

heterogeneity results because the trait actually has no causal relationship with the extent of diversification versus the alternative that it does in some cases, but not in others (Donoghue, 2005).

With these considerations in mind, we may ask what traits, if any, are candidates to have promoted adaptive radiation and species diversification in anoles? To address this question, the first place to look is at traits that arose at the base of the anole radiation.<sup>402</sup> Two obvious candidates are traits that characterize anoles, the toepad and the dewlap. I'll consider each in turn.

#### EXPANDED SUBDIGITAL TOEPADS AS KEY INNOVATIONS

Anoles use a greater range of microhabitats, from leaf litter and grass stems to rainforest canopy and boulder-strewn streams, than other comparable clades of iguanid lizards. One feature that distinguishes anoles from other iguanids is the extent of their arboreality. Most iguanids are either terrestrial or, to the extent that they get off the ground, they use broad surfaces such as boulders, tree trunks, and large branches (Vitt and Pianka, 2003).

In this respect, the evolution of subdigital toepads may represent a key innovation that allowed anoles to interact with their environment in a new way. By allowing these lizards to use a variety of arboreal surfaces such as narrow twigs, leaves, and grass blades that lizards lacking pads have difficulty accessing, the evolution of toepads may have facilitated the radiation of anoles into a variety of ecological niches otherwise little explored by iguanids.

How might this hypothesis be tested? Certainly, toepads provide functional capabilities not available to padless lizards, in particular the ability to adhere to smooth surfaces (Chapter 13). On the other hand, iguanid species that climb on vertical or arboreal surfaces often have sharp, curved claws that provide clinging ability (Zani, 2000). Presumably, toepads allow anoles to use smooth or narrow surfaces upon which claws are ineffective, but this hypothesis has never been tested. One way of examining this idea might be to interfere with the action of the setal hairs on toepads to see whether anoles can still use these habitats with only their claws providing clinging capabilities.

402. Of course, as argued above, traits responsible for diversification in anoles might have arisen in subclades of *Anolis*. The basal split within *Anolis* is between the Dactyloa clade, found primarily on the mainland, and the Caribbean clade, within which *Norops* arose and re-colonized the mainland (Chapter 5). In Chapter 17, I show that both clades have great amounts of morphological disparity; consequently, if a key innovation is responsible for the great disparity of anoles, either it occurred at the base of *Anolis*, or different traits arose independently in both subclades (if the same trait evolved in both subclades, then phylogenetic analysis would infer a single origin at the base of the clade). With regard to species richness, Dactyloa (including *Phenacosaurus*) has 87 species and the Caribbean clade nearly 300. This difference is not statistically significant by at least some tests (Slowinski and Guyer, 1989), which suggests that the base of the tree is the appropriate place to investigate the existence of a trait responsible for the great species diversification of anoles.

No candidates are available for an alternative possibility, that a trait responsible for the great diversity of *Anolis* might have been constructed by sequential evolutionary changes spanning several ancestral nodes.

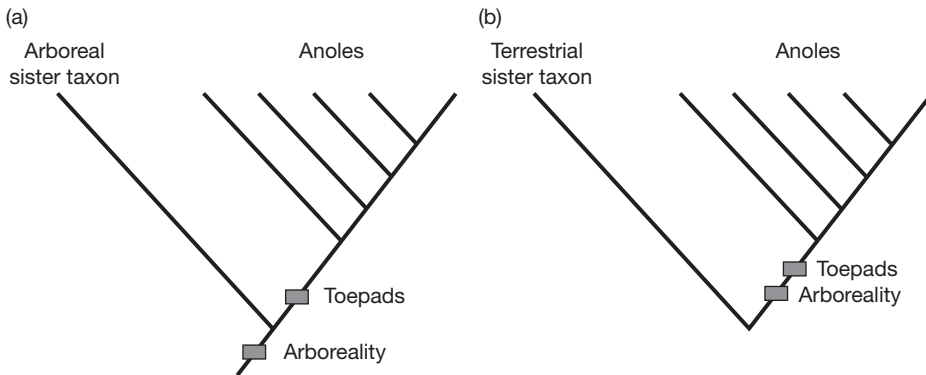


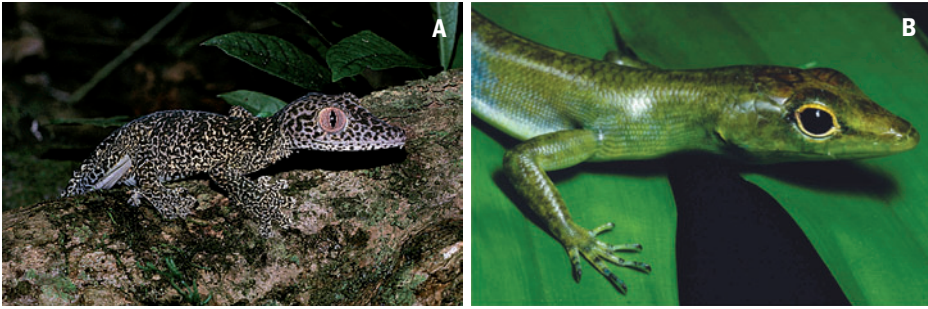
FIGURE 15.5

Evolution of toepads and *Anolis* diversification. (a) If the sister taxon to *Anolis* is arboreal, then the most parsimonious reconstruction is that the ancestral anole was already arboreal when toepads evolved. Alternatively, (b) if the sister taxon is terrestrial, then both the evolution of toepads and the transition to arboreality occurred on the same branch of the phylogeny. Yet another scenario, not illustrated, is possible if more distant outgroups are arboreal. In that event, even if the sister taxon to *Anolis* is terrestrial, the ancestor of *Anolis* may still have been arboreal, with terrestriality being the derived state in the sister taxon.

Phylogenetic evidence generally supports the toepads-as-key-innovation hypothesis. Toepads evolved at the base of the anole phylogeny: shortly thereafter, anoles radiated into a wide variety of ecological niches, just as a key innovation hypothesis would predict. What is not clear is whether anoles moved into the trees before evolving toepads. If, as traditionally believed, *Polychrus* (or some other arboreal clade) is the closest relative of anoles (Chapter 6), then the most parsimonious interpretation is that the ancestor of *Anolis* was also arboreal. In this scenario, the evolution of toepads would have evolved subsequent to the evolution of arboreality (Fig. 15.5a). Alternatively, if the sister group to *Anolis* is terrestrial, as some molecular data suggest (Schulte et al., 2003; see Chapter 6), then toepads may have arisen phylogenetically coincident with the movement of anoles into the arboreal realm (Fig. 15.5b). In this scenario, distinguishing which occurred first—moving into the trees or evolving toepads—is not possible (Arnold, 1994; Larson and Losos, 1996).

In summary, a strong case on functional and phylogenetic grounds has been made that the evolution of toepads permitted anole radiation by allowing the use of a wide variety of ecological habitats not previously accessible. This is about as far as a test of a key innovation can go in most cases when dealing with a single evolutionary event.

However, the evolution of toepads has not occurred just in anoles, but also in two other lizard clades, the Gekkonidae and the skink genus *Prasinohaema* (Fig. 15.6). In both cases, the toepads are covered with microscopic setal hairs and provide enhanced clinging capability (Ruibal and Ernst, 1965; Williams and Peterson, 1982; Irschick et al.,



1996, 2006b). The Gekkonidae is the second most species-rich family of lizards (Vitt and Pianka, 2003) and exhibits a remarkable extent of ecological and morphological diversity. *Prasinohaema*, by contrast, is not species-rich (five species), nor does it seem to be ecomorphologically diverse, although few ecological data are available. Overall, although this hypothesis has never been formally tested, my guess is that the great species richness and ecomorphological disparity of anoles and geckos would lead to a statistical association of both attributes with toepad evolution, the lackluster diversity of *Prasinohaema* notwithstanding. This hypothesis could most profitably be pursued by detailed studies within the Gekkonidae, in which toepads appear to have evolved independently many times (Han et al., 2004).

Thus, the key innovation hypothesis of toepad evolution seems well supported. The way in which the evolution of toepads leads to increased ecomorphological disparity is straightforward: pads give lizards the ability to move effectively on a variety of surfaces on which padless lizards are not competent. But the link between toepads and increased species richness is not so obvious.

Increased species richness can result either from increased speciation rates or decreased extinction rates (Dorit, 1990; Heard and Hauser, 1995). The evolution of features like toepads could plausibly be related to either. On one hand, the possession of toepads could indirectly increase rates of speciation through mechanisms of ecological speciation by opening evolutionary avenues down which populations could diverge. This could happen sympatrically, through disruptive selection, or in allopatry as populations in different localities diverged in different ways, with reproductive isolation evolving as a by-product of this divergence, as discussed in Chapter 14. Alternatively, the possession of toepads might decrease rates of extinction in several ways. For example, if two populations speciated in allopatry but did not diverge ecologically, the possession of toepads would give the two new species increased possibilities for resource partitioning and character displacement if they came into secondary contact, thus potentially decreasing the rate of extinction for young species. Extinction rate might also decrease if the possession of toepads simply made populations better adapted to the environment, and thus more likely to persist over long periods.

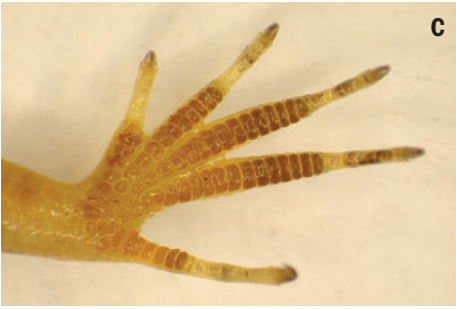


FIGURE 15.6  
Other lizards with toepads. (a) Madagascar leaf-tailed gecko (*Uroplatus fimbriatus*); (b) the skink *Prasinohaema virens* from New Guinea and (c) its toes. Skink photos courtesy of Chris Austin.

These possibilities make clear why linking a putative key innovation to changes in species richness is so difficult and problematic. The possibilities just outlined are plausible, but that is about as far as it goes. Actual direct mechanistic evidence demonstrating a link between evolution of a trait and increased species diversification is rare in most cases, and nonexistent for anoles with regard to toepad evolution.

#### EVOLUTION OF THE DEWLAP AND SPECIES RICHNESS

The flip side of the key innovation coin is the dewlap, the second characteristic feature of anoles. The evolution of the dewlap probably did not open new ecological opportunities for anoles in contrast to the effect of toepad evolution. Thus, the great ecomorphological disparity of the anole clade is probably not a direct result of the evolution of the dewlap. Conversely, the dewlap may explain the great species richness of the clade.

The reason is simple: the use of a visual signal both for intraspecific communication and for species identification increases the possibility that shifts in habitat may lead to divergence in these signals, thus resulting in speciation. The evidence for this hypothesis in *Anolis*, as I reviewed in Chapter 14, is suggestive, but far from conclusive.

A further test of the hypothesis might involve those few anole clades that have greatly reduced dewlaps or none whatsoever. If possession of the dewlap enhances the rate of speciation, then dewlap-deficient clades should have relatively few species compared to other clades. This is exactly what is observed. The only anoles to completely lack a dewlap are *A. bartschi* and *A. vermiculatus*. These species comprise a clade that is very old (Fig. 5.6), but nonetheless only contains two species; other clades of comparable age have dozens of species. Other species with notably reduced dewlaps are *A. poncensis* (a Puerto Rican grass-bush anole), *A. ophiolepis* (the Cuban grass-bush anole that arose within the clade of trunk-ground anoles in the *sagrei* Series), *Chamaelinorops barbouri*, the two small trunk-crown anoles of Hispaniola (*A. singularis* and *A. aliniger*), *A. agassizi*, and the three species, all grass-bush anoles, in the *A. hendersoni* Series (Fig. 15.7; Losos and Chu, 1998). The low species richness of all of these clades of small-dewlapped

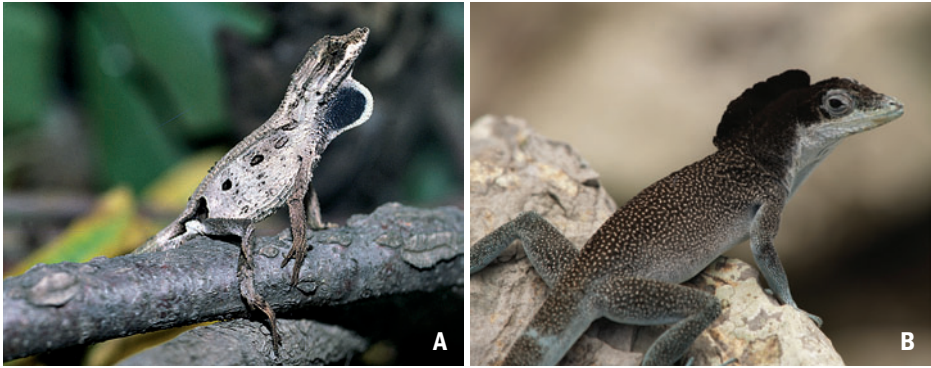


FIGURE 15.7

Small-dewlapped anoles. (a) *Chamaelinorops barbouri* has the second smallest dewlap relative to its body size among 49 West Indian species (not including the two Cuban species that do not have a dewlap [Losos and Chu, 1998]). (b) *A. agassizi* from Malpelo Island off the coast of Colombia also has a very small dewlap; large, reproductively active adult males have a permanently erected nuchal crest, unlike other anoles, in which crest erection is facultative (Rand et al., 1975). Photo courtesy of Margarita Ramos.

species—young or old—suggests that when small dewlaps evolved, for whatever reason,<sup>403</sup> the rate of species differentiation decreased.

Dewlaps or dewlap-like structures have evolved in a number of other lizard clades. The most similar are the dewlaps of several Asian agamid lizards which are strikingly like those of anoles (Fig. 2.3c). This clade, containing the seven species in *Sitana* and *Otocryptis*, is not particularly species rich. In contrast, the flying dragons of southeast Asia, genus *Draco*, sport a structure fairly similar to the anole dewlap (Fig. 2.3b) and are relatively diverse in both species number and ecomorphology (Lazell, 1992; McGuire and Alcalá, 2000; McGuire et al., 2007a).<sup>404</sup> Interspecific variability of the *Draco* dewlap is reminiscent of that seen in *Anolis*, but flying dragons have another trick up their sleeve: during displays, they also extend their wings, which also exhibit interspecific variation in coloration and pattern (Fig. 2.3b; Lazell, 1992; Mori and Hikida, 1994; McGuire and Alcalá, 2000). Further, like anoles, sympatric *Draco* tend to differ in the color of their display structures (Inger, 1983; Lazell, 1992). No research of which I am aware has directly tested the species-recognition role of *Draco* dewlap and wing coloration, much less a hypothesized role in *Draco* speciation. Nonetheless, the parallels are obvious.

403. Fitch and Henderson (1987) suggested that the small dewlap of *A. bahorucoensis*, a member of the *hendersoni* Series, evolved to make display less conspicuous to larger anoles which preyed upon them. Another possibility is that evolving a small dewlap could be another way to differentiate one species from another (Rand and Williams, 1970; Losos and Chu, 1998; Nicholson et al., 2005). No doubt other possibilities exist as well, but the evolution of dewlap size has received little attention.

404. With more than 20 described species, *Draco* is already one of the most species-rich genera of agamids (Stuart-Fox and Owens, 2003). However, many new species have been described recently, and by all indications the number of species may have been greatly underestimated (Lazell, 1987, 1992; McGuire and Alcalá, 2000; McGuire et al., 2007a).

As with the evolution of toepads, some, but not all, clades characterized by the possession of a dewlap have high species richness. No statistical analysis has been conducted, but the great species richness of *Anolis* and *Draco* compared to their close relatives is highly suggestive of a causal relationship, even considering the modest diversity of the *Sitana* + *Otocryptis* clade.<sup>405</sup>

In summary, the evolution of both toepads and dewlaps may have played a role in anole evolutionary diversification. In both cases, a plausible mechanism exists, and comparative data are generally supportive. In addition, these observations suggest a further hypothesis: perhaps evolutionary radiations that combine both great species richness and great adaptive disparity may be the result of the evolution of multiple features that increase both ecological opportunity and rate of speciation. In the case of anoles, the hypothesis would be that the dewlap and the toepads have had an interactive effect: the dewlap has enhanced the production of new species, whereas toepads have increased the likelihood that species would diverge to explore new ecological areas. In Chapter 17, I will explore the extent to which similar scenarios may account for adaptive radiation in other groups.

The study of the factors sparking evolutionary diversification is both fascinating and frustrating. Fascinating, because this is what evolutionary biology is ultimately about, trying to explain the diversity around us. Frustrating because of the difficulty of actually testing the hypotheses that are so easily generated. The discussion in this section, to me, embodies that conundrum: the ideas are interesting, the data somewhat persuasive, but the ability to strongly test the hypotheses limited.

#### DETERMINANTS OF SPECIES DIVERSIFICATION WITHIN ANOLIS

The discussion of the effect of dewlap size on rates of species diversification highlights the fact that species richness varies among anole clades. This variation is evident simply by inspecting the phylogeny in Figure 5.6: clades that originated at approximately the same time vary greatly in species number, from one in the *occultus* Series to 151 in the *Norops* clade. Such variation is highly unlikely if diversification has occurred in a homogeneous fashion among clades ( $p < 0.05$ , methods following Ricklefs [2003], Ricklefs et al. [2007]). Moreover, examination of the phylogeny reveals that many anole clades originated in a short period early in anole history; statistical analysis confirms that the rate of species origination in the Greater Antilles has decreased with time (Harmon et al., 2003).

405. The appropriate statistical evaluation of this hypothesis might take the form of asking: What is the probability that if an investigator randomly selected three clades of iguanian lizards, at least two would have substantially higher species diversity than their sister taxa? Alternatively, one could test whether rates of species diversification on those three branches of the *Iguania* were significantly higher than on branches throughout the rest of the clade. This latter analysis would have the advantage of explicitly incorporating information on evolutionary age, which is always a potential problem when clades—or members of a taxonomic rank such as a genus—differ in age.

A pattern of explosive species diversification early in the history of a clade followed by decreasing rates of diversification later on is found in many radiations (e.g., Gould et al., 1987; MacFadden and Hulbert, 1988; Nee et al., 1992; Lovette and Bermingham, 1999; Rüber and Zardoya, 2005; Seehausen, 2006). Usually this pattern is attributed to the occupation of initially empty ecological space as a result of colonization, extinction of an ecologically dominant form, or evolution of a feature permitting access to previously unavailable resources (Simpson, 1953). This explanation fits anole history well: early on in the radiation, ecomorph types evolved repeatedly; subsequently, ecomorph stasis has been accompanied by lower rates of diversification. An interesting test of the “ecological opportunity” hypothesis might involve mainland *Norops*, which diversified in part of their range in the absence of other anoles, but in the other part in the presence of the *Dactyloa* clade;<sup>406</sup> if this hypothesis is correct, we might expect to see greater rates of diversification among *Norops* in the *Dactyloa*-free region.

Given that rates of diversification are not constant within *Anolis*, we can now ask what accounts for the heterogeneity in rates. I have already discussed the potential role of dewlap size; no other phenotypic character is obviously linked mechanistically to rates of species diversification. However, species richness may be affected by extrinsic factors as well. I will consider two: island area and microhabitat.

#### THE SPECIES DIVERSIFICATION: AREA RELATIONSHIP

The effect of island size on the rate of species diversification is an obvious place to start. The species-area relationship is one of the most consistent findings in all of ecology—across almost any set of islands or island-like entities (e.g., lakes, mountaintops), species richness increases as a function of area (Schoener, 1976b; Lomolino, 2000). The species-area relationship could result purely from ecological processes of extinction and colonization, but recent work has illustrated an evolutionary component as well by demonstrating that rates of species diversification are also a function of island area (Steppan et al., 2003; Gillespie, 2004; Parent and Crespi, 2006). This relationship was first demonstrated for anoles in the Greater Antilles (Fig. 15.8; Losos and Schluter, 2000); statistical analysis indicates that the relationship between rate of diversification and area results primarily from an increase in the rate of speciation with area, rather than a decrease in the rate of extinction.

Why speciation rates should be a function of island area is not clear. One obvious possibility is that the potential for allopatric isolation increases with island area, a hypothesis which appears particularly plausible given the number of mountain ranges on Cuba and Hispaniola. In addition, island area is often correlated with vegetational diversity and the number of different habitats (reviewed in Ricklefs and Lovette, 1999;

406. This assumes that *Dactyloa* wasn't more widespread in the past. *Dactyloa*'s range currently extends as far north as Costa Rica.

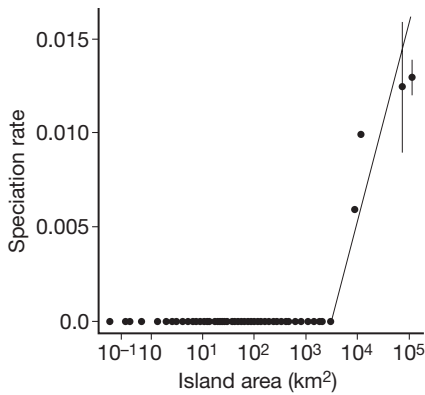


FIGURE 15.8

Speciation-area relationship in West Indian *Anolis*. Rates were calculated with the assumption that the occurrence of sister taxa on the same island is evidence of a cladogenetic speciation event on that island and were calculated relative to branch lengths; the y-axis has no units because branches weren't calibrated to time. Bars indicate ranges resulting from analyses based on different reconstructions of ancestral biogeography. This plot also reveals the threshold island size required for speciation discussed in Chapter 14. Modified with permission from Losos and Schluter (2000).

Whittaker and Fernández-Palacios, 2007), which potentially could increase the available niche space on larger islands. However, as mentioned in Chapter 14, islands the size of Guadeloupe and larger do not seem to differ greatly in habitat availability. Finally, a third possibility is that larger islands have a greater complement of other species—competitors, predators, parasites—which may drive ecological divergence and rates of diversification.

#### ECOMORPHS AND SPECIES RICHNESS

A second factor that may affect the rate of species diversification is microhabitat use. Many aspects of anole biology correlate with ecomorph class: is probability of speciation and extinction yet another? A priori, we can imagine a variety of ecomorph attributes that might have effects on speciation or extinction, such as population size or dispersal ability and its relationship to levels of gene flow.

Analysis of species richness across the Greater Antilles shows a strong effect of both island area and ecomorph (Fig. 15.9). In particular, trunk-ground and grass-bush anoles are particularly species rich, whereas twig and crown-giant anoles tend to be less diverse.

Why these differences exist is not obvious. Clearly, body size is not a factor because the smallest ecomorphs, the twig and grass-bush anoles, differ greatly in the number of species per island. If propensity for habitat fragmentation were responsible, we might predict, in contrast to Figure 15.9, that trunk-ground anoles should be the least



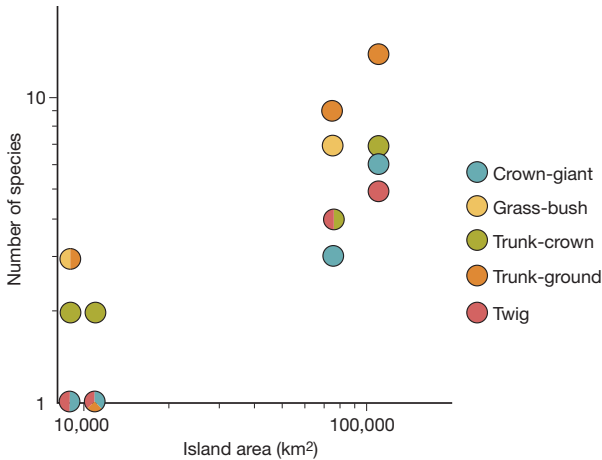


FIGURE 15.9

Differences among ecomorph classes in species richness (circles with more than one color indicate ecomorphs with the same number of species on an island). Ecomorphs differ in species richness across islands (analysis of covariance, heterogeneity of slopes non-significant; ecomorph effect,  $F_{1,4} = 5.74$ ,  $p = 0.007$ ; island area as covariate). Trunk anoles were not included in the analysis because they are only found on two islands; trunk anoles do buck the trend, however, being more species-rich on Hispaniola than on Cuba. Results are qualitatively unchanged if grass-bush anoles, absent from Jamaica, are excluded (Ancova, heterogeneity of slopes non-significant; ecomorph effect:  $F_{1,3} = 4.33$ ,  $p = 0.030$ ). Because ecomorphs are independently derived on each island, statistical significance of the ecomorph effect is not confounded by phylogenetic relationships.

likely to speciate because their populations seem least likely to be isolated by habitat disruptions.<sup>407</sup>

On the other hand, differences in species richness might be a function of extinction, rather than speciation, rates. Both on landbridge islands and throughout the Greater Antilles, trunk-ground anoles are nearly ubiquitous: if anole species are present, trunk-ground anoles are there. On landbridge islands, this pattern results because trunk-ground anoles survive even after other species have perished (see discussion of faunal relaxation in Chapter 4). Although this decreased rate of extinction results because trunk-ground microhabitats are present on even very small islands, it may indicate a general hardiness and resistance to extinction of trunk-ground anoles. Conversely, crown-giants and twig anoles often appear to have low population densities (but see Hicks and Trivers [1983]) and are rarely found on landbridge islands, perhaps bespeaking a high vulnerability to extinction. This line of reasoning, however, breaks down in a comparison of trunk-crown and grass-bush anoles, where the prediction of lower extinction rates of trunk-crown anoles based on patterns of occurrence on landbridge islands and in species-poor sites on the Greater Antilles<sup>408</sup> does not square with the higher species richness of grass-bush anoles.

407. This prediction assumes that trunk-ground anoles are more likely to cross open ground from one habitat patch to another than are more arboreal species.

408. In both situations, trunk-crown anoles are often in places where grass-bush anoles do not occur (see Chapter 4 on landbridge islands; no quantitative data exist for species-poor sites, but my impression is that trunk-crown anoles are usually more likely to be present than grass-bush anoles).

A variety of other aspects of anole biology could, in theory, affect rates of species diversification. Other factors such as environmental stability and seasonality or trophic position might plausibly have an effect. As discussed in Chapter 14, degree of sexual selection has been suggested recently as one factor that may affect rate of species diversification. If ecomorphs differ in extent of sexual selection (which remains to be determined [Chapter 9]), then this hypothesis would be worth investigating.

## SEXUAL DIMORPHISM AND ADAPTIVE RADIATION

Despite the tremendous amount of research over the past several decades on both sexual dimorphism and adaptive radiation, little attention has been paid to the relationship between these two topics. Most research on sexual dimorphism has focused on its causes and consequences within single species and has considered neither the role that sexual dimorphism may play in adaptive radiation, nor how dimorphism might evolve during the course of a radiation.

### THE EVOLUTION OF SEXUAL DIMORPHISM DURING AN ADAPTIVE RADIATION

Imagine the first anole species occupying a Greater Antillean island. Presumably, resources would be abundant and many different ways of making a living—corresponding to the different ecomorph types—would be available. What's a species to do? One possibility is that disruptive selection could drive adaptive radiation as all of the ecomorph types evolve *in situ*. I've already argued in Chapter 14 that sympatric speciation doesn't seem to occur in anoles, so—for whatever reason—this option appears to be out.

Another possibility is niche expansion. As discussed in Chapter 11, anole populations in species-poor localities tend to have broad resource use. An evolutionary response to such wide niche breadth is the evolution of increased intra-population phenotypic variation in which individuals are adapted to use different parts of the resource spectrum. At the extreme, these differences could take the form of discrete morphs, as in the African fire-cracker finch (*Pyrenestes ostrinus*), in which large- and small-billed morphs are adapted to eat seeds of different sizes (Smith, 1993). However, as discussed earlier in this chapter, quantitative analysis indicates that broad resource use is not generally accompanied by increased phenotypic variation within a population, but rather by phenotypically similar individuals with broader resource use (Lister, 1976b); moreover, few examples of ecologically relevant, non-sex-linked polymorphisms exist in anoles.

An alternative response is for populations to evolve sexual dimorphisms in which the sexes use different parts of the ecological spectrum (Schoener, 1986b). Such sexual dimorphism in both size and shape is rampant in anoles and varies by ecomorph (Chapter 9). Consequently, we might predict that the hypothetical initial Greater Antillean anole population would be comprised of individuals with broad resource use and that substantial ecological differentiation would occur between the sexes leading to the evolution of sexual dimorphism in morphology.

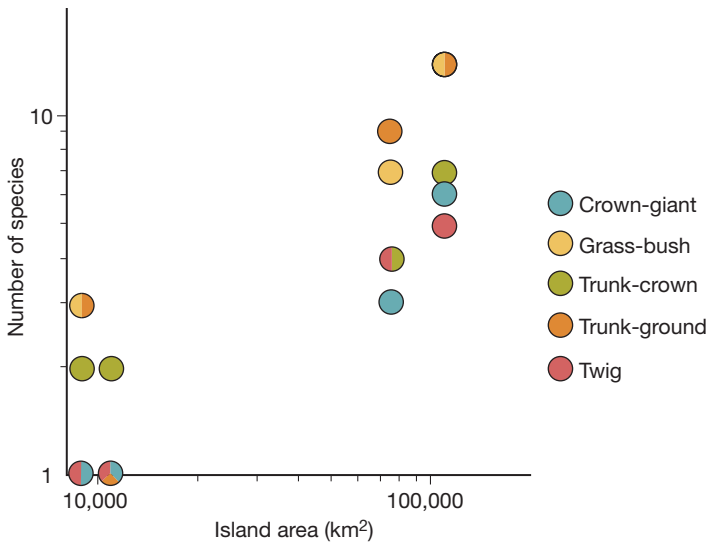


FIGURE 15.10

Sexual size dimorphism as a function of number of coexisting species on an island. Each point represents the median value of sexual size dimorphism for all of the species on one island. Values on the x-axis represent number of described species per island in the mid-1970s. Many species have been discovered since then, particularly on the larger islands. Modified with permission from Schoener (1977).

Eventually, however, more anole species evolve, probably in allopatry, and then become sympatric. As a result, ecological contraction—the opposite of ecological release—should occur, leading to diminished sexual dimorphism. Moreover, as more and more species join the community, this decrease should continue and the extent of sexual dimorphism should get steadily smaller.

This prediction has been tested most thoroughly with regard to size dimorphism. In comparisons both among species and among populations within species, the degree of sexual size dimorphism is negatively correlated with the number of sympatric species (Fig. 15.10; Schoener, 1977). This inverse correlation has several components:

1. Species in depauperate communities on landbridge islands have high levels of dimorphism due to ecological sorting. As landbridge islands decrease in size, ecomorphs drop out in a predictable sequence, and the ecomorphs that tend to persist, trunk-ground and trunk-crown anoles, tend to have high dimorphism (Chapter 4). One possibility is that these ecomorphs are successful in persisting on depauperate islands because of their high dimorphism; however, an alternative is that these ecomorphs are the best adapted to conditions on small islands, unrelated to their great degree of sexual dimorphism.
2. Size dimorphism increases after colonization of solitary islands. Colonizers of empty islands tend to have relatively high levels of size dimorphism, but subsequently evolve even higher levels (Poe et al., 2007). For example, in the Greater Antilles, solitary anole species all have as their sister taxa either

trunk-crown or trunk-ground anoles; comparison to estimates of ancestral size dimorphism indicates increased size dimorphism in these solitary species.<sup>409</sup>

3. Size dimorphism decreases during adaptive radiation with increased species number. Jamaica, the island with the fewest anole species, has the highest median size dimorphism, whereas the two most species-rich islands, Cuba and Hispaniola, have the lowest dimorphism. This trend has several causes. First, among the ecomorphs common to all four islands, size dimorphism within each ecomorph is inversely related to species number on an island (analysis of covariance, heterogeneity of slopes non-significant, island species number effect,  $F_{1,11} = 3.97$ ,  $p = 0.036$ , one-tailed). Second, the ecomorphs found only on the larger, and more species-rich, islands—grass-bush and trunk—have relatively low dimorphism. Third, most Greater Antillean unique anoles, which occur only on the two largest islands (with one exception), also tend to have intermediate-to-low dimorphism.<sup>410</sup>

The relationship between sexual shape dimorphism and number of species has only been examined in one comparison: the species in the Jamaican radiation have a higher mean shape dimorphism than the anoles of Puerto Rico (Butler et al., 2007). Whether, as would be predicted, Lesser Antillean anoles have even greater dimorphism, and Hispaniolan and Cuban anoles even less dimorphism, remains to be tested.

These trends support the hypothesis that sexual dimorphism evolves adaptively in response to the presence or absence of other species, presumably as a result of resource competition. Moreover, they indicate that the degree of dimorphism decreases during adaptive radiation, both because species within microhabitats evolve decreased dimorphism and because the microhabitats occupied only in species-rich radiations tend to be filled by species with low dimorphism.

#### THE RELATIVE IMPORTANCE OF SEXUAL DIMORPHISM VERSUS INTERSPECIFIC DIFFERENTIATION IN ADAPTIVE RADIATION

A second question about sexual dimorphism concerns how substantial a role it plays in adaptive radiation. Most research has implicitly assumed that sexual dimorphism is a minor contributor to the ecomorphological diversity within an adaptively radiating clade. In theory, however, there is no reason that much of the niche differentiation that occurs within a clade could not be manifested as differences between the sexes within species (Fig. 15.11). No study to date has examined the role that sexual dimorphism plays in adaptive radiation.

409. This analysis was limited to species endemic to solitary islands and did not consider populations of species also found on islands with other species.

410. Data from Schwartz and Henderson (1991) and Butler et al. (2000). The Cuban aquatic anole, *A. vermiculatus* and its sister taxon, the rock-wall anole, *A. bartschi*, are conspicuous exceptions to the generalization that unique anoles have low dimorphism.

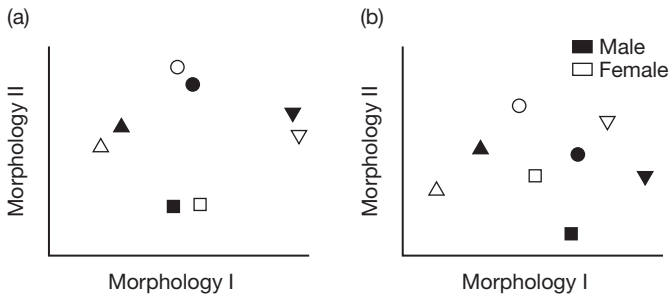


FIGURE 15.11

The role of sexual dimorphism in adaptive radiation. Sexual dimorphism could be a minor (a) or a major (b) component of morphological differentiation. Symbols represent different species, shaded symbols are males and open symbols are females.

