. In the first, which was a feasibility study to determine whether we could successfully raise baby lizards, we recorded behavioral observations. We also took morphological measurements in this experiment. The morphological results were consistent with those from the second, larger scale, experiment; consequently, we only report the morphological results from the second study.

#### *Behavioral observations*

Wild-caught hatchling *A. sagrei* for the first experiment were obtained from Coral Gables and Fort Myers, Florida in August and October 1994. Lizards were placed in 10 gal aquaria, misted daily, and fed hatchling crickets every 2–3 days. The bottoms of the aquaria were covered with cypress mulch. The only perching sites available to the lizards were either four narrow wooden dowels 0.7 cm in diameter and 41 cm long ('narrow' treatment) or two wide pieces of wood with dimensions 51 × 8 × 3.5 cm ('broad' treatment) placed leaning against walls of the aquaria. Sides of the aquaria were painted with Fluon, a substance having very low surface energy to which anoles cannot adhere. No more than two lizards coexisted in an aquarium; lizards placed in the same aquaria were matched for size (differences in snout-vent length [svl] generally < 2 mm).

To examine whether lizards in the two treatments used their limbs in different ways, which might in some way affect limb development, observations were made every 2–3 days. The posture of the hindlimbs was scored in two ways. First, the hindfeet of each lizard were scored as either flat on the substrate or wrapped around a curved surface (a position that could be used only on the narrow perches). Second, the position of the hindlimbs was scored as: Bunched – limbs folded and held next to the body; Stretched Back – one or both hindlimbs stretched backward; Lateral – limbs projecting laterally from the body. For both aspects of posture, some lizards adopted positions that did not conform to the classifications. For each aquarium, we calculated the proportion of observations in which lizards in that aquarium adopted each posture. Observations of lizards in the same aquarium

Table 2. Principal components analyses for *A. sagrei*

	Size	Size-adjusted (Shape)			<i>P</i> **	<i>P</i> ***
	Axis 1	Axis 1	Axis 2	Axis 3		
Variance (%)	80.9	59.9	26.5	8.9		
Snout-vent length*	0.92	0.55	-0.11	0.81	0.151	0.437
Forelimb length	0.80	0.81	0.43	-0.26	< 0.001	0.002
Hindlimb length	0.77	0.86	0.38	-0.02	< 0.001	0.003
Lamella width	0.94	-0.96	0.29	-0.05	0.020	0.033
Mass	0.90	0.33	-0.92	-0.20	0.006	< 0.001
Size axis					0.879	0.796
Shape axis 1					0.002	0.012
Shape axis 2					0.002	< 0.001
Shape axis 3					0.048	0.049

\*Size analysis based on original unadjusted variables. Shape analysis based on Burnaby size-adjusted variables.

\*\**p*-values correspond to an ANOVA on either the size-adjusted variables (above) or the multivariate axes (below).

\*\*\*as above excluding data for Staniel Cay.

Variable loading as correlation coefficients. The size analysis is based on a pooled within-island variance/covariance matrix (see Bookstein 1989), whereas the size-adjusted analysis was based on a procedure developed by Burnaby (1996) to remove size from variables. See text for details.

were considered together because lizards were not individually marked. These values were arcsine-square root transformed for use in statistical analyses. We also attempted to study locomotor behavior, but the lizards generally were inactive in the presence of an observer. This experiment was terminated in February 1995.

#### Morphological measurements

For the second experiment, hatchling *A. sagrei* (svl 26–38.5 mm,  $\bar{x} = 33.1 \pm 0.1$  (s.e.)) were obtained from Fort Myers, FL in November, 1996. Lizards were housed in aquaria as in the first experiment. At the start of the experiment, we measured svl and hindlimb length (distance from insertion of the limb into the body wall to the distal tip of the claw on metatarsal IV) on all individuals, which were toeclipped (one toe on the forelimb) for identification because two lizards were placed in each aquarium. Because of their small size, individuals were not sexed to avoid excessive handling. The experiment was terminated in March 1997, at which times svl and hindlimb length were measured and sex determined.

We used two approaches to determine whether the experimental treatment affected limb growth. First, we compared the relative hindlimb lengths of lizards in the two treatments (narrow and broad) at the end of the experiment using analysis of covariance on

ln-transformed data with sex and treatment as covariates. Preliminary analyses indicated that no interaction terms were significant, validating the assumption of homogeneity of slopes. Second, we calculated for each lizard the slope of limb length growth, which was calculated on ln-transformed data as (final limb length – initial limb length)/(final svl – initial svl). Because data from lizards raised in the same cage might represent pseudoreplication, which could lead to incorrectly low probability values, we repeated analyses producing statistically significant results using average values for each cage. For these analyses, cages with both a male and female lizard had to be omitted.

## Results

### Experimental introductions

#### *Anolis sagrei*

The first principal components axis from a pooled within-island analysis, which we interpret as size (see Bookstein, 1989), loads strongly for all variables and accounts for 81% of the pooled within-island variance (Table 2). The populations did not differ on this axis (Table 2). The first two axes from the principal components analysis using size-adjusted variables account for 86% of the total variance (Table 2). The

