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Detective Work in the West Indies: Integrating Historical and Experimental Approaches to Study Island Lizard Evolution

JONATHAN B. LOSOS

Evolutionary biology is a historical science, like astronomy and geology. Understanding how and why evolution has occurred requires synthesizing multiple lines of inquiry. Historical studies, such as those that estimate phylogenetic trees, can detail the pattern of evolutionary diversification, whereas studies on living species can provide insight into the processes that affect ecological interactions and evolutionary change. The evolutionary radiation of Anolis *lizards in the Greater Antilles illustrates the interplay between historical and modern-day approaches and strongly supports the hypothesis that interspecific interactions drive adaptive diversification. Studies of these species also demonstrate the role that manipulative experiments can play in understanding evolutionary phenomena.*

Keywords: adaptive radiation, Anolis*, community ecology, evolution, lizard*

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 which researchers must take multiple approaches and use whatever types of data are available to construct—and continually test—hypotheses about what happened in the past (Cleland 2001, Mayr 2004). 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 involve using the clues available to fashion the best case of whodunit.

My theme in this article is twofold. First, I argue that to understand what happened in the past, we must take an integrative, multidisciplinary approach. Second, historical and present-day studies can be mutually illuminating: Historical analyses can suggest hypotheses that can be tested, oftentimes experimentally, with data on extant species; in turn, by extrapolating from what happens in present-day ecosystems, researchers can generate hypotheses that can be examined in the evolutionary record.

Building on the pioneering work of Ernest Williams and his students at Harvard's Museum of Comparative Zoology from the 1960s through the 1980s, my colleagues and I have taken this sort of approach in our studies of the *Anolis* lizards of the West Indies (figure 1). Anoles, as they are called, are relatively small, insect-eating lizards that are abundant on islands in the Caribbean, as well as in Central America, northern South America, and the southeastern United States. Their defining traits are enlarged and sticky toe pads that allow them to move with dexterity on slick and narrow surfaces, and the possession by males (and 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.

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.

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Figure 1. Male **Anolis garmani** *from Jamaica displaying (extending its dewlap). Photograph: Jonathan B. Losos.*

One aspect of anole diversity in particular has been the subject of much research. Visitors to any of the islands of the Greater Antilles (Cuba, Hispaniola, Jamaica, Puerto Rico; figure 2) can see a variety of different anole 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 see lizards with long legs running and jumping near the ground, others with large toe pads high in the trees, and still others with narrow bodies and short limbs crawling carefully on narrow surfaces.

What is most remarkable, however, is that essentially the same set of habitat specialists occurs on each of the islands (Williams 1972, 1983). 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 three 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? (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 of the habitat specialists could have evolved only a single time. This latter possibility could result if a species evolved to specialize for a particular habitat on one island, and then subsequently made its way to the other islands and evolved into distinct species. Such a scenario could occur either by overseas colonization (some anole species are quite hardy and able to survive a rafting voyage from one island to another) or by lizards walking from one island to another when they were

Figure 2. Map of the Greater Antilles.