Butler et al. (2007) examined the positions of both sexes of Puerto Rican and Jamaican anoles in multivariate morphological and ecological space. They found that the lion's share of the variation was accounted for by consistent differences among the ecomorph classes. Nonetheless, a substantial additional portion of the variation was explained by sexual differences within species, as well as a small amount due to variation that occurred between sexes in some ecomorphs and not others.<sup>411</sup> Moreover, because of sexual dimorphism, morphological and ecological space were much more fully occupied than if no sexual differences had existed—the morphospace volume occupied by both sexes on these two islands is 59% greater than that occupied just by females and 88% greater than that occupied by males. Similarly, both sexes occupy 33% more multivariate ecological space than females alone and 47% more than males.

These data indicate that sexual size and shape dimorphism play an important role in anole adaptive radiation. In islands with few species, much of the ecomorphological variation among anoles is partitioned between the sexes. As radiation proceeds, dimorphism decreases as species' niches become compressed by the presence of competitors, but it still accounts for an important part of the ecological and morphological variation.

Clearly, work is needed on patterns of shape dimorphism on islands both larger and smaller than the two studied to date. In addition, experimental studies on the evolutionary dynamics of sexual dimorphism could prove quite interesting. One would predict, for example, that the addition of a second species to a site previously occupied by only one species would lead to selection for the sexes to become more similar in the original species. Alternatively, patterns of selection might differ among the sexes, with the sex more similar to the introduced species being affected more greatly.<sup>412</sup> Anoles could prove to be a model system for the study of the evolution of sexual dimorphism, as well as of its role in adaptive radiation.

411. The ecomorph-by-dimorphism interaction term.

412. Alternatively, the same questions could be investigated by looking at the effect of introduced species on the sexual dimorphism of native species.

#### SEXUAL DIMORPHISM AND THE ECOMORPH PHENOMENON

The importance of sexual dimorphism in anole adaptive radiation has one additional implication. As discussed in several previous chapters, the ecomorphs differ in degree of sexual size and shape dimorphism, as well as in social structure and social behavioral traits (e.g., display rate). These differences indicate that the ecomorph phenomenon represents more than just morphological adaptations to moving on different sized structures. Rather, occupation of different structural microhabitats has led to divergent adaptation not just in limb length and toepad size, but also in social structure, display and foraging behavior, size and shape dimorphism, and other characteristics (Chapters 3, 8 and 9). One possibility is that these disparate evolutionary changes are in response to independent aspects of structural microhabitat; that is, limb and toepads may evolve in response to selection for efficient locomotion in the different structural microhabitats, dimorphism may evolve in response to differences among microhabitats that affect the strength of sexual selection, foraging mode may evolve in response to effects of structural microhabitat on prey availability, and so on.

Alternatively, however, these features may be causally linked, representing an evolutionary syndrome of features related to structural microhabitat. For example, the short legs of twig anoles, necessary for locomotion on narrow surfaces (Chapter 13), may make rapid movements to capture prey and escape predators impossible. As a result, twig anoles may need to be more cryptic than other anoles, and thus may display less. In addition, they may need to forage more widely for less active prey, both because their slow speed precludes them from catching more active prey and because their microhabitat limits the area they can scan for active prey. This active lifestyle may lead to increased home range size and a lessened ability to defend territories, thus possibly decreasing the strength of intrasexual selection among males, but increasing the opportunity for female mate choice. At the other extreme, the broad surfaces that trunk-ground anoles use select for long legs: the great sprint speed these legs impart allow these lizards to display frequently in exposed places. Moreover, the large area they can survey for prey allows them to remain stationary, at the same time keeping an eye out for intruders, which can be quickly repelled, thus increasingly the ability of males to exclude others from their territories and possibly limiting opportunities for female choice. In this way, locomotor behavior and morphology, foraging behavior, social structure, and sexual dimorphism all may be integrated aspects of evolutionary adaptation to different structural microhabitats.

#### IS THE TERM “ADAPTIVE RADIATION” MEANINGFUL? A COMPARATIVE TEST TO INVESTIGATE WHETHER A CLADE CONSTITUTES AN ADAPTIVE RADIATION

I'll conclude the chapter by asking a simple question: do anoles constitute an adaptive radiation? Certainly, *Anolis* is speciose and ecologically diverse, and much of this diversification appears to have been adaptive. But this could probably be said about many clades of organisms. Given enough time, almost all clades will diversify, and a substantial

proportion of the ensuing diversity is likely to be adaptive. Does that mean that most clades constitute adaptive radiations? Certainly, many workers who specialize on a particular group refer to their study subject as an adaptive radiation—isn't that more exciting than studying an "ordinary" group?<sup>413</sup>

But this approach renders the term meaningless. If adaptive radiation is the normal, expected outcome of evolutionary diversification, then why have the term at all? Designating a clade as an adaptive radiation would add no extra information. Although arguing about whether a clade is an adaptive radiation or not might seem an insignificant debate over terminology, the issue actually is significant. Evolutionary biologists often are interested in trying to explain why a particular clade is so diverse. Before this question can be investigated, however, we need to know which are the exceptional clades upon which to focus—the diversity of clades that represent the usual expected outcome of evolutionary diversification requires no special explanation. For this reason, reserving the term "adaptive radiation" for those clades which are exceptionally diverse is important.<sup>414</sup>

But how do we recognize those clades that are exceptional? The first question is, what is the metric to compare clades? Many studies have compared the species richness of different clades (e.g., Barraclough et al., 1999; Owens et al., 1999; Ricklefs et al., 2007). Although investigating what causes some clades to be species rich and others to be species poor is interesting and important, it is not the same as asking whether a clade constitutes an adaptive radiation. The reason is simple: clades can be ecologically and morphologically extremely diverse, despite containing few species (consider Darwin's finches, with only 14 species [Grant, 1986; Grant and Grant, 2008]), or they can be species rich, but ecologically and morphologically homogeneous (e.g., plethodontid salamanders [Kozak et al., 2006]). Thus, species richness and ecological and phenotypic disparity are distinct aspects of evolutionary diversification, both of which are considered in this chapter. To examine adaptive radiation, however, we need to focus on phenotypic disparity, which quantifies the extent to which members of a clade have evolved adaptations to using different parts of the environment.

Borrowing a page from community ecology, Miles and I developed a null model<sup>415</sup> to test the hypothesis that a clade has exceptionally great ecomorphological disparity (Losos

413. Of course, some contrarians pride themselves on studying species-rich groups with exceptionally little adaptive variation, which have been given the name "nonadaptive radiations" (in fact, a whole lexicon of types of radiations has been proposed, including "developmental," "architectural," etc. [Erwin, 1992; Givnish, 1997]).

414. Put another way, if *Anolis* is not exceptional, why should we pay particular attention to it, as compared to any other group of lizards? Why should I write this book, and why should you read it? The unusual breadth and integration of research on anoles is certainly an alternative reason, but I think much of the interest in anoles in the general scientific community is based on the idea that anoles are, indeed, special, in the extent of their evolutionary diversification.

415. An ecological null model is "a pattern-generating model that is based on randomization of ecological data or random sampling from a known or imagined distribution. The null model is designed with respect to some ecological or evolutionary process of interest. Certain elements of the data are held constant, and others are allowed to vary stochastically to create new assemblage patterns. The randomization is designed to produce a pattern that would be expected in the absence of a particular ecological mechanism" (Gotelli and Graves, 1996, pp. 3–4). Null models became famous in the context of debates over whether communities exhibited

and Miles, 2002). To employ this null model, one needs to: 1) establish the set of clades included in the comparison;<sup>416</sup> 2) quantify the disparity in putatively adaptive traits (i.e., traits for which an adaptive basis for interspecific variation has been established, such as limb length and lamella number);<sup>417</sup> and 3) determine whether some clades have exceptionally great (or little) disparity compared to what would be expected by chance if clades did not differ in their evolutionary propensities.

Miles and I implemented this approach to ask whether any of the subclades of iguanid lizards are exceptionally disparate in the sort of ecomorphological characters studied in anoles and other lizards. These clades form an appropriate pool to compare because, with one exception, all are similar in basic aspects of natural history such as diet, foraging and territorial behavior, body size and general morphology.<sup>418</sup> Also, the clades all appear to be of approximately the same age (Macey et al., 1997; Schulte et al., 1998; Wiens et al., 2006), so comparisons are not confounded by differences in the amount of time they have had to accumulate differences. To establish a null model of expected disparity, we randomized species among clades (standardizing species' values to account for interclade differences) and then compared the observed values of clade disparity to those generated by the null model.

The results of this analysis are clearcut. The clade to which anoles belong, the Polychrotinae,<sup>419</sup> has the greatest disparity (Fig. 15.12), which is significantly greater than

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nonrandom patterns of species co-occurrence or phenotypic similarity. They were used to ask questions such as “Do particular species co-occur in communities less often than expected by chance?” and “Are coexisting species less similar in body size than would be expected by chance?”. The history of these debates is summarized in Gotelli and Graves (1996); the exchange between Diamond, Gilpin, Simberloff, and Connor in the Strong et al. (1984) volume on community structure is instructive regarding both the science and the sociology of the debate.

416. Adaptive radiation must be viewed as a comparative concept: a clade is judged as an adaptive radiation compared to some universe of other clades comparable in some respects, such as evolutionary age. If not, then all life itself is an adaptive radiation, and all other clades pale in comparison. Or, to make a more narrow comparison, if, as many argue, placental mammals—the clade that includes whales, bats, elephants, and shrews—constitute an adaptive radiation, then any smaller and more restricted clade of mammals would by comparison likely not be considered an adaptive radiation. Thus, for this reason, adaptive radiation is a matter of scale; a clade can only be meaningfully judged in relation to a set of comparable clades.

Some will contend that the only appropriate means to test an evolutionary hypothesis is through sister group comparisons. Based on the logic that sister taxa are of the same age and should be similar in many respects due to their common ancestry, such comparisons are the appropriate and preferred comparison for many questions in evolutionary biology (Cracraft, 1981; Brooks and McLennan, 1991, 2002). However, heretical as it may be to some, sister group comparisons are not always appropriate. In this case, the sister-group approach might judge an unexceptional clade to be exceptional if its sister is even less diverse or, conversely, might fail to identify an exceptional clade if its sister is even more exceptional—compared to placentals, for examples, marsupials, diverse as they are, would not be considered an adaptive radiation (Losos and Miles, 2002). For this reason, the appropriate comparison is between a focal clade and a universe of other clades as similar as possible in age, natural history, geography and other attributes.

417. Disparity can be quantified in a number of ways (Foote, 1997; Erwin, 2007); perhaps the simplest is to calculate the mean pairwise distance between all species in a multivariate space defined by the characters under study: the greater the mean distance, the greater the phenotypic differences among species.

418. The exception are iguanas (the Iguaninae) because they are distinct from all other iguanids (ironically enough) in being herbivorous, with concomitant differences in body size, foraging and territorial behavior, physiology and many other aspects of their biology. For this reason, they were excluded from the analysis. This point is discussed at greater length in Losos and Miles (2002), as are more details about the method.

419. Note that the monophyly of the Polychrotinae has come into question, as discussed in Chapter 6.



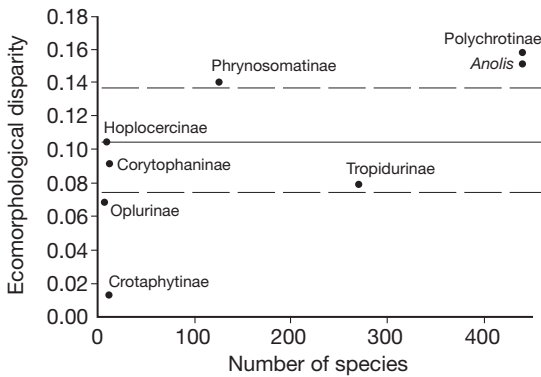


FIGURE 15.12

Ecomorphological disparity of subclades of the Iguanidae. Clades falling above the top dashed line have unusually great ecomorphological disparity, whereas clades falling below the lower line have unusually low disparity. *Anolis*, though younger than the seven subclades, still has exceptionally great disparity, as does the subclade (Polychrotinae) to which it belongs. This analysis also indicates that the relationship between disparity and species richness of clades is positive, but not very strong. Modified with permission from Losos and Miles (2002).

would be expected by chance. Moreover, the disparity value for the anole clade<sup>420</sup> within the Polychrotinae is significantly greater than expected by chance, even though anoles have been diverging for a shorter period of time than the clades that comprise the null pool (Fig. 15.12). The bottom line is that, at least in comparison to a set of similar clades, *Anolis* exhibits exceptional ecomorphological disparity and thus merits designation as an adaptive radiation.

Of course, a theme of this book is that anoles comprise not one radiation, but at least six (four on the Greater Antilles and two, and possibly more, on the mainland). Given that much of the disparity of *Anolis* recurs on each island, each island radiation likely exhibits exceptional disparity, but Losos and Miles (2002) did not sample widely enough to test this proposition. A study directed at this question would require collecting data on appropriate comparison clades (the ones in Losos and Miles [2002] being too old) and would require modifying the test to account for the non-monophyly of most of the anole radiations. Anole phylogeny makes clear that evolutionary diversification has occurred entirely independently only on Jamaica; by contrast, a moderate amount of inter-island reticulation exists among clades on the other three islands of the Greater Antilles (Chapter 6). This pattern of relationship means that the fauna of none of the three islands is the result of a single initial colonizing species. Nonetheless, the number of inter-island connections is small and most of them occurred early in anole history (Chapter 6). Moreover, the observation that sister clades on different islands are almost always ecomorphologically different indicates that the evolutionary diversification that has produced today's anole faunas occurred in situ; the diversity that exists on each island

420. Represented by a variety of Greater Antillean species plus *Anolis Phenacosaurus heterodermus* from the mainland.

today is not the product of species that had already evolved their differences on other islands coming into coexistence by multiple colonization events (i.e., ecological sorting [Chapter 7]).

Thus, although only Jamaica exactly meets the postulated first step of adaptive radiation, the history of the other islands agrees with it in spirit, even if several of the clades present on an island did not initially diverge there. An appropriately designed null model could examine whether the ecomorphological diversity on these islands is greater than expected for a radiation comprised of multiple clades; my feeling is that such a null model would be strongly rejected in all cases, supporting the existence of multiple adaptive radiations in the Greater Antilles and on the mainland.

### **FUTURE DIRECTIONS**

In this chapter, I have attempted to take a synthetic approach to understand the progression of anole adaptive radiation. As has been plainly evident, the speculation-to-empiricism ratio in this chapter has been much higher than in previous chapters, and throughout the chapter I have highlighted what remains to be learned. For this reason, I will not summarize future directions in this and the next two—also synthetic—chapters.

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# 16

## THE FIVE FAUNAS RECONSIDERED

The *Anolis* evolutionary pageant exhibits a fundamental duality. On one hand, the Greater Antillean ecomorphs are renowned for convergence of entire communities, with the same set of ecomorphs evolving repeatedly. On the other hand, only one of the other four anole faunas—the anoles of the small islands of the Greater Antilles—contains many types of ecomorphs. The story of three of the other anole faunas—the mainland, the Lesser Antilles, and the unique anoles of the Greater Antilles—is primarily one of non-convergence, both internally and with the ecomorph radiations.

The simplest explanation for this contrast is that the environments in the Greater Antilles select for the same set of phenotypes, whereas the environments in the other localities select for different phenotypes. By environments, I mean abiotic factors such as temperature and humidity, as well as the structures which anoles use, the food they eat, and the other species with which they interact as predators, prey, and competitors.

This idea can be cast in the framework of an adaptive landscape in which the x- and y-axes represent different aspects of the phenotype and the height of the z-axis represents the extent to which multivariate phenotypes are favored by selection (reviewed in Fear and Price, 1998; Schluter, 2000; Arnold et al., 2001). In this light, the simple hypothesis above would suggest that adaptive peaks are in the same place in the Greater Antilles, and in different places in the other areas (Fig. 16.1).<sup>421</sup>

421. Keep in mind the abstract nature of figures like 16.1. Although the adaptive landscape for a single population in a static environment is mathematically defined and analytically tractable, the extension to consideration of the landscape for multiple co-occurring species in an evolving clade should be viewed as a heuristic analogy. Technically, the adaptive landscape specifically refers to how a population will evolve in a

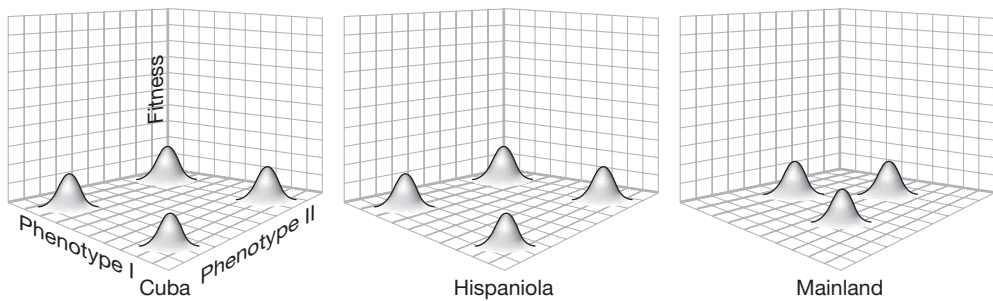


FIGURE 16.1

Similar adaptive landscapes on the islands of the Greater Antilles (represented here by Cuba and Hispaniola) may be responsible for the evolution of the same set of ecomorphs on each island, whereas a different landscape on the mainland could account for the different patterns of morphological evolution found there.

This hypothesis makes a major assumption, that evolution is completely predictable; that is, movement through phenotype space is unhindered such that species will always evolve to the highest available peak (assuming, in addition, that once a peak is occupied by one species, it cannot then be occupied evolutionarily by another species). In addition, as an explanation of ecomorph convergence, the hypothesis also assumes a unitary match between the environmental factors that impose selection and the possible phenotypic responses—that is, that only one phenotypic solution exists for problems posed by the environment.<sup>422</sup>

These assumptions need not be true, and if they are not, then the simple hypothesis above may be incorrect: convergent evolutionary radiations may not necessarily imply similarity in environments, and lack of convergence in radiations may occur even in very similar environments.

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particular selective setting, and multiple peaks on that landscape indicate different regions of phenotypic space favored by selection. However, the existence of multiple peaks for a single population does not necessarily imply that multiple, sympatric species in that environment would evolve to the different peaks. Rather, the landscapes for each of the species would not necessarily be the same, because each species would occur with a different complement of co-occurring species (i.e., each species is part of the environment for other species). Consequently, to envision whether the same set of phenotypes would be favored on different islands, we would need to look at the landscapes for each species separately. However, these landscapes might not be static, but rather might change each time a new species joins the community. In addition, as a species evolves, then so might the adaptive landscapes for all co-occurring species. None of these issues is incorporated into the mathematical underpinning of the adaptive landscape. Consequently, application of this concept to an evolving adaptive radiation should be considered a metaphor, albeit an extremely useful one.

422. This view of selection—the environment creating problems to which populations must adapt—has been criticized because organisms interact with their environment and these interactions shape the way in which natural selection operates (Lewontin, 2000). Certainly this is true in some ways for anoles. For example, by selecting which part of the environment they use, anoles determine the biophysical environment which they experience. Nonetheless, much of the discussion of anole evolution concerns the external environment—vegetation structures, regimes of temperature and humidity—which do set demands to which organisms must adapt if they are to use the environment successfully. In this sense, I feel this metaphor is a useful way to understand anole evolution.

In this chapter, I will examine the hypothesis that convergence among the Greater Antillean ecomorphs and non-convergence with the other anole faunas stems directly from similarities and differences in the adaptive landscapes they occupy. Along the way, I will consider a variety of alternative and interacting explanations for these patterns. At the outset, I want to make clear that expectations should be kept low. We have almost no hard data on any of these ideas. Consequently, this chapter is meant to be forward looking: my hope is to lay out ideas that may profitably be explored in the future, rather than to provide definitive tests of alternative hypotheses. Nonetheless, I will not refrain from providing my own intuition about which factors are most likely to be of primary importance in guiding anole evolution.

### CONVERGENCE AND THE ADAPTIVE LANDSCAPE

Probably the single most notable fact about anole evolution is the convergence of entire communities that has occurred across the four islands of the Greater Antilles. Adaptive radiation on each of these islands presumably followed the scenario detailed in previous chapters, with resource-competition-driven character displacement being of paramount importance. The question is: why have these separate radiations produced extremely similar evolutionary outcomes?

The most parsimonious explanation for the repeated evolution of the ecomorphs is that the selective environment—the adaptive landscape—is the same on all four islands of the Greater Antilles. This is not an easy hypothesis to test. If we could test it, however, we might find one of three outcomes. The hypothesis would be supported if we found that adaptive landscapes are generally the same in the Greater Antilles, but that these landscapes differ from those elsewhere. At the other extreme, we might find either that landscapes everywhere are all the same or that they are all different. Either of these findings would suggest that factors other than the environment have played a role in shaping the anole radiations.

A third possibility, which could occur regardless of whether landscapes in different areas are similar, is that we might find unoccupied adaptive peaks. These vacancies could occur for two reasons. First, they might represent ecological opportunities that, for whatever reason, have not been exploited by anoles. Conversely, they might represent alternative adaptive responses to particular ecological conditions. That is, more than one way of adapting to a given situation might exist. For example, when faced with prey that contains a toxic substance, predators may evolve resistance or simply avoid eating the part of the body that contains the toxin (cf. Farrell et al. [1991] and Berenbaum and Zangerl [1992] on diverse responses in herbivores to plant defenses). In a similar vein, in the presence of predators, potential prey may respond by evolving greater crypticity, ability to flee, or ability to defend themselves (e.g., Losos et al., 2002).

Regardless of the explanation, the presence of unoccupied adaptive peaks would suggest that the external environment may not be solely responsible for determining

patterns of convergence and divergence: factors internal to a population also might play a role in determining which peaks are occupied and which are not.

#### TESTING THE HYPOTHESIS THAT CONVERGENCE RESULTS FROM SIMILARITY IN THE ADAPTIVE LANDSCAPE

In theory, the topography of the adaptive landscape could be discovered in two ways.

##### *MEASUREMENTS OF NATURAL SELECTION COMBINED WITH EXPERIMENTAL APPROACHES*

The first method would be to measure selection on existing species. The expectation would be that selection would maintain ecomorphs in more or less their current state, either through stabilizing selection or through selection that might be directional for one generation, but for which temporal changes in selection ended up with no net change over time (Grant and Grant, 2002). Such a test would confirm the existence of selection favoring the phenotypes of the ecomorphs in an environment occupied by those ecomorphs. It would not, however, be able to assess the form of selection in areas of phenotypic space not currently occupied.

This problem theoretically could be solved by conducting experimental introductions of phenotypically different species to islands on which they did not occur, to measure selection in portions of morphological space not naturally occupied on that island. As suggested in Chapter 14, perhaps introducing only males in experimental enclosures (à la Pacala and Roughgarden, 1982; Rummel and Roughgarden, 1985; Malhotra and Thorpe, 1991) containing the native anole fauna and following their fate through their lifespan might be a way to get around the obvious ethical difficulties with such an approach.<sup>423</sup>

Studies such as these would characterize the selective pressures operating on anole communities today, in the presence of the ecomorphs. They presumably would show that the ecomorph phenotypes that occur today are maintained by selection. What they would show about phenotypes not naturally present on an island is harder to predict. If, for example, one established a population of grass-bush anoles or a rock-wall specialist like *A. bartschi* on Jamaica, would selection favor those phenotypes? This test would have to be conducted in two stages. If all individuals perished, then selection gradients could not be calculated because they involve comparing survivors to non-survivors; nonetheless, this result would strongly indicate that the particular phenotype occurs in an adaptive valley. If there were some survivors, then we could determine how selection would

423. Care would have to be taken to choose species that could not interbreed with native species. Even then, one might worry about the possibility of introducing diseases or parasites to which the native species were not adapted.

Unfortunately, another option, examining localities where species already have been introduced, would not work in this case. The reason is that no cases of introduction of species with ecomorphologies not already occurring on an island have been reported in the Greater Antilles (i.e., there have been no introductions of unique anole species or of the absent ecomorphs on Puerto Rico or Jamaica).

operate on the population's phenotype. Would stabilizing selection maintain their phenotypes or would strong directional selection prevent the phenotype from persisting for long, perhaps by transforming the population into one of the ecomorphs? Ideally, enough different phenotypes could be introduced to cover a broad swath of anole ecomorphospace, though they probably couldn't all be introduced at the same time and place.

Such a study would be incomplete, however, because it would only examine the adaptive landscape in the presence of the ecomorphs. If species interact, then the selective optimum for one species might change depending on what other species are present—character displacement is an example of the different position of adaptive peaks in the presence of competitors. What we are really interested in asking is whether the environments on different islands have driven adaptive radiation in the same direction. To ask this question, we would need to estimate the adaptive landscape in the presence of different numbers and combinations of other species. Perhaps the place to start would be to estimate the landscape for a single species by itself. By placing different phenotypes in an enclosure with no other species, we might be able to estimate the phenotype favored on a Greater Antillean island in the absence of other anole species. Perhaps by then placing different combinations of pairs of species, we could envision the adaptive landscape at the two-species stage. This would be easier if the optimum phenotype at the one-species stage corresponded with the phenotype of an extant species. By examining enough combinations of species numbers and phenotypes, we might be able to get a sense of what the adaptive landscape looks like, and how it changes through the course of a radiation.

Of course, even if such an approach were possible, difficulties would abound. First, we would have to assume that somewhere among the anole phenotypes existing today are species similar to the ancestral anoles that existed in the early stages of radiation. If not, we might fail to estimate a crucial part of the anole landscape.<sup>424</sup> Second, to conduct these experiments thoroughly, they ideally would be carried out over a number of years because selection can vacillate from one year to the next (Grant and Grant, 2002). Third, the experiments should probably be conducted in a wide variety of different localities because environmental conditions vary among and within islands. Finally, fourth, it is a leap of faith to assume that the environments today mirror those encountered by anoles during their evolution, even aside from the vast alterations caused by humans in recent years. Probably for these reasons, as well as the tremendous amount of work that would be required, no study of this sort has ever been conducted on any

424. Some studies have hybridized different forms to create phenotypes not extant today (e.g., Schluter, 1994; Lexer et al., 2003). Unfortunately, most anole species are unlikely to reproduce with other species with very dissimilar phenotypes either because they have been separated evolutionarily for many millions of years and thus are unlikely to be interfertile, or because they coexist with closely related dissimilar forms and have evolved pre-mating reproductive isolating mechanisms. Nonetheless, I am not aware of any study that has tried to hybridize different species either naturally or through *in vitro* means.



organism. Nonetheless, much could be learned—these reservations notwithstanding—and anoles might be a good group on which to attempt such a study.

*PREDICTING THE ADAPTIVE LANDSCAPE FROM KNOWLEDGE OF  
THE ENVIRONMENT AND THE FORM-FUNCTION RELATIONSHIP*

A complementary approach to inferring the adaptive landscape based on measurements of selection would be to derive it from first principles concerning the ways anoles interact with the environment. That is, start with the resources available in the environment and then, based on an understanding of how morphology relates to functional performance and in turn to resource use, predict the phenotypes that would be favored in that environment. In other words, invert the approach that has been taken to date; rather than starting with the species and its morphology and asking why those particular traits are adaptive in the environment in which they occur (Chapter 13), we need to focus on the environment and ask whether we can predict which traits would be favored in that environment.

This approach is exemplified by work on the evolution of beak size in Darwin's finches, which proceeded in several steps (Schluter and Grant, 1984; summarized in Schluter [2000]).<sup>425</sup> The authors proceeded as follows:

1. They quantified the availability of seeds of different sizes on a number of islands.
2. They determined the maximum seed size that could be cracked by a finch with a given beak size.
3. They determined the minimum seed size taken by finches with a given beak size (presumably, the minimum size was related to the efficiency with which small seeds could be manipulated and ingested, but this was not directly examined).
4. For each beak size, they calculated the total density of seeds on an island between the minimum and maximum values.
5. For each beak size, they converted seed density to predicted finch density by means of an empirically derived equation describing the relationship between seed density, finch body mass (which is related to beak size), and population density.
6. For each island, they plotted the relationship between beak size and predicted finch density, with the assumption that the beak sizes with the highest densities represented adaptive peaks.

Based on this analysis, Schluter and Grant (1984) found that most islands had multiple adaptive peaks (Fig. 16.2). Moreover, a reasonably close match was observed between

425. Case (1979) took a somewhat similar approach, minus the functional component, to understand body size evolution in *Cnemidophorus* lizards (see Chapter 17).

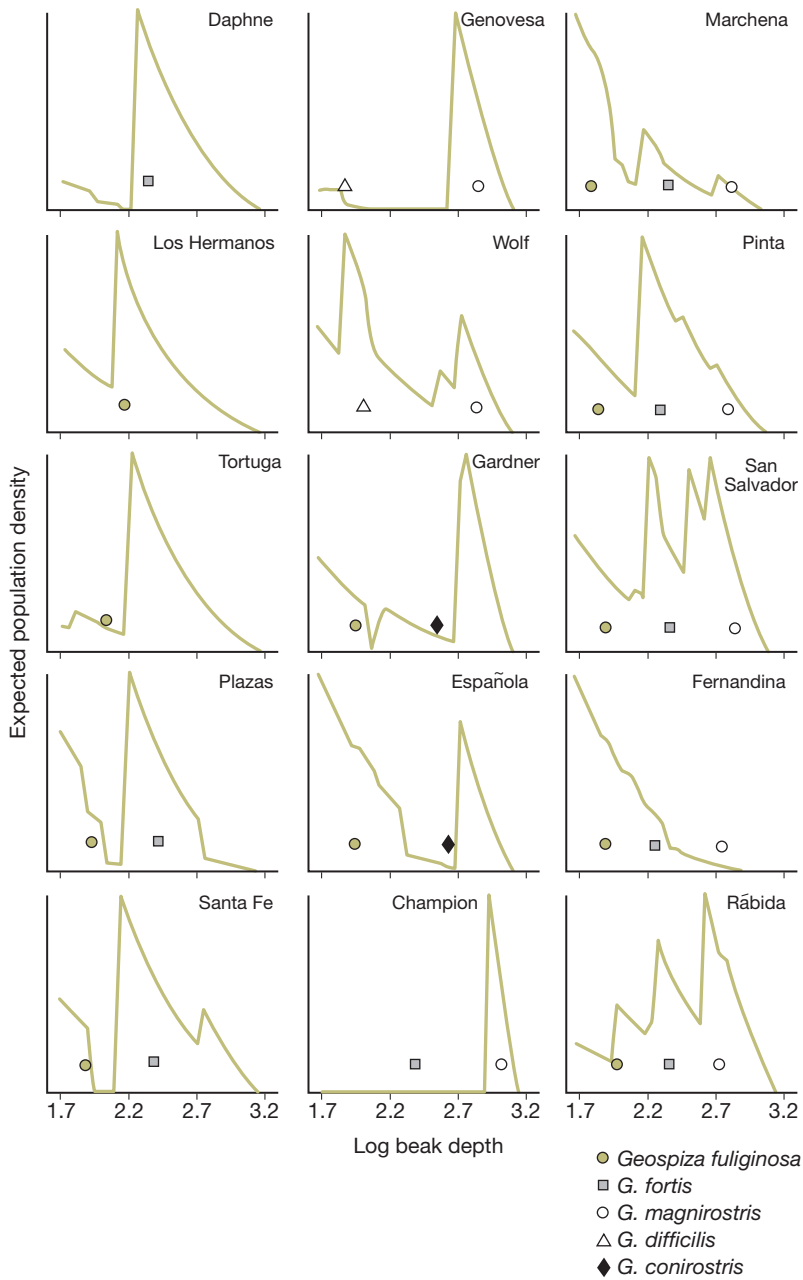


FIGURE 16.2

The adaptive landscape for beak depth in ground finches on the Galápagos. Based on the distribution of seeds on an island and the empirical relationship between beak size and population density, the population size of finches could be predicted as a function of beak depth. Most islands have multiple adaptive peaks, and the morphology of finch species lies close to these peaks on most islands. Modified with permission from Schluter and Grant (1984).

predicted and observed beak size on most islands, and these results were robust to incorporation of information on the beak sizes of sympatric species on an island.

Variation in limb length in anoles is the best candidate as an analog to beak size in finches. Would this approach work for anoles? The relationship for anoles between limb length and surface diameter is not as straightforward as the beak size–seed size function in finches. Two observations seem particularly relevant. First, the extent to which sprint speed is affected by surface diameter is a function of limb length: long-legged species are greatly affected, whereas short-legged species hardly notice differences in surface diameter; second, the more sensitive a species is to perch diameter, the narrower its breadth of habitat use and the more it avoids surfaces on which its sprint speed is greatly sub-maximal (Irschick and Losos, 1999; Chapter 13).

From these data, we can see how derivation of a performance-based adaptive landscape might begin. Clearly, long-legged species should be affected by the availability of broad surfaces. By contrast, short-legged species might be expected to occur everywhere. Three questions would have to be addressed to make progress:

1. What is the relationship between habitat availability and population size? As with the finch example, we can imagine measuring the availability of suitable vegetation (i.e., surface diameters at which a species could run at 50% or 80% [or some other arbitrary cut-off] of maximal speed). Then, we would need to establish the empirical relationship between vegetation availability and population size. Schluter and Grant (1984) simply summed all seeds within the acceptable range; we might want to develop a more precise equation that weighted different-sized supports by how much they affected sprint performance and how frequently they were used.<sup>426</sup> A more sophisticated approach might consider not just how sprint performance changes on different surfaces, but also how prey capture and predator risk vary as well. These would be a function not only of the lizard's performance, but also of the abundance of prey and predators on different surfaces.
2. How does the presence of other species affect habitat use and, as a result, population size? We know that anole species shift their habitat use in the presence of other species (Chapter 11). Presumably this results either from interspecific aggression or resource depletion, or both (or intra-guild predation when the species differ in size; see Chapter 11). These habitat shifts would have to be incorporated into the adaptive landscape model to predict how adaptive peaks would shift in the presence of other species.

426. A comparable approach was tried in the Darwin's finch study, but did not qualitatively change the results (D. Schluter, pers. comm.).

3. How should the distribution of surfaces at different heights be included? Limb length and sprinting capability are not obviously related to perch height in any mechanistic way, yet long-legged species generally occur relatively low to the ground. Most likely, perch height is related to toepad structure (Chapter 13). Two possible approaches would be either to limit measures of habitat availability to the height ranges occupied by different species, or to extend the analysis to a multivariate adaptive landscape and consider toepad structure along with hindlimb length. This would require further examination of the functional and ecological consequences of variation in toepad structure, which is not as well understood as the consequences of limb length variation (Chapter 13).