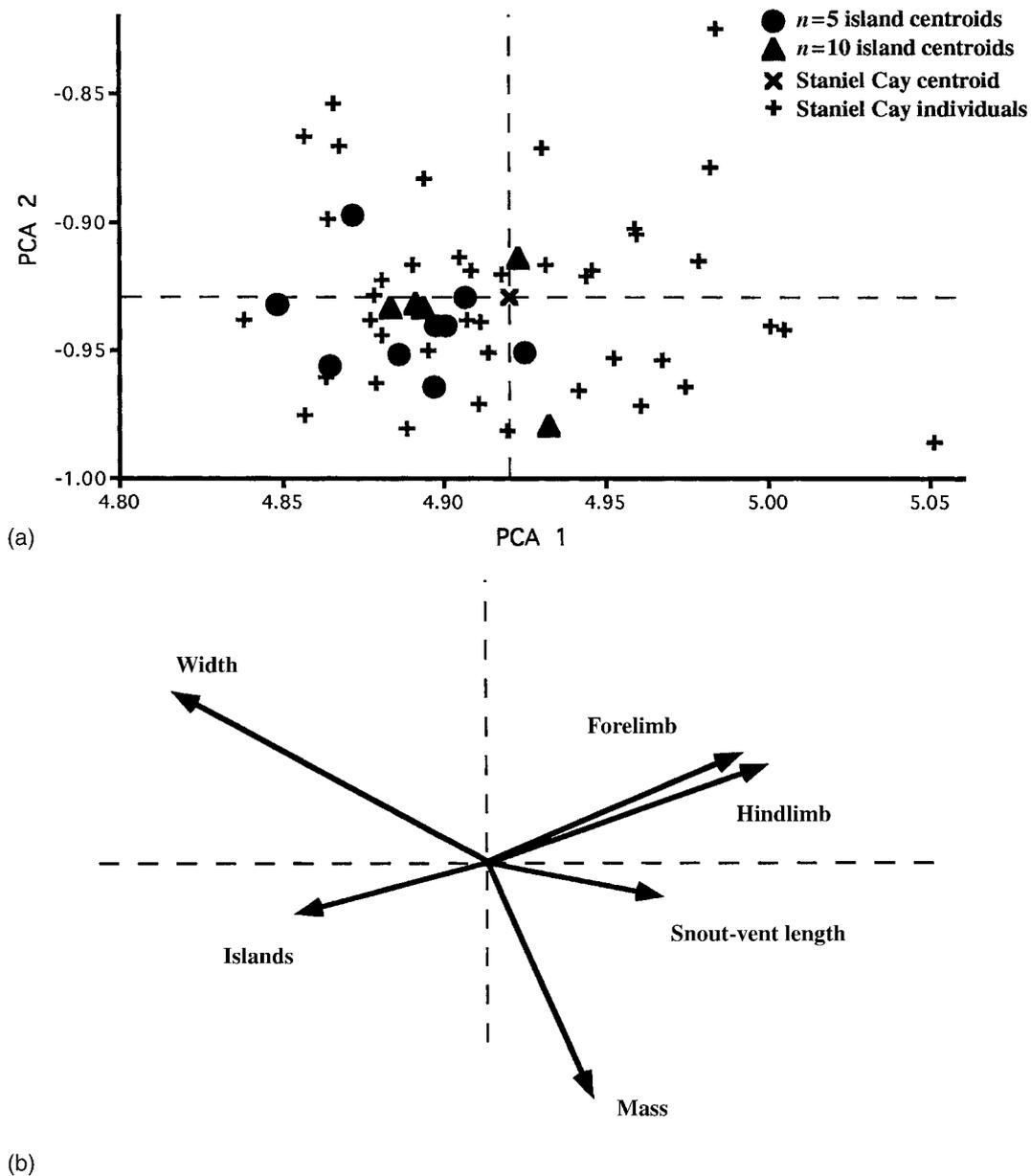


Figure 1. (a) Mean position of experimental populations of *A. sagrei* in a morphological space defined by the first two size-adjusted principal components axes. Circles are the mean position of the islands founded with 5 individuals, triangles are the mean position of the islands founded with 10 individuals, the  $\times$  is the mean position of the Staniel population, and + are individuals from Staniel. (b) Vectors indicate the direction and loading of each variable on the first two principal components axes. The cosine of the angle between any two vectors is equal to the correlation of the variables in that morphological shape. For example, hindlimb length loads strongly and positively on PC I and weakly and positively on PC II. These vectors indicate, for example, that most populations have moved in the opposite direction from the limb vectors, indicating shorter limbs. Modified from Losos et al. (1997).

first axis primarily represents a contrast between fore- and hindlimb length and lamella width, whereas the second axis loads strongly for mass (relative to overall size). The populations differed on both axes regardless of whether Staniel was included (Table 2). The

third shape axis is primarily an svl vector and accounts for an additional 8.9% of the variance. However, this difference is relatively minor given the fact that the third axis accounts for little of the total variance and the population differences are significant at only the

$p = 0.05$  level. Furthermore, the differences among the populations on this axis are more a function of the influence of forelimb and mass on this vector than that of *svl*, and forelimb and mass are more highly correlated to shape axes 1 and 2 than to axis 3 (Table 2).

Figure 1 plots the mean position for Staniel Cay and the experimental islands in a morphological space defined by the first two size-adjusted axes. The experimental islands have clearly differentiated non-randomly with respect to the source population – almost all of them lie in a  $90^\circ$  sector relative to Staniel (Rayleigh's test of circular distribution,  $Z = 7.13$ ,  $p < 0.001$ ). Change in this direction represents primarily shorter limbs, and, to a lesser extent, wider pads and greater mass. The significance of this finding was tested further using the bootstrap by randomly drawing with replacement individuals from the Staniel population. In this manner, we created 500 five-individual and 500 10-individual islands. Relative to the mean Staniel position, these islands showed no directionality (islands founded with 5 individuals:  $Z = 1.00$ ,  $p > 0.20$ ; islands founded with 10 individuals:  $Z = 0.07$ ,  $p > 0.50$ ). Thus, the directionality of the experimental populations is unlikely to be an artifact of sampling from the Staniel population.

Divergence in morphospace appears to be adaptive. A direct relationship existed between how vegetationally different an experimental island was from the source population and how much the experimental population on that island had diverged morphologically from the Staniel population ( $F_{1,12} = 5.09$ ,  $p < 0.025$ , one-tailed, Figure 2; because the veget-

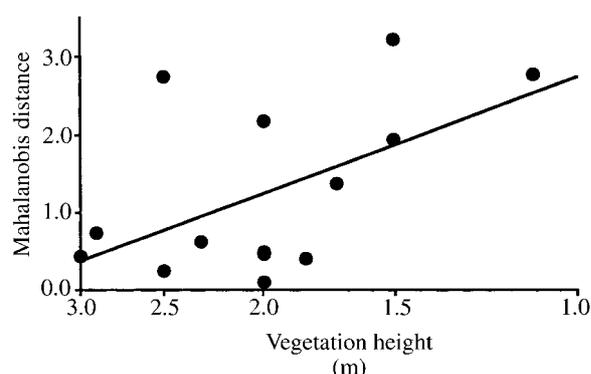


Figure 2. Vegetation height of experimental islands versus the morphological distance of the population on that island from the Staniel population (Mahalanobis distance using PCA 1 and PCA2 as in Figure 1). Because the vegetation on Staniel is higher than on any of the islands, islands with lower vegetation are more dissimilar from Staniel than islands with high vegetation. From Losos et al. (1997).

