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## EVOLUTIONARY IMPLICATIONS OF PHENOTYPIC PLASTICITY IN THE HINDLIMB OF THE LIZARD *ANOLIS SAGREI*

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**Abstract.**—Species of *Anolis* lizards that use broad substrates have long legs, which provide enhanced maximal sprint speed, whereas species that use narrow surfaces have short legs, which permit careful movements. We raised hatchling *A. sagrei* in terraria provided with only broad or only narrow surfaces. At the end of the experiment, lizards in the broad treatment had relatively longer hindlimbs than lizards in the narrow treatment. These results indicate that not only is hindlimb length a plastic trait in these lizards, but that this plasticity leads to the production of phenotypes appropriate to particular environments. Comparison to hindlimb lengths of other *Anolis* species indicates that the range of plasticity is limited compared to the diversity shown throughout the anole radiation. Nonetheless, this plasticity potentially could have played an important role in the early stages of the Caribbean anole radiation.

**Key words.**—*Anolis*, ecomorphology, lizard, phenotypic plasticity.

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The length of the hindlimb of *Anolis* lizards varies tremendously, with some species having limbs twice as long as other species of comparable size (Losos 1990a). This variation reflects adaptation to living in different structural habitats (Williams 1983; Losos 1990a; Larson and Losos 1996):

species utilizing broad surfaces, such as the ground or tree-trunks, tend to have long hindlimbs relative to their body size, whereas species using narrow surfaces, such as twigs, have relatively short limbs (Moermond 1979; Williams 1983; Losos 1990a). Comparisons among recently diverged populations of anoles reveal similar trends, only at a smaller scale. Among Bahamian populations of both *A. sagrei* and *A. carolinensis*, which have probably been separated for several thousand years, a relationship exists between mean perch diameter and mean relative hindlimb length (Losos et al.

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1994); a similar relationship exists among populations of *A. sagrei* experimentally established 20 years previously in the Bahamas (Losos et al. 1997). The similarity in these patterns manifested both intra- and interspecifically over time scales ranging from 20 years to more than 20 million years suggests not only that natural selection is the agent responsible, but also that no distinction might exist between micro- and macroevolutionary processes; the latter simply may be an extrapolation of the former manifest over long periods of time.

However, this conclusion rests on a critical assumption, namely that the differences observed among intraspecific populations reflect genetic differentiation. An alternative hypothesis is that different phenotypes are the result of phenotypic plasticity. Previous work, conducted entirely on endotherms, has revealed that differences in biomechanical forces placed on growing bones, usually as the result of differences in activity levels, can affect limb growth (reviewed in Steinhaus 1933; Booth and Gould 1975; Kiiskinen 1977; Erickson 1997). This work generally indicates that a regimen of strenuous exercise (e.g., running on a treadmill, swimming) leads to a thickening of limb bones, but not to increased bone length (e.g., Jones et al. 1977; Woo et al. 1981; Loitz and Zernicke 1992; see also Erickson 1997). Some exceptions exist, however. For example, the ulna and radius of the serving arm of professional tennis players is longer than the same bones on the nonserving arm (Buskirk et al. 1956; for another example, see Kiiskinen 1977; for theoretical discussion, Wong and Carter 1990). Consequently, lizards living in different island environments, and thus behaving in different ways, might develop differently, thus leading to a plasticity-induced relationship between limb length and habitat use.

To test this possibility, we conducted limb growth experiments on *A. sagrei*, the species that was involved in the previous experimental and natural comparative studies in the Bahamas (Losos et al. 1994, 1997). This species is found naturally throughout the eastern Caribbean and, as a result, is exposed, both within and among populations, to a wide range of environmental circumstances (Schoener 1968, 1975). Thus, this species would seem to be a good candidate for the evolution of adaptive phenotypic plasticity.