Obviously, this proposed work is very conjectural, with many loose ends and much more data needed. Certainly, we would want to include other characteristics beside limb length, not only toepad structure, but tail length, head dimensions and other traits, whether in one big multivariate analysis, or in separate univariate landscapes. Needless to say, this would require considerable effort. Whether we could actually build an anole adaptive landscape from first principles, and thus test the extent to which the environment drives convergence across the Greater Antilles, but not elsewhere, is unclear, but I think it would be worth a try.

In theory, both of these approaches—the development of selective and functional landscapes—are practical, but they may not occur any time soon. In the meantime, we have no actual data supporting the proposition that convergence of the ecomorph radiations is the result of similarity in underlying adaptive landscapes. In the absence of such data, I now turn to consider the evidence, also quite meager, that other factors might have shaped the anole radiations.

#### MORPHOLOGY-PERFORMANCE RELATIONSHIPS

Selection does not act directly on phenotypes, but rather on the functional capabilities produced by phenotypes (Arnold, 1983; Garland and Losos, 1994). For example, selection presumably didn't favor long legs in cheetahs because they are aesthetically pleasing, but because they allow the cats to run very fast. As discussed in Chapter 13, no straightforward relationship may exist between morphology and functional capabilities. Rather, radically different phenotypes may confer the same functional capabilities (Simpson, 1953; Bock and Miller, 1959; Losos and Miles, 1994).

The upshot of many-to-one mapping of morphology onto performance capabilities is that the adaptive landscape is determined by two relationships: the mapping of selection onto performance, and of performance onto phenotype (Fig. 16.3). If a one-to-one relationship exists between phenotype and performance, then selection will favor only a single phenotype for each selective peak in the performance landscape. However, if the

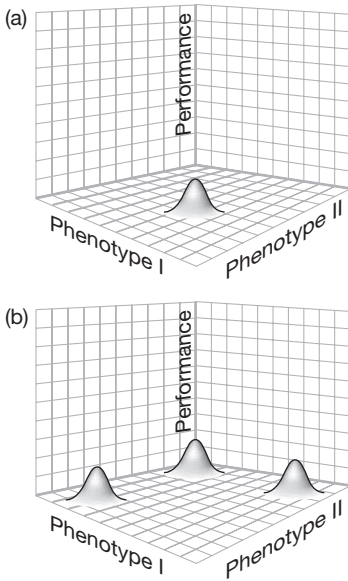


FIGURE 16.3  
Phenotype, performance, fitness and the adaptive landscape. If the relationships between phenotype and performance and between performance and fitness are unimodal, then only a single peak may exist in the adaptive landscape for a population. Conversely, if multiple combinations of phenotypic characters can produce the same performance, then the adaptive landscape will necessarily contain multiple peaks, even if the performance-fitness relationship is unimodal.

relationship between phenotype and performance is many-to-one, then multiple phenotypic optima may exist for each selective peak in the performance landscape. The result is that two clades radiating independently in similar landscapes might nonetheless produce different phenotypes (Alfaro et al., 2005; Stayton, 2006; Collar and Wainwright, 2006; Wainwright, 2007; Young et al., 2007).

Could the many-to-one phenomenon explain differences between the anole faunas? For example, might mainland and Greater Antillean unique anoles be functionally convergent with the ecomorphs, even though they are phenotypically disparate? For the most part, the possibility of many-to-one functional relationships has been little studied, although some preliminary studies hint that they might exist (Chapter 13). However, if that were the case, we would expect to see species that parallel the ecomorphs in ecology and behavior, but not in morphology. This explanation might pertain to some species, but wouldn't apply to the divergent habitat use of many Greater Antillean unique anoles, nor to the behavioral differences between mainland and West Indian anoles (discussed below).

#### EVOLUTIONARY CONSTRAINTS

In the preceding discussion, evolution is dictated solely by external conditions: the environmental setting determines the adaptive landscape, and species necessarily evolve to occupy the highest peaks. This scenario assumes that a species can evolve with equal ease in any direction. However, for a variety of reasons (e.g., the genetic covariances among traits, the way in which development proceeds), evolutionary change may be constrained such that a species may more easily evolve in some directions than in

others, and some phenotypes may not be attainable at all (Arthur and Farrow, 1999; Gould, 2002; Schwenk and Wagner, 2003, 2004; Brakefield, 2006).

The existence of such constraints might make convergence either more or less likely. On one hand, two clades radiating in similar environments might evolve in different ways if their genetic and developmental systems were different such that evolution was constrained to progress in different directions (Fig. 16.4a). Alternatively, if the clades share the same genetic and developmental systems, they might be biased to evolve in similar ways, even in environments that are not identical (Fig. 16.4b).<sup>427</sup>

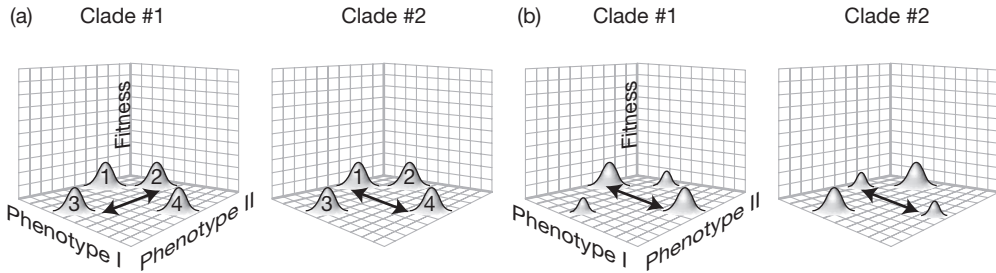


FIGURE 16.4

The effect of constraints on the direction of evolution in an adaptive landscape. In (a) two clades exhibit evolutionary constraints that bias them to evolve in different directions: the arrows indicate the direction in which each clade evolves most readily. Such biases could arise because of genetic linkages (termed covariances) among traits or because the way in which development proceeds, making evolutionary change in the developmental system easier in some ways than in others (these two explanations may represent the same phenomenon, because developmental systems are under genetic control). The result of such biases is that the two clades may radiate in different ways from the same initial starting point in the same adaptive landscape: in the panel on the left, species with phenotypes #2 and #3 would be more likely to evolve, whereas in the panel on the right, phenotypes #1 and #4 likely would evolve. Conversely, in (b), clades with the same biases may radiate the same way, even though occurring in different adaptive landscapes.

427. Perhaps Gould had the anole ecomorphs in mind when he wrote in his usual inimitable style (2002, p. 1174):

... the markedly inhomogeneous occupation of morphospace—surely one of the cardinal, most theoretically, and most viscerally fascinating aspects of life’s history on earth—must be explained largely by the limits and channels of historical constraint, and not by the traditional mapping of organisms upon the clumped and nonrandom distribution of adaptive peaks in our current ecological landscapes. In other words, the inhomogeneous occupation of morphospace largely records the influence of structural rules and regularities emerging “from the inside” of inherited genetic and developmental systems of organisms, and does not only (or even primarily) reflect the action of functional principles realized by the mechanisms of natural selection imposed “from the outside.”

Actually, Gould (2002) probably wasn’t thinking about the anole adaptive landscape because he focused on evolutionary change occurring deeper in phylogenetic history. In fact, although Gould certainly knew *Anolis* from his field work in the Bahamas, to him they were “just a fleeting shadow running across a snail-studded ground” (1997, p. 16). There is no evidence that the anole ecomorph story entered into his thinking at all, even though he occupied an office in the Museum of Comparative Zoology only 24 m from Ernest Williams’ for many years (actually, the distance was only 15 m as the anole hops, but a locked door [under which an anole could pass] required a circuitous sidestep into another hall. Perhaps it was this extra 9-m detour that prevented Gould from fully appreciating the many-splendored lessons of *Anolis*).

Two commonly discussed forms of constraints involve genetic correlations among traits, promoting evolution along the “genetic lines of least resistance” (Schluter, 1996, 2000; Blows and Hoffman, 2005), and developmental pathways, which also would bias the variation available within a population (Maynard Smith et al., 1985; Gould, 2002). If genetic and developmental systems are stable through time, then such constraints could have long lasting effects on evolutionary diversification; this, however, is a big if (Shaw et al., 1995; Schluter, 2000). Currently, few data are available to evaluate the role of constraints in shaping anole evolution. No studies have examined the genetic variance-covariance structure of any *Anolis* species,<sup>428</sup> and little information on anole development is available; in fact, the first embryological staging series for an anole species has just been published (Sanger et al., 2008b).

Although few direct data are available, the hypothesis that evolutionary constraints have played a large role in directing anole evolution seems unlikely. The traits that characterize the different ecomorph types—such as limb lengths, toepad dimensions and body size—are all continuous, quantitative characters. In general, substantial additive genetic variation is usually present for such morphological characters (Mousseau and Roff, 1987; Falconer and Mackay, 1996). Even though genes of large effect that account for substantial amounts of variation among species and populations are increasingly being discovered for all sorts of quantitative characters of this sort (Abzhanov et al., 2004, 2006; Shapiro et al., 2004; Colosimo et al., 2005), including limb length (Storm et al., 1994), these traits generally conform to the properties of heritability and response to selection as predicted by quantitative genetics theory (reviewed in Roff, 2007). For this reason, these traits should readily respond to selective pressures; lack of suitable genetic variation for other phenotypes is unlikely to explain the repeated evolution of ecomorphs.

In theory, genetic correlations among traits may favor the evolution of some multivariate phenotypes and preclude the evolution of others. However, such correlations would have to have persisted for tens of millions of years to have been the primary cause for the repeated evolution of ecomorphs across the Greater Antilles (Revell et al., 2007a). Although no relevant data are presently available to test genetic constraint hypotheses for *Anolis*, the ability to investigate such questions will be facilitated both by the availability of the *A. carolinensis* genome and by ongoing anole breeding projects, and I expect that before too long we will have a better understanding of the genetic architecture underlying ecomorphologically important traits.

Another reason that evolutionary constraint is unlikely to be responsible for the repeated evolution of the ecomorphs on the Greater Antilles is purely empirical: ample evidence exists that, in fact, evolution has produced a plethora of species that do not correspond to any ecomorph. Examples include many Lesser Antillean species, the unique species of the Greater Antilles and, most of the mainland fauna. These species

428. However, phenotypic variance-covariance matrices have been compared among populations of *A. cristatellus* (Revell et al., 2007a).

are interspersed throughout the anole phylogeny, which indicates that the ability to evolve out of the ecomorph mold is not a special condition of a particular clade. This empirical record would seem to contradict the hypothesis that developmental or genetic biases are responsible for the repeated evolution of the ecomorphs. Nonetheless, more data on anole developmental and genetic systems would be extremely useful to examine these ideas directly.

#### HISTORICAL CONTINGENCIES

Gould (1989, 2002) was the strongest proponent of the view that the outcome of evolution is historically contingent, which he defined as “an unpredictable sequence of antecedent states, where any major change in any step of the sequence would have altered the final result. This final result is therefore dependent, or contingent, upon everything that came before—the unerasable and determining signature of history” (Gould, 1989, p. 283).<sup>429</sup>

This perspective considers the predictability of evolution: can we foresee the course of evolution from an initial starting point? Gould’s answer is “no”: unpredictable events will happen along the way, and without foreknowledge of what those events will be, the evolutionary outcome is indeterminate. This view accords with Gould’s (1989) famous analogy of “re-winding the evolutionary tape”: if one could turn back the clock and start over again, from the same ancestral form living in the same place, evolution would be unlikely to take the same course.

In the context of the adaptive landscape and anole evolution, we may look at the question slightly differently and ask: does the history of a clade affect how it diversifies? Or, conversely: is the landscape deterministic such that any clade evolving on the same adaptive landscape will converge upon the same evolutionary outcome, regardless of its history?

Just what aspects of history are we talking about? Two types seem to be the most likely to affect the eventual evolutionary outcome:

1. The starting point of a radiation (Gould’s “happenstance of a realized beginning” [2002, p.1160]): the biology of the ancestral species—its phenotype, natural history, even the amount and type of genetic variation—can affect subsequent evolutionary change (Travisano et al., 1995; Price et al., 2000). Ancestral forms will have their own evolutionary predispositions, resulting from genetic constitution, developmental systems, behavior patterns and a variety of other, interrelated factors that will make evolutionary change more likely in some directions than in others, particularly if these constraints are maintained through the course of a clade’s history (Arnold, 1994; Donoghue, 2005). To exaggerate, had the ancestral anole

429. For a review of Gould’s ideas on contingency and the concept itself, see Beatty (2006, 2008).



been limbless or possessed wings, the course of subsequent evolutionary diversification would have been very different.

2. Chance events: the occurrence and order in which mutations occur might play an important role in directing evolutionary change (Mani and Clarke, 1990; Wichman et al., 1999; Ortlund et al., 2007; but see Weinreich et al. [2006]). Similarly, random events—lightning or a falling tree killing a particular individual, an ill-timed volcanic eruption, or any other matter of happenstance—could push evolutionary change in one direction or another.

Recognition of the importance of historical contingencies does not mean that natural selection and adaptation do not occur. Rather, this perspective emphasizes that even in the presence of natural selection, evolutionary outcomes are not necessarily predictable. An important consideration in this light is the shape of the adaptive landscape. Consider a population evolving in a landscape with a single adaptive peak. Regardless of any of the possible contingencies just discussed, natural selection will tend to drive that population up that peak, or as close to the peak as possible given the variation that can be produced by genetic and developmental systems of the population (Fig. 16.5a).

By contrast, consider a more rugged adaptive landscape in which there are several high peaks, and in which no way exists to move from one peak to another without traversing an adaptive valley (Fig. 16.5b). On this landscape, historical contingencies may matter a great deal. Even if the peaks are the same height—i.e., they are equally favored by selection, none superior to the others—the actual peak that a population ascends may be affected by where the population begins—selection generally favoring movement up the nearest peak—and the pattern of constraint affecting the directions in which the population can most easily move on the landscape. Furthermore, for the same reasons, a population may end up on a suboptimal peak; once on such a peak, selection may have trouble moving the population to a higher peak because it would require first evolving in the direction of lower fitness into an adaptive valley, something selection by itself generally will not do (Fig. 16.5c).<sup>430</sup>

Historical contingency can thus prevent convergence: species evolving on the same adaptive landscape may evolve in different directions. However, contingency is a two-edged sword: species experiencing the same contingent events (e.g., the same ancestral phenotype) might converge, even on adaptive landscapes that are quite different (Fig. 16.6).

The possibility of contingency applies not only to species, but to entire communities. Community ecologists have long known that alternative stable equilibria may exist for the structure of a community (e.g., Scheffer et al., 2001; Chase, 2003a,b; Persson et al., 2007). In other words, given a set of resources in a particular environmental setting,

430. The topic of evolutionary transitions from one peak to another is actually much more complicated than this (Lande, 1986; Arnold et al., 2001), but I present this simple version for heuristic purposes.

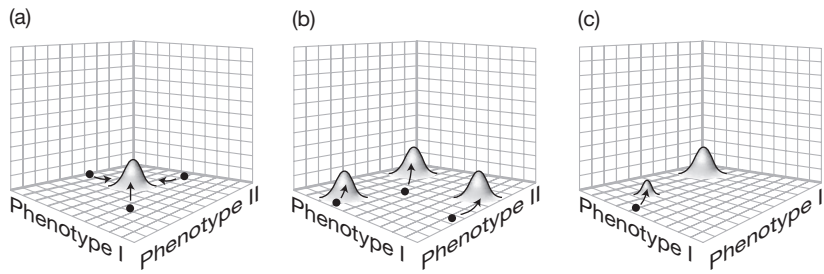


FIGURE 16.5

Historical contingency and the adaptive landscape. In (a) a species is likely to end up on or near the same peak regardless of constraints and where it starts. By contrast, in (b) initial starting conditions, as well as constraints (Fig. 16.4), may determine which peak is occupied because species are most likely to ascend the nearest peak unless constraints push them toward a different peak. This phenomenon can lead to species ending up on a suboptimal peak (c).

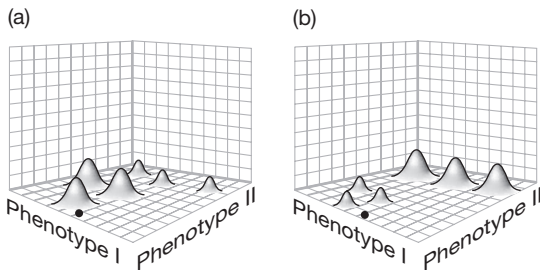


FIGURE 16.6

Initial starting conditions can cause species diversification to converge even in very different adaptive landscapes. In both panels, phenotypes in the lower left quadrant are most likely to evolve due to the clade's initial starting condition, even though the adaptive landscapes are quite different.

multiple ways may exist for a set of species to divide these resources, and each of these community configurations may be stable and resistant to replacement by other possible communities. These multiple ways of existence would correspond to alternative adaptive peaks mentioned at the outset of this chapter. Why one community structure may occur rather than another may be a result of the same historical vagaries—starting conditions, availability of particular mutations, random chance—that affect individual species (Fukami et al., 2007).

How important was historical contingency in anole evolution? For example, would the evolutionary trajectory of an anole radiation have differed depending on whether the ancestor was a twig anole, a crown giant, a grass-bush anole, or something else? This question is difficult to address for two reasons. First, as discussed in the previous chapter, inferring the ancestral phenotype of each of the anole radiations is problematic. For

this reason, determining whether the radiations were initiated from similar phenotypic starting points is not possible. Second, we have little idea of how rugged the adaptive landscape is—that is, how many adaptive peaks there are and how likely a population is to become stuck on a sub-optimal peak. The more rugged the landscape, the more important a species' starting point will be and the more likely that radiations initiated by phenotypically different ancestors would explore different portions of morphological space. For the same reasons, chance events are more likely to have lasting consequences when the landscape is rugged.

We can address this second point to a limited extent. If the adaptive landscape is rugged, then transitions between ecomorph types that are most closely situated in the adaptive landscape might be more likely. The inability to infer ancestral states complicates such an analysis; however, we can ask whether certain pairs of ecomorphs tend to be closely related, which would suggest that transitions from one type to the other occur more readily than other possible transitions. Although no formal analysis has been conducted, examination of the phylogeny of Greater Antillean anoles indicates no obvious patterns of this sort (Chapter 7). However, one intriguing bit of evidence supports the possibility that transitions may occur more readily between adjacent peaks: in all three cases in which one ecomorph type arose from within another ecomorph type (grass-bush/trunk-ground in Cuba and Puerto Rico and trunk-crown/crown-giant in Jamaica [Chapter 7]), the two ecomorphs are ecologically and, to some extent, morphologically proximate.

#### **EVOLUTIONARY DIVERSIFICATION AND THE ANOLIS ADAPTIVE LANDSCAPE**

The preceding discussion makes clear that definitive conclusions about causes of the differences among the anole faunas will be hard to come by. Nonetheless, in the remainder of the chapter, I will discuss what we can and cannot say about the differences among the faunas. I take as my starting point the premise that similarity in adaptive landscapes across the Greater Antilles has driven convergence of the ecomorphs. I begin by examining patterns of occurrence of the different ecomorph types and evolution on species-poor islands in the West Indies to see if any general conclusions can be made about the anole adaptive landscape in the West Indies. I then explore non-convergence in the Lesser Antilles, among the Greater Antillean unique anoles, and on the mainland and discuss why evolution may have gone in different directions in these areas.

#### **PATTERNS OF ECOMORPH OCCURRENCE: THE CASE OF THE MISSING ECOMORPHS**

Not all ecomorphs are present at all locations in the Greater Antilles for two reasons: failure of some ecomorph types to evolve on some islands and failure of ecomorphs present on an island to occur in some localities. Consideration of both of these phenomena suggests that we can make some conclusions about the shape of the anole adaptive landscape.

The ecomorph radiations are not perfectly convergent; rather, trunk anoles are absent from Puerto Rico and trunk and grass-bush anoles from Jamaica. At first glance, the requisite structural habitat for trunk anoles, large tree trunks, appears to occur in abundance on these islands. Hispaniolan trunk anoles are voracious consumers of ants (Chapter 8; the diet of the Cuban trunk anole, *A. loysianus*, is unknown [Rodríguez Schettino, 1999]), and ants also seem common on these islands. Similarly, the prerequisites for grass-bush anoles would seem to be present in Jamaica.<sup>431</sup> Thus, the absence of these ecomorphs is not obviously attributable to environmental deficiencies on these islands.

The concept of “empty niches” has fallen into disfavor in recent years. Lewontin (1978, 1985) summarized the argument against them: one can imagine almost any combination of traits that could exist, such as flying mollusks, so speaking of their absence is pointless; niches don’t exist independent of the organisms that occupy them. On the other hand, Lewontin (2000) also makes clear that his critique is directed toward designation of a niche in the absence of any species that has ever filled it. Convergent evolution has long been considered evidence for a predictable environment-organism interaction which suggests that the environment repeatedly elicits similar evolutionary outcomes (see discussion in Schoener, 1989; Harmon et al., 2005). Thus, it does not seem too much of a stretch to consider the niche for a trunk or grass-bush anole existing prior to its evolution.

Why, then, are some ecomorphs absent on Puerto Rico and Jamaica? One possibility is that their niches don’t actually occur there. As just argued, this seems implausible—grass and tree-trunks abound on both islands<sup>432</sup>—but a more detailed analysis would be useful. In the case of trunk anoles, an alternative ecological possibility is that the trunk ecomorph niche has been usurped by the small trunk-crown anoles, *A. stratulus* (Puerto Rico) and *A. opalinus* (Jamaica), which, though good trunk-crown anoles in terms of morphology and ecology (Chapter 3), do nonetheless often occur on tree trunks. Perhaps this is an example of alternative phenotypes capable of utilizing the same set of resources? By contrast, for some unknown reason, the small trunk-crown anoles of Cuba and Hispaniola are generally restricted to montane localities, thus leaving the “trunk anole niche” open for trunk anoles over most of these islands. This explanation, however, would not account for the missing grass-bush anole of Jamaica; even though Jamaican anoles are less differentiated morphologically than the ecomorphs on other islands, none of the Jamaican species seems to greatly utilize typical grass-bush habitats.

Explanations based on non-adaptive factors should also be explored, though none are particularly compelling a priori. Perhaps genetic or developmental constraints exist in

431. Indeed, as anyone who has walked around tourist areas and been accosted by local peddlers can attest, grass is readily available just about anywhere in Jamaica.

432. Keeping in mind, of course, that the vegetation of these islands has been greatly altered by humans over the last several hundred years. Most of Jamaica was probably forested prior to human arrival (Eyre, 1996). Although open, grassy habitats previously may have been less common in Jamaica than they are today, many grass-bush species (e.g., most Cuban species, Puerto Rican *A. krugi*) occur in forested habitats.

the *grahami* Series (Jamaica) and *crisatellus* Series (Puerto Rico) preventing the production of appropriate phenotypes? These clades have diversified over otherwise much the same ecomorphological space as anoles on the other Greater Antillean islands, so neither this possibility, nor the ancestral starting condition for the radiations, seems likely to have had an impact. Finally, the Jamaican radiation is substantially younger than the other three Greater Antillean radiations, which raises the possibility that not enough time has been available to evolve more than four ecomorph types, although 24 million years<sup>433</sup> would seem long enough (Chapter 6).<sup>434</sup>

In sum, the evolutionary absence of these ecomorphs is a mystery for which we have no good explanation at the present time. However, these are not the only cases of missing Greater Antillean ecomorphs; even when an ecomorph is present on an island, it is often not found everywhere (Chapter 11). Trunk-ground and trunk-crown anoles are generally present in most localities in the Greater Antilles, but other ecomorph types can be more patchy in distribution.

As with the absence of ecomorphs from an entire island, the explanation for these local lacunae relies either on ecology or contingency. Ecologically, the explanations are effectively the same: appropriate habitat is unavailable either because it doesn't exist or is usurped by other taxa. However, the contingency explanation is a little different. Many of the absences seem to relate to thermal and hydric physiology. For some reason, on some islands ecomorph clades exhibit greater physiological versatility—either within or between species—than on other islands. For example, twig anoles occur commonly in the lowlands on Jamaica and Cuba, but not in Hispaniola or Puerto Rico. Assuming that ecological physiology accounts for these distributional patterns, research could be directed toward investigating why some clades are able to evolve greater versatility than others.

In contrast to the Greater Antilles themselves, ecomorph absences on landbridge islands near the Greater Antilles are more readily explainable. Prior to the rise in sea levels, land-bridge islands presumably harbored the full complement of ecomorphs present on the larger landmass to which they were connected (either a Greater Antillean

433. Even the 7 or 13 mya dates for initial within-island divergence suggested by earlier studies seem adequate (Hedges and Burnell, 1990; Jackman et al., 2002).

434. In addition to missing ecomorphs, the island radiations differ in other ways as well. For example, the Jamaican ecomorphs seem less differentiated than those on other islands (Beuttell and Losos, 1999). A quantitative analysis confirmed the imperfection of ecomorph convergence: although most morphological variation among Greater Antillean ecomorph species is explained by ecomorph type, some variation is accounted for by island effects (Langerhans et al., 2006). For example, Cuban ecomorph species tend to have the shallowest heads and Hispaniolan anoles the deepest heads. Differences in the environment across the islands could account for these effects. However, historical/phylogenetic effects—such as constraints or differences in ancestral phenotypes that have persisted to the present—could also be responsible because anoles on each island generally are more closely related to each other than to species on other islands; statistical analysis was unable to separate island and phylogenetic effects.

One particularly interesting phylogenetic effect was evident in the analysis: Cuban trunk-crown anoles have shorter limbs than other trunk-crown anoles, and are also the only trunk-crown anoles that have twig anoles, the shortest-legged of the ecomorphs, as their sister taxa (Langerhans et al., 2006). Possibly, the short-leggedness of the Cuban trunk-crown anoles is related to their being a member of a particularly short-legged clade, thus making them susceptible to whatever short-legged evolutionary biases that clade may possess.

island or the Great Bahama Bank). Consequently, their diminished fauna today is primarily the result of extinction and is related to island area: the smaller the island, the fewer the species. These extinctions have not been random. Rather, trunk-ground species are almost universally present, and if a second species occurs, it is almost always a trunk-crown species. The identity of the third and fourth ecomorph is consistent within a region, but varies across regions (Chapter 4).

The consistency of these patterns strongly argues that the environment determines patterns of ecomorph occurrence and that it does so in substantially the same way throughout the Greater Antilles. These islands might be a good place to develop or test models about the adaptive landscape. One particular question of interest would be whether the environment is unsuitable for ecomorphs that are absent, or whether those ecomorphs are excluded by the presence of other ecomorphs better adapted to environmental conditions. Why, for example, is the twig anole *A. angusticeps* often absent from small islands in the Great Bahamas Bank when appropriate habitat—an abundance of narrow vegetation—occurs on most of these islands? One possibility is that many islands lack some other attribute necessary for these twig anoles, such as the appropriate prey species, but another is that for some reason, other ecomorphs can exclude *A. angusticeps* from these islands, but not from larger ones.

#### EVOLUTIONARY DIVERSIFICATION ON SPECIES-POOR ISLANDS

If the adaptive landscape changes with the addition of new species, we would not expect the four ecomorphs found on Jamaica to also occur on more ecomorph-rich islands (ditto for Puerto Rico's five ecomorphs on Hispaniola and Cuba). The fact that they do suggests that the adaptive landscape is relatively static and that the positions of the adaptive peaks are relatively independent of each other.

We can test this hypothesis by examining patterns of evolutionary diversification on islands with relatively few ecomorphs. Assuming that these islands are environmentally similar to the Greater Antilles (a big assumption), if the adaptive landscape is static, we would expect to find typical ecomorph species.

To examine this idea, I focus only on oceanic islands because landbridge islands probably had a larger fauna in the recent past. Small islands in the Greater Antilles have been colonized primarily by trunk-ground and trunk-crown anoles (although the ancestral form of *A. acutus* on St. Croix is indeterminate [Chapter 4]). For the most part, these species are still recognizable as members of their ancestral ecomorph type; those species that have diverged generally occur in morphological space in positions intermediate between trunk-ground and trunk-crown anoles (Losos et al., 1994; Losos and de Queiroz, 1997; Chapter 15).

Evolutionary diversification in the Lesser Antilles has produced somewhat greater ecomorphological diversity than that seen on 1- or 2-species islands in the Greater Antilles. Although many species appear to be trunk-crown anoles, a few are as large as

crown-giants, and the rest lie in intermediate positions in morphological space, again generally between trunk-crown and trunk-ground anoles (Chapter 4).

The faunas of these small islands could be interpreted in two ways with regard to the idea that the adaptive landscape changes as a function of the number of species present. The occurrence of ecomorph species on these islands might suggest that the same adaptive landscapes exist there as on larger islands, and thus that landscapes do not change depending on the number of species present. Exceptions would be explained as islands that are environmentally different. Alternatively, the glass-half-empty viewpoint would emphasize those species that do not fit neatly into any of the ecomorph categories. Ultimately, direct measurement of the adaptive landscape is needed to assess the extent to which environmental differences among islands drive these patterns.

Nonetheless, two observations are clear. First, when communities—anywhere in the West Indies, including the Greater Antilles—contain 1–2 ecomorphs, those ecomorphs are almost always trunk-ground and/or trunk-crown anoles. Moreover, on species-poor islands, species that do not belong to any ecomorph category are often most phenotypically similar to these two ecomorphs. Second, islands with 1–2 species almost never contain species resembling trunk, grass-bush, or twig species,<sup>435</sup> and nothing like these types has evolved on those small islands on which substantial evolutionary divergence has occurred. Notably, two of these types—grass-bush and trunk—are the ones that are missing from some Greater Antillean islands.

I draw three conclusions from these observations: first, adaptive landscapes throughout the West Indies are similar in that the highest peaks generally correspond to trunk-ground and trunk-crown anoles, or something like them. Second, the twig, grass-bush, and trunk ecomorph peaks seem to be lower, and thus are filled later in the course of faunal development. A corollary of this statement is that the absence of these forms from many islands results not because their niches do not occur on the islands, but simply because not enough species are found there, due to impediments on colonization and speciation. Third, it follows that genetic and developmental constraints and historical contingencies are of secondary importance in shaping patterns of ecomorphological evolution in West Indian anoles.

These are bold statements, perhaps easier to make because they will not be easy to test. Nonetheless, I believe that some of the ideas outlined in this chapter provide the means, at least in theory, to go about testing them. Obviously, the two-species islands of the Lesser Antilles are the biggest challenge, given that many of the species on these islands cannot be assigned to an ecomorph category (see Chapters 4 and 15).

435. Note that in contrast to the situation with landbridge islands—in which the absence of some ecomorph types may be the result of lack of appropriate habitat on small islands—oceanic islands (e.g., the Cayman Islands, St. Croix, the Lesser Antilles) are generally fairly large and contain well developed habitats that seem comparable to habitats which maintain the full complement of ecomorphs on the Greater Antilles.

## NON-CONVERGENCE IN THE LESSER ANTILLES

The two-species islands in the Lesser Antilles are notable in a second respect. Although species from solitary Lesser Antillean islands are quite similar regardless of location, the species composition of two-species islands differs greatly between the north and the south in three ways:

- Although sympatric species almost always differ substantially in body size by approximately the same amount (differences slightly greater in the north), the species are larger in the south (Schoener, 1970b; Roughgarden, 1995).
- Sympatric species in the north differ in perch height, with the larger species found high in the tree and the smaller species near the ground; species on the same island in the south both occur at approximately the same, intermediate height (Roughgarden et al., 1983; Buckley and Roughgarden, 2005b).
- Species on the same island in the south differ in body temperature and segregate by habitat type, whereas species in the north attain similar body temperatures and do not partition habitat types (Roughgarden et al., 1981, 1983; Buckley and Roughgarden, 2005b).

Environmental variables could explain some of these differences. The southern islands are warmer, being closer to the equator, and they also have greater insect abundance (Buckley and Roughgarden, 2005a); both of these factors might promote higher growth rates and hence larger size (e.g., Roughgarden and Fuentes, 1977). In addition, the greater amount of high elevation—hence cooler—habitat in the more mountainous southern islands might promote the evolution of habitat segregation, whereas the more limited range of habitats available in the northern islands might have led to within-habitat niche partitioning (Roughgarden et al., 2003; Buckley and Roughgarden, 2005b).

On the other hand, in this case historical contingencies may play a role as well. The different evolutionary paths taken in the Lesser Antilles could indicate the existence of alternative adaptive peaks and alternative possible community structures. Perhaps either configuration of species is equally likely on these islands and the vagaries of history are responsible for the different outcomes. In this light, the different evolutionary endpoints might be the result of different initial starting conditions. The two areas were colonized by distantly related anole clades, the south by a member of the basal *Dactyloa* clade from South America, and the north by a member of the *cratatellus* Series (Fig. 5.6). These clades differ in a number of respects: *cratatellus* Series anoles are small-to-medium in size and usually heliothermic; by contrast, *Dactyloa* anoles often are quite large. Unfortunately, the ecology of few mainland *Dactyloa* clade anoles is well known, so generalizing about the ecology of this clade is difficult; however, many *Dactyloa* species occur in deep forest and probably are not heliothermic (e.g., Vitt et al., 2003a). Moreover, the phylogeny of *Dactyloa* is not well understood. Given these difficulties, inferring the ancestral condition for the two Lesser Antillean clades is impractical, but the possibility



remains that the clades were initiated from different starting points, and that these differences affected how they subsequently evolved and which adaptive peaks they ultimately occupied.

*Anolis watsi*, a small species from the northern Lesser Antilles that is usually found near the ground, has been introduced to St. Lucia in the southern half of the island chain (Fig. 16.7; Corke, 1987), and also to Trinidad, which was previously inoculated by humans with several southern Lesser Antillean anoles (White and Hailey, 2006). Follow-up studies on the outcome of these introductions might provide some insights about whether environment or contingency is responsible for the different evolutionary pathways taken by anoles in the two halves of the Lesser Antilles: successful invasion of *A. watsi* would support the contingency hypothesis by suggesting that the evolutionary absence of species that use low microhabitats in the southern Lesser Antilles is not the result of environmental inhospitality.

