

Detective Work in the West Indies: Integrating Historical and Experimental Approaches to Study the Evolutionary Diversification of Island Lizards

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One of the great challenges facing scientists—going back to Darwin and even before—is to understand the genesis of biological diversity. How do we account for the great diversity of life we see around us? And why has evolution proceeded in certain directions and not others? These questions have even greater relevance today as we strive to protect both the diversity we currently have and the processes that could replenish it in the future.

Unfortunately, however, evolutionary biology is not like most sciences. We cannot simply conduct experiments to test ideas about the evolutionary events that occurred eons ago. Rather, like astronomy and geology, evolutionary biology is a historical science; in trying to decipher what happened in the past, we must take multiple approaches and use whatever types of data are available to construct—and continually test—the best hypothesis about what happened in the past. In this way, evolutionary biology is more like the study of history than, say, chemistry. More colloquially, I like to compare being an evolutionary biologist to being a detective: both use the available clues to fashion the best possible case.

My theme in this essay is two-fold: first, to argue that to understand what happened in the past, we must take an integrative, multidisciplinary approach; and, second, to suggest that historical and present-day studies can be mutually illuminating: historical analyses can suggest hypotheses that can be tested with data on extant species; in turn, by extrapolating from what happens in present-day ecosystems, we can generate hypotheses that can be examined in the evolutionary record.

Building on the pioneering work of Ernest Williams and his students at the Museum of Comparative Zoology at Harvard University from the 1960s through the 1980s, my colleagues and I have taken this sort of approach in our



FIGURE 1 Male *Anolis lividus* from Jamaica displaying by extending its dewlap. (Jonathan B. Losos)

studies of the *Anolis* lizards of the West Indies. Anoles, as they are called, are relatively small, insect-eating lizards that are abundant on islands in the Caribbean, as well as in Central and northern South America and in the southeastern United States. Their defining traits are enlarged and sticky toepads that allow them to move with dexterity on slick and narrow surfaces, and the possession by males (and by females in some species) of a dewlap, an extensible and often brightly patterned flap of skin on the throat that is used in courtship and territorial encounters. (FIGURE 1)

Anoles are a textbook case for the study of biodiversity. Not only are they abundant and easy to study in many ways, but nearly 400 species are known, with more being discovered every year. Among the group of animals termed the amniotes, which includes birds, mammals, and reptiles, *Anolis* is the most species-rich genus.

One aspect of anole diversity in particular has been the subject of much research. If you were to visit any of the islands of the Greater Antilles (Cuba, Hispaniola, Jamaica, and Puerto Rico; FIGURE 2), you would see a variety of different species. Go, for example, to the Discovery Bay Marine Laboratory on the north coast of Jamaica and quietly take a seat outside. After a few minutes, you will start to see lizards with long legs running and jumping near the ground, others with large toepads high in the trees, yet others with narrow bodies and short limbs crawling carefully on narrow surfaces.



FIGURE 2 Map of the Greater Antilles.

What is most remarkable, however, is that essentially the same set of habitat specialists occurs on each of the islands. So, for example, if you were to go to any of the other islands of the Greater Antilles, you would see a lizard that looks like the Jamaican twig specialist, living in the same sort of habitat and behaving in pretty much the same way (FIGURE 3). The same holds true for the other types of habitat specialists, including the tree-trunk-near-the-ground (“trunk-ground”), tree canopy, and low-lying narrow vegetation (“grass-bush”) specialists, as well as a few others.

The existence of the same set of habitat specialists on different islands raises a series of questions, which I will address in turn: (1)What is the evolutionary history of habitat specialization? (2)Why do species using the same habitat on different islands have the same morphological features (“morphology” refers to the form and structure of an organism)? (3)What evolutionary processes have operated to produce these patterns?

WHAT IS THE EVOLUTIONARY HISTORY OF HABITAT SPECIALIZATION?

Two different scenarios could lead to the existence of the same set of habitat specialists on each island. On one hand, habitat specialists could have evolved repeatedly and independently on each of the islands. On the other hand, each