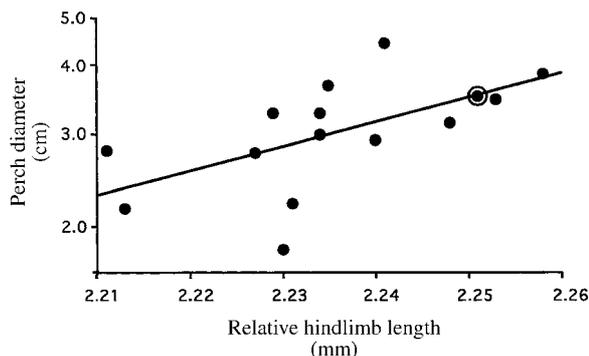


Figure 3. Relationship between perch diameter and relative hindlimb length. Perch diameter on a natural log scale. The circled point is Staniel. From Losos et al. (1997).

ation height on Staniel is greater than that on any of the experimental islands, lower vegetation heights indicate islands that are more dissimilar from the habitat available on Staniel). The relationship between morphological divergence and vegetation differences may be a function of a significant association between size-adjusted hindlimb length and perch diameter, which exists whether the Staniel population is included ( $F_{1,13} = 7.07$ ,  $p < 0.01$ ; Figure 3), or not ( $F_{1,12} = 5.94$ ,  $p < 0.02$ , both comparisons one-tailed). This relationship was confirmed using a series of alternative models: (1) a weighted regression analysis ( $p < 0.005$ , island 24 dropped from analysis because  $n = 1$  for that island and therefore no variance was calculated); a randomized reordering of island values (only 5 of the 500 runs (i.e.,  $p = 0.01$ ) produced an  $r$ -value equal to or greater than the observed value of  $r = 0.59$ ); and a bootstrap procedure (more than 96% of correlation coefficients with a value greater than 0).

The islands founded with 5 and 10 individuals did not differ in the extent of differentiation from Staniel (Mann–Whitney  $U$ -test,  $C_{5,9} = 27$ ,  $p > 0.50$ ). Similarly, no relationship existed between population size (as represented by island area) and distance in morphological space from Staniel ( $F_{1,12} = 0.00$ ,  $p > 0.95$ ). More complicated models, which consider founder and population size plus interaction terms, are also non-significant. No differences existed between the 1977 and 1981 introductions.

#### *Anolis carolinensis*

The results from the morphological analyses of the experimental introductions of *A. carolinensis* are presented in Table 3 and Figure 4. Although these analyses

Table 3. Principal components analyses for *A. carolinensis*

	Size	Size-adjusted (Shape)			<i>P</i> **	Post hoc Test***
	Axis 1	Axis 1	Axis 2	Axis 3		
Variance (%)	84.8	44.7	34.3	15.4		
Snout-vent length*	0.94	-0.18	0.37	0.89	<0.001	Staniel, 16 > 11
Forelimb length	0.87	0.87	-0.26	-0.21	0.024	11 > 16
Hindlimb length	0.80	0.92	-0.12	0.18	0.460	-
Lamella width	0.96	-0.70	-0.70	-0.11	0.033	11 > Staniel
Mass	0.92	-0.10	0.94	-0.32	0.065	-
Size axis					0.006	16 > Staniel, 11
Shape axis 1					0.153	-
Shape axis 2					0.005	Staniel > 11
Shape axis 3					0.005	16 > 11

See Table 1 for details.

\*Size analysis based on original unadjusted variables. Shape analysis based on Burnaby size-adjusted variables.

\*\**p*-values correspond to an ANOVA on either the size-adjusted variables (above) or the multivariate axes (below).

\*\*\*Posthoc analyses were used to test for significant pairwise differences. We show only those differences significant at  $p < 0.05$ , using Bonferroni corrections.

are the same as those conducted on *A. sagrei*, we present the results for *A. carolinensis* in more detail because the *A. carolinensis* analyses involved only two experimental islands (Island 11 and 16) and Staniel, permitting meaningful pairwise comparisons, which is not possible with the larger number of experimental populations of *A. sagrei*.

The difference in microhabitat use between the two experimental populations of *A. carolinensis* is less than the differences among populations of *A. sagrei*. For example, the mean perch diameters for the two *A. carolinensis* populations were 1.59 and 2.57 cm, as compared to the 2.5-fold (1.8–4.9 cm) span among *A. sagrei* populations (Figure 3). Nonetheless, these two populations have differentiated from each other and Staniel in both size and shape. Table 3 presents the result of the principal components analyses. Individuals from Island 16 are larger (defined using the size axis from the pooled within-island analysis) than the individuals from either Staniel or Island 11. In addition, Island 11 differs from Staniel and Island 16 in three size-adjusted dimensions: svl, forelimb length, and lamella width (Table 3). These shape differences are more clearly seen in Figure 4. Individuals from both experimental islands have wider lamellae and perhaps lower mass than Staniel, although the Mahalanobis distance between Island 11 and Staniel is greater than that between Island 16 and Staniel (Figure 4, left). Though this particular morphological analysis

involves shape axes 1 and 2, most of the differences seen here are the result of differences along shape axis 2 which effectively contrasts lamella width and mass (Table 3).

From Table 3 and Figure 4, we conclude that individuals from Island 11 are stockier (i.e., short-bodied) with longer forelimbs and wider lamellae than lizards from Staniel, but individuals from the two populations do not differ in size. In contrast, lizards from Island 16 are larger and longer (see middle of Figure 4) than lizards from Staniel, but have not differentiated in any of the appendicular dimensions. Individuals from Island 11 have also differentiated from Island 16 much in the same direction as Island 11 from Staniel. That is, lizards from Island 11 are smaller, stockier, and with longer forelimbs than lizards from Island 16.