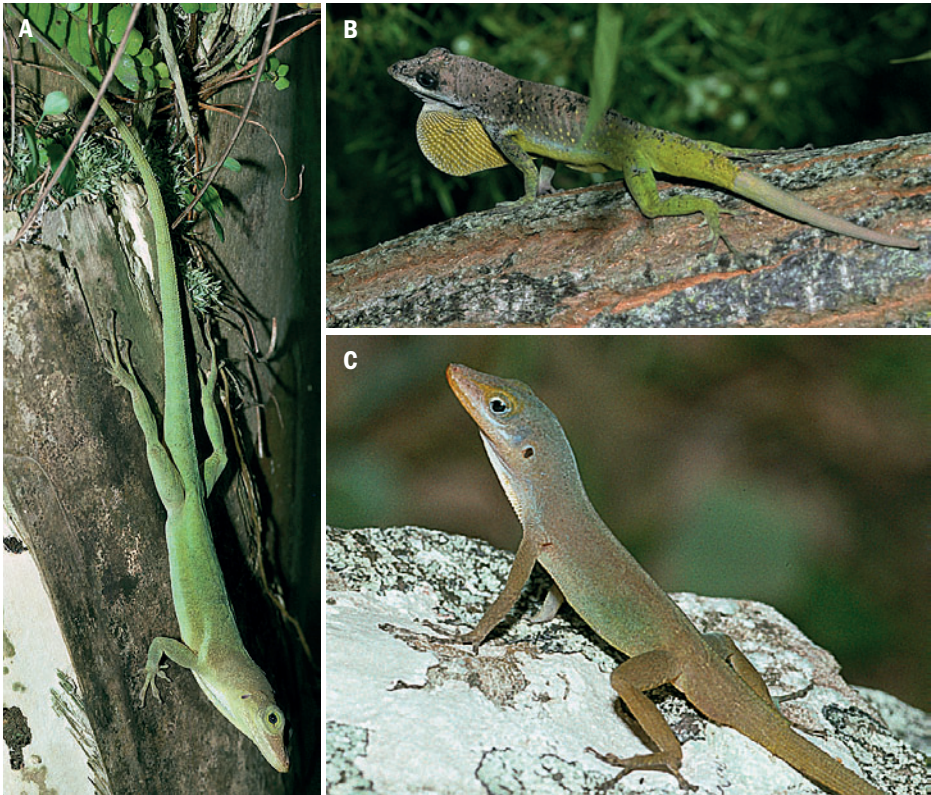


FIGURE 16.7

Hybrid Lesser Antillean community on St. Lucia. Thanks to human introductions, two southern Lesser Antillean species, the native *A. luciae* (a) and *A. extremus* introduced from Barbados (b), now coexist with the small northern Lesser Antillean species, *A. watsi* (c). How these species interact ecologically and evolutionarily may provide insights on why anole communities in the northern and southern Lesser Antilles are structured differently.

The unique anoles of the Greater Antilles are interesting in two respects: first, many of them are greatly divergent from the ecomorphs, in contrast to the pattern seen in the Lesser Antilles and the small islands of the Greater Antilles. This divergence occurs both in morphology—e.g., *Chamaeleolis*, *Chamaelinorops*, *A. vermiculatus*, *A. fowleri*, *A. eugenegrahami*, *A. bartschi*—and in microhabitats occupied—e.g., streams, leaf litter, rock walls, cave entrances (see descriptions in Appendix 4.1). Second, these forms are utterly non-convergent; none of these “unique” anoles has a morphological counterpart, nor an ecological one, on another island.<sup>436</sup>

The second anomaly about the unique anoles is that the Hispaniolan species and the single Jamaican species are found only in the mountains and generally have relatively small geographic ranges. By contrast, most of the Cuban unique species can be found at low elevations and some have quite broad geographic distributions.

What’s going on with these species? Explanations based on environmental differences between islands have already been discussed in Chapter 4 and been found wanting—for the most part, the microhabitats occupied by these species occur across all of the Greater Antilles. But what other explanations are there? One salient observation is that these species are found almost exclusively on the two islands that have both the most species and the greatest number of ecomorphs, Cuba and Hispaniola. Perhaps these anoles have evolved to occupy minor adaptive peaks, ones that only are filled once the ecomorph peaks are already occupied?

If this were the case, we might expect unique anoles to have evolved relatively recently and from an ecomorph ancestor. However, this is not the case. Most unique anoles are on branches that go back deep into the phylogeny, and none has evolved from within a clade composed of another ecomorph type (Fig. 7.1). Of course, the ecomorphs themselves mostly evolved early in anole phylogeny, and the inability to infer ancestral states prevents a clear examination of the history of the unique anoles. Still, the phylogeny provides no support for the idea that unique anoles are late stages added after ecomorph radiation has been completed. Moreover, this hypothesis would not account for the non-convergence of these unique ecomorphological types across islands.

The deep ancestry of the unique anoles also precludes comparisons to sister taxa to see if particular species are similar to their close relatives. For the most part, the sister taxa of unique anoles are large and diverse clades.<sup>437</sup> One exception is *Chamaeleolis*, which is in the same clade as the Hispaniolan and Puerto Rican crown-giants. One

436. The closest appear to be the stream anoles of Cuba and Hispaniola, *A. vermiculatus* and *A. eugenegrahami*. However, not only are they greatly different in morphology, but they also appear to interact with the environment in different ways (Leal et al., 2002). Comparison of species often found on rock surfaces—such as the little-known *A. monticola* Series in Haiti and *A. lucius* and *A. bartschi* in Cuba—might also prove interesting.

437. In other cases, the phylogeny is too uncertain to unambiguously identify sister taxon relationships deep in the tree (Chapter 5).

scenario is that the ancestral *Chamaeleolis* initially was a crown-giant that emigrated from Puerto Rico or Hispaniola, but finding that niche already occupied in Cuba by the *equestris* Series,<sup>438</sup> it diverged to use different parts of the available habitat and food resource spectrum. This might be an example of a historical contingency; the *Chamaeleolis* way of life might most easily evolve from a species that was already very large, so sympatry of two crown-giant clades might be particularly likely to have channeled evolutionary diversification in this direction. This, however, is rampant speculation, particularly given that *Chamaeleolis* and the crown giants do not appear to be sister taxa (even though they are in the same clade), which makes tenuous even the original premise that the ancestral *Chamaeleolis* was a crown-giant.

Speculating about why particular ways of life evolve in one place but not another is always interesting. If it weren't for the existence of the ecomorphs, unique anole species wouldn't be so enigmatic. Rather, the Greater Antilles would be just another case of a species-area relationship, in which larger islands have not only more species, but also a greater diversity of functional types of species. But anole evolution in the Greater Antilles is dominated by convergent evolution, and it is in this light that evolution of the unique anoles is fascinating. Unfortunately, at this point I think we have few good leads to follow.

#### THE ANOLES OF THE MAINLAND

Mainland anoles are comparable to those of the Greater Antilles in the extent of their morphological and ecological diversity (Chapter 4). Nonetheless, most mainland anoles do not belong to any of the ecomorph categories. Quantitative analyses have found only a few cases in which a species qualifies as an ecomorph on both ecological and morphological grounds (Irschick et al., 1997; Velasco and Herrel, 2007): *A. auratus* is a grass-bush anole and *A. frenatus* and *A. biporcatus* may be crown-giants (Fig. 4.9). Qualitatively, a few other species seem to fit the ecomorph bill: both *A. pentaprion*<sup>439</sup> and the species in the *Phenacosaurus* clade appear to be twig anoles (Fig. 4.9), and probably some other arboreal species pass muster as trunk-crown or crown-giant anoles. On the other hand, some mainland species are morphologically similar to one ecomorph class, but ecologically similar to another (e.g., *A. ortonii* [Irschick et al., 1997]), and many mainland anoles are dissimilar to all ecomorphs in morphology, ecology, or both (Chapter 4).

Despite the lack of ecomorphs, mainland anoles for the most part use the same parts of the environment as the West Indian species—basically, all parts of the vegetation from near the ground to the canopy. Even some of the unusual microhabitats of the Greater Antillean unique anoles have their parallels in the mainland, including leaf litter (e.g., *A. humilis*, *A. nitens* [Fig. 4.11; Talbot, 1977; Vitt et al., 2001]), rock wall (*A. taylori* [Fitch and

438. Figure 5.6 suggests that the *equestris* Series originated slightly before the *Chamaeleolis* clade.

439. And probably its close relatives, *A. vociferans* and *A. fungosus* (Myers, 1971).

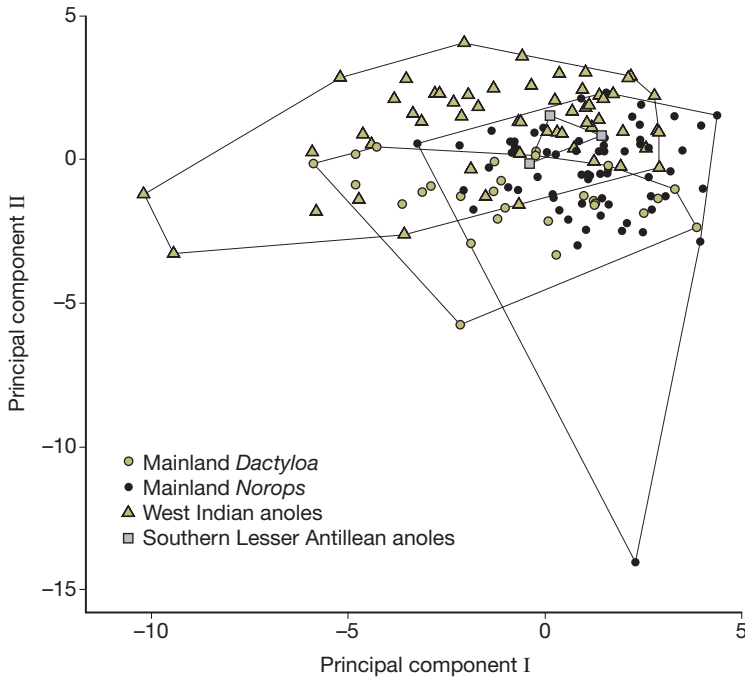


FIGURE 16.8

Relative position of mainland and West Indian anoles in morphological space. Data from a principal components analysis on size-adjusted morphometric variables. Modified with permission from Pinto et al. (2008).

Henderson, 1976), and aquatic anoles (e.g., *A. barkeri*, *A. oxylophus* [Vitt et al., 1995; Birt et al., 2001]).

Although they use the same suite of habitats, mainland and West Indian anoles have adapted to them in different ways, as outlined in Chapter 13. This lack of convergence extends to the entirety of the radiations in the two areas, which overlap only partially in morphological space (Fig. 16.8; Irschick et al., 1997; Velasco and Herrel, 2007; Pinto et al., 2008).<sup>440</sup> Interpreting this difference in position is difficult because the multivariate analyses are not entirely in agreement either within (Velasco and Herrel, 2007) or between studies; nonetheless, one common pattern is that mainland anoles often have more poorly developed toepads relative to Greater Antillean species (in agreement with Macrini et al. [2003]).

While considering explanations for differences between mainland and Greater Antillean anoles, the phylogenetic interrelationships of these two groups should be kept in mind (Chapter 5). The West Indies were colonized twice from Central or South America

440. Keep in mind, however, that these studies have included only a relatively small portion of mainland diversity.

and examination of Figure 16.8 indicates that both West Indian clades have radiated through parts of morphological space not explored by their mainland ancestors (*Dactyloa*). Similarly, the mainland *Norops* clade arose from within this West Indian clade, and members of that clade have radiated in part in an area of morphological space in which West Indian anoles are absent; moreover, to a large extent, this part of the mainland *Norops* radiation has involved returning to space occupied by mainland *Dactyloa*.

One explanation for this pattern of shifts in position in morphological space accompanying island-mainland transitions is that in each case the colonizing species experienced a radical reorganization of its genetic or developmental system that allowed evolutionary exploration of new morphological frontiers; in other words, preexisting constraints were broken, and new ones developed (e.g., Mayr's [1963] "genetic revolutions"). Given the arguments made against the importance of constraints in *Anolis* earlier in the chapter, this hypothesis seems unlikely.

A second possibility is that mainland and West Indian anoles have experienced similar radiations in terms of their functional capabilities, but that different morphological means of producing identical functions have evolved in the two areas. As discussed in Chapter 13, few data are available to evaluate the possibility of many-to-one relationships between morphology and performance in anoles. However, a second point is probably more significant in this context: mainland and West Indian species behave differently (Chapter 8). Consequently, selection in these two areas is likely to favor the different functional capabilities that are appropriate to these behaviors, rendering the many-to-one hypothesis insufficient as an explanation for mainland-island differences.

The other main class of explanation relies on environmental differences between the mainland and the West Indies. Central and South America differ from the West Indies in many ways: topography, climate, geology, to name just a few. The most important differences, however, are probably biotic: the mainland hosts not only many more species in total, but also many more types of species (e.g., salamanders, mammalian carnivores), as well as larger and more complicated food webs.

One or all of these differences could have played a role in sculpting differences in the anole faunas of these areas, but two factors that seem particularly relevant to anoles are the vegetation structure and the abundance of predators. Given that much of the ecomorphological work on anoles has focused on how differences in morphology have evolved to exploit different parts of a tree, vegetation structure would seem to be an important determinant of anole evolution. However, even within a Greater Antillean island, great variety exists in vegetation, from xeric scrub through dry forest to rainforest and cloud forest, yet the same basic ecomorph types occur widely throughout each island. Although certainly some differences in the structure of habitats occur between mainland and West Indian islands, it is not obvious that these differences matter to anoles. That is, anoles use the same variety of structures—e.g., tree trunks, twigs, leaves—in both areas. Even if the mainland in general had taller or broader trees or more lianas, how this would drive anole evolution in significantly different directions is not obvious.

Nonetheless, these thoughts represent just my intuition, and detailed study of how vegetation structure affects anole behavior, ecology, and morphology (e.g., Johnson et al., 2006), both within and between regions, would be instructive.

The difference in predator diversity in the two regions, by contrast, could be of major significance. Consider, for example, the vertebrate predator fauna of La Selva in the Atlantic lowland rainforest of Costa Rica, which includes more than 100 species of snakes, raptors, and members of the Carnivora (Greene, 1988). Although many of these species do not eat anoles, many other types of predators do—e.g., monkeys, peccaries, frogs, a variety of birds, spiders, and army ants. By contrast, the West Indies are a fairly benign place in which to be an anole. Birds and snakes are a threat, of course, but their diversity is less than on the mainland, and many other kinds of potential predators are not represented at all. At the El Verde Field Station in Puerto Rico, for example, anoles are eaten by only 14 species of birds, two species of snakes,<sup>441</sup> and one introduced mammal, as well as several species of frogs and invertebrates (Reagan et al., 1996). A conservative estimate is that at least twice as many species prey on anoles at La Selva (H. Greene, pers. comm.).

Greater predator species richness does not necessarily translate into greater predator abundance and higher rates of predation; each predatory species may be less abundant, or may include anoles as a smaller part of their diet. Nonetheless, the higher mortality rates of mainland anoles are plausibly a result of greater rates of predation (Chapter 8). A similar relationship between predator richness and mortality occurs among Bahamian islands (Schoener and Schoener, 1982b).<sup>442</sup>

More significant than sheer numbers of predators, however, is the diversity of predatory tactics, which is vastly greater on the mainland. The limited number of predatory species in the West Indies means that anoles only have to cope with a few types of predation. By contrast, mainland anoles have to deal with predators of all shapes and sizes, differing in means of locomotion, sensory system, foraging mode, and activity time.

When I first considered the role of predator differences in shaping the anole faunas, I focused on escape performance. I figured that a mainland anole living in the exact same habitat as a West Indian species needed to be faster and stronger to get away from all of these predators. This selection for greater maximal performance in theory could lead to differences in ecomorphological relationships and morphological diversity.

However, in retrospect, this perspective was pretty naïve. Consider an anole in Costa Rica, say *A. limifrons* (Fig. 16.9). Life must be pretty scary for this little lizard. The forest is full of eyes, in the canopy, on the ground, in the trees. And those eyes belong to predators that can attack in many different ways. Although some approaching predators can

441. And probably a third species (Wiley, 2003).

442. Though island size is a confounding factor in this case. More generally, note that even in the absence of increased mortality rates, predators can have a great effect on the ecology—and presumably the evolution—of species and communities by leading to changes in behavior, habitat use, physiology, and even morphology (the latter by inducing phenotypically plastic morphological changes [Lima, 1998; Ripple and Beschta, 2004; Schmidt and Van Buskirk, 2004; Hoverman et al., 2005]).

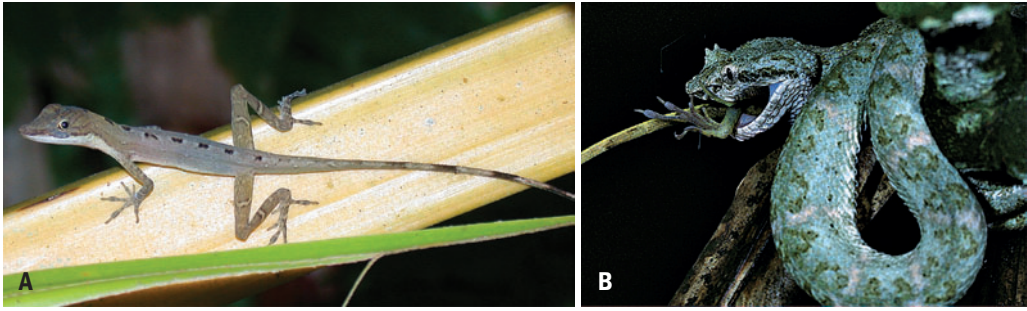


FIGURE 16.9

Predator and prey in the Costa Rican rainforest. *Anolis limifrons* (a) must contend with many different predators with diverse foraging styles, including the sit-and-wait foraging eyelash viper (*Bothriechis schlegelii*) (b). Lizard photo courtesy of J.D. Willson; snake photo courtesy of Harry Greene).

be seen a long way off, others materialize seemingly out of nowhere, either by stealth or quickness. Many of these predators have excellent vision, and some are consummate sit-and-wait foragers, perching in trees and scanning, looking for motion (e.g., Orians, 1969). No matter how fast an anole is, it may have little chance of escaping once a predator notices it.

Consequently, the best way for a mainland anole to avoid being eaten may be to avoid being seen.<sup>443</sup> This hypothesis predicts that a mainland and a West Indian anole using the same structural microhabitat might behave very differently. The mainland anole might be much less active, and might confine its activities to less exposed areas. Such differences might be accentuated by other considerations: fewer intraspecific competitors for food or mates might allow the mainland anole to be more selective about where and when it displayed and chased food. These differences would likely lead to very different selective pressures between mainland and West Indian species occupying the same structural microhabitat; for example, selection for high sprint speed might be less important than selection for crypticity in many mainland anoles.

A corollary to this hypothesis is that the most important factor affecting morphological differentiation among mainland anoles may not be differences in perch height or diameter, as in the West Indies, but distance to cover: some species may spend most of their time in relatively safe microhabitats, whereas others may be out in the open much more often. If this is the case, then we might expect mainland species differing in microhabitat use to experience different selective pressures for functional capabilities and morphology (cf. Pulliam and Mills, 1977; Lima and Valone, 1991).

443. The risks to a mainland anole of conspicuous behavior are well illustrated by Fleishman's (1991) observation of a Panamanian grass anole, *A. auratus*, that began displaying to another anole and was immediately captured by a vine snake, *Oxybelis aeneus*.

The predation hypothesis is consistent with the life history differences that exist between mainland and West Indian species (Chapter 8). In addition, the limited behavioral data also are in agreement: compared to West Indian anoles, mainland species seem warier, forage less, and rely more on crypsis and immobility to avoid predators (Losos et al., 1991; see Chapter 8).

The hypothesis that these life history and behavioral defenses are a result of differing predation pressures is plausible, but can they explain differences in morphological variation? The hypothesis makes three predictions: first, that mainland anoles interact with the environment in a fundamentally different way than do West Indian anoles; second, that differences in predation pressures are the cause; and third, that as a result, mainland anole evolutionary diversification has occurred in very different ways than in the West Indies.

Although differences in the relationship between habitat use and morphology have been reported (Table 13.3), we need much more detailed information on how mainland anoles interact with their environment. Is it correct that two species—one on the mainland, the other West Indian—using essentially the same microhabitat (e.g., tree trunks near the ground) nonetheless behave in very different ways? Assuming that these differences exist, the next question is whether differences in predation regime are the cause. This is a difficult prediction to test, but comparative analyses of habitat use and behavior between areas differing in predator faunas could be instructive;<sup>444</sup> examination of localities in which some predators have been introduced or extirpated by humans could add a quasi-experimental perspective.<sup>445</sup> In addition, experimental additions or removals could examine the extent of potential behavioral plasticity inherent within species, although evolved differences may be much greater in magnitude.

Testing the macroevolutionary sequelae of this hypothesis will be more difficult. A fairly large body of theoretical literature predicts that the presence of predators can spur diversification in different directions than would occur in their absence, but empirical data are relatively few (reviewed in Vamosi, 2005; Langerhans, 2006). For example, Zimmerman (1970) attributed some of the unusual behaviors and lifestyles of Hawaiian insects to lack of predators and noted that introduced predators have wiped out some of the species. Conversely, Doucette et al. (2004), working on Icelandic sticklebacks, suggested that the presence of predators may lead prey species to partition refuges sites, promoting subsequent morphological divergence (see also Rundle et al., 2003). Similarly, the evolution of different anti-predator strategies (e.g., fight versus flight) might lead to divergence in a variety of different behavioral, physiological and anatomical traits (e.g., Losos et al., 2002).

444. For example, Lister and Aguayo (1992) report that Mexican *A. nebulosus* males are much more active and display considerably more on an offshore island that lacks most predators than in a nearby population on the Mexican mainland (see Chapter 8 for examples of predator-induced shifts in habitat use).

445. For example, in the West Indies, introduction of mongooses resulted in the extinction of a number of ground snakes (Tolson and Henderson, 2006).



In addition, predator-prey coevolutionary dynamics may also have a large effect on patterns of prey diversification. For example, the development of greater predatory ability (faster speed, better shell-crushing ability) in predators may be parried by the evolution of counter-adaptations among prey (faster speed, thicker shells [Bakker, 1983; Vermeij, 1987]). Studies of the fossil record have shown how this escalation can lead to evolutionary diversification of prey in ways that do not occur in the absence of the predators (Vermeij, 1987). Nonetheless, for mainland anoles, the effect of predators probably results more from their increased presence, relative to the West Indies, than from predator-prey coevolution; the selective pressure probably comes not from functional improvements in mainland predators, but rather from an increase in the number and types of predation threats.

The approach that will need to be taken to study the effect of predation on anole diversification will need to be the same as for the study of evolutionary adaptation in general (Chapter 13): careful examination of the functional demands caused by the environment (in this case, predators), analysis of the behavior and ecology of the anoles in the context of these demands, and evaluation of functional and behavioral consequences of phenotypic differences that have evolved in the presence of different predator faunas. This approach can be coupled with studies of selection to examine how selective pressures vary in areas differing in predator communities; experimental approaches would certainly be possible with at least some types of predators.

Although I have focused on the role of predators, the greater species richness of mainland localities could affect anoles in other ways. An obvious alternative candidate is interspecific competition resulting from the greater diversity of insectivores on the mainland. The increased prey size and reduced foraging rate of mainland species was interpreted as a result of reduced intraspecific competition because of lower population densities that result from increased predation (Chapter 8). Alternatively, however, reduced population sizes could result from increased interspecific competition from non-anoles (although the observed higher growth rates, larger prey and greater feeding rates wouldn't be predicted results of increased competition; see Chapters 8 and 11). Moreover, independent of population size effects, the presence of more non-anole competitors may have forced anoles to shift to capturing different types of prey or foraging in different ways. The competition and predation hypotheses are not mutually exclusive; investigations of the effects of competitors should be conducted with the same approaches taken to studying predation.

One broader issue remains concerning mainland anole evolution. Clearly, the mainland radiation has not followed the path of the West Indian ecomorphs. But does a different ecomorph syndrome exist on the mainland? We know that convergence is rampant in the West Indies; is it equally prevalent on the mainland, but in the form of a different set of ecomorphs?

Currently, I have no answer to this question. No data are available to evaluate whether mainland communities are composed of similar sets of habitat specialists. Moreover,

given uncertainties concerning phylogenetic relationships among mainland anoles, even if community similarity exists across the mainland, we wouldn't know whether ecologically similar species in different localities were the result of convergent evolution or close relationship. To date, the existence of two clades of twig anoles and three of aquatic anoles are the only clearcut cases of convergence in the mainland (Chapter 7).

Obviously, I have many more questions than answers. Moreover, many of the questions are posed in very vague terms, without clearly defined approaches to answer them. I can understand how those who like clearly defined hypotheses and research programs would be unhappy with the research agenda laid out in this chapter. In my defense, all I will say is that the general issues discussed here are not specific to anoles. Rather, many of the most exciting and challenging questions in evolutionary biology revolve around the processes generating large scale patterns of macroevolution. Methods for their study are still very much in their infancy, and I propose that *Anolis* may be an excellent group in which to develop and fine-tune them.

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# 17

## ARE ANOLES SPECIAL, AND IF SO, WHY?

What's so great about anoles? Why have I written a whole book about them—and spent more than 20 years studying them—and why have you read the book? Of course, they're attractive and engaging little creatures, with great variety and entertaining behavior. But if that were their only claim to fame, this book would be of limited interest.

Quite the contrary, anoles are receiving ever-increasing attention: more and more papers, by more and more research groups, on increasingly diverse topics; even the anole genome is being sequenced. What, if anything, makes them so special?

I suggest that the interest in anoles stems from three factors:

1. The exceptional extent to which the adaptive radiation of anoles has been studied.
2. The great diversity and disparity exhibited by anole evolution.
3. The replicated adaptive radiations in the Greater Antilles.

In this last, concluding chapter, I will consider whether anoles really are so special and if so, why. I'll then conclude the book by looking forward to consider what the future holds for the lizards themselves.

## ANOLIS AS A MODEL TAXON FOR STUDIES OF BIOLOGICAL DIVERSITY

In the Prologue, I suggested that *Anolis* is nearly unrivalled in the depth and breadth of knowledge about its biological diversity, spanning fields as disparate as phylogenetics, ecology, physiology, behavior and evolution, and including both laboratory and field studies and experimental and observational approaches. After having read through the book, you can decide for yourself whether our knowledge of anoles is broader and more integrated than that of other diverse groups of organisms.

Why has so much work been conducted on anoles? The answer is simple. For many types of studies, anoles—particularly Greater Antillean species—are ideal subjects. They are often abundant and easy to observe, they can be manipulated in the field to answer behavioral and ecological questions, they can be brought into the lab for a wide variety of different studies, and they can be marked and followed over reasonably short generation times. Plus, many species co-occur, facilitating studies of interspecific interactions. Finally, the patterns of convergence add statistical replication to evolutionary analyses. The only glaring shortcoming in our knowledge of anoles is our lack of understanding of the genetic basis underlying phenotypic variation, and that is likely to change radically in the near future.

For these reasons, anoles have been useful subjects to develop new approaches and to test important and general questions in a wide variety of fields. Moreover, the ability to integrate knowledge concerning so many different aspects of their biology has made them an ideal group for synthetic studies of biodiversity and evolution, an attribute that will only grow in the future as we learn more about them.

Anoles are particularly useful for macroevolutionary studies for two additional reasons. Grant (1986), following Lack (1947), suggested that Darwin's finches are at just the right stage of evolutionary diversification to combine studies of pattern and process; that is, they are diverse enough to illustrate interesting patterns of adaptive radiation, yet they are similar enough that process-based studies in behavioral, ecological and microevolutionary time can provide meaningful insight about how and why adaptive diversification occurred. I would argue that the same can be said about anoles; indeed, that has been the primary theme of this book.

We can contrast cases like Darwin's finches and anoles with case studies at either end of the spectrum. On one hand, studies of closely related species in the process of diverging and speciating provide wonderful insights into these processes. Studies on sticklebacks, walking sticks, and columbines (e.g., Rundle et al., 2000; Nosil et al., 2004; Colosimo et al., 2005; Whittall et al., 2006)—to name just three—are at the cutting edge of evolutionary biology, applying modern methods and approaches to advance our knowledge of the evolutionary process. Nonetheless, groups such as these are not adaptive radiations; they simply don't display enough ecological and phenotypic diversity. Studies on these groups certainly are informative concerning microevolutionary processes, and

the groups themselves may be nascent adaptive radiations,<sup>446</sup> but adaptive radiations they are not, and the extent to which we can scale up from studies of groups such as these to macroevolutionary levels is not clear.<sup>447</sup>

At the other end of the spectrum, some of the most famous examples of adaptive radiation—such as beetles, placental mammals and angiosperms—represent old and extremely diverse groups. Although their disparity is the hallmark of adaptive radiation, these clades are so diverse in so many ways that it is hard to imagine how process-based studies could be informative about the origin of these differences (Grant, 1986). Consider placental mammals, and more specifically the subclade Afrotheria: what sorts of studies could help us understand why this clade differentiated to produce golden moles, aardvarks, elephants, and other taxa? In other words, the macroevolutionary pattern is present, but it is not clear how we can devise studies to understand the processes that drove evolutionary diversification in these old and disparate groups.

Anoles exhibit a second advantage for the study of adaptive diversification, one not shared by Darwin's finches and some other groups: the ability to conduct manipulative experiments in nature, over both ecological and evolutionary timescales.<sup>448</sup> For the last quarter century, ecologists have emphasized the importance of manipulative experiments for hypothesis testing; in recent years, evolutionary biologists are increasingly taking the same approach, though experimental studies in natural settings are still rare (Reznick, 2005). Studies in laboratory microcosms have demonstrated the utility of experimental methods to the study of adaptive radiation (Rainey et al., 2000; MacLean and Bell, 2002; Kassen et al., 2004; Meyer and Kassen, 2007); now is the time to extend this approach to the field.

This is where anoles have their greatest advantage as a macroevolutionary study system. Experimental work on anoles is feasible at all time scales: behavioral, ecological, and microevolutionary. Moreover, quasi-experiments established by anole introductions and natural experiments created by nature via replicated evolution all provide powerful means for hypothesis testing. By synthesizing these experimental approaches with observational studies on extant taxa and phylogenetic studies of evolutionary history, *Anolis* is an excellent system for the yin and yang of hypothesis generation and testing, as well as for the mutual illumination of historical and present-day studies discussed in Chapter 1.

It is for these reasons that *Anolis* has been—and continues to be—an excellent group for a wide variety of studies, and particularly for synthetic, broad-scale integrative work.

446. Or members of larger clades that do constitute adaptive radiations.

447. In the most authoritative treatment of adaptive radiation in half a century (and maybe ever), Schluter (2000) relied heavily on *Anolis* and Darwin's finches as examples, but he and I differ slightly in emphasis: whereas I focus on adaptively disparate groups, he emphasizes the ability to study processes in recently diverging clades (see pp. 8–9 of his book).

448. Such studies cannot be conducted on Darwin's finches because research in the Galápagos is stringently regulated and limited.

A major goal of this book has been to not only make this point, but to illustrate that abundant opportunity still exists to jump on the *Anolis* bandwagon—all are welcome, and the more, the merrier!

#### ANOLIS ADAPTIVE RADIATION

But enough cheerleading—let's get down to the nitty-gritty: is the evolutionary diversification of *Anolis* exceptional and, if so, why have these lizards evolved such diversity and disparity?

#### ARE ANOLES SPECIAL?

To decide if *Anolis* is exceptional, we need to delineate an appropriate pool of comparison clades. In Chapter 15, I presented one approach, arguing that the appropriate comparison is to a sample of clades that share similarities in biology, natural history, and age. Based on this approach, I found that both *Anolis* and the Polychrotinae (the larger clade to which *Anolis* belongs) exhibit significantly great ecomorphological disparity (Fig. 15.12).

A second, more traditional, approach is to compare *Anolis* to its sister group.<sup>449</sup> As discussed in Chapter 6, uncertainty currently exists about the sister taxon of *Anolis*. Nonetheless, all of the candidates that have been mentioned in the literature are clades that contain few species and little ecological and morphological variety. It seems safe to conclude that, in comparison to its sister group, *Anolis* is exceptionally species rich and ecomorphologically diverse.

A third approach would be to compare *Anolis* to other clades which diversified in the same biogeographic region. If we consider first the West Indies, no reptile clade comes even remotely close to rivaling *Anolis* in species richness or ecomorphological diversity. Expanding to all vertebrates, the only comparable group is eleutherodactyline frogs, with about 150 species and extensive, though little studied, ecomorphological diversity (Hedges, 1989; Hedges et al., 2008). Even if we expand the scope to consider the Neotropics, anoles, eleuths, and perhaps dendrobatid frogs (Grant et al., 2006) seem to be exceptional, certainly among amphibians and reptiles. Comparisons in this case are more difficult because there are so many more groups on the mainland, but few other candidates exhibit comparable diversity and disparity. Of course, one could argue that the comparison is unfair; anoles and eleuths are exceptionally old clades (Chapter 6; Heinicke et al., 2007; Hedges et al., 2008), so the appropriate comparison should be to Neotropical clades of comparable age. In the absence of detailed and dated phylogenies for other groups, this point cannot be resolved, but few contenders exist among other amphibian and reptile groups, nor all that many among mammals, birds, or fish, either.<sup>450</sup>

449. For reasons discussed in Footnote 416, I prefer the first approach.

450. Poeciliid fish (Meffe and Snelson, 1989; Hrbek et al., 2007) and hummingbirds (McGuire et al., 2007b) are possible examples.

In summary, by whatever criterion one wants to use, *Anolis* stands out as an exceptionally diverse and ecomorphologically disparate clade.

#### WHAT IS RESPONSIBLE FOR THE EXCEPTIONAL DIVERSIFICATION OF ANOLES?

##### *ECOLOGICAL OPPORTUNITY*

Ecologists and evolutionary biologists often identify ecological opportunity as an important stimulus to adaptive radiation (Simpson, 1953; Schluter, 1988a,b, 2000). Remote islands are particularly good candidates because their depauperate faunas mean that colonizing species may find a surfeit of resources and few competitors. Indeed, many of the most famous examples of adaptive radiation occur on distant oceanic islands, such as Hawaii and the Galápagos, and in their aquatic counterparts, inland lakes such as the African Rift Lakes and Lake Baikal.<sup>451</sup>

Groups radiating on such islands often exhibit substantially greater ecomorphological disparity than their close relatives in mainland settings (Carlquist, 1974). This evolutionary ebullience is usually credited to niche expansion in the absence of other competing taxa. The result is that species in the radiating clade diverge, occupying a wide array of different niches that are usually utilized by other clades in mainland settings (reviewed in Schluter [2000]; for a recent example, see Chiba [2004]). As outlined in Chapter 11, Greater Antillean *Anolis* fulfill this scenario very well.