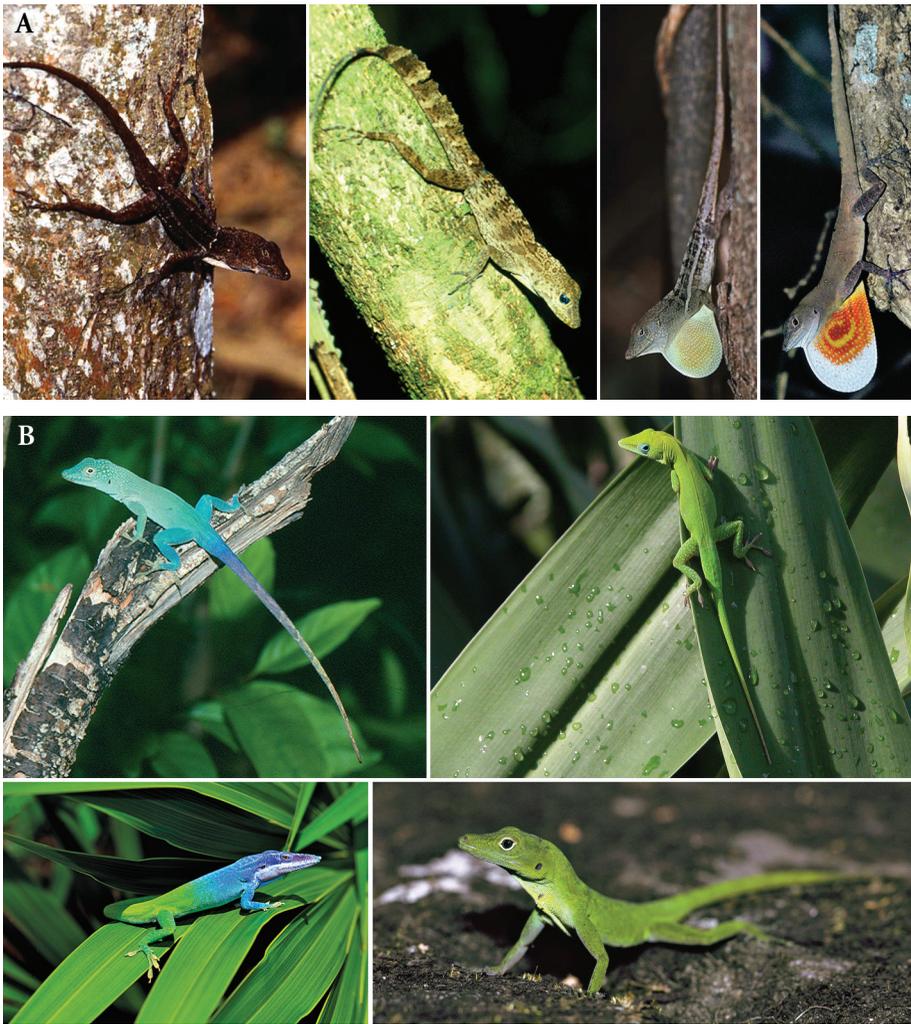


FIGURE 3 Five habitat specialist types, shown here and on the facing page: (a) **trunk-ground anoles** (from left to right: *Anolis cybotes* [Hispaniola], *Anolis gundlachi* [Puerto Rico], *Anolis lineatopus* [Jamaica], and *Anolis allogus* [Cuba]); (b) **trunk-crown anoles** (top row, left to right: *Anolis grahami* [Jamaica], *Anolis chlorocyanus* [Hispaniola], bottom row, left to right: *Anolis allisoni* [Cuba] *Anolis evermanni* [Puerto Rico]); (c) **crown-giant anoles** (upper left: *Anolis cuvieri* [Puerto Rico], lower left: *Anolis equestris* [Cuba], right: *Anolis garmani* [Jamaica]); (d) **grass-bush anoles** (from left to right: *Anolis vanidicus* [Cuba], *Anolis olssoni* [Hispaniola], and *Anolis pulchellus* [Puerto Rico]); and (e) **twig anoles** (top row: *Anolis valencienni* [Jamaica], *Anolis insolitus* [Hispaniola], bottom row: *Anolis angusticeps* [Cuba], and *Anolis occultus* [Puerto Rico]). Grass-bush anoles are found on only three islands. Crown-giant anoles are also found on Hispaniola (not shown). A sixth habitat specialist, the trunk anole, is found only on Hispaniola and Cuba and is not illustrated. (Photographs of *A. chlorocyanus*, *A. vanidicus*, *A. valencienni*, and *A. insolitus* Kevin de Queiroz; photograph of *A. occultus* William E. Rainey; all other photographs by Jonathan B. Losos)





of the habitat specialists could have evolved only a single time. This latter possibility could have resulted if a species evolved to specialize for a particular habitat on one island and then subsequently made its way to the other islands and then evolved into distinct species. Such a scenario could occur either by overseas colonization (some anole species are quite hardy and are able to survive a rafting voyage from one island to another) or by lizards walking from one island to another when they were connected at some time in the past (the geological history of the Caribbean is still surprisingly little known, so we can't say for sure about the extent to which the various islands were previously in contact, although we do know that at least some of them were connected at some point in the past).

All we need to distinguish between these hypotheses is a tree of evolutionary relationships of the species (termed a “phylogeny”). Phylogenies are now regularly constructed by evolutionary biologists using DNA-sequence data; by comparing the same stretch of DNA for different species using sophisticated computer algorithms, the hypothesis of evolutionary relationships that is best supported by the data can be discovered.

The two hypotheses about the evolution of habitat specialists make different predictions that can be tested with a phylogeny. If each habitat-specialist type has evolved only a single time, then species belonging to that type on different islands should be more closely related to each other than they are to other species of different types on their own islands (FIGURE 4). Alternatively, if species have evolved the same habitat specializations independently, then these species should not be so closely related to each other.