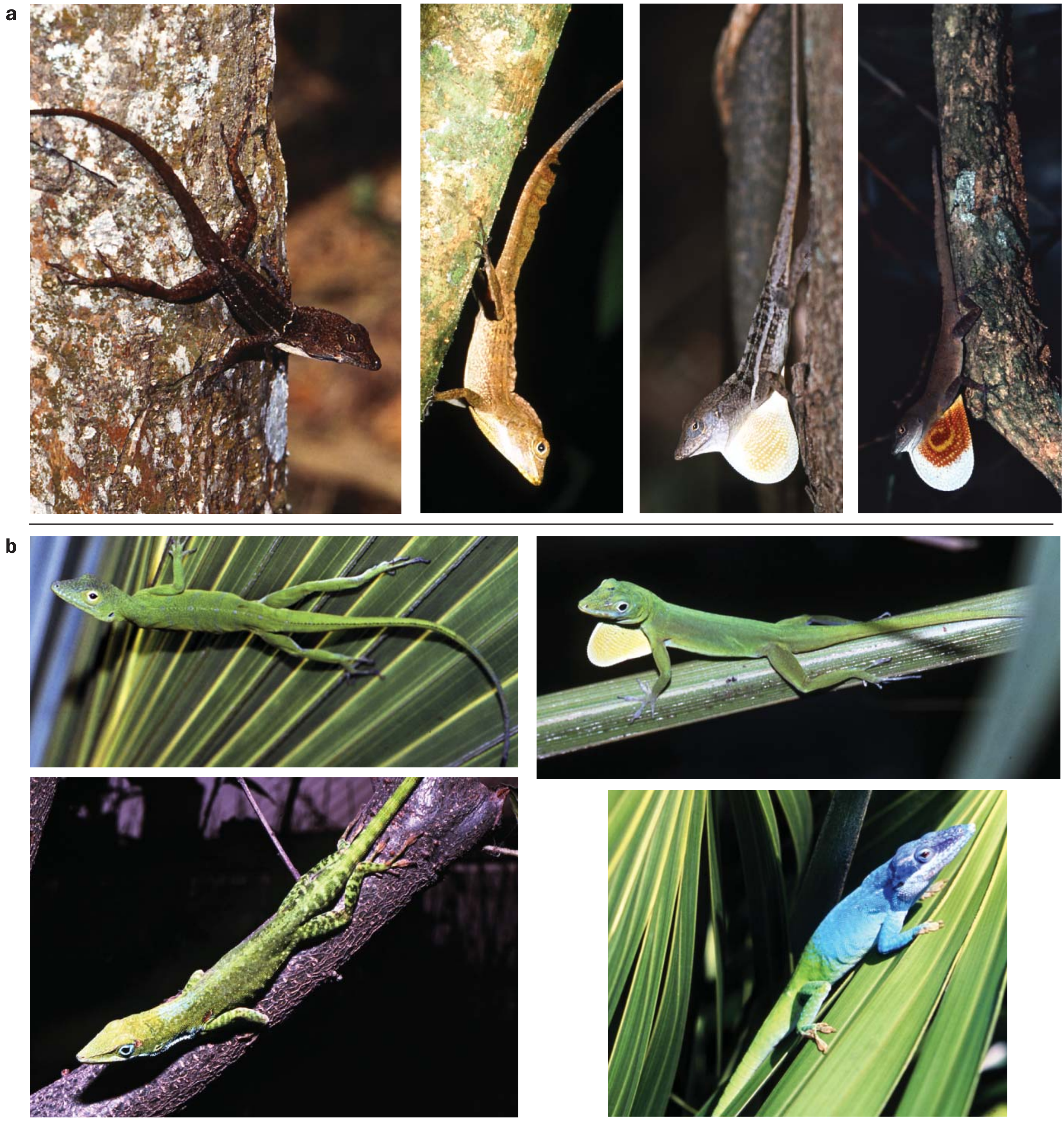

*Figure 3. Five habitat specialist types, shown here and on the following two pages (from left to right in each panel): (a) trunk–ground anoles (*Anolis cybotes *[Hispaniola],* Anolis gundlachi *[Puerto Rico],* Anolis lineatopus *[Jamaica], and* Anolis allogus *[Cuba]); (b) trunk–crown anoles (*Anolis grahami *[Jamaica],* Anolis evermanni *[Puerto Rico],* Anolis chlorocyanus *[Hispaniola], and* Anolis allisoni *[Cuba]); (c) crown-giant anoles (*Anolis cuvieri *[Puerto Rico],* Anolis luteogularis *[Cuba], and* Anolis garmani *[Jamaica]); (d) grass–bush anoles (*Anolis vanidicus *[Cuba],* Anolis olssoni *[Hispaniola], and* Anolis pulchellus *[Puerto Rico]); and (e) twig anoles (*Anolis valencienni *[Jamaica],* Anolis insolitus *[Hispaniola],* 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 *courtesy of Kevin de Queiroz; photograph of* A. occultus *courtesy of William E. Rainey; all other photographs by Jonathan B. Losos.*

connected some time in the past (the geological history of the Caribbean is surprisingly little known, so we can't say for sure to what extent the islands previously were in contact, although we know that at least some of them were connected at some point in the past; for a recent review, see Graham [2003]).

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 researchers can test with a phylogeny. If each habitat specialist type has evolved only once, 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 independently evolved the same habitat specializations, then they should not be closely related to each other.

The phylogeny that my colleagues and I have developed for anoles (Jackman et al. 1999, Nicholson et al. 2005; see also Poe 2004) 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 members of the same habitat specialist type on different islands one another's closest relatives, presumably as a result of a relatively recent dispersal event.