Nonetheless, ecological opportunity cannot be the whole story, because not all clades radiate under such conditions. In the Galápagos, for example, Darwin's finches are the only birds to have diversified to any extent; similarly, some plant, insect and mollusk groups have radiated extensively in this archipelago, but many others have not (Jackson, 1994). In Hawaii and any other isolated island or island group, the story is the same (e.g., Zimmerman, 1970; Carlquist, 1974). Greater Antillean anoles again fit the picture: in the West Indies, few other taxa (including only one other reptile clade, *Sphaerodactylus* geckoes) have radiated to any substantial extent, even though most have been present in the West Indies as long as anoles (Crother and Guyer, 1996; see Thorpe et al., 2008).<sup>452</sup>

##### *DIVERSITY OF A CLADE'S CLOSE RELATIVES*

Why, then, do some clades radiate and not others? One predictor may be the diversity of a clade's relatives elsewhere (Carlquist, 1974). Consider, for example, Hawaiian honeycreepers and Darwin's finches. Both of these clades have radiated extensively,<sup>453</sup> and their sister taxa on the mainland also exhibit substantial—though not as great—ecomorphological diversity (Burns et al., 2002; Lovette et al., 2002). By contrast, two

451. Lakes surrounded by terrestrial habitats are, for freshwater denizens, the evolutionary equivalent of islands surrounded by water.

452. Length of residence in an area is an important consideration because the radiation of an early colonist may preclude diversification by later arrivals (Carlquist, 1974; for an interesting counterexample, see the discussion of the tropheine cichlids in Lake Tanganyika in Salzburger et al. [2005]).

453. They have radiated so much that their ecomorphological disparity is almost as great as that seen within all passerine birds (Burns et al., 2002; Lovette et al., 2002).



clades that have not radiated to any substantial extent despite having been present on these islands just as long, Hawaiian thrushes and Galápagos mockingbirds, belong to clades that also show little disparity on the mainland (Lovette et al., 2002; Arbogast et al., 2006; Grant and Grant, 2008). A corollary of this pattern is that some clades seem to diversify repeatedly on different islands, whereas others diversify rarely. For example, some clades of African cichlids radiate in many different lakes, whereas other clades never exhibit much diversification (Seehausen, 2006).

However, it is probably premature to consider this to be a general rule of adaptive radiation because some clades that radiate on islands are not diverse elsewhere in their range, such as *Tetragnatha* spiders and aglycyderid weevils (Gillespie et al., 1994; Paulay, 1994) and cichlid fish in most African rivers (Joyce et al., 2005), and no overall assessment of the generality of this phenomenon has been conducted. Clearly, whether the clades that adaptively radiate on islands can be predicted by the diversity of their relatives elsewhere would make for an interesting study. Nonetheless, to the extent that this rule does hold, anoles would seem to be a good example, given that they have diversified greatly both in the West Indies and on the mainland.

#### ECOLOGICAL OPPORTUNITY AND THE MAINLAND RADIATION

All in all, Greater Antillean *Anolis* would seem to be a classic example of island adaptive radiations resulting from ecological opportunity. Nonetheless, this conclusion leads to a question: if ecological opportunity prompted the anole radiation in the West Indies, how do we account for the comparable ecomorphological variety on the mainland (Chapter 16)? Has ecological opportunity played a role there, as well?

It is easy to imagine anoles arriving on a proto-West Indian island brimming with empty niches, but the mainland is a different story. Today the mainland is full of animals of all sorts that vie with anoles for arboreal insects (Chapter 11). In the absence of fossils and detailed phylogenetic analyses, we don't know what other taxa were present on the mainland 40 or more million years ago, and thus whether anoles initially diversified in the presence of other arboreal insectivores. Nonetheless, we might expect that mainland communities were diverse and species rich in the distant past, even if we don't know what kind of species were present. And if that is the case, then the evolutionary success of mainland anoles suggests that ecological opportunity may not be a prerequisite for anole adaptive radiation.

On the other hand, few data support such a supposition, and we shouldn't discount the possibility that ecological opportunity was abundant in the early days of mainland anole diversification. For example, few mammalian insectivores<sup>454</sup> are known from the Neotropics in the Eocene and Oligocene (MacFadden, 2006). Although the fossil record of bird diversity is scant, molecular studies suggest that modern Neotropical clades, at least, were not diverse in the Eocene or much of the Oligocene. In particular, Amazonian

454. Or, for that matter, any potential mammalian predators of anoles.

forest canopy and scrub habitats today are dominated by North American clades, which began to diversify in Amazonia only 12 million years ago. Perhaps the most likely scenario is that these clades displaced suboscine passerines, but even those avian clades have only been diversifying in South America for the last 32 million years (Ricklefs, 2002). Although many lizard clades have probably been present in the neotropics for a long period of time, few of these clades contain arboreal insectivores (Chapter 11); similarly, being primarily nocturnal, frogs probably do not compete with anoles to a great extent (Chapter 11). Thus, it is conceivable that mainland anole diversification, at least in its early stage, occurred in a relatively empty ecological theater. This possibility applies particularly to the older *Dactyloa* clade; by contrast, the more diverse *Norops* clade colonized the mainland more recently (Fig. 6.1), when birds and mammals were more diverse and *Dactyloa* also was already present (although possibly restricted to southern Central America and South America, as it is today).

#### WHY HAVE ANOLES RADIATED WHERE OTHER TAXA HAVE NOT?

Regardless of the role that ecological opportunity has played in anole diversification, we still must ask why anoles have diversified to so much greater an extent than other taxa with which they coexist. Even if ecological opportunity was the stimulus to diversification, many other clades had the same opportunity but failed to take evolutionary advantage of it.

In Chapter 15, I put forth my hypothesis: the evolution of toepads provided anoles with the evolutionary flexibility to adapt to many different aspects of arboreal existence, allowing species to specialize to use twigs, grass blades, the canopy, and other parts of the environment. In this regard, the evolution of toepads in anoles would be a classic example of a key innovation allowing a clade to utilize the environment in a different way and thus leading to adaptive diversification within this new adaptive zone, just as the evolution of wings prompted the adaptive radiation of birds into a variety of niches unavailable to their theropod ancestors.

One way of distinguishing the power of the toepad versus ecological opportunity would be to see how anoles do when introduced to other parts of the world (Chapter 11). The success of anoles in Bermuda (Wingate, 1965), Micronesia (Rodda et al., 1991), and islands near Japan (Hasegawa et al., 1988; Okochi et al., 2006) indicates that anoles can infiltrate other ecosystems; however, these are all islands, where ecological opportunity may have been great. The real test will be if and when anoles are introduced to continental settings in the Old World, where ecological opportunity may be limited.<sup>455</sup> Will the

455. I have mentioned the utility of studying introduced populations repeatedly in the last few chapters, so I want to reemphasize that I in no way condone such introductions. Nonetheless, given the extent of global commerce and the ease with which anoles stow away, it is probably inevitable that *A. sagrei*, *A. carolinensis* or some other species will eventually arrive in many far-off destinations. Of course, in some places, such as Madagascar, toepadded, arboreal and diurnal insectivorous lizards already exist and have radiated widely, as I will discuss shortly. Even if toepads are a key innovation, they may be of little use to invading anoles in such places because their potential niches may already have been preempted.

possession of toepads be sufficient to allow anoles to become established and diversify in such settings?

As important as toepads may have been, they are not the whole story. Toepads may have allowed anoles to diverge into different structural microhabitats, but anoles also show repeated divergence and convergence in their occupation of thermal microhabitats. Repeatedly within ecomorph clades, species have differentiated in the thermal microhabitats they occupy, with concomitant adaptation in thermal physiology. Indeed, the rate of evolution in thermal biology is even higher than in ecomorphology (Hertz et al., in review). The lability in thermal biology is particularly notable because thermal biology is evolutionarily conservative among most lizard clades (Bogert, 1949; Huey, 1982; Hertz et al., 1983; Andrews, 1998; but see Castilla et al. [1999]). Why anoles exhibit so much greater evolutionary flexibility in thermal physiology than other types of lizards is unknown.

Another factor that may be important in adaptive radiation is “evolvability,” simply the ability to evolve readily into diverse forms (Schluter, 2000). Perhaps this seems self-evident, but taxa that are limited in their ability to evolve will change more slowly or not at all; populations that can readily adjust will be able to adapt to local circumstances (Lovette et al, 2002; Arbogast et al., 2006). Evolvability is an attribute of a population; consequently, data on genetics and response to selection is the best way to measure it. For the time being, we don’t have a good measure of anole evolvability; however, interspecific comparisons indicate that anoles are evolutionarily labile, displaying great variety in both morphology and thermal physiology compared to other clades (e.g., Warheit et al., 1999). To the extent that anoles are more evolvable than other taxa, a variety of different factors could be responsible.

- *Modularity.* Phenotypically and genetically, aspects of the anole phenotype may be structured independently (i.e., they are compartmentalized or modular), allowing aspects of the phenotype to evolve independently of each other. This idea has been discussed in phenotypic (Liem, 1974; Vermeij, 1974) and quantitative genetic (Cheverud, 1996; Wagner and Altenberg, 1996) terms for many years; recently the parallel idea has been developed at the genomic level (Kirschner and Gerhart, 1998; Rutherford and Lindquist, 1998). How this idea might apply to anoles is not clear. Interspecific morphometric variation in toepad characteristics, limb dimensions, body size, and sexual size dimorphism are uncorrelated (Harmon et al., 2005), and none of these characteristics is likely to covary with thermal physiology, so in this sense anole adaptive responses may occur along several independent pathways. Whether analogous compartmentalization exists in anole genomes is unknown, though such questions will be increasingly amenable to study in the near future.
- *Broad Niche Use.* Although specialized to use particular parts of the environment, anoles are nonetheless highly flexible in their habitat use and behavior: any

species can be found almost anywhere in the environment, at least occasionally (Chapter 3).<sup>456</sup> A similar phenomenon is seen in cichlid fish which, despite specializations of the jaw for particular trophic niches, can eat a broad range of different types of food (Galis and Metz, 1998; Kornfield and Smith, 2000). As a result, given the opportunity to expand their habitat use by the absence of competitors or predators, or forced to shift habitat use by their presence, anoles can do so and subsequently adapt to the new conditions in which they occur (Chapters 11–13).

- *Phenotypic Plasticity.* The potential evolutionary significance of phenotypic plasticity has attracted increasing interest in recent years (e.g., West-Eberhard, 1989, 2003; Schlichting and Pigliucci, 1998; DeWitt and Scheiner, 2004; Ghalambor et al., 2007). Adaptive phenotypic plasticity has been discovered in two anole species: individuals of *A. carolinensis* and *A. sagrei* that grow up using broad surfaces develop relatively longer hindlimbs than those that grow on narrow surfaces (Chapter 12). Presumably, such plasticity could allow a population of lizards to persist in a habitat in which it would otherwise perish; given enough time, advantageous genetic variation would appear and spread through the population, leading to genetic adaptation and elaboration of the traits.<sup>457</sup> Whether hindlimb plasticity, much less plasticity in other traits, occurs to a greater extent in anoles than in other taxa is unknown.
- *High Rate of Speciation.* An alternative perspective is that anoles speciate at a rate greater than that of other clades, and the resulting abundance of species sets the stage for evolutionary divergence in adaptive phenotypic traits. In Chapter 15, I suggested that the reliance of anoles on visual signals for communication increases the likelihood that populations in different environments will diverge and become reproductively isolated. A high rate of speciation could promote adaptive diversification in two ways. First, the incidence of ecologically similar species becoming secondarily sympatric and undergoing character displacement is likely to be a function of the number of species in a region. Second, to the extent that gene flow constrains evolutionary divergence (Mayr, 1963; Moore et al., 2007), then an increased likelihood that populations will become reproductively isolated should increase the rate of evolutionary divergence (Futuyma, 1987).

Whether, in fact, any of these possibilities explains the extensive evolutionary diversity of anoles relative to other taxa is unknown. For one thing, we don't even know

456. This refers more to structural than thermal microhabitat. Crown-giants occasionally are seen on the ground, and trunk-ground and grass-bush anoles every now and then climb high into a tree. However, deep forest anoles aren't often found in the middle of a sunny field, nor open habitat anoles in deep forest.

457. Note that mutations are random with respect to their selective value. Particularly beneficial mutations do not arise in response to particular environmental exigencies. For this reason, the potential for phenotypic plasticity to facilitate subsequent evolutionary adaptation is in no way Lamarckian, as sometimes is supposed.

whether these factors differ between anoles and other taxa. Whether anoles exhibit particularly great compartmentalization, niche breadth, or plasticity compared to other lizard clades or other Neotropical taxa is unknown and would make for an interesting study, as would investigation of the extent to which greater species diversity promotes phenotypic differentiation.

In sum, anoles display many of the characteristics exhibited by other adaptive radiations. At least in the Greater Antilles, and possibly on the mainland, they took advantage of ecological opportunity to diversify widely. The possession of toepads allowed them to diversify throughout the arboreal realm, which was underutilized by other taxa. In addition, anoles exhibit a variety of other characteristics that may explain their great evolutionary lability. In many of these regards, anoles appear exceptional relative to most other lizard clades and most other neotropical taxa, but share similarities with other clades that have radiated adaptively.

## REPLICATE ADAPTIVE RADIATIONS

What is particularly exceptional about *Anolis* is the fact that independent radiations on four separate islands have produced communities composed of the same set of habitat specialists. The idea that communities in similar environments—such as deserts or Mediterranean habitats—should exhibit similar structure and composition has a long pedigree (Orians and Paine, 1983; Blondel et al., 1984; Pianka, 1986; Wiens, 1989; Losos, 1996; Kelt et al., 1996). If these habitats occur in far-off lands, they usually will be occupied by distantly related taxa, and thus similarity in community structure likely would be convergent (Schluter, 1986). Note, however, that communities can converge in overall structure (e.g., species richness, pattern of spacing in ecological or morphological space) while their constituent species may differ greatly (Ricklefs and Travis, 1980; Schluter, 1990). Communities that are composed of species exhibiting the same set of convergently evolved phenotypes—termed “species-for-species” matching—are quite rare, and it is this phenomenon that is *Anolis*’s number one claim to fame.<sup>458</sup>

458. The null model debate of the late 1970s and early 1980s (Chapter 11 and Footnote 415), acrimonious as it was, had one salutary effect: it made clear that before making a claim that a community is structured by deterministic processes, one must first assess the possibility that the community patterns could have resulted from random processes.

In this vein, it would be nice to conduct a null model analysis of the Greater Antillean anole radiations to ask if the apparent species-for-species matching is greater than would be expected by chance (cf. Schluter [2000]). The observations are that the same four ecomorphs occur on all four islands, the same five ecomorphs occur on three islands, and the same six on two islands; and that phylogenetic analysis indicates that in almost all cases, the presence of the same ecomorph on multiple islands is the result of convergence (Chapter 7).

This species-for-species matching is impressive, but imperfect, given the absence of several ecomorphs from two islands. Moreover, the unique anoles—one in Jamaica, eight in Hispaniola, 12 in Cuba—are not matched. The question then becomes: given these non-matched components, is the extent of species-for-species matching among the ecomorphs greater than would be expected to occur by chance? Put another way, if evolutionary diversification occurred randomly (i.e., morphological change occurred in random directions as species diversified), producing the same number of species on each island as are observed today with the same

In laboratory experiments, replicated microbial systems will diversify to produce identical communities composed of the same set of 2–3 habitat specialists (Rainey and Travisano, 1998; Meyer and Kassen, 2007). By contrast, among communities of organisms in nature, very few examples of species-for-species matching exist. Evidence from mainland settings is almost non-existent; communities in different mainland areas, even in similar environments, tend to be composed of dissimilar species;<sup>459</sup> this is true even when higher level properties of these communities, such as species richness or niche packing, do show evidence of convergence (see reviews in Orians and Paine [1983]; Wiens [1989]; Melville et al. [2006]).

Replicate adaptive radiations, when they do occur, are almost always found on islands or in lakes. Young, post-glacial lakes in the northern hemisphere provide the most extensive example of replicated adaptive radiation (see reviews in Schluter [2000] and Snorason and Skúlason [2004]). In such lakes, which have only been colonized since the end of the last Ice Age and which generally have low diversity, fish repeatedly diversify into two ecomorphs that utilize pelagic and benthic habitats. Examples of this divergence are known from Alaska, Canada, Iceland, Ireland, Scandinavia, Scotland and elsewhere; in some clades, the same pattern of divergence has occurred independently in multiple

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phylogenetic relationships, how likely would it be to generate a pattern in which there is as much species-for-species matching as there is today among the Greater Antilles? A more elaborate null model might also include the caveat that not only would there have to be as much species-for-species matching, but the species or clades that converge across islands would have to be those that are among the most abundant and geographically widespread on the island (i.e., the convergence wouldn't include a clade with an extremely restricted range on one island, because none of the ecomorph clades on any of the islands has such a distribution).

Even the simpler analysis would be complicated in many ways. For example, the existence of clades of similar species, all members of the same ecomorph category, means that the match across islands would sometimes be between species and sometimes between clades. Moreover, given the stasis in ecological morphology evident in recent times (as evidenced by these clades of morphologically similar species), simulations would need to use a non-Brownian Motion model of character evolution to incorporate this pattern of evolution into the null model.

I have not conducted such an analysis. Nonetheless, I think it unlikely that the convergence of the ecomorphs across four islands is likely under a random model. Given the vast swath of morphological space occupied by anoles, even just by Greater Antillean anoles, it seems unlikely that a radiation producing six species (i.e., Jamaica) would manage to produce four ecomorphs that also have evolved on all three other islands. Similarly unlikely would be a radiation of 10 species (Puerto Rico) producing four types shared by three other islands, and a fifth type shared by two others. That Hispaniola and Cuba could produce the same six set of ecomorphs by chance seems less implausible; if these were the only two islands, I would be less convinced, but the congruence of the four islands seems to me to be highly unlikely to have arisen by coincidence.

459. Molecular systematic studies sometimes reveal that morphologically dissimilar species in a local area are not, as previously thought, each related to morphologically similar species elsewhere, but, rather, are closely related to each other and thus represent an in situ radiation (e.g., Australian corvids [Sibley and Ahlquist, 1990; Barker et al., 2002]; Malagasy songbirds [Yamagishi et al., 2001]). In some cases, these findings indicate the existence of multiple cases of convergence across regions, such as in Malagasy and Asian ranid frogs (Bossuyt and Milinkovitch, 2000), *Myotis* bats (Ruedi and Mayer, 2001; Stadelmann et al., 2007), and African and Laurasian mammals (Madsen et al., 2001). However, such cases usually fall short of constituting replicate adaptive radiations because most species in each region are probably not convergent with species in the other region. This lack of widespread convergence is certainly true for the placental mammal faunas of different regions; more complete analyses of ranid frogs and *Myotis* are needed to evaluate the extent to which those radiations are matched across regions. As discussed in the previous footnote, quantitative statistical methods are needed to investigate whether in any of these cases, radiations in different regions are more similar than would be expected by chance.

lakes (e.g., Taylor and McPhail, 2000; Østbye et al., 2006; Landry et al., 2007). This pattern of evolution into pelagic and benthic ecomorphs has occurred in a wide variety of fish, including sticklebacks, charr, salmon, trout, and whitefish. Patterns of morphological divergence usually are similar, with the pelagic planktivores tending to be smaller, more slender and possessing a greater number of gill rakers than the benthic carnivores.

In some cases, evolutionary divergence in these lakes has proceeded beyond the two-species stage. As with Greater Antillean anoles, ecomorph occurrence is nested among post-glacial lakes, with the ecomorphs present in two-species lakes always present in lakes with a greater number of species. In all cases, lakes with three or four species include at least one benthic and one pelagic ecomorph; additional species either subdivide the benthic niche according to depth or are piscivorous.

The most famous case of replicated adaptive radiation in lake fish is the cichlids of the East African Great Lakes (reviewed in Fryer and Iles, 1972; Stiassny and Meyer, 1999; Kornfield and Smith, 2000; Kocher, 2004; Salzburger and Meyer, 2004; Salzburger et al., 2005; Seehausen, 2006; Genner et al., 2007). Approximately 2000 species occur in these lakes, but what is particularly remarkable is the extraordinary radiations that have occurred in Lake Tanganyika (9–12 million years old, 250 species), Lake Malawi (2–5 million years old, 1000 species) and Lake Victoria (less than—possibly much less than—200,000 years old, 500–1000 species). These lakes have experienced independent evolutionary radiations and have each produced a dazzling array of ecomorphological diversity, including plankton grazers, algae scrapers, sand filterers, egg predators, piscivores, sit-and-wait and rapid pursuit predators, species that pluck insect larvae from crevices, fish scale eaters that rasp scales off the sides of other fish (with species with curved heads and jaws specialized to eat from either the left or the right side of the prey), molluscivores, and piscivores (Fryer and Iles, 1972). Moreover, a number of these habitat specialists have evolved convergently in two or all three of these lakes (Fig. 17.1; Fryer and Iles, 1972).

There can be no doubt that the extent of adaptive radiation of African lake cichlids is extraordinary, particularly given the young age of the Lake Victoria radiation. Further, a picture is a worth a thousand words, and illustrations such as Figure 17.1 convincingly suggest that adaptive convergence has occurred among fish in the different lakes. Nonetheless, in many respects, our understanding of replicated adaptive radiation in cichlids lags well behind that of anoles. In particular, two sorts of data are still lacking.

First, although cases of ecomorphological convergence between the lakes certainly exist, we have no idea how common this convergence is: no quantitative analyses have examined the entire faunas of the lakes (although Joyce et al. [2005] is a nice start in this direction). Are these faunas ecomorphologically matched, or do only a few instances of convergence exist, embedded in a larger sea of non-convergence between the lakes? That is, is the situation in the African lakes more like that of the anoles of the Greater Antilles, in which a few unique forms exist, but to a large extent, species-for-species matches occur across islands; or are the lakes more similar to the comparison of placental and

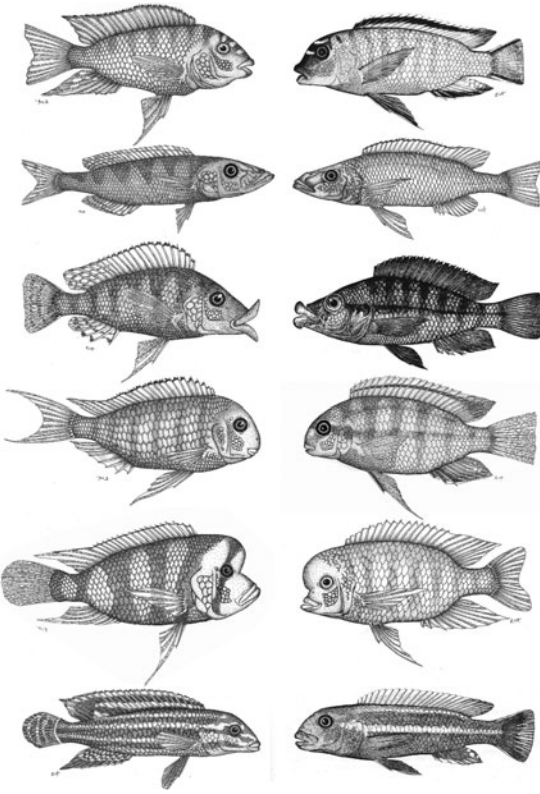


FIGURE 17.1

Convergent evolution in cichlid fishes in the African Great Lakes. Fish in the left column are from Lake Tanganyika and fish on the right are from Lake Malawi. Phylogenetic analyses indicate that independent evolutionary radiations have occurred in these lakes, and thus that these forms are convergent (Kocher et al., 1993). Reprinted with permission from Albertson and Kocher (2006).

marsupial mammals, in which some convergent examples exist, but the faunas are overall not all that similar.<sup>460</sup> Fryer and Iles' (1972) monograph suggests that the lake situation may be more like the latter; although a number of cases of convergence exist, the lakes differ in their degree of divergence and specialization, and many ecomorphological types in each lake apparently have no counterpart in the others.<sup>461</sup>

Second, although visually compelling, documentation of cichlid convergence would be more convincing if it were supplemented by quantitative morphometric analysis indicating that forms truly are convergent (e.g., Rüber and Adams, 2001; Joyce et al.,

460. The marsupial-placental example is a favorite of textbook writers (including me!), but as an example of replicated adaptive radiation, the case falls short. First, Australian marsupials are generally not compared to the fauna of any particular place, but rather to placentals in general. Second, although stunning examples of convergence exist (thylacine-wolf, dasyurid-cat, phalanger-flying squirrel), these are cherry-picked case studies with no overall quantitative assessment. Certainly, there are no marsupial equivalents of cetaceans, bats, and many other placentals, nor any placental equivalent to kangaroos (for a nice introduction to marsupial diversity and parallels, or lack thereof, to placentals, see Springer et al. [1997]). I make these points not to cast aspersions on the wonderful utility of the marsupial-placental comparison as an example of convergent evolution, but simply to say that this example is not a case study of replicated adaptive radiation. See also Leigh et al. (2007), which provides a fascinating discussion of convergence of other mammalian faunas.

461. Fryer and Iles (1972, p. 517) provided a table listing 16 types of "morphologically and/or ecologically equivalent species" found in all three lakes, but point out that in some of these cases, species filling the same ecological niche are not morphologically similar. Thus, the extent of species-for-species matching of ecological equivalents across these lakes is unclear.



2005), and by functional, ecological, and behavioral data investigating the adaptive basis for this convergence.<sup>462</sup>

The number of examples of replicated adaptive radiation on islands is quite small. Probably the best case of replicated adaptive radiation in a terrestrial setting, other than *Anolis*, is the land snails of the genus *Mandarina* in the Bonin Islands near Japan (Chiba, 2004). Ecologically, four types of microhabitat specialists exist: arboreal, semi-arboreal, sheltered ground, and exposed ground. Sympatric species differ in microhabitat use and members of the same microhabitat specialist class do not coexist. Morphologically, the snails cluster into four groups corresponding to their microhabitat use. Phylogenetic analysis indicated that these different ecomorphs have evolved independently multiple times among the islands, except possibly the exposed ground ecomorph, which may be ancestral to the others (Fig. 17.2).

The spiny leg clade of Hawaiian long-jawed spiders (*Tetragnatha*) is another example (Gillespie, 2004). These spiders come in four microhabitat specialist types: species morphologically adapted to leaf litter, moss, twigs, and bark. Communities contain 2–4

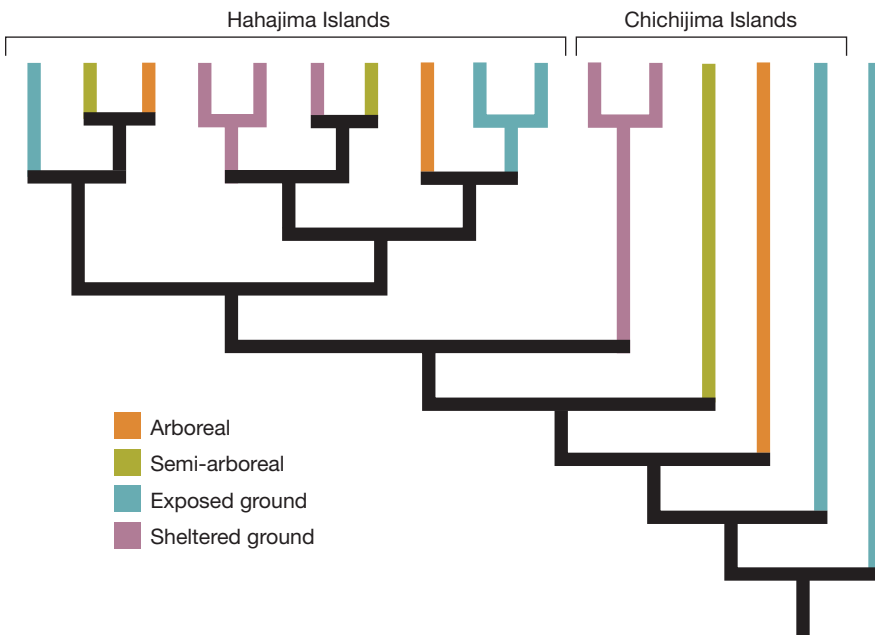


FIGURE 17.2

Replicated adaptive radiation of *Mandarina* snails in islands near Japan. Multiple islands with distinct snail species occur in both the Hahajimas and Chichijimas. Species occupying different microhabitats are morphologically differentiated. Modified from Chiba (2004) with permission.

462. Indeed, although the adaptive basis for ecomorphological differentiation is well studied in pelagic-benthic species pairs (reviewed in Schluter, 2000), for most other cases of replicated adaptive radiation, it has not received much detailed investigation along the lines discussed in Chapter 13.



FIGURE 17.3  
 Evolutionary diversification of *Tetragnatha* spiders in the Hawaiian Islands. The occurrence of similar ecomorphs on different islands results in part from convergent evolution and in part from colonization. Modified with permission from Gillespie (2004).

“ecomorphs,” but no site has more than one member of an ecomorph class. At least three of the ecomorphs are found on every island, but this similarity is only in part a result of convergent evolution; although some ecomorphs have evolved independently, and thus are more closely related to different ecomorphs on the same island, other ecomorphs have evolved only once or twice and have dispersed from one island to another (Fig. 17.3). Overall, a parsimony reconstruction of ecomorph evolution suggests the occurrence of six transitions from one ecomorph to another and eight instances of dispersal of an ecomorph from one island to another.

From this review, we can draw a number of conclusions about replicated adaptive radiations: in particular, they are quite rare, and limited almost exclusively to closely related taxa with poor dispersal ability that occur on islands or lakes in the same region. I will examine each of these points in turn.

THE RARITY OF REPLICATED ADAPTIVE RADIATIONS

Given the amount of attention paid to adaptive radiation in recent years, as well as the fact that the idea of community convergence has been discussed for more than three decades, the paucity of well documented cases can’t be a result of no one looking for them. Certainly, as more and more taxa are studied, additional unexpected cases will come to light, particularly in non-morphological characters, for which divergence within radiations and convergence among them may be harder to detect. Nonetheless, it seems

unlikely that replicated adaptive radiation is a widespread phenomenon that simply has not yet been noticed.

#### SPECIES-FOR-SPECIES MATCHING IS LIMITED TO CLOSELY RELATED TAXA

Many cases of evolutionary convergence of communities have been investigated for distantly related taxa, but evidence for species-for-species matching is rarely found (Wiens, 1989; Schluter, 1990; Price et al., 2000). Species-for-species matching has almost exclusively been detected among relatively closely related species, such as cichlid fish or anoles. The only exception to this generality is the possibility that benthic and pelagic fish are matched in postglacial lakes in different regions, even though they occur in distantly related fish families. However, such matching has not been demonstrated.<sup>463</sup>

Consider, for example, the adaptive radiation of day geckos (*Phelsuma*) on Indian Ocean islands (Fig. 17.4). Despite their nocturnal, gekkonid heritage, day geckoes—diurnal, as their name implies—show many similarities to anoles (see references in



FIGURE 17.4

Day geckos (*Phelsuma*). (a) *P. astriata*, Seychelles; (b) *P. ornata*, Mauritius. Photo courtesy of Luke Harmon.

463. Although divergence into benthic and pelagic ecomorphs has occurred in many different fish families, I am unaware of any study that has quantitatively compared the morphologies of different species pairs to investigate whether the pelagic ecomorphs of different types of fish are more similar to each other than any pelagic ecomorph is to its benthic counterpart, as the replicated adaptive radiation hypothesis would suggest. An alternative possibility is that even though evolutionary divergence has occurred in the same manner in each lake, this differentiation has not been great enough to override preexisting differences among clades (Stayton, 2006; Revell et al., 2007b).

Harmon et al., 2007, 2008). They are relatively small, arboreal, insectivorous, sit-and-wait foraging lizards which have large toepads and are usually green. Further like anoles, they are highly territorial and communicate through head movements.<sup>464</sup> *Phelsuma* has experienced independent radiations in the Mascarene, Seychelles, and Comoros islands, all of which are embedded phylogenetically in the much larger radiation on Madagascar, the presumed ancestral home of these lizards (Austin et al., 2004; Rocha et al., 2007; Harmon et al., 2008). Within each radiation, species have diversified morphologically and ecologically; as many as five species can occur sympatrically, and ecomorphological relationships similar to those in anoles have been detected (Harmon, 2005; Harmon et al., 2008). Moreover, sympatric species partition the habitat and shift their habitat use in the presence of other species (Harmon et al., 2007).

In other words, if ever there were two distantly related clades that seemed likely to have produced replicated adaptive radiations, *Phelsuma* and *Anolis*—separated evolutionarily by approximately 175 million years since their last common ancestor (Wiens et al., 2006)—are the ones. Yet, their radiations aren't mirror images. Compared to anoles, *Phelsuma* exhibits relatively little variation in limb or tail length, toepad size or habitat use. No twig day geckos exist, nor grass-bush species. There are—or were<sup>465</sup>—giant day geckos as large as the largest anole, but they tended to use rocks frequently and the largest species apparently was nocturnal (Vinson and Vinson, 1969). Microhabitat partitioning among sympatric day geckos sometimes occurs by tree type (palm versus non-palm), a phenomenon unknown in anoles (Thorpe and Crawford, 1979; Harmon et al., 2007). All in all, despite their many similarities, *Anolis* and *Phelsuma* have not diversified in the same ways, although in broad terms their radiations exhibit many similarities.<sup>466</sup>

Why haven't anoles and day geckos traveled down exactly the same evolutionary paths? All of the potential explanations for non-convergence mentioned in Chapter 16 are possibilities. For example, Indian Ocean and West Indian island environments may be different. One obvious example is that Madagascar, the ancestral cradle of *Phelsuma*,

464. But they move their heads side to side, rather than vertically up and down like iguanid lizards (Marcellini, 1977; Delheusy and Bels, 1994; Murphy and Myers, 1996).

465. The largest day gecko, *P. gigas*, which reached 190 mm SVL, went extinct on Rodrigues Island in the 19th century (Vinson and Vinson, 1969). The largest living species, *P. guentheri*, reaches a respectable 160 mm SVL (Austin et al., 2004), larger than most crown-giant anoles.

466. We might also wonder whether the *Phelsuma* radiations in the different island groups in the Indian Ocean have produced matched outcomes. This question has not yet been explicitly analyzed: a preliminary morphometric analysis suggests some cases of cross-island convergence, but also some species on one island—particularly in the Mascarenes and Madagascar—are unlike any species found on other islands (Harmon et al., in press).