#### Laboratory studies of phenotypic plasticity

##### Behavioral observations

Lizards in the narrow dowel treatment more frequently perched with their feet wrapped around the dowel than did the lizards in the broad treatment (ANOVA  $p < 0.001$ ; Figure 5(a)). Similarly, narrow-treatment lizards more frequently perched with their hindlimbs stretched behind them (ANOVA  $p < 0.001$ ; Figure 5(b)).

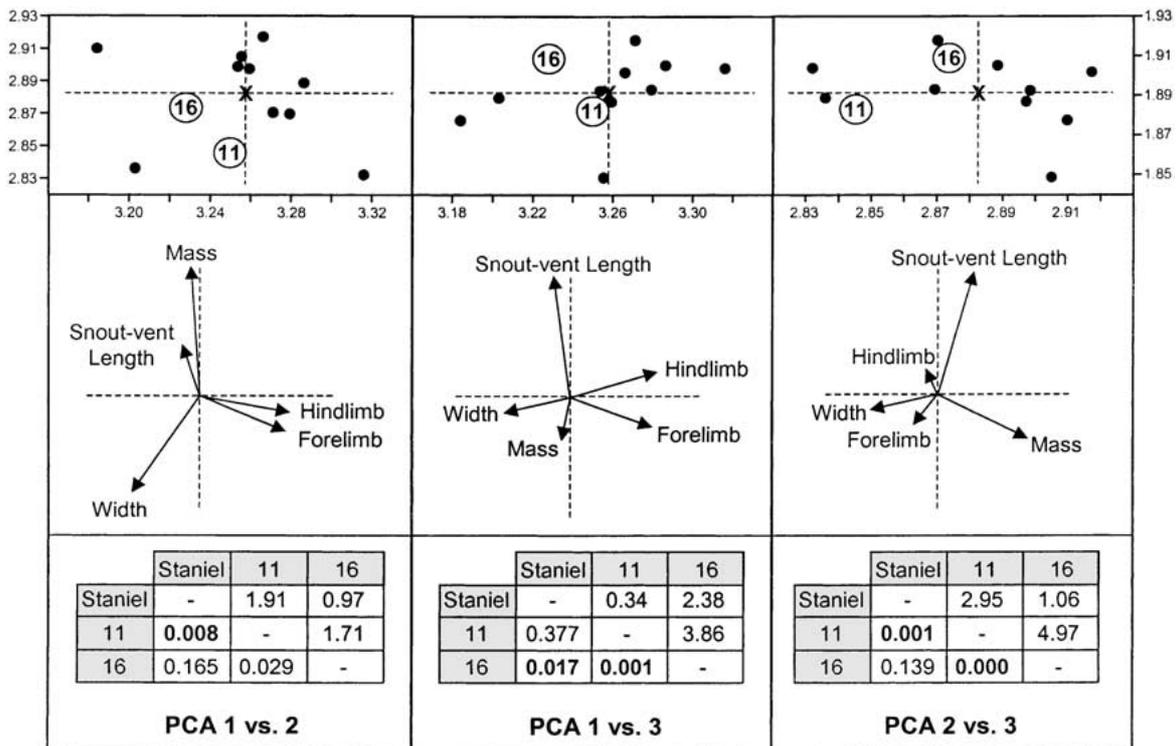


Figure 4. Results from the size-adjusted principal component analysis for *A. carolinensis*. Top panels indicate morphological space defined by two of the first three axes. Circles are data points for individuals from Staniel, whereas the x, 11, and 16 show the positions of the centroids for Staniel, Island 11, and Island 16. The middle panels show the relationships of the variables for each of the pairwise axes. Vectors indicate the direction and loading for each variable. The cosine of the angle between any two vectors is equal to the correlation of the variables in that morphological space. The distance matrices in the bottom panels are Mahalanobis distances (above the diagonal) and the  $p$ -values for those distances (below the diagonal). Values in bold are those that are significant at the  $p = 0.05$  level after adjustment for experiment-wise error rates using the Bonferroni correction. Therefore, the figure can be read as follows (using PCA 1 vs. 2 as an example): Lizards on Island 11 and 16 have diverged from those on Staniel (top panel) mostly in the direction of having wider lamellae (middle panel). The divergence for Island 11 is greater than that for Island 16, and is significant for Island 11 only.

### Morphological measurements

At the start of the experiment, the two groups of lizards did not differ in relative limb length, either when all individuals are considered ( $t = 0.59$ , 114 d.f.,  $p = 0.56$ ) or when only lizards that survived the experiment are considered ( $t = 0.56$ , 63 d.f.,  $p = 0.58$ , two-tailed). In addition, the sexes did not differ in relative limb length (analysis of covariance, differences in slope,  $p = 0.43$ ; differences in intercepts,  $p = 0.52$ ; determined only for lizards that survived and could be sexed at the end of the experiment).

At the end of the experiment, lizards in the two treatments did not differ in svl (narrow treatment:  $\bar{x} = 41.9 \pm 0.6$  (1 s.e.); broad treatment:  $\bar{x} = 42.6 \pm 0.7$ ;  $t = 0.71$ , 64 d.f.,  $p = 0.48$ ). However, an analysis of covariance did reveal an effect of both sex (males with relatively longer hindlimbs than females;  $F_{1,62} = 13.52$ ,  $p < 0.0005$ ; one-

tailed) and treatment (lizards in the broad treatment with longer legs than lizards in the narrow treatment;  $F_{1,62} = 5.04$ ,  $p = 0.014$ , one-tailed; Figure 6). Results were nearly identical when cage averages were used (sex:  $F_{1,42} = 11.52$ ,  $p = 0.001$ ; treatment:  $F_{1,42} = 6.66$ ,  $p = 0.007$ ).

Potentially, the difference in hindlimb length between the treatments could have been the result of natural selection if relatively short-limbed lizards had higher mortality in the broad dowel treatment and relatively long-limbed lizards had higher mortality in the narrow dowel treatment. To examine this possibility, we compared the initial relative hindlimb measurements on survivors versus non-survivors in each treatment separately. In neither treatment was there a significant difference (narrow dowels:  $t = 0.61$ , 56 d.f.,  $p = 0.27$ , one-tailed; broad dowels:  $t = 0.25$ , 56 d.f.,  $p = 0.40$ , one-tailed).