#### MATERIALS AND METHODS

116 juvenile lizards (snout-vent length [SVL] 26–38.5 mm,  $\bar{x} = 33.1 \pm 0.1$  SE) were obtained from Fort Myers, Florida in November 1996. Lizards were placed in 37.9-L glass aquaria, misted daily, and fed hatchling crickets dusted with mineral supplements every two to three days. The bottoms of the aquaria were covered with cypress mulch. Lighting was provided by a cool fluorescent bulb and a Sylvania 350 BL black light bulb placed on the top of each aquarium. 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  $51 \times 8 \times 3.5$  cm ("broad" treatment) placed leaning against walls of the aquaria. Sides of the aquaria were painted with Fluon, a substance to which anoles cannot adhere. Only 65 aquaria were available, so most aquaria initially contained two lizards. Lizards were haphazardly assigned to treatment and aquaria with the proviso that lizards placed in

the same aquarium were matched for size (differences in SVL generally  $< 2$  mm). Aquaria were arranged on tables in such a way as to alternate treatments (i.e., each aquarium was flanked on both sides by aquaria in the other treatment).

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 one of the forelimbs) for identification. Because of their small size and to avoid excessive handling, individuals were not sexed. The experiment was terminated in March 1997, at which time SVL and hindlimb length were measured and sex determined. At this time, most lizards were sexually mature.

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 with sex and SVL as covariates. Preliminary analyses indicated that no interaction terms were significant, validating the assumption of homogeneity of slopes. Second, we estimated limb growth relative to overall growth, which we term "relative hindlimb growth" (RHG) 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 a female lizard had to be omitted. Variables were natural-log transformed in all analyses.

#### RESULTS

At the start of the experiment, analysis of covariance (ANCOVA) revealed that the two groups of lizards did not differ in the relationship between relative limb length and SVL, either when all individuals are considered (difference in intercepts,  $F_{1,113} = 0.04$ ,  $P = 0.85$ , two-tailed; here and in all results below, the hypothesis that slopes were homogeneous was first tested and not rejected) or when only lizards that survived the experiment are considered ( $F_{1,62} = 0.00$ ,  $P = 0.99$ ). In addition, the sexes did not differ in hindlimb length relative to SVL ( $F_{1,62} = 0.43$ ,  $P = 0.52$ ; 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:  $\bar{x} = 41.9 \pm 0.6$  SE; broad treatment:  $\bar{x} = 42.6 \pm 0.7$ ;  $t = 0.71$ ,  $n = 66$ ,  $P = 0.48$ ). ANCOVA revealed an effect of both sex (males with longer hindlimbs relative to SVL than females;  $F_{1,62} = 13.52$ ,  $P < 0.0005$ , one-tailed) and treatment (lizards in the broad treatment with relatively longer legs than lizards in the narrow treatment;  $F_{1,62} = 5.04$ ,  $P = 0.014$ , one-tailed; Fig. 1). Results were nearly identical when cage averages were used (sex:  $F_{1,42} = 11.52$ ,  $P = 0.001$ ; treatment:  $F_{1,42} = 6.66$ ,  $P = 0.007$ ) and when cages averages were used and the sexes analyzed separately (males, treatment effect:  $F_{1,6} = 5.62$ ,  $P = 0.028$ ; females, treatment effect:  $F_{1,34} = 4.02$ ,  $P = 0.027$ ; cages with one male and one female lizard omitted).

The difference in hindlimb length between the treatments

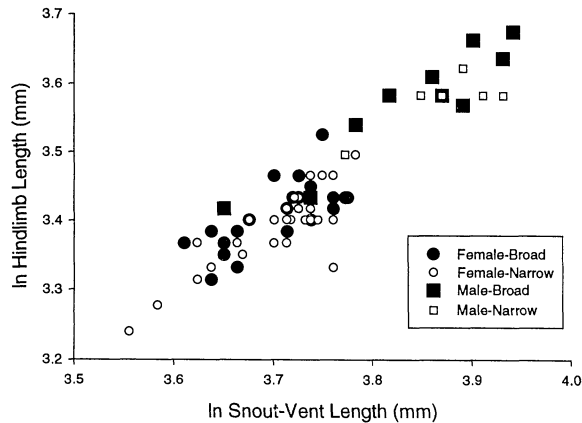


FIG. 1. Hindlimb length versus snout-vent length for lizards from the two treatments at the end of the four-month experiment. Lizards in the broad treatment were housed in aquaria with two pieces of wood with dimensions  $51 \times 8 \times 3.5$  cm, whereas lizards in the narrow treatment had four narrow (0.7-cm diameter) wooden dowels. Heavy outlined symbols represent multiple individuals with identical measurements.