A question more suited for *Animal Planet* concerns what would happen if *Anolis* and *Phelsuma* ever came together. Would the species interact? If so, who would win? This is more than a thought experiment, as both anoles and day geckos have been introduced to Hawaii (McKeown, 1996), and the Madagascar giant day gecko, *P. madagascariensis*, has not only been introduced to the Florida Keys (Krysko et al., 2003), but has been observed eating an *A. carolinensis* (J. Kolbe, pers. comm.). Anecdotal reports from Oahu claim that the day geckos are kicking the anoles' butts (i.e., supplanting them from areas previously colonized), but I am unaware of any scientific study of this battle of the arboreal green lizard radiations.

is also home to another large radiation of arboreal, diurnal, and insectivorous lizards. The presence of chameleons—specialized to use narrow, arboreal surfaces<sup>467</sup>—may have constrained the ecological diversification of day geckos.<sup>468</sup>

Alternatively, the differences in anole and day gecko radiations may reflect the different evolutionary potentialities of geckos and iguanid lizards. Geckos, for example, tend to have more laterally oriented limbs than iguanid lizards, which may place limits on the way geckos can adapt to different microhabitats. Moreover, gecko toepads have setal hairs that are elaborated to a much greater extent than the relatively simple setae of anoles, but anole setal densities are higher (Ruibal and Ernst, 1965; Williams and Peterson, 1982). Although a preliminary study found no difference in clinging ability between anoles and geckos (Irschick et al., 1996), further study would be useful because anecdotal evidence suggests that geckos are better clingers (e.g., many geckos will readily run across a ceiling upside down, something that anoles rarely do). If day geckos do, indeed, have greater clinging ability than anoles, then they may not have needed to diverge in limb length as much as anoles to adapt to using different microhabitats.<sup>469</sup> These, as well as a myriad of other differences, may have steered anole and day gecko evolution down different evolutionary paths, even if the adaptive landscapes in the two areas were extremely similar.

The *Anolis*–*Phelsuma* example is probably representative of most similar situations. As discussed in Chapter 16, similar clades diversifying in what appears to be similar environmental situations may realize very different evolutionary trajectories for two primary reasons. First, they are unlikely to occupy identical adaptive landscapes. For the most part, distantly related clades that are ecologically similar are unlikely to radiate in the same geographic area. As a result, such clades are not likely to experience the same patterns of selection because environments in different areas are unlikely to be the same; if nothing else, interactions with different sets of other clades are likely to produce different evolutionary outcomes. Conversely, when distantly related clades diversify in the same geographic area, they are likely to radiate in different ways to prevent competitive exclusion (Malagasy chameleons and day geckos possibly being an example).<sup>470</sup>

Second, distantly related clades tend to differ in so many ways that it is unlikely that entire evolutionary radiations will unfold in the same way. The differences between *Phelsuma* and *Anolis* would constitute different initial starting points for radiation, but also probably reflect different genetic and development constraints (see Chapter 16).

467. Although, paradoxically, one clade, *Brookesia*, is primarily terrestrial, despite possessing the modifications of the hands and feet for grasping narrow surfaces.

468. Chameleon species also occur naturally alongside *Phelsuma* in the Comoros and on some islands in the Seychelles, but are not found naturally in the Mascarene Islands.

469. In this regard, I should add that day geckos have no claws! Whether this clawlessness is a testament to the efficacy of gecko toepads or a constraint on habitat use, or both, is unknown.

470. In theory, one could imagine an archipelago in which Clade A radiates in half the islands and Clade B in the other half so that the two clades do not coexist, but I am unaware of any such cases.

Certainly, cases of convergence among distantly related species are common (Conway Morris, 2003), but it may be too much to expect that entire radiations of distant relatives will evolve in lockstep. Only closely related clades are likely both to start with similar initial phenotypes and to have developmental and genetic systems that bias evolutionary diversification to occur in similar ways.

#### REPLICATED ADAPTIVE RADIATIONS LIMITED TO ISLANDS AND LAKES

The reason that replicated adaptive radiations are limited to islands and lakes is an extension of the reason they only occur among closely related clades. Radiations on different continents usually, though not always, will be accomplished by distantly related clades which are likely to diversify in different ways (Pianka, 1986; Cadle and Greene, 1993; Losos, 1994a). Moreover, clades radiating on different continents are unlikely to experience identical selective pressures. Not only will the different biota lead to divergent adaptive landscapes due to variation in regimes of predation, competition, disease, and so on, but the number of simultaneously radiating clades that co-occur in continental settings will be greater. That is, the depauperate faunas on islands allow a single clade to radiate by itself into wide open ecological space. By contrast, when such space occurs in continental settings (perhaps due to appearance of a new resource or extinction of a previously dominant group), many clades may radiate simultaneously, limiting the opportunities available to any one clade.

#### POOR DISPERSAL ABILITY

Few cases of replicated adaptive radiation are known in flying organisms.<sup>471</sup> The reason is obvious. Evolutionary replication is most likely when it occurs on separate islands or lakes in the same region, so that the environments are likely to be as similar as possible. However, if species in the radiating clade are able to move back and forth between evolutionary arenas, then independent radiations will not occur. The faunas in the different areas may end up being matched perfectly, but that will result because the matching species are closely related, rather than convergent. This phenomenon is seen to some extent in the Hawaiian *Tetragnatha* discussed above. By contrast, for non-flying animals such as lizards or frogs, dispersal between islands probably occurs much less frequently (Chapter 6), setting the stage for replicated adaptive radiation.

In summary, replicated adaptive radiations are very rare, and *Anolis* is perhaps the most extensive and best documented example. Why replicated adaptive radiation has occurred in these lizards seems straightforward. Earlier in the chapter I discussed why

471. The only potential example of which I'm aware is the convergence of *Myotis* bats in different regions of the northern hemisphere discussed in Footnote 459.

*Anolis* has radiated to such a great extent; here I've shown that the reason for evolutionary replication is that Greater Antillean *Anolis* has all the necessary ingredients: radiation of closely related, relatively poorly-dispersing species on isolated islands with low diversity in the same general region.

Still, we might ask why replicated adaptive radiation is so uncommon, particularly given that it is seen so readily in laboratory experiments with microbial systems. One possibility, of course, is that the environment—so easy to control in the laboratory—is rarely so similar in different localities in nature. In other words, the lack of replicated adaptive radiation reflects a lack of replicated adaptive landscapes. The other possibility is that adaptive radiation doesn't occur all that often, and rarely occurs multiple times in closely related clades—with sufficiently similar phenotypes, ecology and evolutionary potentiality—in sufficiently similar environments. If we accept the view that the acquisition of different developmental and genetic systems and other constraining factors prevent all but closely related taxa from diversifying in the same way, then it may simply be that closely related taxa rarely get the opportunity to radiate multiple times in highly similar environments, and *Anolis* on Greater Antillean islands may be one of those few exceptions.

#### **PARALLELISM, GENETIC CONSTRAINT, AND ANOLE ADAPTIVE RADIATION**

One reason that closely related clades may diversify in the same way is that they share similar developmental and genetic systems. Hence, when species from such clades are subjected to the same selective conditions, they may adapt in genetically and developmentally similar ways (Haldane, 1932; Gould, 2002; Hoekstra, 2006). Recent studies have provided many examples in a wide range of organisms and traits in which parallel phenotypic change in multiple populations or closely related species is caused by similar genetic changes (e.g., Sucena et al., 2003; Colosimo et al., 2005; Derome and Bernatchez, 2006; Derome et al., 2006; Hoekstra et al., 2006; Protas et al., 2006; Shapiro et al., 2006; Whittall et al., 2006).<sup>472</sup> Whether convergence of the anole ecomorphs similarly has been accomplished by the same genetic means remains to be seen; the combination of the *A. carolinensis* genome and the status of the vertebrate limb and craniofacial region as model systems in developmental biology (e.g., Niswander, 2002; Tickle, 2002; Abzhanov et al., 2004, 2006; Stopper and Wagner, 2005) suggests that we may soon have an answer to this question.

In the previous chapter, I argued that genetic constraints are unlikely to have played a role in shaping the convergence of the anole ecomorphs. Nonetheless, if this convergence

472. Of course, this is not always the case; some times convergent phenotypic evolution is accomplished by different genetic changes, even in closely related species (e.g., Hoekstra and Nachman, 2003; Hoekstra et al., 2006; Wittkopp et al., 2004).

has been accomplished by the same genetic changes, then we may have to look more carefully at the possibility that not just adaptation alone, but the interplay between adaptation and constraint, has been responsible for the replicated adaptive radiation of Greater Antillean anoles (Gould, 2002).

However, even if convergence in *Anolis* has occurred by way of identical genetic changes, it does not necessarily follow that limited genetic options—i.e., constraints—have played an important role in shaping the anole radiations. Rather, even if they were completely unconstrained in terms of the direction in which they could evolve, species with similar genetic architecture might be expected to adapt to similar selective conditions by means of the same genetic changes (Gould, 2002).

### **ANOLE FUTURES: BIODIVERSITY, CONSERVATION, AND THE FATE OF ANOLIS**

It seems appropriate to end this book by discussing anole biological diversity and the extent to which it is likely to be imperiled in the years to come. On the positive side, anole biodiversity may be substantially greater than we presently realize. New species are being discovered at a high rate, mostly in Central and South America, but also in Cuba, primarily in the mountains in the east (e.g., Fong and Garrido, 2000; McCranie et al., 2000; Garrido and Hedges, 2001; Köhler et al., 2001, 2007; Köhler and Sunyer, 2008; Navarro et al., 2001; Pacheco and Garrido, 2004; Hulebak et al., 2007; Poe and Ibañez, 2007; Poe and Yañez-Miranda, 2007; Ugueto et al., 2007). Most of these are genuinely new, previously unknown taxa, although in some cases the new species result from breaking of one species into several.<sup>473</sup> Given the regularity with which these new forms are being discovered, who knows how many anole species there are? Moreover, as discussed in Chapter 14, molecular data raise the possibility that many widespread species may actually be complexes of parapatric species. Anole diversity is probably substantially underestimated.

On the negative side, anoles experience the same pressures that confront much of the world's fauna and flora: habitat destruction, global climate change, invasive species, and overexploitation (Wilcove et al., 1998; Gibbon et al., 2000). Some of these, however, are much graver threats than others.

#### **HABITAT DESTRUCTION**

As is often the case (Wilcove et al., 1998; Gibbon et al., 2000), habitat destruction is probably the biggest threat. The most extreme case is Haiti, where less than 1% of the land has forest cover (Hedges and Woods, 1993) and several species—most notably the aquatic anole, *A. eugenegrahami*—are in grave jeopardy. More generally, approximately

473. This taxonomic “splitting” perhaps has been excessive in a few cases.



90% of most West Indian habitats have been degraded; to a large extent, much of the change in West Indian habitats has involved a shift from closed forest to open forest and agricultural lands (Mittermeier et al., 1999). The disappearance of *A. roosevelti*, last seen more than 75 years ago, may be a result of the extensive habitat destruction that occurred on the islands near Puerto Rico early in the last century (Mayer, 1989). Similarly, much of the original forest—both rainforest and dry forest—in Central America is gone or severely degraded and deforestation rates in some areas are among the highest in the world (Janzen, 1988; Mittermeier et al., 1999). One species from Mexico, *A. naufragus*, is known only from one locality, which was almost totally deforested subsequent to its discovery (Campbell et al., 1989). Other than *A. roosevelti* and *A. naufragus*, no species are currently suspected to have gone extinct, but this will change in the years to come.

One ironic twist resulting from this habitat degradation is that the most common anoles today probably were much less plentiful before the arrival of humans. In Cuba, for example, the most abundant species are *A. sagrei* and the green anoles, *A. porcatius* and *A. allisoni*, species which occur in open, sunny habitats and which are common in and around human habitations. In contrast, within intact forests throughout much of the island, *A. sagrei* is much less abundant and the green anoles less commonly seen (although they may be more abundant in the sun-drenched canopy). In prehistoric times, when Cuba was mostly forested, these species must have been much less plentiful and more patchily distributed than they are today. Similarly, *A. sericeus*, a Central American species often found in edge habitats, is probably more common today than it was in the past (Henderson and Fitch, 1975). Conversely, many forest-dwelling species, particularly those that require pristine forest, probably were much more abundant in times past.<sup>474</sup> Such species, particularly those with small geographic ranges today, face an uncertain future in many places.

#### GLOBAL CLIMATE CHANGE

Global warming poses many threats to species and ecosystems. The most direct is from increased temperature and changes in precipitation, to which populations could respond in three ways: by adapting, by shifting their range, or by going extinct (Parmesan, 2006). Given the evolutionary lability of anole thermal and hydric physiology (Chapters 10 and 12), we might expect that anoles—more than many other taxa—may be able to adapt

474. These recent shifts caution against evolutionary interpretations based on current distributions and abundance. On the other hand, the major conclusions of this book concerning ecomorph ecology and evolution are not affected by the realization that much forested habitat has been converted to more open habitats because the ecomorphs usually occur in all but the most degraded habitats, albeit sometimes represented by different species in closed and open forest. Thus, general conclusions from work conducted today about ecomorph ecology and evolution probably apply to the conditions that existed prior to the arrival of humans, even if the relative mix of open and closed habitats has changed. Research conducted in the most degraded habitats (e.g., agricultural fields), where usually only 1–2 anole species occur, usually at low densities (e.g., Glor et al., 2001a), probably has little applicability to prehistoric times, but relatively little work is conducted in such areas.

to changing temperatures and precipitation regimes. On the other hand, these changes may occur too rapidly and anole species may be forced to shift their ranges if they are to avoid extinction.

Broad scale predictive analyses using interpolated climate data and remote sensing approaches (Chapter 10) have not yet been performed for anoles, but one such study for Mexican butterflies, birds, and mammals predicted relatively few extinctions, but widespread range shifts and changes in the composition of local communities (Peterson et al., 2002). Montane populations may be particularly vulnerable because their geographic ranges are often small and the potential to shift to higher elevations as temperature increases may be limited; at the extreme, populations shifting upward may run out of mountain (Parmesan, 2006). Just that has apparently happened in the cloud forests of Costa Rica, where many frog species have disappeared (Pounds et al., 1999, 2006). Even in lowland areas, relatively cool-adapted, closed forest species may be imperiled as temperatures increase and the habitat becomes more suitable for more warm-adapted, open habitat species (Tewksbury et al., 2008).

The only relevant data on anoles comes from the Monteverde Cloud Forest Preserve at 1,540 m elevation in Costa Rica, where two formerly abundant montane species, *A. tropidolepis* and *A. altae*, disappeared in the mid-1990s, while *A. intermedius*, a species also found at lower elevations and thus presumably better adapted to warmer conditions, has not experienced a change in population size (Fig. 17.5; Pounds et al., 1999, 2006).

Climate change can also affect populations in many indirect ways, by altering the composition of communities and by changing the functioning of ecosystems (Parmesan, 2006). For example, the disappearance of montane frogs may not be due to changes in temperature and moisture levels per se, but rather to the resulting spread of pathogenic chytrid fungus facilitated by these changes (Pounds et al., 2006). One possible example involving anoles relates to the substantial decline in leaf-litter anoles at the La Selva Biological Station in Costa Rica, which may be related to reduced litter accumulation due to changing patterns of rainfall (Whitfield et al., 2007).

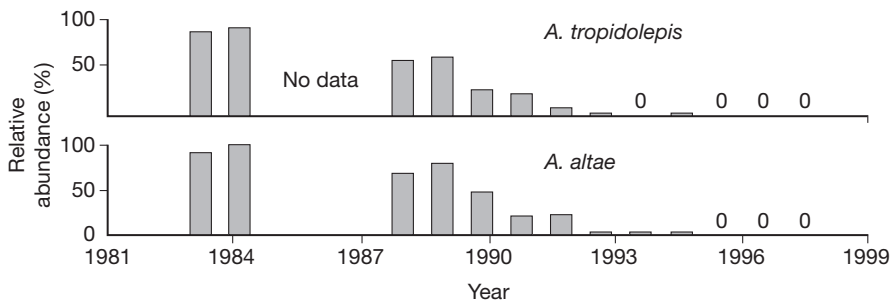


FIGURE 17.5 Decline in Costa Rican montane anole populations. No data were collected 1984–1987. Modified with permission from Pounds et al. (1999).

Invasive species have had calamitous impacts on native species and ecosystems (Wilcove et al., 1998; Mooney and Hobbs, 2000). Documented effects on anoles, however, have been relatively minor. Despite the many introductions of anoles from one place to another throughout the West Indies and elsewhere, few examples exist of introduced species negatively affecting the natives. Rather, in most cases, introduced anoles have had relatively little success when invading in the presence of ecologically similar species (Chapter 11), and many invaders are restricted to human environs and severely disturbed habitats (e.g., Fitch et al., 1989; Henderson and Powell, 2001; Greene et al., 2002; White and Hailey, 2006; Powell and Henderson, 2008b).

Probably the best known counterexample is the effect of *A. sagrei* on *A. carolinensis* in Florida. Concomitant with the expansion of *A. sagrei* throughout Florida, *A. carolinensis* has apparently become much scarcer. There can be no doubt that *A. sagrei* has a negative effect on *A. carolinensis* (or its close relatives elsewhere [Schoener, 1975; Losos and Spiller, 1999; Campbell, 2000]), but the conversion of much of Florida into parking lots, roadways, and other prime *A. sagrei* habitat probably has something to do with *A. carolinensis*'s decline as well. More generally, though, the survival of *A. carolinensis* is probably not threatened. Rather, after colonizing Florida several million years ago, *A. carolinensis* probably experienced ecological release in the absence of other anoles. Now that *A. sagrei* is present, *A. carolinensis* seems to have retreated to its ancestral, trunk-crown niche, reestablishing the pattern of niche partitioning and sympatric coexistence that initially evolved in Cuba between the *carolinensis* and *sagrei* clades and which is evident today throughout Cuba, the Bahamas, and Little Cayman (Chapter 11; Losos, 1996c).

Aside from this case, few examples of negative effects of an introduced anole on other anole species have been reported. In several cases, an introduced species has caused habitat shifts in other species, either native (e.g., Losos et al., 1993a) or introduced (e.g., Wingate, 1965; Salzburg, 1984). Evidence of population declines resulting from the introduced species is also scant and limited to urban settings. For example, in parts of Santo Domingo, the introduced Cuban green anole, *A. porcatius*, seems to have had a negative effect on the Hispaniolan green anole, *A. chlorocyanus* (Powell et al., 1990; Powell and Henderson, 2008b; see also Fitch et al. [1989] for a similar example).

Effects of other introduced species on anoles have also been rarely documented. The only clearly detrimental impact is the introduction of the brown tree snake to Guam, which has eliminated *A. carolinensis*, also introduced, from natural habitats (Fritts and Rodda, 1998). Mongooses have been widely introduced throughout the West Indies and have ravaged populations of many species of mammals, birds, and reptiles (Seaman and Randall, 1962; Case and Bolger, 1991; Powell and Henderson, 2005). Although anoles are often a major component of mongoose diets (Waide and Reagan, 1983; Vilella, 1998; Wilson and Vogel, 1999), I am unaware of any reports of substantial population level effects, although they probably occur in some places.

## OVEREXPLOITATION

Anoles are not widely used by local people for any purpose. As far as I know, anoles are not eaten by people anywhere—for good reason, as I imagine they'd be pretty crunchy. On the other hand, anoles are commercially collected, primarily for export for the pet trade. I am unaware of global data on the magnitude of the trade, but it can be substantial. For example, from 1998–2002, more than 250,000 *A. carolinensis* and more than 100,000 *A. sagrei* were legally exported from the United States; in the same period, as many as 30,000 anoles of various species may have been imported into the U.S. (M. Schlaepfer, pers. comm.).<sup>475</sup> Figures for imports into other countries are unavailable, but may be large because there are many reptile hobbyists in Europe. The United States is the only country likely to have much domestic trade in anoles, and these numbers, too, are great because many *A. carolinensis* and *A. sagrei* are captured and sold within the United States, not only for the pet trade, but also to laboratories, educational supply companies, and zoos.<sup>476</sup> Data on the magnitude of this trade is scarce, but more than 250,000 anoles were collected in Florida in a four-year period in the early 1990s (Enge, 2005);<sup>477</sup> in Louisiana, nearly a million *A. carolinensis* a year were collected in the mid-1990s, but that number has declined to around 350,000 per year in 2006, apparently as a result of declining demand, rather than shortage of anoles (J. Boundy, pers. comm.).

These are not insignificant numbers, and the pet trade can certainly threaten species, particularly if they have small geographic ranges and are easily collected (Stuart et al., 2006). Nonetheless, most of the anole species being collected are very abundant and the trade in most other species is probably much smaller. Occasionally there are claims on the internet or elsewhere that collecting is threatening particular anole species, usually those found on small islands. Although this is certainly possible, no data are available to substantiate such claims.

## WHITHER ANOLIS?

What will the future hold for *Anolis*? Certainly, species will be lost. Indeed, who knows how many species—unknown and unlamented—have disappeared in Central and South America as a result of loss of their habitat before they could be discovered? No doubt, more species will perish as their environment is destroyed. Moreover, habitat fragmentation will hinder the ability of species to shift their geographic and elevational ranges as climate changes. Invasive species and collecting for the pet trade may have some effect as well. Without question, anole biodiversity will take a hit.

475. Data from the Lemis data base of the United States Fish and Wildlife Service. Importation numbers may be overestimates because exports are sometimes mistakenly recorded as imports (Schlaepfer et al., 2005).

476. Where they are often fed to other animals!

477. This number may be a substantial underestimate because dealers were not required to report the number of the introduced *A. sagrei* and as a result, most did not do so.

On the other hand, the survival of the clade as a whole is not jeopardized, and anoles will fare much better than many other taxa. Quite a few anole species do well in human-disrupted habitats (Henderson and Powell, 2001; Powell and Henderson, 2008b) and, with their great behavioral and evolutionary flexibility, anoles are better prepared than most species to adjust to changing conditions in both the short- and long-term.

A theme of this book has been the marriage of observation and experiment, of historical inference and present-day investigation. It is regrettable that humans have messed up the world in so many ways, and that our fellow fauna and flora have paid so heavy a price, and will continue to do so. Nonetheless, these disruptions set the evolutionary stage for the sort of research that could scarcely be imagined, much less intentionally be put into practice.

Several of the hallmarks of anole evolution are that they they adapt quickly to new environmental conditions; they respond behaviorally, ecologically, and evolutionary to selective pressures resulting from the presence of other species; and they diversify evolutionarily in response to ecological opportunity and the absence of other, similar species. In this book, I have laid out the evidence to support these claims and have suggested small scale ways to test them.

But we humans are creating the opportunity to test these ideas on a much more massive scale. Can anoles really adapt rapidly to environmental change? We're changing the environment in a myriad of ways, and we will see just how rapidly they can evolve, whether some types of change are more easily accommodated than others, and whether some types of species are more evolutionarily adept than others. Does the presence of other species spark evolutionary adjustment? We're adding and subtracting species all over the place. Does adaptive radiation result when anoles colonize new areas with open environmental space? Let's see what they'll do in Hawaii, Taiwan, Guam, and the many other previously anole-free places they'll eventually occupy.

Don't get me wrong, I'd much rather appreciate and study anoles in pristine habitats in a world spared the ravages of mankind. But this is the world in which we live. History is in the past, and usually we are hard pressed to study the processes underlying it, but anoles may be an exception. Environmental disruptions have recreated all aspects of the factors thought to have been important in the genesis of their incredibly rich biological diversity. Even as we strive to minimize further environmental damage, it is our rare opportunity to study in the present the same phenomena and processes that were so generous to *Anolis* in the past.

Of course, such studies are just an adjunct to ongoing studies of natural populations in less disrupted habitats. We have learned much from such studies over the course of the past four decades, knowledge that has been valuable not only for understanding anole biology, but also for addressing broader questions in ecology, evolutionary biology, and other disciplines. As this book has made clear, however, we have much more yet to learn. Indeed, the more we learn, and the more we develop new methods and new ideas, the more we realize what we have yet to discover. Most of the general statements about

anole biology made in this book are based on data from relatively few species, usually less than 10% of the nearly 400 described anole species. For many interesting and important topics, we have data only from a handful of species. More detailed study on many species—directed, where possible, toward addressing questions of broad and general interest—is needed to fully comprehend the patterns and underlying processes involved in the genesis of anole biological diversity.

Anoles are an evolutionary marvel. They, along with eleutherodactyline frogs, are the dominant vertebrate element of West Indian ecosystems. In the mainland neotropics, they are nearly unrivalled in terms of their species diversity. They are excellent—nearly perfect—subjects for scientific studies of biological diversity. More generally, they are simply delightful creatures to observe and study. Reverend Lockwood (1876, p.16) had it right more than a century and a quarter ago when he said that *Anolis* “is everything that is commendable: clean, inoffensive, pretty and wonderfully entertaining; provoking harmless mirth, and stirring up in the thinker the profoundest depths of his philosophy.”

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## AFTERWORD

### AN ANOLE BESTIARY

In this section, I present a list of all West Indian anole species and of all mainland species mentioned in the text. In addition, Figure A.1 presents the complete phylogeny from Nicholson et al. [2005] that served as the basis for several figures in this book and was used for all original statistical analyses presented here.

### WEST INDIAN SPECIES

This list is based primarily on Caribherp (<http://evo.bio.psu.edu/caribherp/lists/wi-list.htm>), last modified December 6, 2007 (at the time of writing). I have not included several island populations that are normally considered as subspecies of *A. marmoratus* or *A. sagrei* (e.g., *A. m. kahouannensis* from the island of Kahouanne offshore from Guadeloupe and *A. s. luteosignifer* from Cayman Brac) and for which no recent phylogenetic analysis has presented a compelling argument for elevation to species status. The two species from Isla Providencia and San Andrés in the southwestern Caribbean are included. Islands in the Lesser Antilles are only distinguished into northern and southern groups because some species occur on multiple islands. Ecomorph designations are based on Beuttel and Losos (1999); species not included in that study are assigned to ecomorph based on natural history information in the literature and examination of specimens. Ecomorph designations are not applied to Lesser Antillean species, although



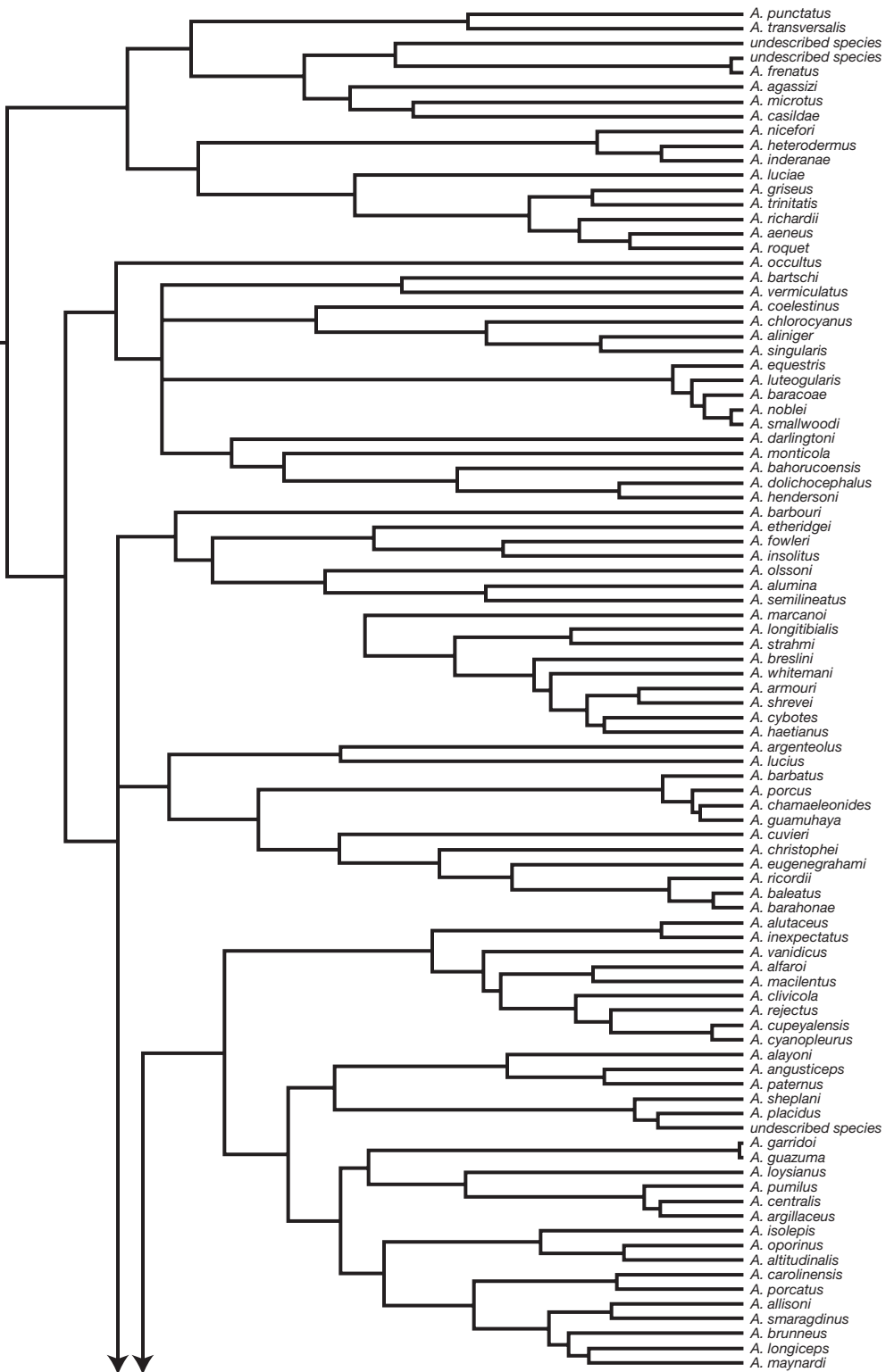
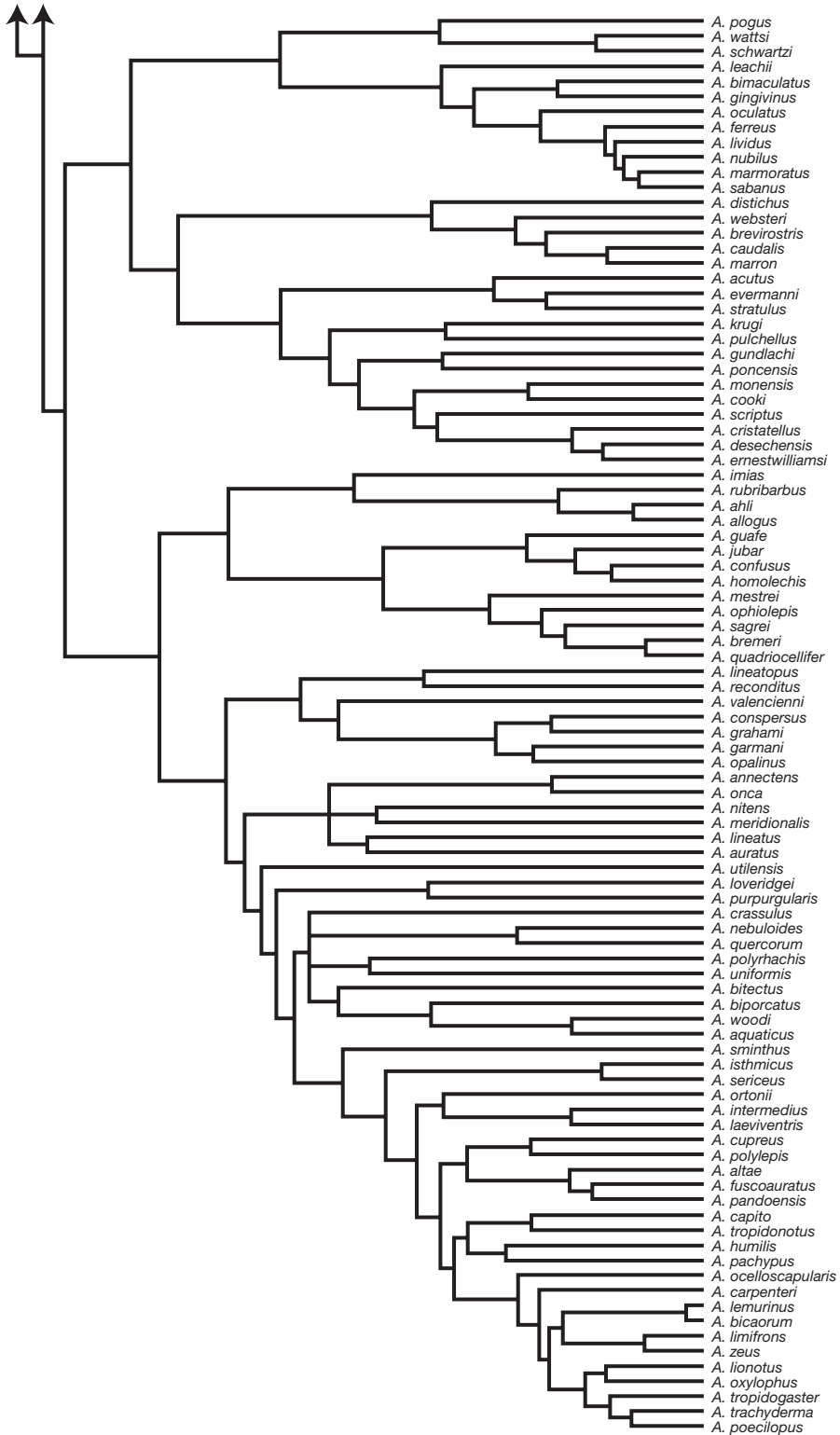


FIGURE A.1  
 Phylogeny of anoles used for figures and analyses in this book from Nicholson et al. (2005). Branch lengths were made proportional to time using the program r8s (Sanderson, 2003).



some species qualify as members of particular ecomorph classes (see Chapter 4 and Losos and de Queiroz [1997]). This column is also left blank for unique anoles.

Series/Clade names correspond to those in Fig. 5.6 and follow Savage and Guyer [1989] and Brandley and de Queiroz [2004]. The following Series were recognized so that all taxa would be monophyletic: the *insolitus* Series, comprised of *A. insolitus*, *A. etheridgei*, and *A. fowleri*; the *bartschi* Series composed of *A. bartschi* and *A. vermiculatus*; and the *alutaceus*, *hendersoni*, and *semilineatus* Series (each raised from Species Group status). The clades Chamaeleolis and Chamaelinorops might also be considered series. The two members of the mainland Norops radiation that have recolonized the West Indies are listed simply as Norops because phylogenetic relationships within this clade are not well established (Chapter 5).