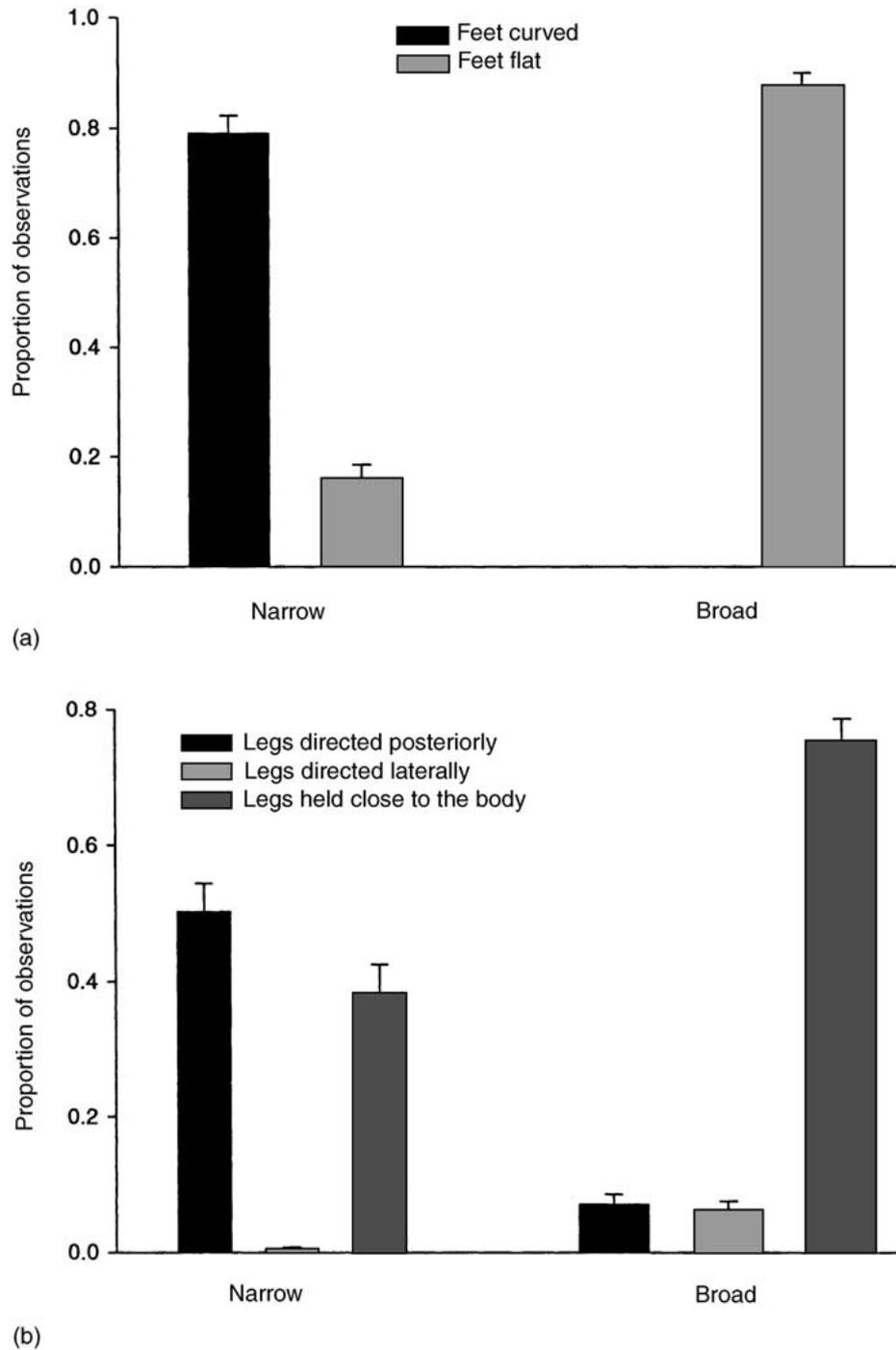


Figure 5. Differences in posture between lizards in the narrow and broad dowel treatments. (a) Position of feet; (b) Position of hindlimbs.

Comparisons of the growth slopes indicate that limb length increased more rapidly relative to svl in lizards on the broad dowels than in lizards on the narrow dowels ( $t = 2.33$ , 63 d.f.,  $p = 0.012$ , one-tailed;

Figure 7). Two-way ANOVA reveals effects of both treatment ( $F_{1,62} = 3.96$ ,  $p = 0.026$ , one tailed) and sex ( $F_{1,62} = 8.97$ ,  $p = 0.002$ , one tailed) on growth slope. This result holds when cage averages are used