Convergent evolution, in which 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 (Pagel 1994). However, convergence of entire assemblages of species is much less common; anoles are one of the best examples, if not the best, 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 cannot explain 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 on 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 in two areas: How does trait variation affect the functional capabilities of lizards, and what are the lizards actually doing in their environments (Wainwright 1988, Garland and Losos 1994, Irschick 2002)? For example, one of the traits that varies greatly among the habitat specialists is hind limb length: At the extremes, trunk–ground anoles have extremely long hind limbs, 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 lizard functional abilities is much like orchestrating a "Lizard Olympics," as individuals are put through their paces to determine 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: Our basic premises about lizard functional morphology have been confirmed, but many of the more detailed findings were surprising. As predicted, lizards with longer limbs—which can cover more ground in each stride, and which accelerate for a longer period during the launch phase of a jump—can run faster and jump farther (Losos 1990, Irschick and Losos 1998, Toro et al. 2004, Vanhooydonck et al. 2006). Also as predicted, lizards with larger toe pads—and thus more of the microscopic hairlike structures responsible for adhesive force (Peterson 1983, Autumn et al. 2000, 2002)—can cling better (Losos 1990, Irschick et al. 1996). Failure to find support for these predictions would have suggested that our basic understanding of lizard biomechanics was inadequate, so finding support for these hypotheses was important.

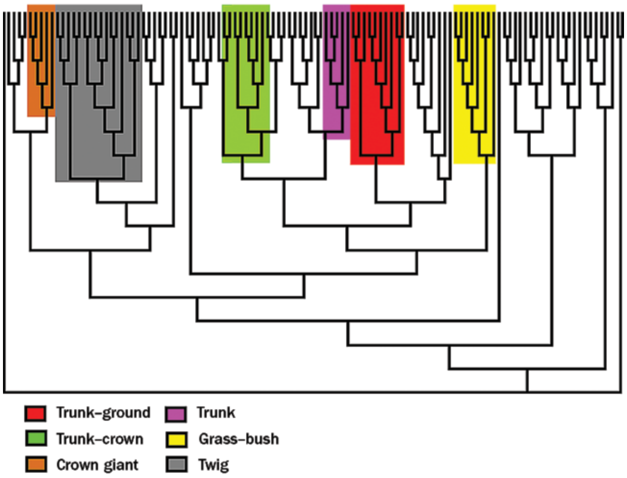

Figure 4. Hypothetical phylogenetic tree illustrating a scenario in which* Anolis *lizard species of the same habitat specialist type, although on different islands, are more closely related to each other than they are to members of other habitat specialist types.

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 should run fastest on broad surfaces and twig species on narrow surfaces.

These predictions were only partly supported. Long-legged species do, in fact, run fastest on broad surfaces and experience a marked decline in sprinting ability as the diameter of the surface on which they are running declines (figure 7). But short-legged species do not run faster on narrow surfaces than on broader surfaces. Moreover, the phylogeny indicates that short legs are a derived feature in twig anoles: The short-legged species 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 as or faster than a short-legged one on narrow surfaces, without giving up its much greater capabilities on broader surfaces (Losos and Sinervo 1989, Irschick and Losos 1999).