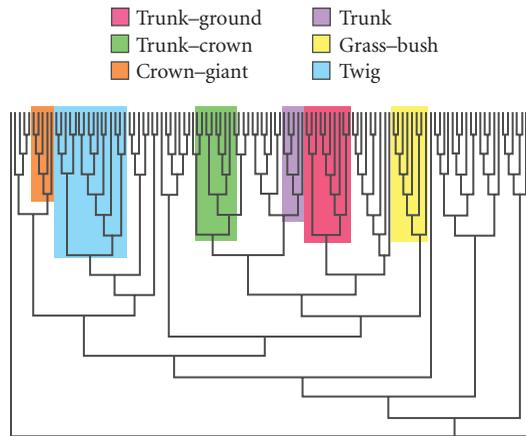


FIGURE 4 Hypothetical phylogenetic tree illustrating a scenario in which *Anolis* lizard species of the same habitat specialist type, although on different islands, are more closely related to each other than they are to members of other habitat specialist types.

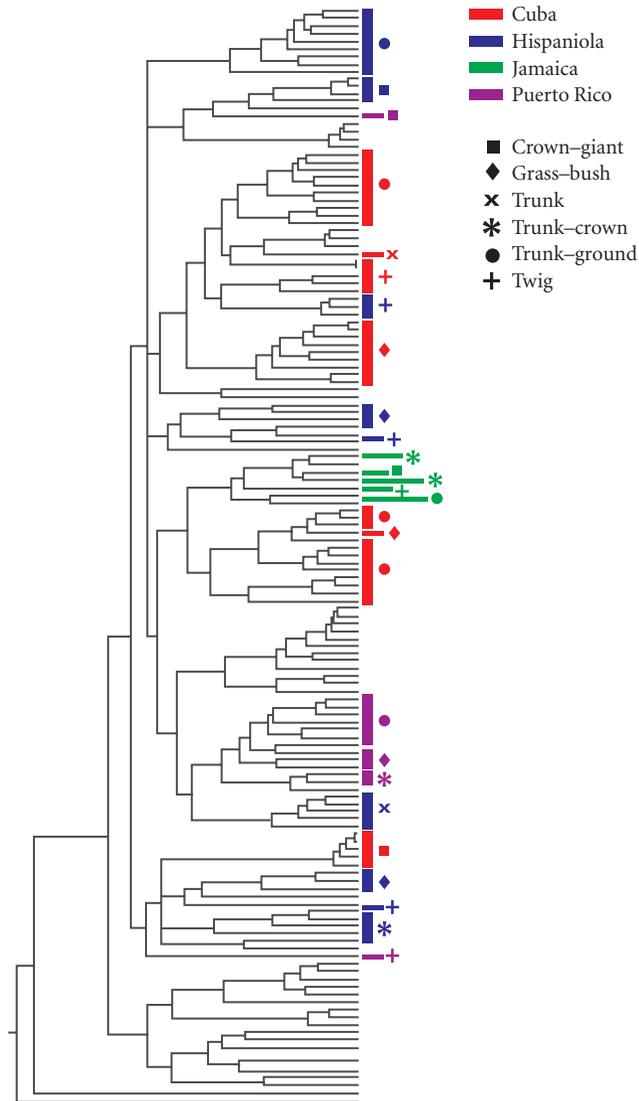


FIGURE 5 Phylogenetic relationships of *Anolis*. Symbols represent the different habitat specialist types; color represents the four islands of the Greater Antilles. Tips of the phylogeny with no symbol represent species from areas other than the Greater Antilles and species from the Greater Antilles that are not one of the convergent habitat specialist types. The figure demonstrates that members of the same habitat specialist type on different islands are not closely related.

The phylogeny we have developed for anoles is unequivocal on this count: habitat specialists have evolved independently on each of the islands of the Greater Antilles (FIGURE 5). In only one case are the members of the same habitat-specialist type on different islands each other's closest relatives, presumably the result of a relatively recent dispersal event from one island to the other.

Convergent evolution, when species facing the same environmental pressures evolve the same phenotypic responses, has long been considered evidence that those phenotypes represent adaptations to those particular circumstances. However, convergence of entire assemblages of species is much less common, and anoles provide one of the very best examples of this phenomenon.

WHY DO SPECIES USING THE SAME HABITAT ON DIFFERENT ISLANDS HAVE THE SAME MORPHOLOGICAL FEATURES?

Phylogenetic approaches can demonstrate the occurrence of convergence, but they can't tell us why it occurred. Convergent evolution of each of the habitat specialists indicates that adaptation to using different parts of the structural habitat (i.e., the arrangement and architecture of the surfaces upon which the lizards move) is pervasive in anole evolution. Nonetheless, this simple correlation between morphology and habitat does not explain why particular features are favored by natural selection in particular habitats.