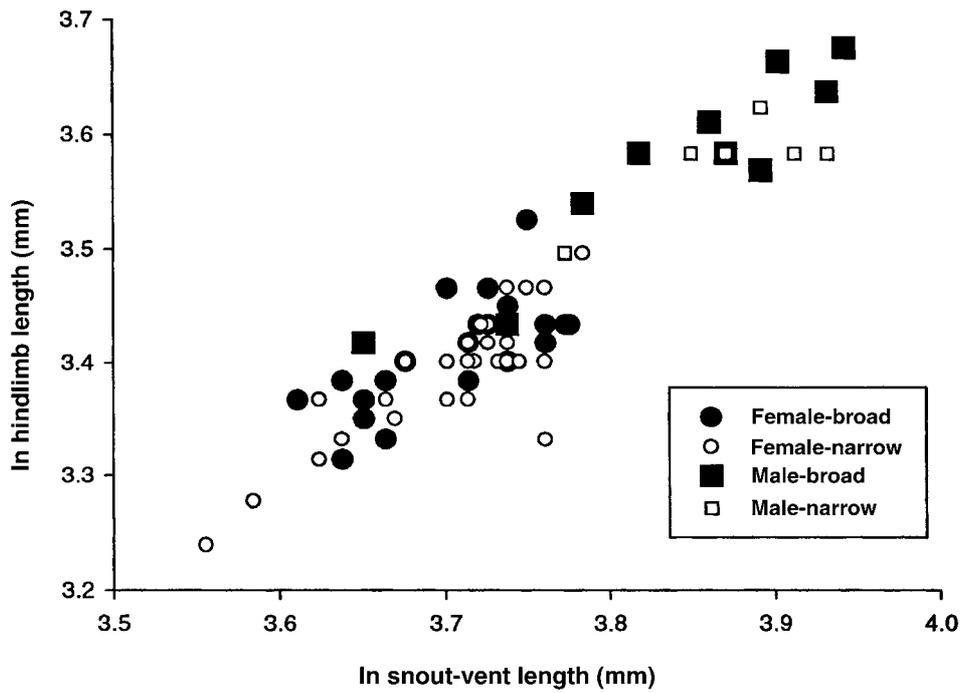


Figure 6. Hindlimb length versus snout-vent length for lizards from the two treatments at the end of the four-month experiment. Lizards in the broad treatment were housed in aquaria with two pieces of wood with dimensions  $51 \times 8 \times 3.5$  cm, whereas lizards in the narrow treatment had four narrow (0.7 cm diameter) wooden dowels. Heavy outlined symbols represent multiple individuals with identical measurements (from Losos et al., 2000).

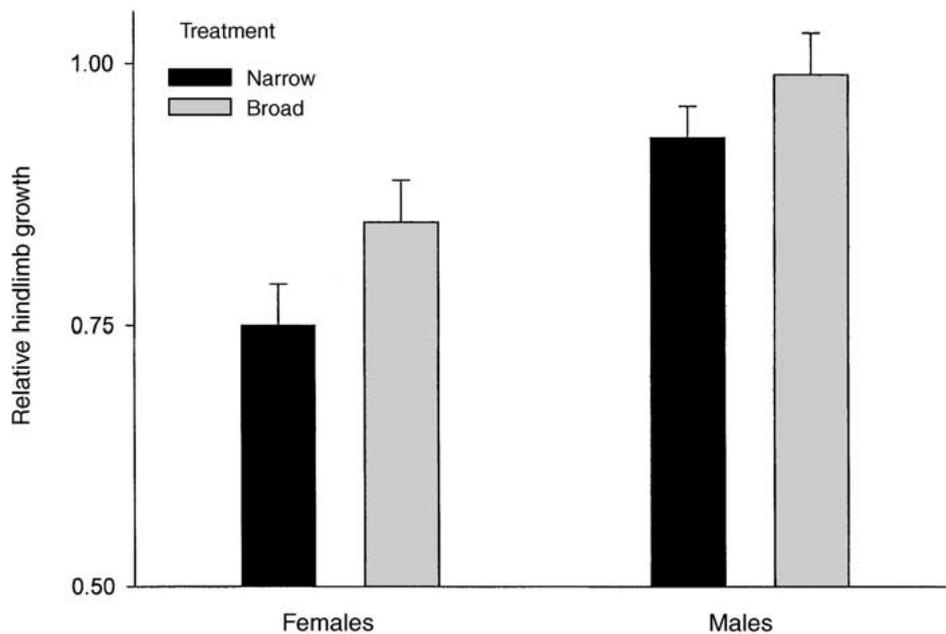


Figure 7. Relative hindlimb growth (calculated as  $[\text{final hindlimb length} - \text{initial hindlimb length}] / [\text{final snout-vent length} - \text{initial snout-vent length}]$ , all variables  $\ln$ -transformed) from the two treatments (from Losos et al., 2000).

(treatment:  $F_{1,42} = 3.09$ ,  $p = 0.043$ ; sex:  $F_{1,42} = 8.18$ ,  $p = 0.004$ ; cages with individuals of both sexes omitted).

## Discussion

Experimental populations of *A. sagrei* and *A. carolinensis* have differentiated, some populations markedly, within 15 years or less of their introduction. Differentiation of *A. sagrei* clearly has been non-random relative to the ancestral population on Staniel Cay (Figure 1); the two experimental populations of *A. carolinensis* have also diverged, but in a manner different from *A. sagrei*. Although such rapid rates of differentiation are not uncommon in introduced populations, rarely has the adaptive nature of this change been obvious (Hendry & Kinnison, 1999; Reznick & Ghalambor, this volume). In this case, however, the extensive knowledge of anole natural history allows *a priori* prediction and *a posteriori* interpretation of patterns of differentiation among introduced populations.

Comparisons among species of West Indian *Anolis* and among populations of both *A. carolinensis* and *A. sagrei* (Losos et al., 1994) reveal a strong correlation between relative hindlimb length and perch diameter, the adaptive basis of which has been corroborated by laboratory and field investigations (Irschick & Losos, 1998, 1999). If differentiation among the experimental islands has been adaptive, we might expect to find similar patterns. The source of the introductions, Staniel Cay (approximately  $3 \times 1$  km), is covered by a variety of vegetation including substantial amounts of coppice, a scrubby to moderately tall forest formation (Coker, 1905). This contrasts markedly with the experimental islands, which exhibit a paucity of large trees and are generally covered by low-lying and narrow-diameter vegetation. Considerable variation exists among the experimental islands as well (Figure 2). Consequently, following from the among-population and interspecific relationships, we can make two predictions: experimental populations should have relatively shorter hindlimbs than the Staniel population and, among the experimental populations, a relationship should exist between perch diameter and limb length. Both predictions are strongly supported for *A. sagrei* (Figures 2–3), leading us to conclude that differentiation among these populations has been adaptive. However, hindlimb length is not significantly different among the *A. carolinensis* populations. This suggests that if morphological di-

vergence in this species is adaptive, its adaptive nature is different from that of *A. sagrei*.

