To what extent does this interisland study of size offer evidence for the role of adaptation in speciation? In the north, the larger species are of the *bimaculatus* group and the smaller belong to the *wattsi* group. These are distinct lineages (Stenson 2000), so within a given island the two species will not be sister taxa. Hence there is no question of a common ancestor split by adaptive speciation. In the south, the phylogenetic relationships of the *roquet* group are resolved only partially (see Thorpe and Stenson 2003 and references therein), so it is not always possible to know if a pair of species on an island (Plate 9) are sister taxa that could have speciated *in situ* by adaptive speciation. Work on the phylogeny and colonization sequence of this group is ongoing.

Within islands there is evidence of parapatric forms with restricted gene flow among them on both Dominica (Stenson *et al.* 2002) and Martinique (Ogden and Thorpe 2002). The latter case was interpreted as evidence in favor of the process of ecological speciation, as the forms are defined by patterns of current habitat rather than past allopatry. Adaptive speciation may occur on an ecological gradient (Doebeli and Dieckmann 2003; Chapter 7), but as pointed out in Chapter 1, such a parapatric situation may, or may not, involve adaptive speciation. Consequently, whether the Martinique (Ogden and Thorpe 2002), and other (Thorpe and Richard 2001) lizard cases represent examples of adaptive speciation (Tautz 2003) remains to be investigated fully.

16.3   Adaptation and Speciation in Greater Antillean Anoles

Jonathan B. Losos

This section first reviews the evidence that both speciation and adaptation played important roles in anole diversification, focusing primarily on the anoles of the Greater Antilles (Cuba, Hispaniola, Jamaica, and Puerto Rico). It then addresses the extent to which the two processes are intimately linked. The theory of adaptive speciation presents one mechanism by which the two processes might occur in an integrated fashion, but there are other possibilities. In part this requires a discussion of what constitutes a species of *Anolis*, so that it is possible to recognize when two lineages have diverged to the level of different species. Finally, this section addresses some exciting new developments that affect our understanding of the processes important in anole adaptive radiation.

Evidence for speciation

The extent of speciation in Caribbean anoles can be viewed at several levels. Most generally, the number of Caribbean anole species indicates the high rates of speciation that have occurred. *Anolis* is the most species-rich genus of vertebrate in the Caribbean and phylogenetic studies indicate that Caribbean anoles are the descendants of only two colonizations from mainland taxa (Jackman *et al.* 1999). Hence, the Caribbean anole radiation has resulted almost entirely from *in situ* speciation, rather than from repeated colonization. Examination of anole phylogeny (Figure 16.5), however, can tell us considerably more about patterns of speciation.
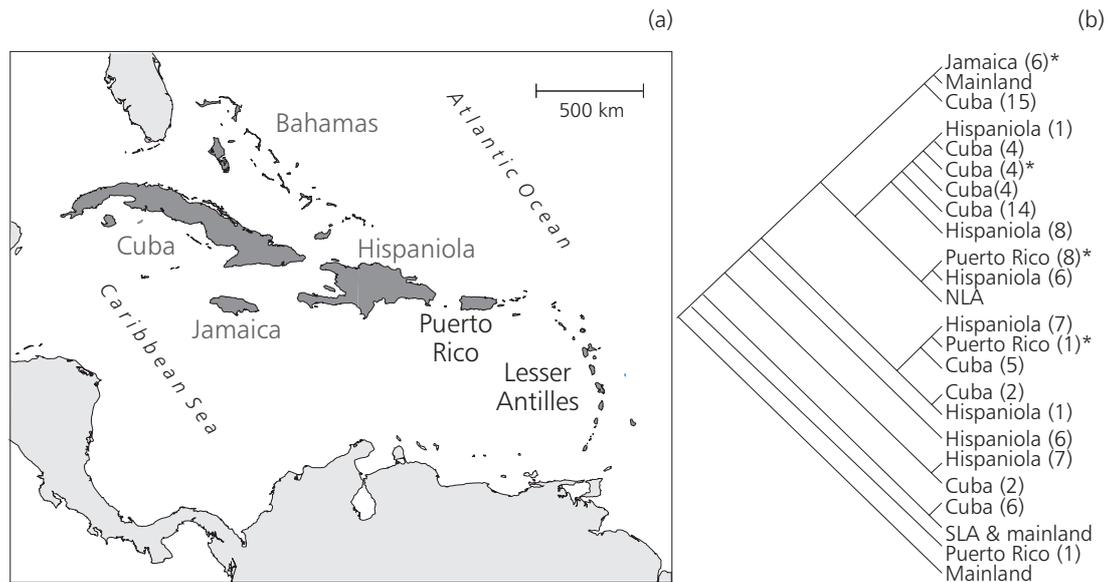
Figure 16.5 (a) Map of the Caribbean. (b) Phylogeny of *Anolis* based on mtDNA (Jackman *et al.* 1999). Relatively few interisland movements are required to account for the more than 100 species of anoles on the Greater Antilles. Numbers in parentheses indicate the number of species within each terminal clade. Monophyly of these terminal clades is based on traditional morphological data. Molecular phylogenetic analyses using DNA indicated that the placement of species into species groups based on morphology is nearly always correct (e.g., Jackman *et al.* 1999; Schneider *et al.* 2001; Jackman *et al.* 2002). Species from small islands in the Caribbean (e.g., *A. acutus* on St Croix, *A. conspersus* on Grand Cayman) occur within terminal clades (designated with an asterisk) and are not indicated. In all cases, these species are apparently derived from clades on one of the Greater Antilles [e.g., *A. conspersus* from Jamaica, *A. acutus* from Puerto Rico (Jackman *et al.* 2002)].