To understand the mechanistic link responsible for these repeated evolutionary patterns, we need knowledge of two types: how does trait variation affect the functional capabilities of lizards, and what are the lizards actually doing in their environments? For example, one of the traits that varies greatly among the habitat specialists is hindlimb length: at the extremes, trunk-ground anoles have extremely long hindlimbs, whereas twig anoles have very short ones. What are the functional differences that result from these differences in limb length, and how do these differences relate to how the lizards interact with their environments?

This is where the fun comes in. Measuring the functional abilities of lizards is much like orchestrating a Lizard Olympics, as individuals are put through their paces to determine, for example, how fast they can run, how far they can jump, and how well they can cling (FIGURE 6).

The results have produced the best of all possible worlds. As we predicted, lizards with longer limbs—which can cover more ground in each stride and which accelerate for a greater period of time during the launch phase of a jump—can run faster and jump farther, and lizards with larger toepads—and thus more of the microscopic hair-like structures responsible for adhesive force—can cling better. Failure to find support for these predictions would



FIGURE 6 *Anolis carolinensis* jumping from a round wooden dowel in a laboratory trial. (Bob Lalonde)

have suggested that our basic understanding of lizard biomechanics was inadequate, so finding support for these hypotheses was important.

On the other hand, we have learned some important lessons that were completely unexpected. One example concerns the adaptive advantage of short legs for species using narrow surfaces. Our initial prediction was that species would run fastest on surfaces corresponding to those they use in nature: trunk-ground species would run fastest on broad surfaces and twig species would run fastest on narrow surfaces.

These predictions were only partly supported. Long-legged species do, in fact, run fastest on broad surfaces, and they experience a marked decline in sprinting ability as the diameter of the surface upon which they are running declines (FIGURE 7). But short-legged species do not run faster on narrow surfaces. Moreover, the phylogeny indicates that short legs are a derived feature in twig anoles—they evolved from a longer-legged ancestor. But why evolve shorter legs? The data in Figure 7 indicate that a long-legged lizard can run just as fast or faster than a short-legged one on narrow surfaces, but without giving up its much greater capabilities on broader surfaces.

The answer to this dilemma was revealed by another measure of locomotor performance that we collected during the sprint trials: the number of times lizards tripped or stumbled. On broad surfaces, none of the species had much difficulty. However, on the narrow surfaces, trunk-ground species had trouble on more than 75% of the trials. By contrast, twig anoles experienced only a minor decrease in “sure-footedness” on narrower surfaces.

With these data in mind, we went back into the field to see what the lizards are actually doing in their natural environment. Sure enough, trunk-ground

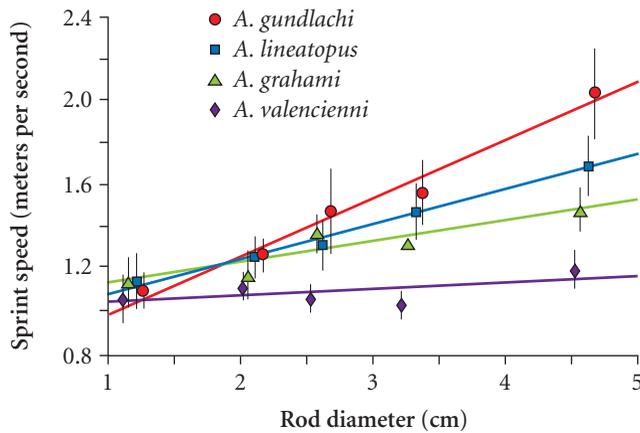


FIGURE 7 Sprint speed versus surface diameter for several anole species. *Anolis valencienni*, a twig anole, has substantially shorter legs than the other three species illustrated here. Modified from Losos and Sinervo (1989).

lizards zip around on the ground and on other broad surfaces, using their quickness to capture prey and to elude predators. By contrast, twig anoles are much more deliberate; they creep slowly along twigs. Rapid sprints rarely occur, but moving without difficulty on their narrow and irregular surfaces is essential to discovering the motionless prey that they eat and for avoiding being detected by predators.

This example illustrates how a combination of functional studies and basic natural history can elucidate the selective pressures leading to convergent evolutionary specialization. Studies of this sort have revealed much of the adaptive basis of anole diversification, but some questions remain. For example, grass anoles have extremely long tails—sometimes as much as four times the length of the body. The adaptive benefits these elongated tails provide is still a matter of conjecture.

WHAT EVOLUTIONARY PROCESSES HAVE OPERATED TO PRODUCE THESE PATTERNS?

The term “adaptive radiation” refers to the situation in which an ancestral species diversified to produce a set of descendant species that are adapted to using a wide variety of different ecological niches. Classic examples of adaptive radiation include Darwin’s finches on the Galápagos Islands, Hawaiian silversword plants, and cichlid fishes in the lakes of the Rift Valley in Africa. West Indian

Anolis lizards also exemplify adaptive radiation, replicated four times and with much the same outcome on each island.