SPECIES	ISLAND	ECOMORPH	SERIES/CLADE
<i>Anolis acutus</i>	St. Croix		<i>crisatellus</i>
<i>Anolis aeneus</i>	Southern Lesser Antilles		<i>roquet</i>
<i>Anolis Chamaeleolis agueroi</i>	Cuba		Chamaeleolis
<i>Anolis ahli</i>	Cuba	Trunk-Ground	<i>sagrei</i>
<i>Anolis alayoni</i>	Cuba	Twig	<i>angusticeps</i>
<i>Anolis alfaroii</i>	Cuba	Grass-Bush	<i>alutaceus</i>
<i>Anolis aliniger</i>	Hispaniola	Trunk-Crown	<i>chlorocyanus</i>
<i>Anolis allisoni</i>	Cuba	Trunk-Crown	<i>carolinensis</i>
<i>Anolis allogus</i>	Cuba	Trunk-Ground	<i>sagrei</i>
<i>Anolis altavelensis</i>	Hispaniola	Trunk	<i>distichus</i>
<i>Anolis altitudinalis</i>	Cuba	Trunk-Crown	<i>carolinensis</i>
<i>Anolis alumina</i>	Hispaniola	Grass-Bush	<i>semilineatus</i>
<i>Anolis alutaceus</i>	Cuba	Grass-Bush	<i>alutaceus</i>
<i>Anolis anfiloquioi</i>	Cuba	Grass-Bush	<i>alutaceus</i>
<i>Anolis angusticeps</i>	Cuba, Bahamas	Twig	<i>angusticeps</i>
<i>Anolis argenteolus</i>	Cuba		<i>lucius</i>
<i>Anolis argillaceus</i>	Cuba		<i>angusticeps</i>
<i>Anolis armouri</i>	Hispaniola	Trunk-Ground	<i>cybotes</i>
<i>Anolis bahorucoensis</i>	Hispaniola	Grass-Bush	<i>hendersoni</i>
<i>Anolis baleatus</i>	Hispaniola	Crown-Giant	<i>ricordii</i>
<i>Anolis baracoae</i>	Cuba	Crown-Giant	<i>equestris</i>
<i>Anolis barahonae</i>	Hispaniola	Crown-Giant	<i>ricordii</i>
<i>Anolis Chamaeleolis barbatus</i>	Cuba		Chamaeleolis
<i>Anolis Chamaelinorops barbouri</i>	Hispaniola		Chamaelinorops

SPECIES	ISLAND	ECOMORPH	SERIES/CLADE
<i>Anolis bartschi</i>	Cuba		<i>bartschi</i>
<i>Anolis bimaculatus</i>	Northern Lesser Antilles		<i>bimaculatus</i>
<i>Anolis birama</i>	Cuba	Trunk-Ground	<i>sagrei</i>
<i>Anolis bremeri</i>	Cuba	Trunk-Ground	<i>sagrei</i>
<i>Anolis breslini</i>	Hispaniola	Trunk-Ground	<i>cybotes</i>
<i>Anolis brevirostris</i>	Hispaniola	Trunk	<i>distichus</i>
<i>Anolis brunneus</i>	Bahamas	Trunk-Crown	<i>carolinensis</i>
<i>Anolis caudalis</i>	Hispaniola	Trunk	<i>distichus</i>
<i>Anolis centralis</i>	Cuba		<i>angusticeps</i>
<i>Anolis Chamaeleolis chamaeleonides</i>	Cuba		Chamaeleolis
<i>Anolis chlorocyanus</i>	Hispaniola	Trunk-Crown	<i>chlorocyanus</i>
<i>Anolis christophei</i>	Hispaniola		<i>christophei</i>
<i>Anolis clivicola</i>	Cuba	Grass-Bush	<i>alutaceus</i>
<i>Anolis coelestinus</i>	Hispaniola	Trunk-Crown	<i>chlorocyanus</i>
<i>Anolis concolor</i>	San Andrés		Norops
<i>Anolis confusus</i>	Cuba	Trunk-Ground	<i>sagrei</i>
<i>Anolis conspersus</i>	Grand Cayman	Trunk-Crown	<i>grahami</i>
<i>Anolis cooki</i>	Puerto Rico	Trunk-Ground	<i>cristatellus</i>
<i>Anolis cristatellus</i>	Puerto Rico	Trunk-Ground	<i>cristatellus</i>
<i>Anolis cupeyalensis</i>	Cuba	Grass-Bush	<i>alutaceus</i>
<i>Anolis cuvieri</i>	Puerto Rico	Crown-Giant	<i>ricordii</i>
<i>Anolis cyanopleurus</i>	Cuba	Grass-Bush	<i>alutaceus</i>
<i>Anolis cybotes</i>	Hispaniola	Trunk-Ground	<i>cybotes</i>
<i>Anolis darlingtoni</i>	Hispaniola	Twig	<i>darlingtoni</i>
<i>Anolis delafuentei</i>	Cuba	Trunk-Ground	<i>sagrei</i>
<i>Anolis desecheensis</i>	Desecheo	Trunk-Ground	<i>cristatellus</i>
<i>Anolis distichus</i>	Hispaniola, Bahamas	Trunk	<i>distichus</i>
<i>Anolis dolichocephalus</i>	Hispaniola	Grass-Bush	<i>hendersoni</i>
<i>Anolis equestris</i>	Cuba	Crown-Giant	<i>equestris</i>
<i>Anolis ernestwilliamsi</i>	Carrot Rock	Trunk-Ground	<i>cristatellus</i>
<i>Anolis etheridgei</i>	Hispaniola		<i>insolitus</i>
<i>Anolis eugenegrahami</i>	Hispaniola		<i>eugenegrahami</i>
<i>Anolis evermanni</i>	Puerto Rico	Trunk-Crown	<i>cristatellus</i>
<i>Anolis extremus</i>	Southern Lesser Antilles		<i>roquet</i>

(Continued on following page)

SPECIES	ISLAND	ECOMORPH	SERIES/CLADE
<i>Anolis fairchildi</i>	Bahamas	Trunk-Crown	<i>carolinensis</i>
<i>Anolis ferreus</i>	Northern Lesser Antilles		<i>bimaculatus</i>
<i>Anolis fowleri</i>	Hispaniola		<i>insolitus</i>
<i>Anolis fugitivus</i>	Cuba	Grass-Bush	<i>alutaceus</i>
<i>Anolis garmani</i>	Jamaica	Crown-Giant	<i>grahami</i>
<i>Anolis garridoi</i>	Cuba	Twig	<i>angusticeps</i>
<i>Anolis gingivinus</i>	Northern Lesser Antilles		<i>bimaculatus</i>
<i>Anolis grahami</i>	Jamaica	Trunk-Crown	<i>grahami</i>
<i>Anolis griseus</i>	Southern Lesser Antilles		<i>roquet</i>
<i>Anolis guafe</i>	Cuba	Trunk-Ground	<i>sagrei</i>
<i>Anolis Chamaeleolis guamuhaya</i>	Cuba		Chamaeleolis
<i>Anolis guazuma</i>	Cuba	Twig	<i>angusticeps</i>
<i>Anolis gundlachi</i>	Puerto Rico	Trunk-Ground	<i>crstatellus</i>
<i>Anolis haetianus</i>	Hispaniola	Trunk-Ground	<i>cybotes</i>
<i>Anolis hendersoni</i>	Hispaniola	Grass-Bush	<i>hendersoni</i>
<i>Anolis homolechis</i>	Cuba	Trunk-Ground	<i>sagrei</i>
<i>Anolis imias</i>	Cuba	Trunk-Ground	<i>sagrei</i>
<i>Anolis incredulus</i>	Cuba	Trunk-Crown	<i>carolinensis</i>
<i>Anolis inexpectatus</i>	Cuba	Grass-Bush	<i>alutaceus</i>
<i>Anolis insolitus</i>	Hispaniola	Twig	<i>insolitus</i>
<i>Anolis isolepis</i>	Cuba	Trunk-Crown	<i>carolinensis</i>
<i>Anolis juangundlachi</i>	Cuba	Grass-Bush	<i>alutaceus</i>
<i>Anolis jubar</i>	Cuba	Trunk-Ground	<i>sagrei</i>
<i>Anolis koopmani</i>	Hispaniola	Grass-Bush	<i>monticola</i>
<i>Anolis krugi</i>	Puerto Rico	Grass-Bush	<i>crstatellus</i>
<i>Anolis leachii</i>	Northern Lesser Antilles		<i>bimaculatus</i>
<i>Anolis lineatopus</i>	Jamaica	Trunk-Ground	<i>grahami</i>
<i>Anolis litoralis</i>	Cuba		<i>angusticeps</i>
<i>Anolis lividus</i>	Northern Lesser Antilles		<i>bimaculatus</i>
<i>Anolis longiceps</i>	Navassa	Trunk-Crown	<i>carolinensis</i>
<i>Anolis longitibialis</i>	Hispaniola	Trunk-Ground	<i>cybotes</i>
<i>Anolis loysianus</i>	Cuba	Trunk	<i>angusticeps</i>
<i>Anolis luciae</i>	Southern Lesser Antilles		<i>roquet</i>
<i>Anolis lucius</i>	Cuba		<i>lucius</i>
<i>Anolis luteogularis</i>	Cuba	Crown-Giant	<i>equestris</i>
<i>Anolis macilentus</i>	Cuba	Grass-Bush	<i>alutaceus</i>

SPECIES	ISLAND	ECOMORPH	SERIES/CLADE
<i>Anolis marcanoii</i>	Hispaniola	Trunk-Ground	<i>cybotes</i>
<i>Anolis marmoratus</i>	Northern Lesser Antilles		<i>bimaculatus</i>
<i>Anolis marron</i>	Hispaniola	Trunk	<i>distichus</i>
<i>Anolis maynardi</i>	Little Cayman	Trunk-Crown	<i>carolinensis</i>
<i>Anolis mestrei</i>	Cuba	Trunk-Ground	<i>sagrei</i>
<i>Anolis monensis</i>	Mona	Trunk-Ground	<i>cratatellus</i>
<i>Anolis monticola</i>	Hispaniola		<i>monticola</i>
<i>Anolis noblei</i>	Cuba	Crown-Giant	<i>equestris</i>
<i>Anolis nubilis</i>	Northern Lesser Antilles		<i>bimaculatus</i>
<i>Anolis occultus</i>	Puerto Rico	Twig	<i>occultus</i>
<i>Anolis oculatus</i>	Northern Lesser Antilles		<i>bimaculatus</i>
<i>Anolis olssoni</i>	Hispaniola	Grass-Bush	<i>semilineatus</i>
<i>Anolis opalinus</i>	Jamaica	Trunk-Crown	<i>grahami</i>
<i>Anolis ophiolepis</i>	Cuba	Grass-Bush	<i>sagrei</i>
<i>Anolis oporinus</i>	Cuba	Trunk-Crown	<i>carolinensis</i>
<i>Anolis paternus</i>	Cuba	Twig	<i>angusticeps</i>
<i>Anolis pigmaequestrus</i>	Cuba	Crown-Giant	<i>equestris</i>
<i>Anolis pinchoti</i>	Providencia		Norops
<i>Anolis placidus</i>	Hispaniola	Twig	<i>angusticeps</i>
<i>Anolis pogus</i>	Northern Lesser Antilles		<i>bimaculatus</i>
<i>Anolis poncensis</i>	Puerto Rico	Grass-Bush	<i>cratatellus</i>
<i>Anolis porcatius</i>	Cuba	Trunk-Crown	<i>carolinensis</i>
<i>Anolis Chamaeleolis porcus</i>	Cuba		Chamaeleolis
<i>Anolis pulchellus</i>	Puerto Rico	Grass-Bush	<i>cratatellus</i>
<i>Anolis pumilus</i>	Cuba		<i>angusticeps</i>
<i>Anolis quadriocellifer</i>	Cuba	Trunk-Ground	<i>sagrei</i>
<i>Anolis reconditus</i>	Jamaica		<i>grahami</i>
<i>Anolis rejectus</i>	Cuba	Grass-Bush	<i>alutaceus</i>
<i>Anolis richardii</i>	Southern Lesser Antilles		<i>roquet</i>
<i>Anolis ricordii</i>	Hispaniola	Crown-Giant	<i>ricordii</i>
<i>Anolis rimarum</i>	Hispaniola		<i>monticola</i>
<i>Anolis roosevelti</i>	Puerto Rico Bank	Crown-Giant	<i>ricordii</i>
<i>Anolis roquet</i>	Southern Lesser Antilles		<i>roquet</i>
<i>Anolis rubribarbus</i>	Cuba	Trunk-Ground	<i>sagrei</i>
<i>Anolis ruibali</i>	Cuba		<i>angusticeps</i>
<i>Anolis rupinae</i>	Hispaniola		<i>monticola</i>

(Continued on following page)

SPECIES	ISLAND	ECOMORPH	SERIES/CLADE
<i>Anolis sabanus</i>	Northern Lesser Antilles		<i>bimaculatus</i>
<i>Anolis sagrei</i>	Cuba, Bahamas, Other islands	Trunk-Ground	<i>sagrei</i>
<i>Anolis schwartzi</i>	Northern Lesser Antilles		<i>bimaculatus</i>
<i>Anolis scriptus</i>	Inagua	Trunk-Ground	<i>crisatellus</i>
<i>Anolis semilineatus</i>	Hispaniola	Grass-Bush	<i>semilineatus</i>
<i>Anolis sheplani</i>	Hispaniola	Twig	<i>angusticeps</i>
<i>Anolis shrevei</i>	Hispaniola	Trunk-Ground	<i>cybotes</i>
<i>Anolis singularis</i>	Hispaniola	Trunk-Crown	<i>chlorocyanus</i>
<i>Anolis smallwoodi</i>	Cuba	Crown-Giant	<i>equestris</i>
<i>Anolis smaragdinus</i>	Bahamas	Trunk-Crown	<i>carolinensis</i>
<i>Anolis spectrum</i>	Cuba	Grass-Bush	<i>alutaceus</i>
<i>Anolis strahmi</i>	Hispaniola	Trunk-Ground	<i>cybotes</i>
<i>Anolis stratulus</i>	Puerto Rico	Trunk-Crown	<i>crisatellus</i>
<i>Anolis terraecaltae</i>	Northern Lesser Antilles		<i>bimaculatus</i>
<i>Anolis terueli</i>	Cuba		<i>angusticeps</i>
<i>Anolis toldo</i>	Cuba	Trunk-Crown	<i>carolinensis</i>
<i>Anolis trinitatis</i>	Southern Lesser Antilles		<i>roquet</i>
<i>Anolis valencienni</i>	Jamaica	Twig	<i>grahami</i>
<i>Anolis vanidicus</i>	Cuba	Grass-Bush	<i>alutaceus</i>
<i>Anolis vermiculatus</i>	Cuba		<i>bartschi</i>
<i>Anolis vescus</i>	Cuba	Grass-Bush	<i>alutaceus</i>
<i>Anolis wattsi</i>	Northern Lesser Antilles		<i>bimaculatus</i>
<i>Anolis websteri</i>	Hispaniola	Trunk	<i>distichus</i>
<i>Anolis whitemani</i>	Hispaniola	Trunk-Ground	<i>cybotes</i>

#### MAINLAND SPECIES

The many mainland species described since the last published list of anole species (Savage and Guyer, 1989) preclude an accurate listing of all species. For this reason, I only list those mainland species mentioned in the text. I mention notable ecomorphological information in “Notes.” Some species are assigned to an ecomorph class following Irschick et al. (1997), information in the literature (particularly Savage [2002]), or personal observations. I indicate only whether species belong to the Norops or Dactyloa clades because the lower level systematics of mainland anoles is in flux (see Chapter 5). I include in this list several species that occur on islands in the Pacific Ocean off the coast of northern South America.

SPECIES	LOCALITY	CLADE	NOTES
<i>Anolis agassizi</i>	Malpelo Island	Dactyloa	Rocky surfaces, large
<i>Anolis altae</i>	Costa Rica	Norops	Low to ground
<i>Anolis aquaticus</i>	Costa Rica and Panama	Norops	Aquatic anole
<i>Anolis auratus</i>	Widespread in Central America to northern South America	Norops	Grass-Bush anole
<i>Anolis barkeri</i>	Mexico	Norops	Aquatic anole
<i>Anolis biporcatus</i>	Widespread in Central America to northern South America	Norops	Crown-Giant <sup>478</sup>
<i>Anolis capito</i>	Widespread in Central America	Norops	Near ground, relatively large
<i>Anolis cupreus</i>	Widespread in Central America	Norops	Low to ground
<i>Anolis frenatus</i>	Costa Rica to Colombia	Dactyloa	Crown-Giant
<i>Anolis fungosus</i>	Costa Rica and Panama	Norops	Twig anole
<i>Anolis fuscoauratus</i>	Amazonia	Norops	Low to ground
<i>Anolis gadovi</i>	Mexico	Norops	
<i>Anolis gorgonae</i>	Gorgona Island	Dactyloa	Arboreal
<i>Anolis humilis</i>	Costa Rica and Panama	Norops	Ground litter inhabitant
<i>Anolis insignis</i>	Costa Rica and Panama	Dactyloa	Crown anole, large
<i>Anolis intermedius</i>	Costa Rica and Panama	Norops	Low to ground
<i>Anolis limifrons</i>	Widespread in Central America	Norops	Near the ground; often narrow diameter vegetation
<i>Anolis macrolepis</i>	South America	Norops	Aquatic anole
<i>Anolis naufragus</i>	Mexico	Norops	
<i>Anolis nebulosus</i>	Mexico	Norops	Ground to high in trees

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478. Mean perch height for *A. biporcatus* in Irschick et al. [1997], based on observations of five individuals, was lower than that of West Indian crown-giants. However, my unpublished observations in Panama and Costa Rica and those of others (e.g., Leenders [2001]) indicate that it often goes high into the canopy, much like crown-giants.



SPECIES	LOCALITY	CLADE	NOTES
<i>Anolis nitens</i>	Amazonia	Norops	Leaf litter
<i>Anolis onca</i>	Venezuela	Norops	Ground-dwelling, sandy areas
<i>Anolis ortonii</i>	Amazonia	Norops	Low to ground
<i>Anolis oxylophus</i>	Widespread in Central America	Norops	Aquatic anole
<i>Anolis pentaprion</i>	Widespread in Central America to Colombia	Norops	Twig anole
<i>Anolis polylepis</i>	Costa Rica and Panama	Norops	Moderately arboreal
<i>Anolis proboscis</i>	Ecuador	Dactyloa	
<i>Anolis sericeus</i>	Widespread in Central America	Norops	Moderately arboreal
<i>Anolis taylori</i>	Mexico	Norops	Rocky surfaces
<i>Anolis transversalis</i>	Amazonia	Dactyloa	Arboreal
<i>Anolis tropidolepis</i>	Costa Rica	Norops	Montane, low to ground
<i>Anolis vociferans</i>	Costa Rica	Norops	Twig anole
Phenacosaurus clade	South America		Twig anoles, some quite large

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# INDEX

Page numbers followed by *f* refer to figures, *t* refer to tables and *n* refer to notes.

- acceleration capabilities, 265, 268*n*, 324
- adaptive divergence, 291–293, 294, 297, 312
- adaptive landscape
  - and convergence, 353–366
  - evolution on species-poor islands, 369–370
  - hypothesis, 351–353
  - non-convergence cases, 371–381
  - occurrence patterns, 366–369
- adaptive radiation
  - comparative test for, 345–349
  - of day geckos, 398–400
  - definition and process, 205–207
  - and ecological interactions, 230–231
  - ecological opportunity, 387
  - evolutionary biologists' perspective, 99
  - factors in, 389–392
  - genetic constraints, 402–403
  - Greater Antillean anoles, 326–328
  - historical inference of patterns of, 318–328
  - parallelism, 402
  - of *Phelsuma*, 398–400
  - phenotypic diversification rates, 329
  - predictors of, 206, 387–389
  - replication, 392–398, 401–402
  - and sexual dimorphism, 341–345
  - stages of, 324–328
  - timing, 99–101, 109–112
  - uniqueness of *Anolis*, 386–387
- African fire-cracker finch, 341
- aggressive behavior, 164–167, 170
- allopatric speciation, 292–293, 303, 304, 325*n*, 396
- Alsophis portoricensis*, 144–145
- alutaceus* Series, 326
- amber fossils, 3*n*, 8, 119*n*, 160, 324
- Ameiva*, 144
- American kestrel, 140, 141*n*, 182
- ancestral anoles, 104, 109, 303, 318–324, 363–364
- ancestral reconstruction, 84–89, 104, 105, 117–119
- Andrews, R.M., 156
- Anguilla, 123*f*
- Anguilla Banks, 129
- angusticeps* Series, 97–98
- Anolis*
  - area of origin, 103–104
  - characteristics, 11–19
  - geographic distribution, 19
  - as model taxon, 384–386
  - origin of name, 10*n*, 12
  - phylogenetics, 90–92
  - pronunciation, 10*n*, 12
  - species diversity and recognition, 20–27
  - taxonomy, 95–97
  - See also specific species*

- Anolis acutus*, 122, 414<sup>t</sup>  
*Anolis aeneus*, 414<sup>t</sup>  
 backcross with *Anolis trinitatis*,  
 24<sup>n</sup>, 37  
 body size, 123<sup>f</sup>, 127–129  
 diet, 153  
 dispersal, 139  
 egg-laying behavior, 138  
 female sperm storage, 176  
 growth rate, 160<sup>n</sup>, 207  
 habitat shifts, 198  
 head bobs, 300  
 mating behavior, 171, 172  
 phylogenetic relationships, 124<sup>f</sup>  
 resource partitioning, 212<sup>f</sup>  
 survey position, 162  
 territories, 167, 170  
*Anolis agassizi*, 419<sup>t</sup>  
*Anolis ahli*, 414<sup>t</sup>  
*Anolis alayoni*, 414<sup>t</sup>  
*Anolis alfaroi*, 414<sup>t</sup>  
*Anolis aliniger*, 414<sup>t</sup>  
*Anolis allisoni*, 414<sup>t</sup>  
*Anolis allogus*, 414<sup>t</sup>  
*Anolis altae*, 419<sup>t</sup>  
*Anolis altavelensis*, 414<sup>t</sup>  
*Anolis altitudinalis*, 414<sup>t</sup>  
*Anolis alumina*, 414<sup>t</sup>  
*Anolis alutaceus*, 414<sup>t</sup>  
*Anolis anfiloquioides*, 414<sup>t</sup>  
*Anolis angusticeps*, 414<sup>t</sup>  
 of Bahamas, 66, 67, 369  
 foraging behavior, 148  
 future research directions, 186  
 life span, 139  
 natural selection study, 235  
 oceanic island colonization, 63  
 prey attack behavior, 151, 272  
*Anolis aquaticus*, 419<sup>t</sup>  
*Anolis argenteolus*, 414<sup>t</sup>  
*Anolis argillaceus*, 414<sup>t</sup>  
*Anolis armouri*, 414<sup>t</sup>  
*Anolis auratus*, 419<sup>t</sup>  
*Anolis bahorucoensis*, 414<sup>t</sup>  
*Anolis baleatus*, 414<sup>t</sup>  
*Anolis baracoae*, 414<sup>t</sup>  
*Anolis barahonae*, 414<sup>t</sup>  
*Anolis barkeri*, 419<sup>t</sup>  
*Anolis bartschi*, 415<sup>t</sup>  
*Anolis bimaculatus*, 415<sup>t</sup>  
 body size, 123<sup>f</sup>, 126<sup>n</sup>, 165, 129, 130<sup>f</sup>  
 interspecific interaction with *Anolis schwartzi*,  
 217–218, 221, 225<sup>n</sup>, 289, 229  
 phylogenetic relationships, 125<sup>f</sup>  
 resource partitioning, 212<sup>f</sup>, 229  
*Anolis biporcatus*, 419<sup>t</sup>  
*Anolis birama*, 415<sup>t</sup>  
*Anolis bonairensis*, 125<sup>f</sup>  
*Anolis bremeri*, 415<sup>t</sup>  
*Anolis breslini*, 415<sup>t</sup>  
*Anolis brevirostris*, 415<sup>t</sup>  
*Anolis brunneus*, 415<sup>t</sup>  
*Anolis capito*, 419<sup>t</sup>  
*Anolis carolinensis*, 414<sup>t</sup>  
 aggressive behavior, 166  
 on *Anguilla*, 220  
 bite force, 278  
 body size, 168<sup>f</sup>, 169  
 color and pattern, 279  
 dewlap, 14<sup>f</sup>  
 ecological release, 222, 252  
 egg laying process, 138  
 exotic pet trade, 407  
 in Florida, 218, 406  
 foraging behavior, 149–150  
 genome sequence, 251–252, 402  
 on Guam, 219<sup>n</sup>, 284  
 habitat shifts, 199  
 head-bobbing patterns, 187<sup>f</sup>  
 hindlimb length and perch  
 diameter, 246  
 hybridization with *A. porcatus*, 64<sup>n</sup>, 90  
 hydric environment adaptation, 285  
 mating behavior, 171, 172, 173, 174, 176  
 origins, 110<sup>n</sup>, 142  
 perch height, 221  
 phenotypic plasticity in hindlimb length,  
 249–250  
 predators, 140  
 prey attack behavior, 151  
 reproductive system, 137  
 sexual dimorphism, 182  
 sexual selection, 172, 173, 181  
 surface diameter use and limb length,  
 261–262  
 territorial behavior, 167, 170, 175<sup>n</sup>,  
 231, 177  
 time budgeting, 162, 163  
*Anolis caudalis*, 415<sup>t</sup>  
*Anolis centralis*, 415<sup>t</sup>  
*Anolis Chamaeleolis agueroi*, 414<sup>t</sup>  
*Anolis Chamaeleolis barbatus*, 414<sup>t</sup>  
*Anolis Chamaeleolis chamaeleonides*, 415<sup>t</sup>  
*Anolis Chamaeleolis guamuhaya*, 416<sup>t</sup>  
*Anolis Chamaeleolis porcus*, 417<sup>t</sup>  
*Anolis Chamaelinorops barbouri*, 414<sup>t</sup>  
*Anolis chlorocyanus*, 152–153<sup>f</sup>, 415<sup>t</sup>  
*Anolis christophei*, 415<sup>t</sup>  
*Anolis clivicola*, 415<sup>t</sup>  
*Anolis coelestinus*, 415<sup>t</sup>  
*Anolis concolor*, 415<sup>t</sup>  
*Anolis confusus*, 415<sup>t</sup>

- Anolis conspersus*, 415t  
*Anolis cooki*, 415t  
*Anolis cristatellus*, 415t  
 aggressive behavior, 164n, 212  
 and *Anolis desechensis*, 64n, 90  
 carnivory, 154f  
 head bobs, 299  
 learning experiment, 185  
 light environment, 197  
 oceanic island colonization, 63  
 predators, 144–145  
 prey attack behavior, 225f  
 sexual selection, 176  
 species-area relationship, 67  
 territoriality, 214  
 thermoregulation, 190, 191f, 192, 282–283  
*Anolis cupeyalensis*, 415t  
*Anolis cupreus*, 419t  
*Anolis cuvieri*, 415t  
*Anolis cyanopleurus*, 415t  
*Anolis cybotes*, 415t  
*Anolis darlingtoni*, 133n, 172, 415t  
*Anolis delafuentei*, 415t  
*Anolis desechensis*, 415t  
*Anolis distichus*, 415t  
 ant consumption, 155  
 dewlap, 300n, 359  
 in Florida, 35n, 46  
 fossil data, 241  
 life span, 139  
 oceanic island colonization, 63  
 pectoral girdle shape, 289  
 perch height, 221  
 species-area relationship, 67, 68n, 95  
 territories, 169  
*Anolis dolichocephalus*, 415t  
*Anolis equestris*, 415t  
*Anolis ernestwilliamsi*, 415t  
*Anolis etheridgei*, 415t  
*Anolis eugenegrahami*, 415t  
*Anolis evermanni*, 122, 155, 415t  
*Anolis extremus*, 123f, 125f, 127, 415t  
*Anolis fairchildi*, 416t  
*Anolis ferreus*, 123f, 125f, 416t  
*Anolis fowleri*, 416t  
*Anolis frenatus*, 419t  
*Anolis fugitivus*, 416t  
*Anolis fungosus*, 419t  
*Anolis fuscoauratus*, 419t  
*Anolis gadovi*, 419t  
*Anolis garmani*, 416t  
*Anolis gingivinus*, 416t  
 on Anguilla, 220  
 ant consumption, 155  
 body size, 123f, 126n, 165, 129, 130–131, 130f  
 diet alteration, 221  
 experimental studies, 217  
 on Martin, 211n, 268, 328  
 parasites, 145, 226–227  
 phylogenetic relationships, 125f  
*Anolis gorgonae*, 419t  
*Anolis grahami*, 416t  
*Anolis conspersus* origins, 301n, 361  
 ant consumption, 155  
 body size, 241n, 299  
 dewlap, 65f  
 diet, 153  
 dispersal over water, 301  
 display behavior, 166f  
 geographic variation, 247  
 introduced population on Bermuda, 218n, 282, 219n, 284  
 learning experiment, 185  
 mitochondrial divergence, 307  
 oceanic island colonization, 63, 64  
 perch height, 221  
 phylogenetic relationships, 26  
 Starburst experiment, 146n, 189  
*Anolis griseus*, 123f, 125f, 127, 416t  
*Anolis guafe*, 416t  
*Anolis guazuma*, 416t  
*Anolis gundlachi*, 416t  
 body temperature, 283  
 display behavior, 27f  
 head bobs, 299  
 head shape, 277f  
 hydric environment, 196  
 light environment, 197  
 parasites, 145  
 prey, 152  
 thermoregulation, 192, 193, 195  
*Anolis haetianus*, 416t  
*Anolis hendersoni*, 133n, 172, 416t  
*Anolis homolechis*, 155, 416t  
*Anolis humilis*, 419t  
*Anolis imias*, 416t  
*Anolis incredulus*, 416t  
*Anolis inexpectatus*, 416t  
*Anolis insignis*, 419t  
*Anolis insolitus*, 416t  
*Anolis intermedius*, 419t  
*Anolis isolepis*, 416t  
*Anolis juangundlachi*, 416t  
*Anolis jubar*, 416t  
*Anolis koopmani*, 133n, 172, 134, 416t  
*Anolis krugi*, 416t  
*Anolis leachii*, 123f, 124f, 125f, 126n, 165, 129, 130f, 416t

- Anolis limifrons*, 419t  
 dietary differences in females vs. males, 154–155  
 dispersal, 138–139  
 egg laying behavior, 137  
 habitat use and morphology, 73  
 hydroregulation, 196  
 mating behavior, 171  
 population fluctuation, 146, 147f  
 predators, 140f, 377–378  
 time budgeting, 163
- Anolis lineatopus*, 416t  
 and *A. reconditus*, 79  
 bite force, 278  
 body size and territory, 169  
 body temperature and sprint speed, 283  
 display behavior, 164  
 geographic variation in color, 247  
 habitat use, 221  
 mitochondrial divergence, 307  
 sleeping sites, 201  
 supplemental food, 160n, 206
- Anolis litoralis*, 416t
- Anolis lividus*, 123f, 124f, 125f, 416t
- Anolis longiceps*, 416t
- Anolis longitibialis*, 416t
- Anolis loysianus*, 416t
- Anolis luciae*, 123f, 125f, 416t
- Anolis lucius*, 416t
- Anolis luteocularis*, 416t
- Anolis macilentus*, 416t
- Anolis macrolepis*, 419t
- Anolis magnaphallus*, 136f
- Anolis marcanoii*, 417t
- Anolis marmoratus*, 123f, 125f, 417t
- Anolis marmoratus setosus*, 71n, 103
- Anolis marmoratus terraaltae*, 72n, 102
- Anolis marron*, 417t
- Anolis maynardi*, 417t
- Anolis mestrei*, 417t
- Anolis monensis*, 417t
- Anolis monticola*, 417t
- Anolis naufragus*, 419t
- Anolis nebulosus*, 419t  
 display behavior, 164, 379n, 444  
 foraging behavior, 150, 199  
 headbob displays, 23  
 mating behavior, 172  
 monogamy, 169  
 sleeping site, 200n, 254  
 territory size, 168f  
 time budgeting, 163
- Anolis nitens*, 420t
- Anolis noblei*, 417t
- Anolis nubilus*, 123f, 125f, 417t
- Anolis occultus*, 417t
- Anolis oculatus*, 123f, 125f, 152–153f, 417t
- Anolis olssoni*, 417t
- Anolis onca*, 420t
- Anolis opalinus*, 155, 417t
- Anolis ophiolepis*, 417t
- Anolis oporinus*, 417t
- Anolis ortonii*, 420t
- Anolis oxylophus*, 420t
- Anolis paternus*, 417t
- Anolis pentapirion*, 131, 420t
- Anolis phyllorhinus*, 184
- Anolis pigmaequestris*, 417t
- Anolis pinchoti*, 417t
- Anolis placidus*, 417t
- Anolis pogus*, 417t  
 on Anguilla, 129n, 168  
 body size, 123f  
 interspecific interactions, 217  
 parasites, 226–227  
 phylogenetic relationships, 125f  
 on St. Martin/Maarten, 129n, 168
- Anolis polylepis*, 420t
- Anolis poncensis*, 417t
- Anolis porcatus*, 417t  
 body size, 210  
 dorsal patterning, 184f  
 of Great Bahama Bank islands, 66  
 interpopulational divergence, 308  
 introduced population in Santo Domingo, 406  
 oceanic island colonization, 63, 64  
 phylogenetic relationships, 26
- Anolis proboscis*, 420t
- Anolis pulchellus*, 417t
- Anolis pumilus*, 417t
- Anolis punctatus*, 75f
- Anolis quadriocellifer*, 417t
- Anolis reconditus*, 417t
- Anolis relictus*, 417t
- Anolis richardii*, 123f, 125f, 127–129, 417t
- Anolis ricardii*, 417t
- Anolis rimarum*, 417t
- Anolis roosevelti*, 417t
- Anolis roquet*, 417t  
 body size, 123f  
 character displacement, 127  
 dewlap, 300  
 intraspecific variation, 71  
 on Martinique, 310  
 morphological shift with environmental change, 312f, 313  
 phylogenetic relationships, 125f
- Anolis rubribarbus*, 417t