Many islands in the Lesser Antilles and elsewhere in the Caribbean, such as the Bahamas and the Virgin Islands, contain more than one anole species. However, these co-occurring species are almost invariably distantly related, which suggests that the ancestors of these species independently colonized the island, and are not the result of a speciation event that occurred on that island. By contrast, in the Greater Antilles, the situation is quite different. Many monophyletic clades are found only on a single island, which indicates that substantial speciation has occurred within an island. On Puerto Rico, for example, eight of the ten species are members of the *cristatellus* group, whereas in Jamaica, six of the seven species belong to the *grahami* group. Similarly, the *alutaceus* group of grass anoles, found only on Cuba, contains 14 species. In each case, the most parsimonious explanation is that the ancestor of the group occurred on the island in question and then, by a series of divergent speciation events, the single ancestral species gave rise to numerous descendants. Indeed, anole phylogeny suggests that as few as 11 interisland colonization events are necessary to explain the distribution of the 110 or more Greater Antillean species (Jackman *et al.* 1997); thus, all remaining species are the result of within-island diversification (Losos and Schluter 2000).

Evidence for adaptation

Several lines of evidence indicate the great extent of anole adaptive diversity. First, convergent habitat specialization is widespread in the Greater Antilles. Williams (1972, 1983) noted, for anole assemblages within the Greater Antilles, that species exhibit specializations to using different parts of the structural habitat. Thus, for example, twig species are streamlined with extremely short limbs and tails and trunk–ground species (which perch low on the trunk and frequently descend to the ground) are stocky with extremely long hind limbs and poorly developed toe pads. The similarities even extend to patterns of sexual size dimorphism: trunk–ground anoles, for example, are always highly dimorphic, whereas twig anoles exhibit little dimorphism (Butler *et al.* 2000). In all, six types of habitat specialists have been recognized.

Such a pattern of assemblage similarity could result either because each specialist evolved once only and made its way to each of the islands, or because highly similar assemblages evolved independently on each island. Phylogenetic studies make clear that the latter explanation is correct (Losos *et al.* 1998). Habitat specialists on different islands are almost never closely related; hence, these similar assemblages are the result of convergent evolution.

Patterns of divergent evolution also provide evidence of adaptation. For example, correlations exist between habitat use and morphology within both Lesser (Section 16.2) and Greater Antillean anoles (Lister 1976; Losos *et al.* 1994). Among populations of *A. sagrei*, for instance, a correlation exists between mean perch height and mean number of toe-pad lamellae (Lister 1976). Similar examples are presented from Lesser Antillean taxa (Section 16.2)

Convergent evolution and correlations between morphology and environment have long been taken as evidence of adaptation (reviewed in Harvey and Pagel 1991; Losos and Miles 1994). Nonetheless, to understand fully the adaptive basis of character evolution, we need to understand why particular traits evolved in particular environments. Doing so requires an understanding of the functional consequences of character variation, as well as detailed information of what organisms actually do in nature (Lauder 1981; Arnold 1983; Greene 1986; Wainwright 1988; Losos 1990b; Arnold 1994).