The standard explanation for adaptive radiation is the following scenario: for some reason (perhaps due to colonization of an island or mass extinction), an ancestral species finds itself in an environment with an abundance of resources. Speciation occurs, leading to a number of co-occurring species that initially use the same resources. As the species' populations increase in abundance, resource levels fall and interspecific competition occurs for the now scarce resources. As a result, species may alter their resource use, shifting to utilize resources that are not used by the other species. Over time, the species evolve adaptations to use their different ecological niches, and the end result is a set of species adapted to use different parts of the environment—that is, an adaptive radiation.

In the absence of a time machine, testing historical hypotheses such as this is difficult. Moreover, the fossil record for anoles is extremely limited. Consequently, our best bet for understanding the processes that may have occurred in the past is to examine how those processes operate today. In particular, this scenario suggests three testable hypotheses: (1) Coexisting species compete for resources; (2) In the presence of competitors, species shift their use of their habitat to minimize overlap in resource use; (3) As a result of shifts in habitat use, species adapt to their new conditions.

One point to keep in mind when evaluating these predictions is that species of *Anolis* that occur together today invariably differ in their resource use. Consequently, even if interspecific competition leads ecologically similar species to diverge, the result might be that species that co-occur have already diverged to the extent that they don't compete any more. In this case, studying interactions among present-day species would not help us to decipher what happened in the past. Conversely, if present-day, already ecologically differentiated species, compete, we might safely assume that ancestral species that hadn't already differentiated and thus were much more similar in their resource use would have competed even more strongly.

HYPOTHESIS 1: COEXISTING ANOLE SPECIES COMPETE FOR RESOURCES

A wide variety of studies have demonstrated negative effects on one anole species resulting from the presence of a second anole species. For example, in an experimental investigation on the island of St. Martin, a number of cages 144 m² in area were constructed. Into each of these cages, either one or both species native to that island were placed. Individuals of the focal species, *A. gingivinus*, grew at higher rates, ate more, reproduced more quickly, and attained a larger adult size in the cages in which they were alone, when compared to those

in which individuals of the other species were also present. Similarly, on tiny islands in the Bahamas, populations of *A. smaragdinus* reached higher population densities when they were the only anole species placed on the island when compared to the population densities of *A. smaragdinus* on islands onto which *A. sagrei* was also introduced (FIGURE 8).

Evidence of another sort comes from human introduction of anole species throughout the Caribbean. Although introduced species are a grave environmental problem, they do present the opportunity to examine situations that could not be created intentionally. Examination of the record of anole introductions revealed a stark contrast: in cases in which an ecologically similar anole was not already present, seven of 11 introduced species had become widespread, and none had become extinct. In contrast, in 12 cases in which an ecologically similar species was already present, none of the introduced species had become widespread, and two had perished.

In recent years, ecologists increasingly have emphasized the importance of other types of negative interactions among species besides resource competition. For example, adult anoles of one species may prey on the young of another species. In anoles, the evidence for resource competition is strong, but more work is needed to investigate other possibilities.



FIGURE 8 One of the larger Bahamian islands on which experiments have been conducted. Experiments have been conducted in several parts of the Bahamas; this island is in Snake Creek, Abaco. (Jonathan B. Losos)

HYPOTHESIS 2: ANOLE SPECIES SHIFT HABITAT USE IN THE PRESENCE OF OTHER SPECIES

Evidence for habitat shifts is widespread, and it occurs at the individual level and at the landscape level. On one hand, observations of single lizards have revealed that individuals of one species will move away when individuals of a second species appear in their environment. Experimental studies such as those described in the last section reveal a similar population-level response; in the experiments on St. Martin, for example, individuals of *A. gingivinus* perch much higher in the trees in cages containing the second species of anole than they do in the cages in which they occur alone. Similar shifts are documented in the presence of an introduced species. Lastly, comparisons of populations throughout a species' geographic range show consistent changes in habitat use depending on whether other anole species are present.

HYPOTHESIS 3: SHIFTS IN HABITAT USE LEAD TO EVOLUTIONARY ADAPTATION

Evidence pertaining to this hypothesis comes mostly from comparisons of populations of a species that differ in habitat use. Based on our understanding of how anole species adapt to using different parts of the environment, we can predict the changes that would occur at a smaller scale as populations adjust their habitat use. For example, species using narrower surfaces should evolve shorter limbs, and species becoming more arboreal should evolve more highly developed toepads. Comparisons of populations of several species have confirmed these predictions.

The occurrence of introduced species provides the opportunity to test these predictions over a shorter time scale. For example, the Cuban brown anole, *A. sagrei*, was introduced into southern Florida sometime in the latter half of the nineteenth century. As it continues its spread throughout the southeastern United States, studying the ecological and evolutionary effects of the introduced species on the native *A. carolinensis* would prove fascinating. Surprisingly, such studies have not yet been conducted.