No differences in body size exist among populations of *A. sagrei*, including the Staniel population. By contrast, the *A. carolinensis* population on Island 16 is significantly larger than the populations on Island 11 and Staniel (Table 3; in fact, the difference is so great that there is no overlap in non-size-adjusted svl between individuals on the two experimental islands). The *A. carolinensis* populations on Island 11 and 16 also differ in size-independent shape variables and in shape axis 3, even though the islands are not very different vegetationally and habitat use is quite similar between the two populations. The *A. sagrei* populations on these two islands are fairly similar and have not differentiated much from the Staniel population. Of the two island populations of *A. carolinensis*, the Island 11 population seems to be the most divergent from Staniel (Table 3, Figure 4) and this divergence seems centered mostly on lamella width. Thus, the Island 16 population is divergent in size and the Island 11 population in shape. However, further work is necessary to determine the causal basis of this differentiation.

### *Evolutionary change or environmental response?*

Rapid differentiation of introduced populations has been interpreted as evolutionary change resulting from the action of natural selection (see references cited above). However, in recent years, there has been a growing awareness of the importance of non-genetic environmentally-determined effects on morphological size and shape (e.g., James, 1983, 1991; Bernays, 1986; Meyer, 1986; Sultan, 1987; Patton & Bryl-ski, 1988; Rhymer, 1992; Trussell & Etter, 2001; see Schlichting and Pigliucci (1998) for a recent review).

Our laboratory studies indicate the existence of adaptive phenotypic plasticity in hindlimb length of *A. sagrei*. Indeed, the degree of such plasticity matches the amount of such change in the experimentally introduced populations (Figure 8). However, the existence of such plasticity in a Florida population of *A. sagrei* does not rule out the possibility that observed differences among Bahamian populations of *A. sagrei* and *A. carolinensis* are genetically-based; common-garden studies are planned to evaluate this possibility.

The reason that perch diameter affects limb growth in these lizards is not known. Studies (none involving reptiles) have investigated how differences in physi-

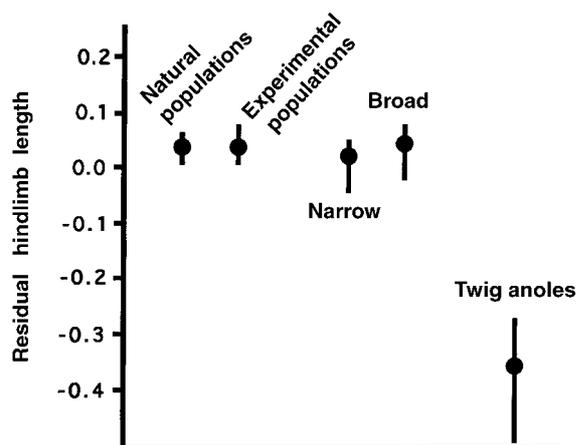


Figure 8. Relative hindlimb length for natural populations of *Anolis sagrei* in the Bahamas (Losos et al., 1994), the experimental Bahamas populations reported in this study, the lizards raised on the broad and narrow surfaces in the plasticity experiment, and Caribbean *Anolis* lizards specialized to use very narrow surfaces (termed 'twig anoles,' [Losos et al., 1998 and references therein]). Relative length was calculated as the residual from a regression of  $\ln(\text{hindlimb length})$  versus  $\ln(\text{snout-vent length})$  that included all lizards from the plasticity study, population means for natural and experimental Bahamian populations, and species mean values of Greater Antillean *Anolis* species (Losos et al., 1998). For the narrow and broad treatments, circles represent mean values and bars represent the range of variation. For the Bahamian *A. sagrei* populations and twig anole species, means and ranges are calculated from the mean value of each population or species in the sample (from Losos et al., 2000).

cal exertion can affect limb dimensions (reviewed in Steinhaus, 1933; Booth & Gould, 1975; Kiiskinen, 1977). Commonly, these studies utilized exercise regimes involving daily treadmill runs, though some studies examine effects of heavy workloads on young children (Kato & Ishiko, 1966) or compare the arms of professional tennis players (Buskirk, Andersen & Brozek, 1956). In many cases, differences in bone density or diameter were observed (e.g., Jones et al., 1977; Woo et al., 1981; Loitz & Zernicke, 1992; see also Erickson, 1997), but in other cases, effects on relative limb length occurred (e.g., Kiiskinen, 1977). No study has examined the effect of substrate characteristics (e.g., diameter) on limb dimensions. Certainly, locomotor performance in lizards is affected by diameter (Losos & Sinervo, 1989; Sinervo & Losos, 1991; Losos & Irschick, 1996), and our study documents that lizards on different substrates use their limbs in different ways. Consequently, it is plausible that the stresses involved in locomotion and position maintenance vary as a function of substrate diameter, which could affect bone growth.

More generally, two kinds of hypotheses exist for this experimentally produced increase in limb length. First is the direct, physical cause-and-effect: limbs 'stretch' and grow longer when perches are thicker (or some such effect of differing forces). Second is the developmental-cuing process hypothesis: exposure to thicker perches somehow stimulates developmental pathways for longer limbs (and maybe other aspects of morphology) that are suitable in forests as opposed to scrub.

Few data allow us to distinguish between these possibilities. Erickson (1997) has shown that alteration in long bone growth in response to changes in loading is an ancestral trait of vertebrates. Although his studies did not focus specifically on limb length, they raise the possibility that the response observed in this study in anoles represents a general response of vertebrates. If so, then its occurrence in *A. sagrei* is fortuitous; although beneficial, the trait may have evolved for other reasons. Of course, it is possible that a less pronounced plastic response existed ancestrally, but was greatly enhanced by natural selection.

Alternatively, the developmental-cuing hypothesis suggests that the plasticity mechanism evolved specifically because it was advantageous for species that occupy multiple habitats. Whether such a mechanism actually could exist is unknown; moreover, if plasticity in limb length is an ancestral trait in tetrapods, it is not clear that selection would favor the evolution of a developmental-cuing mechanism rather than just elaborating upon the direct growth-related plasticity process already in place.