In the case of anoles, laboratory functional studies have revealed how variations in limb length and toe-pad dimensions affect the ability to run, jump, and cling (Irschick *et al.* 1996; Irschick and Losos 1999, and references therein). As might be expected, species with longer hind limbs have greater sprinting and jumping abilities, whereas toe-pad dimensions are related to clinging abilities. Moreover, functional capabilities are not independent of the environment. Long-legged lizards, for example, can run faster than short-legged species on broad surfaces, but not on narrow ones (Losos and Sinervo 1989; Losos and Irschick 1996).

In turn, field studies have revealed some of the contexts in which maximal performance is important. Most species run at maximal speed to escape predators, but not to capture prey (Irschick and Losos 1998). Moreover, species that run quickly

tend primarily to use habitats in which they can run at top speed (i.e., broad surfaces), whereas slow species, which rely more on crypsis and slow locomotion, are less constrained in their habitat use (Irschick and Losos 1999).

In a similar vein, physiological studies have established how species adapted to different thermal environments by altering their physiological capabilities. Thus, species that use cooler, forest habitats thermoregulate at lower temperatures, whereas species in hot, open habitats maintain higher temperatures. Further, research on Caribbean and mainland species has established that peak functional capabilities correspond to preferred temperatures (e.g., Hertz 1979, 1992; Hertz *et al.* 1979; Huey 1983; Van Berkum 1986). Thus, although many questions remain unanswered, we do have a solid understanding of the functional consequences of observed variation in traits. This understanding supports the conclusion, based on convergence and correlation, that the extensive variation in traits – such as limb length, toe-pad dimensions, and thermal physiology – observed among anole species represents adaptation to living in different parts of the environment.

Has adaptive speciation occurred?

The observations that sympatric anoles almost always differ in habitat use, with attendant morphological or physiological adaptations, and that most speciation has occurred within islands in the Greater Antilles suggest that adaptive speciation has played an important role in anole adaptive radiation (Dieckmann and Doebeli 1999). Consider Jamaica, for example. Five species are widespread throughout the island, and often occur sympatrically. All five descended from a common ancestor on Jamaica, and each has adapted to its own specific niche. One ready explanation is that this diversity arose via adaptive speciation, as disruptive selection led first to polymorphism within a single ancestral species and then, as reproductive isolation evolved, to speciation and the production of an assemblage of species adapted to different parts of the environment. Indeed, given that the species now occur island wide, that it is not clear that the island was ever divided into separate parts by climate change or sea-level rise, and that there are few peripherally isolated offshore islands (Lazell 1996), a scenario of allopatric speciation is in some ways distinctly less parsimonious. Although opportunities for allopatric speciation are greater on the other Greater Antillean islands, which are larger and more varied topographically, the argument for adaptive, sympatric speciation still remains.

However, before the process of speciation can be discussed meaningfully, an understanding of what constitutes a species is necessary. Thus, before the evidence relative to modes of speciation in anoles is examined, first a digression is needed to discuss what defines an anole species and how one recognizes whether different taxa belong to the same species.

Concepts of anole species and speciation.   Recent years have seen much criticism of the biological species concept and a proliferation of other ideas about what a species is [e.g., Howard and Berlocher (1998), and references therein]. Nonetheless, the vast majority of sympatric anoles coexist without interbreeding. Indeed, despite 40 years of extensive fieldwork in the Caribbean, hybridization has only

Table 16.2 Reported cases of hybridization in Caribbean *Anolis*.

Species	Island	Notes	References
A. aeneus × *A. trinitatis*	Trinidad	Infertile; species introduced to island, not naturally sympatric	Gorman and Atkins 1968; Gorman *et al.* 1971
A. allisoni × *A. porcatus*	Cuba	Hybridization suggested by morphological intermediacy	Ruibal and Williams 1961
A. brevirostris × *A. distichus*	Hispaniola	Abnormal meiosis, thus probably infertile; dewlaps very similar; hybridization possibly frequent	Webster 1977
A. caudalis × *A. websteri*	Hispaniola	Will intermate, but no documented hybrids; dewlaps different color	Jenssen 1996
A. chlorocyanus × *A. coelestinus*	Hispaniola	Hybridization suggested by the presence of morphologically intermediate forms and interspecific courtship in staged trials	Garcia *et al.* 1994
A. grahami × *A. lineatopus*	Jamaica	One individual; probably infertile because of chromosomal irregularities	Jenssen 1977

been suggested between six pairs of Caribbean species, most at a single locality only (Table 16.2). Further, the evidence in several of these cases is far from compelling. Thus, as a general rule, Caribbean anoles are characterized by premating reproductive isolation.