Overall, the extensive data on anoles, which I have skimmed only briefly here, strongly support the predictions of the adaptive-radiation hypothesis: anole species interact strongly when they co-occur; as a result, they shift their habitat use; and, over time, they adapt to their new habitat.

EVOLUTIONARY BIOLOGY AS AN EXPERIMENTAL SCIENCE

Evolutionary biologists revere Charles Darwin. *On the Origin of Species* and Darwin's other works provide a wealth of data and ideas that are relevant to scientists a century and a half later. Nonetheless, Darwin wasn't right about everything. His conception of heredity was completely wrong, for example. In addition, Darwin thought that evolution proceeded only at a glacial pace, and thus its workings would be evident only after thousands of years. This view persisted for more than a century, and thus led to the widespread notion that evolution could be studied only through the lens of a historian.

In recent years, however, it has been revealed very clearly that Darwin got this one wrong. Given strong enough selection, evolution can occur extremely rapidly, not only over the course of an individual scientist's career, but even over the course of a few years (see the essay by David Reznick in this volume). The result is not only that evolution is observable as it occurs, but also that it may be possible to conduct experiments to test evolutionary hypotheses. One famous example is the translocation of guppies to predator-free environments, which led to substantial evolutionary changes in body coloration in less than two decades (see essay by Reznick in this volume).

In a series of experiments, two of my collaborators (Thomas Schoener and David Spiller) and I have attempted to test experimentally certain ideas that are fundamental to the hypothesis of adaptive radiation. These experiments have been conducted on tiny islands in the Bahamas, using species that occur naturally in the area (FIGURE 9). The results are as yet somewhat inconclusive, but they illustrate the perils and pitfalls of fieldwork in evolutionary biology.



FIGURE 9 Common Bahamian anoles: *Anolis smaragdinus* (left, previously considered conspecific with *Anolis carolinensis*, the only anole native to the United States) and *Anolis sagrei* (right). (Jonathan B. Losos)

Our first experiment examined the ecological and evolutionary consequences of interspecific interactions between *A. smaragdinus* and *A. sagrei*. The experiment clearly indicated the negative effect of *A. sagrei* on *A. smaragdinus*: the density of *A. smaragdinus* populations that occurred with *A. sagrei* were consistently lower than the densities of *A. smaragdinus* populations that occurred by themselves. Moreover, *A. smaragdinus* perched higher on the two species islands, evidence that they were shifting up into the vegetation in the presence of the more terrestrial *A. sagrei*. Unfortunately, before we had a chance to detect evolutionary changes in morphology, populations of *A. smaragdinus* on all islands crashed, presumably due to adverse weather (although the exact cause is not clear). Then, a hurricane swept through the area and eliminated most of our populations, thus ending the experiment (and also confirming our hypothesis about why these low-lying islands were not occupied prior to the experiment: although anoles can colonize over water, such colonizations occur at a relatively low rate, and hurricanes passing through periodically are sufficient to keep most of the islands unoccupied by anoles).

In our second experiment, we decided to focus on a different ecological process: predation. In this case, we introduced a larger, ground-dwelling lizard, the curly-tailed lizard, *Leiocephalus carinatus* (FIGURE 10), to examine the ecological and evolutionary effects of predation on anoles. We chose 12 islands that naturally contained *A. sagrei* and on six of them we introduced curly-tailed lizards from the nearby mainland (curly-tailed lizards also naturally colonize these small islands, so we were again mimicking a natural and ongoing process). Although curly-tailed lizards are known to eat anoles, we did not know



FIGURE 10 A curly-tailed lizard (*Leiocephalus carinatus*). (Jonathan B. Losos)

