However, an alternative hypothesis is that limb length is a phenotypically plastic trait. Perhaps young *A. sagrei* that grow up using narrower supports develop shorter limbs than individuals that grow up using broader supports. Surprisingly, a laboratory study found just that: hind-limb length is a phenotypically plastic trait affected by perch diameter (Losos *et al.* 2000).

This study has two implications. More narrowly, it suggests that the differences observed between both experimental and natural populations in the Bahamas may be the result of plasticity, rather than genetic differentiation. Studies in which individuals from different islands are raised in the same environment are needed to test this hypothesis more directly.

More generally, these findings suggest the intriguing possibility that plasticity may play an important role in adaptive evolution. By permitting lizards to occupy a new habitat in which they otherwise might not be able to survive, plasticity may allow anoles to occupy new habitats. Once in these habitats, lizard behavior might change and, as new mutations arise, these could be selected for and thus greatly accentuate the initial, relatively minor, changes in limb length. In this way, plasticity might represent the first stage in major adaptive shifts. If nothing else, it is striking that phenotypic plasticity produces the same morphology–environment correlation as observed among habitat specialists [note that the differences in limb length among habitat specialists are vastly greater than those produced in the plasticity experiment and surely represent genetic differences (Losos *et al.* 2000)].

The hypothesis that plasticity might be important in adaptive differentiation was originally put forth 50 years ago by Schmalhausen (1949), Waddington (1953a, 1953b), and others. Long ignored, the idea has recently been revived (West-Eberhard 1989; Schlichting and Pigliucci 1998). Anoles may represent a good system in which to further explore these ideas.

In: Adaptive Speciation. U. Dieckmann, M. Doebeli, J.A.J. Metz, and D. Tautz, eds. Cambridge Univ. Press. 2004.

16.4 Concluding Comments

Roger S. Thorpe and Jonathan B. Losos

The previous two sections on one of the most speciose genera of amniote vertebrates emphasize the Lesser Antilles (Section 16.2) and the Greater Antilles (Section 16.3) systems. These two systems have many basic differences. The former is dominated by solitary anole species (or at most two natural species in sympatry); no, or relatively low, congeneric competition; numerous colonization events between island banks associated with “speciation”; and somewhat arbitrary allopatric species. The latter is dominated by multiple-species sympatry, competition, few colonization events, speciation within islands, and a relatively high degree of confidence in what constitutes a species.

Despite these basic differences, the conclusions suggested by the two sections are very similar. In both the Lesser and Greater Antillean models, there is substantial speciation and substantial evidence of adaptation. In the former, evidence of adaptation comes from intraspecific, within-island adaptation to different habitat types (ecotypes) supported by correlational evidence, parallels, translocation experiments, and common-garden experiments. In the latter it comes from convergent habitat specialization among species (ecomorphs) supported by functional and physiological studies. Even though both speciation and adaptation are substantial in both systems, currently neither system shows hard evidence of adaptive speciation.

Perhaps we have not been able to reveal any clear-cut cases of adaptive speciation because it does not occur in this group. However, it may occur and our failure to reveal it may be because either the criteria used are too demanding or the appropriate studies have not been carried out. If the definition of adaptive speciation in Chapter 1 is used, an important subset of cases involve speciation in sympatry. In this subset of cases, anoles are unlikely models for adaptive speciation as there are no well-supported cases of sympatric speciation in squamates with normal sexual reproduction and without chromosomal changes. However, if adaptive speciation could occur where adaptation plays a key role in the speciation of populations in ecological (parapatric) contact, as indicated in Chapter 7, then adaptive speciation may play a role in the speciation of anoles and other squamates.

For the Greater Antilles, Losos (Section 16.3) suggests the possibility that adaptation to new habitats could trigger speciation indirectly by leading to changes in the behavioral or morphological facets of sexual signals, but this remains to be demonstrated. So in the Greater Antilles, perhaps, parapatric adaptive speciation may have played a part that future studies will reveal. However, the dewlap, which is thought to play a key role in sexual signaling, may show relatively little difference among habitat types within Lesser Antillean islands (e.g., *A. oculatus* in Malhotra 1992), an observation that does not provide support for the above proposal. Yet, more recent studies using spectrometric analysis of dewlap hue, in the *roquet* group, show distinct variation in relation to habitat type (Thorpe 2002; Thorpe and Stenson 2003).

With regard to the Lesser Antilles model, there is evidence (Ogden and Thorpe 2002) of a reduction in gene flow between parapatric habitat forms (incipient speciation), but this is not complete speciation, and even if these parapatric forms have become partially isolated *in situ*, this is not necessarily adaptive speciation (Chapter 1). With other contact zones within Martinique, which may warrant full species recognition, further work is required to exclude confidently a role for divergence in allopatry.

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