Fortunately, we have a good idea of what factors promote reproductive isolation in anoles. Anoles are visually oriented animals and communicate by visual displays that involve vertical movements of the head, termed head bobs, and by extending their colorful dewlaps. Several lines of evidence indicate that anoles are able to distinguish conspecifics from nonconspecifics by the form of their bobbing display and by the appearance of the dewlap. With regard to the head-bobbing patterns, each species has its own stereotyped pattern of movements, which differ, among species, in rhythm and amplitude (Jenssen 1978). A video playback experiment with one Central American species indicated that female *A. nebulosus* can discriminate males that perform their normal, unaltered displays from males whose displays have been experimentally altered (Jenssen 1970; see also Macedonia *et al.* 1993).

With regard to dewlaps, it is notable that sympatric species always differ in the size, color, or patterning of their dewlaps (Plate 10; Rand and Williams 1970; Williams and Rand 1977; Losos and Chu 1998). In itself, this decidedly nonrandom pattern suggests that the dewlap is used as a species-recognition signal. Moreover, an experimental study with a pair of sympatric species indicates that

anoles use the color of the dewlap as a cue to determine how to respond to another male (Losos 1985; see also Macedonia and Stamps 1994).

This understanding of reproductive isolating mechanisms [or specific mate-recognition systems (Paterson 1982)] is important in two regards. First, it provides a mechanistic understanding of what goes on during speciation; before two species can coexist in sympatry, they apparently must evolve differences in these systems. Second, it permits an objective means of evaluating whether allopatric populations have differentiated to the extent that they would interact as distinct species were they to become sympatric: if the populations differ in dewlap color or head-bobbing pattern, they constitute distinct species. Of course, the converse is not always true. It is possible that allopatric populations may evolve postzygotic reproductive isolation and thus be isolated reproductively, even in the absence of premating isolating mechanisms. Thus, this method for determining specific status may, in some cases, fail to recognize populations that already constitute different biological species, a situation that may exist in some Lesser Antillean taxa (Section 16.2).

Evidence for adaptive speciation.   Given this understanding of what constitutes speciation in anoles, under what conditions has speciation occurred? The adaptive speciation hypothesis suggests that speciation was sympatric and that speciation and adaptation are related intimately, as discussed elsewhere in this volume (Chapter 1). Despite years of work on the evolutionary ecology of Caribbean anoles, little direct evidence exists to determine the geographic context in which speciation has occurred. However, data do exist from which the hypothesis that speciation and adaptation are related can be evaluated. Although far from conclusive, these data indicate that no necessary link exists between these two processes.

This argument has two lines of evidence. First, many examples indicate that adaptation can occur in the absence of speciation in Caribbean anoles. As discussed above, comparisons indicate that populations of the same species adapt to different environments in both the Lesser and Greater Antilles. Although detailed phylogeographic studies have been conducted for only a few of these species, such studies confirm that populations of several of these species are part of a single species, rather than distinct but unrecognized species (see Section 16.2). Thus, adaptive evolution can occur in the absence of speciation.

Conversely, speciation can occur, but it produces species that are adaptively undifferentiated. Evidence for this claim comes from complexes of allopatrically distributed species on the islands of Cuba and Hispaniola. On Cuba, for example, the monophyletic *alutaceus* group of grass anoles contains 14 species. Two of these species are found island wide, but the other 12 have narrow distributions, mostly centered on different mountain ranges. For the most part, these species are little differentiated, both ecologically and morphologically. However, differences in their dewlaps suggest that the species are isolated reproductively and, thus, valid species. Similar complexes of mostly allopatric species are seen in the *sagrei* group in Cuba (14 species) and the *cybotes* group in Hispaniola (eight species), as well as in a number of smaller complexes. This phenomenon reveals

both the efficacy of allopatric speciation and the possibility that speciation can occur without substantial adaptive divergence (it could, of course, be suggested that these populations initially arose in sympatry and only later attained allopatry, but given the small and disjunct ranges – often centered on mountain ranges – of many of these species, such an explanation seems decidedly unlikely).

Adaptation can occur without speciation, and speciation can occur without adaptation. Does this indicate that adaptive, sympatric speciation does not occur? Of course not. No one would claim that adaptive speciation must account for all of the speciation and adaptation evident in the anole radiation. Moreover, although adaptive differentiation does occur intraspecifically, the amount of divergence is relatively limited and does not approach the extent of differentiation between different habitat specialists, such as the difference between twig and trunk–ground specialists. All that can be said is that no evidence exists to support the occurrence of adaptive speciation, and alternative mechanisms have been demonstrated that can produce adaptation and speciation in other ways.