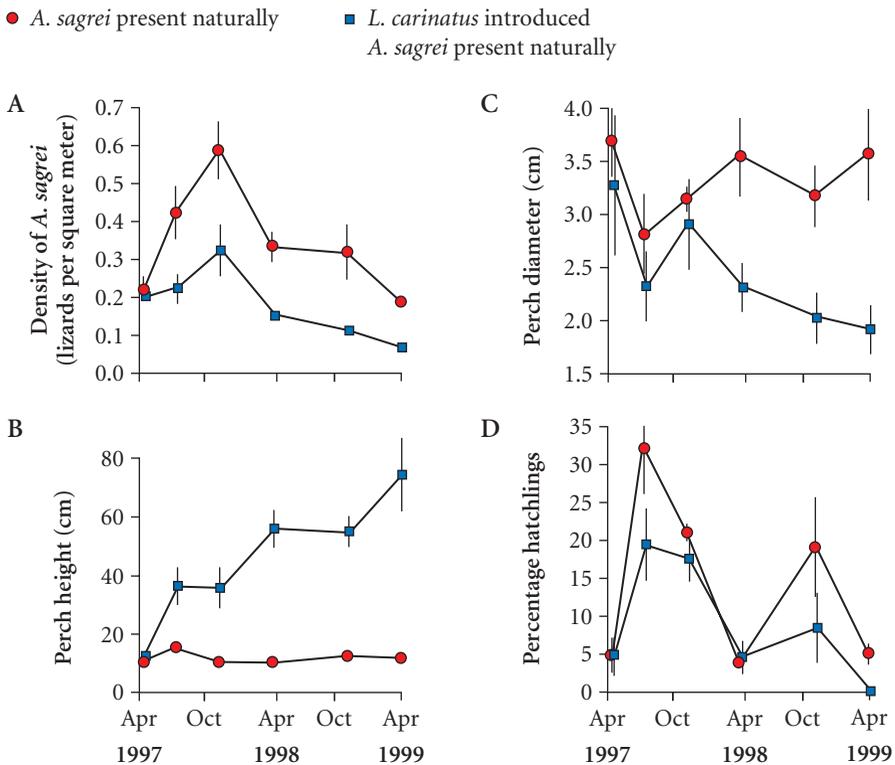


FIGURE 11 Effect of introduction of predatory lizards (*Leiocephalus carinatus*) on *Anolis sagrei* populations in terms of (a) population density, (b) perch height, (c) perch diameter, and (d) percentage of lizards observed that were hatchlings. Modified from Schoener and colleagues (2002).

whether such predation was a rare event or whether the anole populations would be greatly affected.

The results were dramatic. On islands with curly-tailed lizards, anole populations plummeted and the mean perch height of the remaining anoles skyrocketed: the surviving anoles were moving up into the bushes to avoid the terrestrial predators (FIGURE 11). *Anolis sagrei* is a trunk-ground habitat specialist, but, on these islands, it was being forced to use narrow surfaces, leading to the prediction that the populations would evolve shorter legs to adapt to their new circumstances. Unfortunately, this experiment, too, was terminated by a hurricane.

We did make one unexpected finding, however: lizard eggs can survive immersion in the high water resulting from a hurricane. As a result, even

though all of the lizards were washed off our islands, the lizard eggs in the ground subsequently hatched, and the *A. sagrei* populations quickly recovered (although the curly-tailed lizard populations did not, perhaps because their breeding season may have been already finished for the year).

As a result, we were able to reinitiate the experiment within a few years. Confident that curly-tailed lizards would have a large effect on the population of *A. sagrei*, we did something new in the next round of the experiment: we measured and individually marked the *A. sagrei* prior to the start of the experiment. Our prediction was that, in the first generation, predation by curly-tailed lizards would favor those anoles with the longest legs because they would be faster and thus more able to escape (even on islands on which curly-tailed lizards are introduced, anoles still use the ground to some extent). Over the longer term, as individuals of *A. sagrei* became more arboreal, we predicted that selection would reverse its course as the species adapted to using narrow, arboreal perches.

By going back after six and 12 months, we could determine which lizards had survived and which had not. By examining the measurements we made of the lizards at the start of the experiment, we could ask whether survival was related to limb length; in other words, we were looking for evidence that natural selection had occurred. More importantly, we were interested in determining whether the form of natural selection differed between the islands with and without the predator.

As predicted, selection favoring longer limbs was stronger on experimental islands than on controls over the first six months. Further, and again as predicted, selection reversed course and began to favor shorter legs. However, that reversal occurred in the second six-month period, much sooner than we had expected.

Because selection on the experimental islands had first favored longer legs and then shorter legs, the overall effect for the entire 12 months was not different from selection on the control islands. However, with the lizards now shifted into the bushes, we expected that selection would continue to favor shorter legs. Consequently, we would predict that selection over many generations would lead to the evolution of shorter limbs in populations on the experimental islands.

What happened? More hurricanes, of course. In 2004, not one, but two hurricanes passed over our experimental islands, terminating yet another experiment. It took four years, but the *A. sagrei* populations have recovered, and round III of the experiment is now underway. Hopefully, in this trial, we will be able to follow the experiment long enough to test the hypothesis that predation-driven selection can lead to rapid evolutionary change.

ANOLE GENETICS AND GENOMICS

The theory of evolution by natural selection requires three conditions: (1) Individuals must vary; (2) This variation must lead to differences in reproduction or survival (i.e., selection must occur); (3) Variation among individuals must have a heredity basis, such that offspring tend to resemble their parents.

Conditions 1 and 2 are met for anoles, but studies on the genetic basis of phenotypic differences have lagged behind. In part, this is probably because the large sample sizes required by laboratory genetic studies are hard to obtain from anoles, which only lay one egg at a time. However, females of many species of the genus can produce an egg every 7 to 10 days, and now several laboratories are studying the extent to which variation in anole traits is transmitted between generations. Early reports indicate high levels of heritability.