In any case, if something like the developmental-cuing mechanism is occurring, this relates to the question of how much adaptive flexibility a single genotype with elaborately rigged developmental pathways can produce. A species like *A. sagrei* would be expected to have a flexible developmental system even on the more forested (tall, thick trees) small islands because offspring may easily find themselves spending a lifetime in a much scrubbier habitat than the forested one. Thus, on Staniel Cay, if juveniles from forests dispersed to the shoreline or scrubby hilltops, they would spend their lives in a habitat more like that of the very small introduction islands than that of their parent's habitat. On Bimini, a somewhat larger island than Staniel, *A. sagrei* is common in all the vegetation types studied, from forest to scrub (Schoener & Schoener, 1980). In contrast, the other species on Bimini, especially *A. distichus* and *A. angusticeps*, are not found in all vegetation types and so might be

expected to have a much less flexible ontogeny. Hence, repeating the plasticity experiment with such species could give quite different results and thus reveal the extent to which this plasticity is an adaptive, derived trait of the broad-niched *A. sagrei*.

Whether the substantial difference in size between populations of *A. carolinensis* results from different genotypes also requires further investigation. Size is a phenotypically plastic trait in many animal species (e.g., Patton & Brylski, 1988) and one study is suggestive of such plasticity in anoles (Roughgarden & Fuentes, 1974). In addition, differences in age structure resulting from different patterns of mortality also could result in interpopulational differences in body size (although such differences in mortality may eventually lead to selection for differences in body size (Schoener & Schoener, 1978; Stamps, 1993; Stamps, Krishnan & Andrews, 1994)). Whether either of these processes could produce differences in body size as great as observed between the two populations remains to be determined.

#### *Macroevolutionary parallels*

An interesting parallel exists between patterns of adaptive differentiation exhibited by *A. sagrei* in this study and among species of *Anolis* in the Greater Antillean radiation. In both cases, differences in limb and toe-pad dimensions are related in a similar manner to differences in microhabitat structure, although the differences are considerably greater in magnitude among Greater Antillean species (Figure 8; Rand & Williams, 1969; Williams, 1983; Mayer, 1989; Losos, 1990b; Losos, Irschick & Schoener, 1994). If the differences among experimental populations prove to be genetically based, then one might conclude that the differences among species simply represent the continued action of natural selection, extended over considerably longer periods of time.

Alternatively, it is possible that large and (presumably) genetically based differences among species represent a magnification of environmentally-determined adaptive phenotypic plasticity exhibited within populations, a scenario discussed by Schmalhausen (1949), Waddington (1975) and others. This continuum might indicate that what had originally begun as a norm of reaction within a population had been canalized into discrete phenotypes characterizing different species, with the difference between phenotypes subsequently greatly amplified by natural selection during the *Anolis* radiation (see also Huxley, 1942; Simpson, 1953).

The hypothesis that phenotypic plasticity may play an important role in initiating adaptive radiation is receiving renewed attention (West-Eberhard, 1989; Schlichting & Pigliucci, 1998); *Anolis* may prove to be a good group on which to test such ideas.

#### *Number of founding individuals*

The role of founder effects in enhancing rates of evolutionary change and speciation is controversial (e.g., Carson & Templeton, 1984; Barton & Charlesworth, 1984; Barton, 1989; Rice & Hostert, 1993; Rundle, Mooers & Whitlock, 1998, 1999; Templeton, 1996, 1999). We predicted that if founder effects are important, then we might observe differences in degree of differentiation among the 5- and 10-propagule populations of *A. sagrei*. No such differences were observed. The failure to support our prediction could be explained in two ways. First, founder events may not have an important effect on these species. Weedy colonizing species, such as the two anole species in this study, should commonly experience founder events and may thus have a genetic architecture that is not affected by them (Carson & Templeton, 1984). Alternatively, the founder events and subsequent population bottlenecks in this study may have been too slight in magnitude to have had much effect on genetic variation and structure. Anoles are known to store sperm (Fox, 1963), so the populations may actually have had a considerably larger effective population size than the number of actual founders. Further, population size increased extremely rapidly on at least some of the islands (e.g., a ten-fold increase in the first year on one island [Schoener & Schoener, 1983]), mitigating the effects of the founder event (Nei, Maruyama & Chakraborty, 1975).

#### *Rapid adaptive differentiation in small populations*

The fate of small isolated populations is of central importance to the fields of evolutionary and conservation biology. Theories of enhanced evolutionary change in small populations have been criticized because such populations are likely to be lacking in additive genetic variation (Barton & Charlesworth, 1984; Barton, 1989). In a similar vein, conservationists worry that small populations will experience heightened risk of extinction due to loss of variation and enhanced vulnerability to stochastic processes (Frankel & Soulé, 1981; Gilpin & Soulé, 1986).

While our results suggest that, at least in the short term, these concerns do not apply to experimental

populations of *A. sagrei* and *A. carolinensis*, we must point out that our introduction study took place in nature, with the consequent uncertainty about the conditions that such field experiments entail. Relevant here is the possibility of genetic variation entering the small-island populations from natural immigrants. Natural colonization by *A. sagrei* in the central Bahamas, while uncommon, does occur (Schoener, 1986; Schoener, Spiller & Losos, unpublished), and even a small amount of such gene flow can be an important factor in determining levels of genetic variation within a population (Wright, 1977).

Were colonists to come from other small islands, only somewhat larger than the experimental ones, the immigrants might bring alleles from populations already adapted to small island conditions. While such islands are much smaller in area than the Staniel mainland (the source of the founding individuals), and thus perhaps less likely to be the source of immigrants, some of the smaller islands are closer to the experimental islands and thus more likely to be a source of colonists. Consequently, although parallels to truly isolated populations, such as those that may have initially colonized some of the larger and more distant islands of the Caribbean, must therefore be drawn with care, we do not view our experiment as somehow flawed because of its natural setting. Rather, real colonizations always take place in such 'quasi-isolation.'

Regardless of whether the variation has an underlying genetic basis, these populations have been able to differentiate adaptively with respect to environmental differences on the experimental islands. The ability of small founding populations of *Anolis* to differentiate rapidly and adaptively, as demonstrated in this study, may have been an important factor in the extensive diversification of Caribbean *Anolis*.

Of course, in the long-term, lack of genetic variation could preclude adaptive response to changing environmental conditions (Franklin, 1980; Soulé, 1980; Frankham et al., 1999). Only continued monitoring of these populations will allow evaluation of their evolutionary potential.

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