potentially could have been the result of natural selection if relatively short-limbed lizards had higher mortality in the broad treatment and relatively long-limbed lizards had higher mortality in the narrow treatment. To examine this possibility, we used ANCOVA to compare the relationship between the initial hindlimb length and initial SVL of survivors versus that of nonsurvivors in each treatment separately. In neither treatment was there a significant difference, which suggests that relative limb length was unrelated to survival (narrow:  $F_{1,54} = 0.29$ ,  $P = 0.29$ , one-tailed; broad:  $F_{1,56} = 0.00$ ,  $P = 0.47$ , one-tailed).

Comparisons of RHG indicate that limb length increased more rapidly relative to SVL in lizards in the broad treatment than in lizards in the narrow treatment ( $t = 2.33$ ,  $df = 63$ ,  $P = 0.012$ , one-tailed; Fig. 2). Using cage means provides the same result ( $t = 2.60$ ,  $df = 43$ ,  $P = 0.023$ ). 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 RHG. This result holds when cage averages are used (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) and when sexes are analyzed separately using cage means (males:  $t = 1.85$ ,  $df = 7$ ,  $P = 0.054$ ; females:  $t = 1.49$ ,  $df = 34$ ,  $P = 0.072$ ; because these are independent tests of the same hypothesis, we can calculate an overall probability using Fisher's test for combining probabilities,  $P < 0.05$ ).

## DISCUSSION

### *Phenotypic Plasticity in Hindlimb Length*

In this study, we found that hatchling *A. sagrei* that lived on broad surfaces as they grew developed relatively longer hindlimbs than conspecifics raised on narrow surfaces. This result, which is among the first demonstrations of plasticity in limb length in vertebrates and the first in an ectotherm, has a number of important implications for our understanding of the evolutionary radiation of *Anolis* lizards, which has

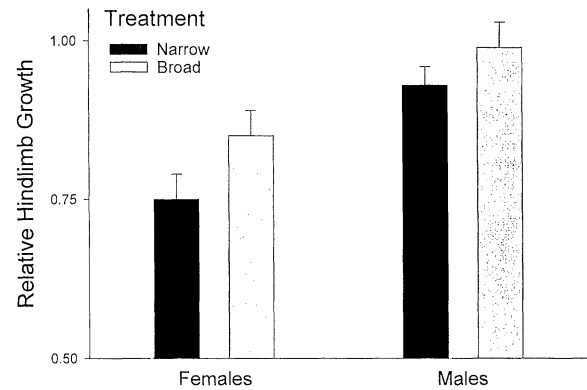


FIG. 2. Relative hindlimb growth (calculated as [final hindlimb length – initial hindlimb length]/[final snout-vent length – initial snout-vent length]) for lizards from the two treatments.

produced more than 400 species in the Caribbean and tropical mainland America.

Most immediately, these findings suggest that a substantial component of the differences observed among Bahamian populations, both natural (Losos et al. 1994) and introduced (Losos et al. 1997), may result from phenotypic plasticity. Only future common-garden or breeding experiments can determine whether a genetic component exists as well. Consequently, at this point, the parallel patterns of differentiation seen in intra- and interspecific comparisons cannot be taken as evidence that the same processes are at work and that macroevolution is simply “microevolution writ large.”

These results might also lead one to question whether the differences seen among species of Caribbean *Anolis* that have specialized to use different habitats (“ecomorphs,” Williams 1983; Losos et al. 1998) also might be the result of plasticity. This seems unlikely because the differences displayed among such species are vastly greater than those produced in this study. For example, even though the narrow dowels used in this study are comparable in size to those used by twig specialists in nature (Losos 1990a; Irschick and Losos 1996), the limbs of *A. sagrei* raised on narrow perches were much longer than those of twig species (Fig. 3). Given that the breadth of perch diameters employed in this study was, in functional terms, extreme (from very narrow to essentially flat), it seems unlikely that raising lizards on a greater range of surfaces would have yielded significantly greater morphological divergence. Consequently, differences in hindlimb length among anole species are substantially greater than differences produced by plasticity and thus almost surely represent genetic differences.