Nonetheless, the existence of genetic variation for a trait does not guarantee that phenotypic variation among individuals within a population, or among populations in different environments, is the result of genetic differences. The reason is that a single genotype can produce different phenotypes in different environments—the phenomenon of phenotypic plasticity. We are all aware of such plasticity in plants: grow clones of the same plant in different light or moisture environments, and the resulting plants will look very different. However, in recent years, evidence for plasticity in animals has increased greatly. Because of phenotypic plasticity, scientists need to be cautious in interpreting the variation they see within and among populations, which may result from the differences environments in which individual organisms have developed, rather than reflecting genetic differences.

The potential significance of phenotypic plasticity in anoles was driven home years ago in a study on variation in limb length in *A. sagrei*. Having grown tired of botanists pestering me with questions after seminars, I conducted an experiment at the St. Louis Zoo in which we raised baby anoles in cages with either broad or narrow perches on which they could sit. To our surprise, at the end of the experiment, the lizards in the cages with broad surfaces had longer legs than those in cages with narrow surfaces. This result was not due to differences in size or survival; legs actually grow longer when a young lizard grows up on a broader surface. A subsequent study on *A. carolinensis* yielded the same result.

The existence of plasticity in anoles has several implications. First, differences among populations may not indicate that populations have evolved genetically to adapt to different environments. Second, selection within a population may not lead to evolutionary change if the selection operates on variation among individuals that is not genetically based: if individuals with long and short legs do not differ genetically, then it doesn't matter which ones survive and reproduce; the gene pool of the next generation will remain unchanged.

Before dismissing the entire phenotypic diversity of anoles as a result of phenotypic plasticity, however, keep in mind that the differences produced in our laboratory studies were quite modest. Despite growing on surfaces approximating tree trunks (broad and flat) and twigs, the differences in limb length among individuals of *A. sagrei* were quite minor compared to differences that characterize species adapted to living on tree trunks or on twigs. These much more substantial differences between species are surely the result of genetic change. Moreover, in the only study to examine the genetic basis of differences among populations of anoles, baby *A. oculatus* from different places on the island of Dominica were raised in the same locality. If differences among populations were the result of phenotypic plasticity, then we would expect the differences to disappear in such a “common garden.” However, the among-population differences persisted for the most part, suggesting an underlying genetic basis for interpopulation differences.

More generally, evolutionary biologists are paying increasing attention to phenotypic plasticity as a process that could accelerate evolutionary diversification. Although variation among individuals may not have a genetic basis, plasticity itself is a genetically based trait that is subject to selection and that can evolve. Thus, species that tend to occur in highly variable populations may evolve a great capacity for plasticity to produce phenotypes that are appropriate for different conditions. Moreover, phenotypic plasticity, in theory, could jump-start adaptive radiation by allowing a population to occupy a new environment in which it otherwise might not be able to become established. Once there, the population might subsequently evolve enhanced phenotypic adaptations through genetic means, as beneficial mutations occur and are favored by natural selection.

Discussion of anole genetics would not be complete without mention of the impending genomic tidal wave. The genome of *A. carolinensis* has recently been sequenced at the Broad Institute in Cambridge, Massachusetts. Once the results are analyzed and reported, a variety of approaches will be available to identify the genes that affect specific phenotypic characters, as well as the mutations responsible for variation within populations and between species. The developmental genetics of some traits of particular significance in anoles, such as limb or head dimensions, have been extensively studied in other vertebrates. Many genes are evolutionarily conservative; consequently, anole researchers may be able to take advantage of work on other groups to study diversification in these traits. A question of particular interest will be whether convergence in such phenotypic traits as limb length has been accomplished through convergent changes at the DNA level.

A lot of hard work stands between obtaining a genome sequence and actually finding the genetic differences responsible for phenotypic variation, but

already the impending publication of the *A. carolinensis* sequence is generating widespread interest. I look forward to the day, perhaps not far off, when we can identify the genes and even the DNA base-pair substitutions responsible for phenotypic variation within populations and between species. This knowledge will allow us to study anole adaptive radiation synthetically, uniting investigations of genomics with those of community ecology, behavior, and macroevolution.

CONCLUSIONS

I have tried to demonstrate two points in this essay. First, evolutionary biology is inherently multidisciplinary and synthetic. To study what happened in the past, we must combine a variety of different approaches. Each approach has its advantages and its shortcomings. Historical analysis can reveal patterns of evolutionary change, but not why they occurred; study of extant populations can reveal how processes operate in the here and now, but not their outcome over geological time. When these approaches are synthesized, they can be mutually illuminating, allowing us to formulate and test hypotheses about how and why evolution has followed a particular course.

Second, evolutionary biology can incorporate an experimental approach. Such studies are not easy and take a long time, but they do allow hypotheses generated from historical data to be tested on present-day populations. The synthesis of history and the present, of observation, inference, and experiment, is a powerful means for studying the origin and maintenance of biological diversity.

SUGGESTED READINGS

- Losos, J. B. 2009. *Lizards in an Evolutionary Tree: Ecology and Adaptive Radiation of Anoles*. University of California Press: Berkeley, CA.
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