An alternative hypothesis is that species arose in allopatry and perhaps differentiated adaptively to some extent. Then, when they came back into sympatry, interspecific interactions – most likely competition – lead to habitat partitioning and subsequent adaptation and specialization to different habitats. Such a scenario of character displacement is a standard view of the manner in which adaptive radiation proceeds (Grant 1986; Schluter 2000). Much experimental and observational data indicate that anole species do alter their habitat use in the presence of congeners and some data suggest that this leads to morphological change (reviewed in Losos 1994). However, the extent of habitat shifts and morphological change are minor relative to the differences between different habitat specialists. Thus, further investigation is required of both adaptive speciation and character displacement hypotheses for the adaptive radiation of anoles.

An alternative link between adaptation and speciation. Adaptation and speciation may be linked directly in a manner different from that envisioned in the adaptive speciation hypothesis. As discussed above, speciation in anoles results when changes occur in the species-recognition systems, the dewlap and head-bobbing patterns. These systems may evolve, in turn, when populations adapt to new habitats. The reason is that these signals, being visual, must be seen to be effective. Consequently, if a population for some reason occupies a new habitat in which the visual environment is different, natural selection may favor evolutionary change in the signal to maximize the effectiveness of communication, both intra- and interspecifically [this is the sensory drive hypothesis of Endler (1992); see Fleishman (1992, 2000)].

For example, the most visible color for a dewlap varies depending on the environment. In closed forests, light levels are reduced and the light that does penetrate is mostly in the yellow and green parts of the spectrum. As a result, white or yellow dewlaps are optimal because they reflect the little light that is available. By contrast, in open areas there are few limits in the light availability and the most effective dewlaps are nonreflective and dark, producing a darkness contrast to the

bright background (Fleishman 1992, 2000). Indeed, in a survey of Caribbean anole dewlap colors, Fleishman (1992, 2000) found that most closed-forest anole species have yellow or white dewlaps, whereas the majority of open-habitat species have orange, red, black, or blue dewlaps.

Thus, if an open-habitat species for some reason moved into a closed habitat [or perhaps the open area itself is transformed and the populations stay put, akin to Vanzolini and Williams' (1981) vanishing refugium hypothesis], selection would favor change in dewlap color to maximize the ability to communicate intraspecifically. An indirect by-product of this adaptation, however, may be that the population becomes reproductively isolated from other populations remaining in the original habitat. Thus, adaptation to a new visual environment may lead to speciation. This scenario could operate whether the populations are initially sympatric or allopatric; it could easily result as allopatric populations differentiate in different habitats, but it also might be the result of adaptive speciation in sympatry.

Similar arguments may apply to head-bobbing patterns. To be detected, the movements of a displaying lizard must differ from movements of the background vegetation. In habitats in which there is not much background vegetation, or in which the vegetation tends not to move much, small amplitude displays may be conspicuous. By contrast, when background vegetation moves greatly, more pronounced displays may be needed to catch the attention of other lizards (Fleishman 1992). As with dewlap color, adaptive change in head-bobbing patterns thus could produce speciation.

In addition, new habitats may select for other features as well as those used in communication, because the structural and thermal environments may differ also. Consequently, adaptations in a variety of different traits may all be linked to speciation because of the relationship between communication, light environments, and specific mate-recognition systems. This hypothesis is not easy to test, but important advances in our understanding of anole visual ecology and physiology are being made by Fleishman and colleagues (Fleishman *et al.* 1997; Persons *et al.* 1999; Leal and Fleishman 2002).

Phenotypic plasticity and anole adaptive radiation.   Recent work has suggested an intriguing new hypothesis: phenotypic plasticity might play an important role in anole adaptation and adaptive radiation. The background for this work was a pair of studies on populations of *A. sagrei* in the Bahamas. A comparison of natural populations revealed a correlation between the mean diameter of perches used and mean relative limb length (Losos *et al.* 1994). Further, examination of populations experimentally established on tiny Bahamian cays 10–15 years previously (Schoener and Schoener 1983) revealed a similar trend (Losos *et al.* 1997). These correlations paralleled – at a lesser scale – the trend seen among anole habitat-specialists, exemplified by the extremely long-legged trunk–ground anoles that inhabit tree trunks and the short-legged anoles that inhabit twigs. Thus, one interpretation is that microevolutionary change over relatively short periods produced the same pattern as evident over macroevolutionary time; by extrapolation, the latter was simply an extension of the former over longer periods of time.

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.

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

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