### *Beneficial Phenotypic Plasticity and the Role of Plasticity in Adaptive Evolution*

The functional and behavioral significance of interspecific variation in hindlimb length among anoles is clear. On broad surfaces, limb length is directly correlated with maximum sprinting speed (Losos and Sinervo 1989; Losos 1990b; Losos and Irschick 1996). Longer legs are thus beneficial to permit rapid locomotion to capture prey and escape predators; field studies affirm that long-legged species run frequently in these contexts (Irschick and Losos 1998). In contrast, on

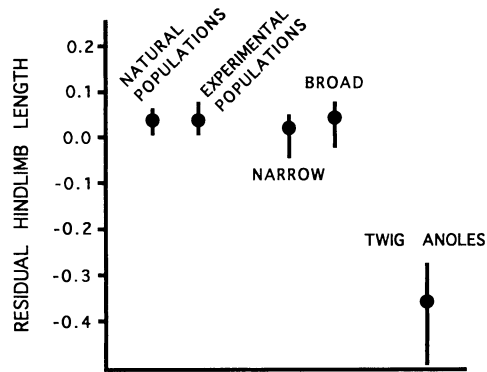


FIG. 3. Relative hindlimb length for lizards in this study; natural populations of *Anolis sagrei* in the Bahamas (Losos et al. 1994); experimental populations introduced to small islands near Staniel Cay, Bahamas (Losos et al. 1997); and Caribbean *Anolis* species specialized to using very narrow surfaces (termed "twig anoles," [Losos et al. 1998 and references therein]). Relative hindlimb length was calculated as the residual from a regression of  $\ln(\text{hindlimb length})$  versus  $\ln(\text{snout-vent length})$  that included all lizards in this study, population mean values for *A. sagrei* in previous studies (Losos et al. 1994, 1997), and species mean values of Greater Antillean *Anolis* (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.

narrow surfaces, longer-legged lizards cannot run faster than shorter-legged species. Furthermore, shorter limbs are advantageous for careful movement; long-legged lizards tend to lose their balance and stumble or even fall off narrow surfaces (Losos and Sinervo 1989; Losos and Irschick 1996; Irschick and Losos 1999). As one might expect, shorter-legged lizards rely more on slow locomotion both to find immobile prey and to avoid detection (Hicks and Trivers 1983; Irschick and Losos 1998). In this context, the enhanced agility of shorter-legged species is advantageous.

Although these studies have been conducted on species differing markedly in limb length, the biomechanical factors underlying this tradeoff should apply equally within species. Consequently, the plasticity observed in this study is likely to be advantageous in that it leads to the production of phenotypes well suited for the environment in which they occur. Such beneficial (sometimes termed "adaptive") plasticity is being increasingly recognized (reviewed in Schlichting and Pigliucci 1998), but this is the first example involving vertebrate hindlimbs.

A major theme in the extensive evolutionary radiation of *Anolis* lizards, both in the Caribbean and in Central and South America, has been adaptation to diverse structural habitats differing in perch dimensions by evolutionary alterations in limb length (Pounds 1988; Losos 1994; Irschick et al. 1997 and references therein). Consequently, our results suggest the intriguing hypothesis that plasticity may play an important role in the early stages of anole adaptive evolution. Phenotypic flexibility provided by plasticity may allow anole populations to occupy novel habitats that otherwise would be inaccessible. Once a population occupies these habitats, natural selection would then favor any new genetic variation that enhanced organismal performance in this habitat. In this

way, what initially begins as relatively minor morphological change resulting from plasticity subsequently could be amplified greatly by natural selection. Given that variation in limb length is one of the major factors in the anole radiation, phenotypic plasticity thus might play an important role in adaptive radiation. This hypothesis, which was originally proposed by Schmalhausen (1949) and Waddington (1953a,b) and recently elaborated by West-Eberhard (1989), has received little empirical investigation. Further research on the evolution of phenotypic plasticity in anoles may provide an ideal system to examine the macroevolutionary significance of phenotypic plasticity.

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