- Anolis ruibali*, 417t  
*Anolis rupinae*, 417t  
*Anolis sabanus*, 123f, 125f, 418t  
*Anolis sagrei*, 418t  
 of Bahamas, 157  
 body size, 241  
 body temperature, 194, 223  
 climatic microhabitat  
 partitioning, 51  
 dewlap, 24f, 173n, 228, 298f  
 dorsal patterning, 184f  
 ecomorphology, 68, 115n, 148  
 exotic pet trade, 407  
 foraging behavior, 148  
 geographic variation, 246  
 growth rates, 138  
 hurricane-induced colonization,  
 64n, 89  
 interpopulational divergence in morphology  
 and genetics, 314  
 interpopulational genetic  
 differentiation, 308f  
 interspecific competition, 228  
 introduced populations, 157  
 life span, 139  
 marking using elastomer  
 injection, 255f  
 mating behavior, 171, 172, 177  
 multiple paternity, 176  
 natural selection studies, 235–239  
 oceanic island colonization, 63  
 perch height/diameter, 49, 221  
 phenotypic plasticity in hindlimb length,  
 249–250  
 predators, 141–143  
 running, 270f  
 skin pattern, 281  
 species-area relationship, 67  
 sperm storage, 176  
 and spider density, 158  
 surface diameter use and limb length,  
 261–262  
 territories, 168, 169  
*Anolis sagrei luteosignifer*, 301n, 361  
*Anolis sagrei nelsoni*, 301n, 361  
*Anolis schwartzi*, 123f, 125f, 418t  
*Anolis scriptus*, 418t  
*Anolis semilineatus*, 418t  
*Anolis sericeus*, 420t  
*Anolis sheplani*, 418t  
*Anolis sheplani* + *Anolis placidus*, 115  
*Anolis shrevei*, 418t  
*Anolis singularis*, 418t  
*Anolis smallwoodi*, 418t  
*Anolis smaragdinus*, 418t  
 and *A. porcatius*, 64n, 90  
 and *A. sagrei* presence, 228  
 foraging behavior, 148  
 of Great Bahama Bank islands,  
 66, 68  
 introduced populations, 217, 242  
 life span, 139  
 species-area relationship, 67  
 sprinting, 271  
 subfossil data, 241  
*Anolis spectrum*, 418t  
*Anolis strahmi*, 418t  
*Anolis stratulus*, 418t  
 and *Anolis acutus*, 122  
 diet, 152  
 ecomorph class, 53  
 experimental studies, 216n, 278  
 habitat shifts, 199  
 oceanic island colonization, 63  
 population density, 145, 158  
 in Puerto Rico, 35, 51  
 territories, 168n, 217  
 in Virgin Islands, 67  
*Anolis taylori*, 420t  
*Anolis terraealtae*, 123f, 125f, 418t  
*Anolis terueli*, 418t  
*Anolis toledo*, 418t  
*Anolis transversalis*, 420t  
*Anolis trinitatis*, 123f, 125f, 127, 418t  
*Anolis tropidolepis*, 420t  
*Anolis valencienni*, 418t  
 body size, 54, 61  
 dewlap, 182  
 egg laying behavior, 137  
 escape from predators, 273f  
 foraging behavior, 148, 150  
 jumping ability, 267f  
 mating behavior, 171, 172, 174,  
 175, 186  
 phylogeny position, 322  
 resource partitioning, 52n, 64  
 sprint speed, 271  
 territories, 169, 170, 186  
*Anolis vanidicus*, 418t  
*Anolis vermiculatus*, 418t  
*Anolis vescus*, 418t  
*Anolis vociferans*, 420t  
*Anolis wattsi*, 123f, 124f, 125f,  
 130f, 418t  
*Anolis websteri*, 418t  
*Anolis whitemani*, 418t  
 Antigua, 123f  
 ants, 155  
 aquatic anoles, 61n, 77, 131, 146, 213n, 272, 375,  
 381, 403  
 area of origin, 103–104  
 Aves ridge, 108n, 138



- Bahamas  
*A. sagrei*, 157  
 anole population density, 146  
 curly-tailed lizard introduction experiment, 142  
 ecomorphology, 68  
 geography, 64–66  
 niche complementarity, 215  
 survival rate study, 139
- Barbados, 123*f*
- Barbuda, 123*f*
- Barro Colorado Island, 146, 147*f*
- Basiliscus basiliscus*, 140*f*
- Basiliscus galeritus*, 213*n*, 272
- behavioral data, 45–49
- Bequia, 123*f*
- Bermuda, 218*n*, 282
- bimaculatus* Series, 70, 97, 122, 211, 319
- Biological Species Concept (BSC), 21–22
- birds, 155
- bite force, 278
- body size  
 co-occurring species, 51  
 and diet, 153–155  
 effects of, 259–261  
 fossil data, 241  
 general range, 11–12  
 geographic variation, 248  
 and habitat shifts, 198  
 heritability, 251  
 of introduced populations, 242  
 Lesser Antillean anoles, 120–131  
 and male territory, 168*f*, 169  
 and mating frequency, 172, 175*f*  
 and perch diameter, 215  
 and phenotypic plasticity, 248–250  
 and population density, 239  
 and predation, 225  
 sexual dimorphism, 177–184  
 and sprint speed, 264–265  
 of sympatric species, 209–210, 215
- body temperature, 190–196, 203–204, 223, 281–284
- Boiga irregularis*, 140
- brain, 166–167
- brown tree snake, 140, 406
- Bubulcus ibis*, 140
- Burgess Shale fauna, 6*n*, 10
- cannibalism, 141
- carnivory, 155
- carolinensis* Series, 97
- Carriacou, 123*f*
- cattle egret, 140
- Central America, 71–73, 112, 404. *See also*  
 mainland anoles
- Chamaeleolis*, 91, 94, 95, 96,  
 373–374
- Chamaeleolis barbatus*, 25*f*
- Chamaeleolis clade, 61–62, 76
- Chamaelinorops*, 91, 94, 95, 96. *See* Anolis  
*Chamaelinorops barbouri*
- chance events, 364
- character displacement, 126–131
- chlorocyanus* Series, 98
- Chuckles experiment, 146*n*, 189
- cichlid fish, 391, 394–395
- claws, 276–277, 289
- climate change, 404–405
- clinging ability, 275–277, 285–286
- Cnemidophorus*, 124*n*, 163
- coevolution, 380
- colonization, 132–133
- color and pattern, 23*n*, 36, 146*n*, 189, 182–183,  
 279–281
- communication, 13
- community structure, 208–216, 230. *See also*  
 ecological interactions
- competition, interspecific. *See* interspecific  
 competition
- convergent evolution, 353–366, 364, 394–396,  
 402–403
- Costa Rica, 216, 405
- crisatellus* Series, 126*n*, 165
- crown giants,  
 ancestral reconstruction, 120–121*f*  
 characteristics, 32*t*, 37–38  
 claws, 227*n*, 338  
 ecological and behavioral characteristics, 47*f*  
 evolution, 114*f*  
 foraging behavior, 150  
 movement rate, 149*f*  
 perch height and diameter, 46*f*  
 sexual dimorphism, 178*f*, 179*f*  
 size differences, 52*n*, 64  
 species richness, 340*f*  
*See also specific species*
- cryptic female mate choice, 176–177
- Ctenosaura similis*, 15*f*
- Cuba  
 evolutionary patterns, 115, 116  
 geological history, 108  
 map of, 30*f*  
 number of species, 21  
 phylogenetic relationships, 102*f*, 103  
 sexual dimorphism, 343  
 unique species, 61, 76, 373
- curly-tailed lizard, 141–143, 213*n*, 270,  
 237–238
- cybotes* series, 119
- Dactyloa clade, 131
- Darwin, C., 84*n*, 107, 164*n*, 212, 233–234*n*, 292
- Darwin's finches, 297, 356–358, 384, 387–388
- Daudin, F. M., 10*n*, 12

- day geckos, 398–400
- Dendrobatid frogs, 383–409
- dewlaps
  - of anoles generally, 12–14
  - detectability, 298–299
  - differences in, 295–297
  - display behavior, 23, 136, 164–165, 173, 187
  - evolution of, 335–337
  - future research directions, 28
  - geographic variation, 300
  - mating, 136, 173
  - sexual differences, 182, 183*f*
  - size of and bite force, 278*n*, 340
  - species-recognition significance, 23
  - territory defense, 164–165
- Dial, R., 156*f*, 157
- diet, 146–156, 221, 229
- dimorphism, sexual, 49, 177–184, 280–281, 341–345
- Diplolaemus darwinii*, 103*f*
- dispersal, 109, 138–139, 301
- displays
  - dewlaps, 23, 136, 164–165, 173, 187
  - mating, 136, 171, 173
  - to predators, 144–145
  - research, 187
  - selection for, 295–297
  - and species recognition, 23, 297–297, 316
  - for territorial defense, 163–166
  - See also* headbob displays
- distichus* Series, 150
- divergence, adaptive, 291–293, 294, 297, 312
- divergence, dates of, 129
- divergence, genetic. *See* genetic divergence
- Dobzhansky, T., 292
- Dominica, 123*f*
- Dominican Republic, 3, 308*f*, 323. *See also* Hispaniola
- dorsal patterning, 183, 184*f*
- Draco*, 336
- Draco jarecki*, 15*f*
- ecological data, 45–49
- ecological interactions
  - and adaptive radiation, 230–231
  - experimental studies, 216–220
  - future research directions, 231–232
  - and habitat shifts, 220–221
  - interspecific competition, 227–229
  - niche breadth, 222–223
  - niche complementarity, 209, 215–216
  - parasitism, 226–227
  - predation, 224–226
  - research evidence, 208–209, 223–224
  - resource partitioning, 209–215
- ecological opportunity, 387, 388–389
- ecological release, 222, 252
- ecomorphology, 56*n*, 70, 68, 318–321
- ecomorphs
  - absence of on certain islands, 366–369
  - adaptive radiation, 326–328, 353
  - appearance of, 122
  - definition of, 29–31, 52–55, 56*n*, 70
  - ecological and behavioral approaches, 45–49
  - evolutionary patterns, 126
  - future research directions, 55
  - as interspecific variation explanation, 49–50
  - vs. mainland species, 73
  - morphological approaches, 41–45, 49
  - resource partitioning of sympatric species, 209–211
  - sexual dimorphism, 345
  - species diversity within, 50–52
  - species richness, 339–341
  - sympatric speciation, 303
  - testing hypothesis of existence of, 40–49
  - time budgets, 163
  - use of term, 40*n*, 51
- ecosystem role, 157–159
- elastomer injection, 255
- Eleutherodactylus*, 110
- Eleutherodactylus coqui*, 213*n*, 271, 226
- empty niches, 367
- environmental factors, 189–197, 356–359, 371
- equestris* Series, 98, 374
- evolution
  - body size, 122–131
  - constraints, 350–363
  - ecomorphs in Greater Antilles, 113–121
  - historical contingencies, 363–366
  - phylogenetic analysis, 132–133
  - timing and biogeography, 99–112
- evolvability, 390–391
- exotic pet trade, 407
- experiments
  - “Chuckles,” 146*n*, 189
  - for convergence tests, 354–356
  - curly-tailed lizard introduction, 142
  - ecological interactions, 216–220
  - ecosystem role, 157–159
  - food supplementation, 159–160
  - learning, 185
  - limitations, 1, 7
  - “natural,” 221
  - natural selection, 236–240, 354–356
  - sympatric species, 208
- extinctions, 241–242, 334, 338, 340, 369, 404
- extra-pair copulation, 174–175
- Falco sparverius*, 140, 141*n*, 182
- faunal relaxation, 67–68

- females
- diet, 154–155
  - fitness assessments, 240
  - foraging behavior, 150
  - growth rate, 138
  - perches, 201
  - reproduction, 12, 19, 24, 136–138, 171–177, 186
  - sexual dimorphism, 49, 177–184
  - skin color and pattern, 280–281
  - territories and territoriality, 170
  - time budgets, 163
- fish, 324, 391, 394–394
- fitness, 240
- Florida, 106, 218, 219–220, 222, 232, 242, 310, 406
- flying dragons, 336
- food limitation, 159–160
- food web, 158
- foraging behavior, 147–151, 159, 162, 163, 199
- fossils
- advantages/disadvantages, 3, 84*n*, 107, 88*n*, 110
  - anoles' origins, 99–100, 111
  - ecomorph evolution, 323–324
  - evolutionary diversification of prey, 380
  - molecular evolution rate, 101
  - subfossil data, 241
- founder effects, 301–302
- frogs, 213*n*, 271, 226, 386
- frugivory, 155–156
- functional capabilities
- adaptive basis of variation, 274–281
  - future research directions, 287–290
  - and hydric environment, 284–285
  - limb length variation, 264–271
  - mainland anoles, 285–287
  - and morphology, 260*t*, 359–360
  - research approaches, 258–260
  - and thermal environment, 281–284
  - use of maximal capabilities, 271–274
- Galápagos mockingbirds, 388
- geckos, 16–17, 19*n*, 26, 213*n*, 272, 333–334, 398–400
- gel electrophoresis, 91*n*, 117
- gender differences, in functional capabilities, 290. *See also* females; males
- genetic constraints, 402–403
- genetic correlation, 362
- genetic divergence
- mitochondrial DNA studies, 306–311
  - and morphological differentiation, 311–314
  - research history, 306
  - trait variation, 248, 250–252
- genetic drift, 301–302
- genomics, 251–252, 253
- geographic distribution, 19–20
- Geographic Information Systems (GIS), 197–198
- geographic variation, 244–248, 279, 302–306
- global warming, 404–405
- Gonatodes humeralis*, 213*n*, 272
- Gould, S. J., 6*n*, 10, 234*n*, 292, 317, 361*n*, 427, 363
- grahami* Series, 97, 368
- Grand Cayman, 64, 65*f*, 218
- grass-bush anoles, 40*f*
- absence on Jamaica, 367
  - ancestral reconstruction, 120–121*f*
  - body temperature, 195*f*
  - characteristics, 32*t*, 38–39
  - ecological and behavioral characteristics, 47*f*
  - evolution, 114*f*
  - foraging behavior, 150
  - locomotive abilities, 274
  - movement rate, 149*f*
  - perch height and diameter, 46*f*
  - predator approach response, 144
  - sexual dimorphism, 178*f*, 179*f*
  - species richness, 340*f*
  - subdivision of, 54–55
  - sympatry, 51
  - See also specific species*
- Great Bahama Bank, 65–66, 68, 369
- Greater Antilles
- interpopulational divergence in morphology and genetics, 314
  - phylogeography, 307–309
  - smaller islands, 62–66
  - species-area relationships, 66–68
  - unique species, 73, 121–122
  - within-island geographic trait variation studies, 246–248
  - See also ecomorphs; specific islands*
- Grenada, 123*f*, 127–129, 129–130
- Grenadines, 123*f*, 129–130
- growth rate, 138, 159
- Guadeloupe, 123*f*
- Guam, 219*n*, 284, 406
- Gulf of California, 124*n*, 163
- Guyer, C. 131
- habitat
- destruction of, 403–404
  - and ecological interactions, 133, 220–221
  - environmental factors, 189–197
  - future research directions, 202–203
  - and hindlimb length, 288
  - niche breadth, 222–223
  - night use, 200–202
  - and population size, 358
  - and presence of other species, 358
  - research variables, 45–46
  - selection, 199–200
  - shifts in, 49, 197–198
- Haiti, 22*n*, 32, 59–60. *See also Hispaniola*
- hatchling size, 138
- Hawaii, day geckos in, 399*n*, 466

- Hawaiian honeycreepers, 387–388  
Hawaiian long-jawed spiders, 396–397  
Hawaiian thrushes, 388
- headbob displays  
context, 187  
detectability, 299–300  
differences in, 295  
display action graphs, 26f  
future research directions, 27–28, 186, 187  
mating, 136, 171  
research, 187  
species-recognition significance, 23–24  
stereotyped patterns, 187  
territory defense, 164–165
- head shape and size, 181, 277–279
- hearing, 12
- heritability, 250–252
- hindlimb length, 246, 249–250, 251, 253, 288.  
*See also* limb length
- Hispaniola  
anoles' arrival, 111, 119, 121  
common ecomorph species, 33f  
evolutionary patterns, 115  
geological history, 108  
map of, 30f  
phylogenetic relationships, 102f, 103  
sexual dimorphism, 343  
trunk anoles, 35–36  
unique species, 61, 77, 373
- historical analysis, 2–4, 5
- historical contingencies, 363–366, 371–372
- home range, 168n, 216
- Hurricane Floyd, 142n, 184, 238, 251n, 311
- Hurricane Francis, 142n, 184
- Hurricane Gilbert, 64
- Hurricane Hugo, 157
- hurricane impact on smaller islands, 242
- hybridization, 21, 22, 24, 25n, 38, 64n, 90
- hydric environment, 196, 202, 247, 284–285
- hyoid, 12–13
- hypotheses, 2, 5, 7, 133
- Icelandic sticklebacks, 379
- identification techniques, 254–255
- iguanas, 347–348
- Iguania, 14n, 23, 15f
- Imantodes cenchoa*, 226
- insects, 158
- interactions, ecological. *See* ecological interactions
- interspecific competition  
evidence for, 227–229  
and evolutionary diversification, 133  
experiment limitations, 1  
future research directions, 232  
hypotheses, 133  
and predation, 224, 232, 380  
uniformitarian assumption, 5–6
- Interspecific variation in lesser atilles, 70–71
- introduced species  
*A. grahami*, 218n, 282, 219n, 284  
*A. porcatus*, 406  
*A. sagrei*, 157  
*A. smaragdinus*, 217, 242  
body size, 242  
fate of, 218–220  
research opportunities, 232, 240, 252, 354–355
- invasions  
*A. cristatellus*, 305n, 370  
*A. sagrei*, 252  
*A. watsi*, 372  
co-invasions of Lesser Antilles, 252
- invasive species, 406
- Isla Juventud, 62–63
- Jamaica  
absence of certain ecomorphs, 367  
adaptive radiation, 348, 349  
anoles' arrival, 110  
evolutionary patterns, 117–119, 322  
geological history, 63n, 85, 108  
map of, 30f  
niche complementarity, 215  
phylogenetic relationships, 102f, 103  
sexual dimorphism, 343, 344  
trunk-crown anoles, 53  
unique species, 61, 79
- jumping ability, 267–268, 270–274
- juveniles, 170, 198
- karyology, 91n, 117
- key innovations, 329–335
- Lack, D., 384
- La Desirade, 123f
- lakes, 393–395, 401
- lamellae, 235–236, 246, 275, 276, 288
- landbridge islands, 62–63, 66, 342,  
368–369
- landscape, adaptive. *See* adaptive landscape
- La Palma, 57
- Lazell, J.D., 70–71
- leaf warblers, 324, 326
- learning, 185
- Leiocephalus*, 104n, 135, 213n, 270
- Leiocephalus carinatus*, 141–143, 158, 228, 237–238
- Lepidodexia blakeae*, 145
- Lesser Antilles  
adaptive radiation, 327–328  
allopatric speciation, 304  
evolutionary patterns, 121–125, 369–370  
interpopulational divergence in morphology  
and genetics, 312–314  
map, 69f  
non-convergence in, 371–372

- Lesser Antilles (*continued*)  
 phylogenetic relationships, 102*f*, 103  
 regional differences, 371  
 resource partitioning of sympatric species, 211  
 sexual dimorphism, 343  
 size differences, 132, 215  
 size divergence, 126  
 species of, 70–71  
 subfossil data, 241  
 within-island geographic trait variation  
   studies, 244–246  
*See also specific islands*
- Lewtontin, R., 367
- life span, 139
- light environment, 196–197, 199, 202
- limb length  
 adaptive basis of variation, 274–281  
 adaptive significance of interspecific variation,  
   261–265  
 functional consequences of variation, 264–271  
 and habitat use, 288  
 heritability, 251  
 and perch diameter, 246, 261–262, 358  
 and performance capabilities, 259–260  
 phenotypic plasticity in, 249–250, 253
- lizard cuckoo, 140, 141*n*, 182
- locomotive abilities, 46, 274
- Los Tuxtlas, Mexico, 21
- Luquillo Mountains, 156*f*
- mainland anoles  
 body temperature, 194*f*  
 colonization of West Indies, 104–106  
 community structure, 230, 232  
 diet, 156  
 diversity, 72–73  
 ecological opportunity, 388–389  
 evolutionary patterns, 131  
 functional capabilities, 285–287  
 future research directions, 73  
 vs. island anoles, 159–160  
 movement rates, 149  
 niche complementarity, 216  
 non-convergence in, 374–381  
 Norops clade, 106  
 phylogenetic relationships, 102*f*, 103  
 population density and constancy, 146  
 predator approach response, 144  
 research, 71–72  
 resource partitioning of sympatric species,  
   211–213  
 sexual dimorphism, 182  
 species list, 418–420  
 time budgets, 163
- malaria parasites, 145, 226–227
- males  
 diet, 154–155  
 foraging behavior, 150  
 growth rate, 138  
 perches, 201  
 reproduction, 12, 19, 24, 136–138, 171–177, 186  
 sexual dimorphism, 49, 177–184  
 skin color and pattern, 281  
 territorial behavior, 163–164, 167–171  
 time budgets, 163
- Malpelo Island, 104, 106*n*, 136, 146*n*, 189, 170
- Mandarina*, 396
- manipulative experiments, 4, 5, 221, 385
- Margarops fuscatus*, 140
- Marie Galante, 123*f*
- marking techniques, 254–255
- marsupials, 395*n*, 460
- Martinique, 123*f*
- mating behavior, 136, 171–177, 186
- maximum likelihood method, 87*f*, 101, 104
- microclimate, 50
- microevolution, 240–243, 252–253
- microhabitats, 31, 50–51, 57, 148, 179–180, 199,  
 229, 327–328, 339
- mitochondrial DNA, 97, 100, 105, 306–311, 315
- model lizards, 203
- modularity, 390
- moisture, 196, 202, 247, 284–285
- molecular clock approach, 100–101
- molecular dating, 100–101, 111
- Mona Passage, 108
- mongooses, 406
- monticola* Series, 98
- Montserrat, 123*f*
- morphology  
 ecomorph hypothesis testing, 41–45, 49  
 future research directions, 55  
 vs. genetics, 311–314  
 Greater Antillean species, 32*t*  
 history of, 56–57  
 performance correlations, 260*t*, 359–360
- Movement rates, 149*f*
- mortality, 142, 377
- muscles, 289
- myrmecophagy, 12
- nasal appendages, 184
- natural experiments, 221
- natural selection  
 adaptive landscape inferred by, 354–356  
 environmental factors imposing, 352  
 experimental studies, 236–240, 354–356  
 and functional capabilities, 258–259  
 in natural populations, 235–236  
 research issues, 233–234, 234, 240  
*See also adaptive radiation*
- nectarivory, 156
- Nevis, 123*f*
- niche breadth, 222–223
- niche complementarity, 209, 215–216
- niche expansion, 341

- niches, 133  
 Norops, 131  
 null models, 214–215, 346–347, 392*n*, 458  
  
 Oahu, 219  
 observations, 221  
 oceanic islands, 63–64, 66, 68  
 ontogenetic habitat shifts, 198  
 osteological analysis, 92  
*Otocryptis*, 14, 336, 337  
 overwater dispersal, 109  
 owls, 200  
  
 Pacala, S.W., 157  
 pair bonding, 171  
 paleoclimate modeling, 315  
 parallelism, 402  
 parapatric speciation, 294, 311–314  
 parasites, 145, 226–227, 228  
 parrotfish, 324  
 parsimony, 85*f*, 86, 318  
 pattern and color, 23*n*, 36, 146*n*, 189, 182–183, 279–281  
 pearly-eyed thrasher, 140  
 pectoral girdle, 289  
 perch diameter  
   and acceleration capabilities, 268*n*, 324  
   of ecomorph species, 46*f*  
   and jumping ability, 270–271, 274  
   and lamella number, 275  
   and limb length, 246, 261–262, 358  
   niche complementarity, 215  
   and sprint speed, 268–270, 271  
   and toepad area, 286*f*  
   and tree type, 49  
 perch height  
   of ecomorph species, 46*f*  
   and lamella number, 246, 275  
   seasonal shifts, 199  
   and toepad structure, 359  
 perch use  
   and light environment, 197  
   natural experiments, 221  
   for sleeping, 200–202  
 performance capabilities. *See* functional capabilities  
 pet trade, 407  
*Phelsuma*, 124*n*, 163  
*Phenacosaurus*, 131  
 phenotypic differences, 257–258  
 phenotypic diversification rates, 329  
 phenotypic plasticity, 248–250, 251*n*, 312, 253, 391  
 phylogenetics  
   advantages/disadvantages, 4, 82–90  
   colonization direction, 105–106  
   DNA-based studies, 92–95  
   evolutionary patterns, 132–133  
   future research directions, 97–98  
   history/patterns of *Anolis*, 90–92, 101–103  
   toepads, 333  
   tree thinking approach, 81–82  
   unique anoles, 373  
   Williams's early use of, 324  
 phylogenetic species concept (PSC), 22, 26–27  
 phylogenetic trees, 104  
 phylogeography, 306–309  
*Plasmodium* infection, 145  
*Poecilia reticula*, 234  
*Polychrus*, 13, 103, 333  
*Polychrus liogaster*, 103*f*  
 population density, size, and constancy, 145–146, 159, 239, 358  
 Praslin Island, 124*n*, 163  
*Prasinochaema*, 334  
 predation, among anoles, 224–226, 228, 232  
 predators  
   escape from, 272, 273*f*, 274, 377–378  
   of Greater Antilles vs. mainland, 159–160, 377–380  
   types of, 12, 139–145  
 prey, 50, 51, 61, 146–156, 159, 380  
 Puerto Rico  
   absence of certain ecomorphs, 367  
   diet of anoles, 151  
   ecosystem experiments in, 157  
   evolutionary patterns, 115, 117–119, 322, 324  
   geological history, 108  
   habitat shifts, 199  
   map of, 30*f*  
   phylogenetic relationships, 102*f*, 103  
   sexual dimorphism, 344  
   unique species, 61, 79  
*Pyrenestes ostrinus*, 341  
  
 racetracks, 264–265  
 radiation. *See* adaptive radiation  
 Rand censuses, 208*n*, 263  
 range, 19–20  
 Redonda, 123*f*  
 reinforcement, 293  
 replicated adaptive radiation, 392–398, 401–402  
 reproduction, 12, 19, 24, 136–138, 171–177, 186  
 reproductive isolation, 22–28, 292–293, 294, 297–298, 301, 309–311  
 research  
   *A. carolinensis*/*A. porcatius*, 64*n*, 90  
   *Anolis* as model taxon, 384–386  
   dewlaps, 28  
   diet, 160  
   display behavior, 187  
   ecological interactions, 208–209, 223–224, 231–232  
   ecomorphs, 55  
   evolutionary patterns, 133–134  
   functional capabilities, 258–260, 287–290  
   genetic divergence, 306  
   habitat, 45–46, 202–203

- research (*continued*)
- headbob displays, 27–28, 186, 187
  - interspecific competition, 232
  - mainland anoles, 73
  - microevolution, 252–253
  - morphology, 55
  - natural selection, 233–234, 234, 240, 252–253
  - phylogenetics, 97–98
  - reproductive isolation, 27
  - speciation, 314–316
  - time budget data, 186
  - timing and biogeography of anole evolution, 112
  - unique species, 73–75
  - video, 27
- resource partitioning, 51–52, 209–215, 229, 230, 231
- robotic techniques, 27
- roquet* Series, 70, 97, 103, 104, 105–106, 122, 211, 319
- Roughgarden, J., 156*f*, 157
- Saba, 123*f*
- sagrei* Series, 97
- Santa Maria, 52*n*, 64
- Santo Domingo, 406
- satellite data, 197–198
- Saurothera vielloti*, 140, 141*n*, 182
- Savage, J.M., 131
- scales, 246, 249, 251, 285
- Sceloporus*, 194
- Sceloporus occidentalis*, 250*n*, 308
- Schoener, T.W., 123*f*
- seasonal habitat shifts, 198–199
- seed consumption, 155–156
- sensory drive theory, 298, 300–301
- sexual dimorphism, 49, 177–184, 280–281, 341–345
- sexual maturity, 138, 170*n*, 220
- sexual reproduction, 12, 19, 24, 136–138, 171–177, 186
- sexual selection, 161–163, 172–177, 179, 186, 302
- signals. *See* displays
- Siphlophis compressus*, 140*f*
- Sitana*, 14, 336, 337
- Sitana ponticeriana*, 15*f*
- skin color and pattern, 23*n*, 36, 146*n*, 189, 182–183, 279–281
- sleeping sites, 200–202
- smell, 12
- snails, 396
- snakes, 140, 144–145, 200, 201*f*, 226, 377, 406
- snout-vent length (SVL), 11. *See also* body size
- social behavior, 163–172, 186
- solitary anoles, 318–319, 342–343
- Soroa, Cuba, 24*f*, 25*f*, 216
- South America, 71–73. *See also* mainland anoles
- South Bimini, 215, 216*f*, 235, 304
- speciation
- and adaptive divergence, 291–293
  - allopatric, 292–293, 303, 304, 325*n*, 396
  - approaches to, 294–302
  - definition of, 291*n*, 349
  - on ecological gradients, 292–293
  - future research directions, 314–316
  - geographic context, 302–306
  - high rates of, 391
  - as incidental bi-product of adaptation, 297–301
  - intraspecific genetic divergence, 306–311
  - morphological-genetic differentiation
    - relationship, 311–314
  - parapatric, 294, 311–314
  - See also* sympatric species and speciation
  - species-area relationships, 66–68, 338–339
  - species concepts, 21–27
  - species diversification, 20–27, 50–52, 109, 337–341
  - species-for-species matching, 392–393, 398–401
  - species recognition, 316
  - species richness, 56, 334, 337, 339–341, 346
  - sperm storage, 176–177

*Sphaerodactylus*, 213*n*, 270

  - spiders, 158, 396–397
  - sprinting, 264–267, 268–274, 283
  - St. Barthélemy, 123*f*
  - St. Croix, 122
  - St. Eustatius, 123*f*, 157
  - St. Kitts, 123*f*
  - St. Lucia, 123*f*
  - St. Martin, 123*f*, 129*n*, 168
  - St. Vincent, 123*f*
  - Staniel Cay, 242, 243*f*
  - subfossil data, 241
  - surface diameter. *See* perch diameter
  - survey posture, 162
  - survival rates, 139, 159
  - sympatric species and speciation
    - and character displacement, 129–130
    - dewlap differences, 295
    - ecological interaction, 133, 206, 208–216
    - experimental studies, 208
    - lack of in anoles, 305
    - microhabitat use, 57
    - number of and niche breadth, 223*f*
    - vs. reinforcement, 293*n*, 350
    - and reproductive isolation, 292–293
    - resource partitioning, 51–52, 209–215
- tail length, 288–289
- taxonomy, 95–97
- teeth, 289
- teid lizards, 144, 148*n*, 193
- temperature, 190–196, 199, 223, 404–405
- Terre-de-Bas, 123*f*
- Terre de Haute, 123*f*

- territorial behavior, 163–171  
*Tetragnatha*, 396–397  
 thermoregulation, 190–193, 199, 202, 203–204, 281–284, 390  
 time budgets, 162–163, 186  
 toe-clipping, 254  
 toepads, 15–18, 274–277, 285–286, 288, 332–335, 359, 389–390  
 tongue displays, 166*n*, 214  
 trait distributions, 236  
 trait evolution, 84–89  
 Trinidad, 24*n*, 37  
 Trinidadian guppies, 234  
 trogon, 141*f*  
 trunk anoles, 31*f*, 32*t*  
   absence on Jamaica, 367  
   absence on Puerto Rico, 367  
   ancestral reconstruction, 120–121*f*  
   body temperature, 195*f*  
   characteristics, 32*t*, 35–36  
   ecological and behavioral characteristics, 47*f*, 53  
   evolution, 114*f*  
   foraging behavior, 147, 150  
   movement rate, 149*f*  
   perch height and diameter, 46*f*  
   resource partitioning, 209–210  
   sexual dimorphism, 178*f*, 179*f*  
 trunk-crown anoles, 31*f*, 37*f*  
   as ancestor anoles, 318–321  
   ancestral reconstruction, 120*f*  
   body temperature, 195*f*  
   characteristics, 32*t*, 35  
   ecological and behavioral characteristics, 47*f*  
   evolution, 114*f*  
   foraging behavior, 147, 150  
   movement rate, 149*f*  
   nectarivory, 156  
   perch height and diameter, 46*f*  
   predator approach response, 144  
   sexual dimorphism, 178*f*, 179*f*  
   size differences, 52*n*, 64  
   species richness, 340*f*  
   sympatry, 51  
 trunk-ground anoles, 31*f*  
   ancestral reconstruction, 120*f*  
   body temperature, 195*f*  
   characteristics, 32*t*, 33–35  
   ecological and behavioral characteristics, 47*f*  
   evolution, 114*f*  
   foraging behavior, 150  
   movement rate, 149*f*  
   perch height and diameter, 46*f*  
   predator approach response, 144  
   sexual dimorphism, 178*f*, 179*f*  
   species richness, 340*f*  
   sympatry, 51  
 twig anoles, 43*f*  
   absence on certain islands, 368  
   ancestral reconstruction, 120*f*  
   body size, 52*n*, 64, 54, 61  
   characteristics, 32*t*, 39  
   ecological and behavioral characteristics, 47*f*  
   evolution, 114*f*, 115  
   foraging behavior, 147–148, 150  
   movement rate, 149*f*  
   perch height and diameter, 46*f*  
   sexual dimorphism, 178*f*, 179*f*  
   species richness, 340*f*  
 unique anoles, of Greater Antilles, 73, 121–122,  
 unweighted pair group method with arithmetic means (UPGMA), 42–44  
*Uromacer frenatus*, 226  
 van der Waals forces, 16–17  
 variation, interspecific. *See* interspecific variation  
 vegetation structure, 148, 236–237, 352*n*, 422, 376–377  
 video research, 27  
 Virgin Islands, 62, 67  
 vision, 12, 18–19, 198*n*, 251  
 vocalizations, 12, 166*n*, 214  
*wattsi* Series, 123*n*, 162  
 West Indies  
   anole movement rate, 149*f*  
   anole population density, 146  
   geologic history, 106–108  
   map of, 30*f*  
   number of species, 21  
   sexual dimorphism, 181–182  
   species list, 411–418  
 Wetmore, A., 141*n*, 182  
 Williams, E. E., 29–30, 45, 52, 53*n*, 67, 54, 55, 56, 57, 61*n*, 76, 78, 91, 94, 115, 321, 324  
 Windward Passage, 108