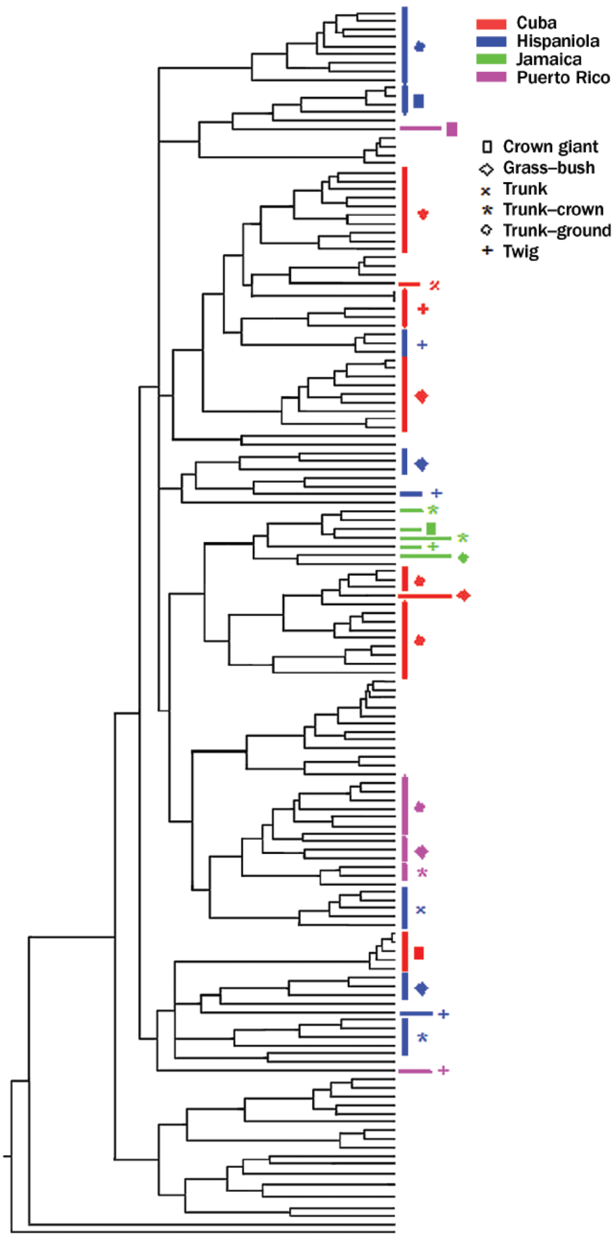

Figure 5. Phylogenetic relationships of* Anolis. *Symbols represent the different habitat specialist types; color represents the four islands of the Greater Antilles. (Tips of the phylogeny with no symbol represent species from areas other than the Greater Antilles and species from the Greater Antilles 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.

Figure 6.* Anolis carolinensis *jumping in a laboratory trial. Photograph: Bob Lalonde.

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, the long-legged trunk–ground species *Anolis gundlachi* had trouble in more than 75 percent of the trials. By contrast, short-legged twig anoles experienced only a minor decrease in surefootedness (as we called it) on narrower surfaces (Losos and Sinervo 1989).

With these data in mind, we went back into the field to see what the lizards actually do in their natural environment. Sure enough, trunk–ground lizards zip around on the ground and on other broad surfaces, using their quickness to capture prey and elude predators. By contrast, twig anoles are much more deliberate; they creep slowly along twigs (Irschick and Losos 1999). Rapid sprints rarely occur, but moving without difficulty on narrow and irregular surfaces is essential to discover the motionless prey these anoles eat and to avoid 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 (Irschick 2002). 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!

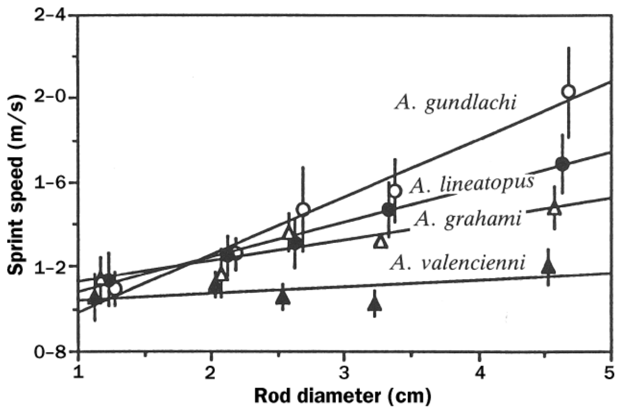

Figure 7. Sprint speed versus surface diameter for several anole species. **Anolis valencienni,** *a twig anole, has substantially shorter legs than the other three species illustrated here. Modified from Irschick and Losos (1999).*

What 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, producing a set of descendant species that are adapted to use a wide variety of different ecological niches (Givnish 1997, Futuyma 2005). Classic examples of adaptive radiation include Darwin's finches on the Galápagos Islands, Hawaiian silversword plants, and cichlid fishes in the great lakes of the African rift valley. 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 as follows (Simpson 1954, Schluter 2000): For some reason (perhaps due to the colonization of an island or a 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 alter their resource use, shifting to utilize resources not used by the other species. Over time, the species evolve adaptations to use their different ecological niches, and the 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 (de Queiroz et al. 1998, Polcyn et al. 2002). 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 anole species compete for resources; (2) in the presence of competitors, species shift their habitat use to minimize overlap in resource use; and (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 (Schoener 1968, Schoener and Schoener 1971a, 1971b). Consequently, even if interspecific competition leads to the divergence of anole species, the result might be that present-day species no longer compete ("the ghost of competition past," in the words of Connell [1980]). In this case, studying interactions among present-day species would not help us decipher what happened in the past. Conversely, if present-day, already ecologically differentiated species compete, we might safely assume that ancestral species, which had not yet diverged 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 species. For example, in an experimental investigation on the island of St. Maarten, either one or both anole species native to the island were placed in one of several 144-square-meter enclosures. Individuals of the focal species, the Anguilla Bank tree anole (*Anolis gingivinus*), grew at higher rates, ate more, reproduced more quickly, and attained larger adult size in the cages in which they were alone compared with those in which the other species was present (Pacala and Roughgarden 1985). Similarly, on tiny islands in the Bahamas, populations of the Bahamian green anole (*Anolis smaragdinus*) reached higher population densities when they were the only anole species placed on the island, compared with *A. smaragdinus* populations on those islands onto which the Cuban brown anole, *Anolis sagrei,* was also introduced (figure 8; Losos and Spiller 1999).

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 (Sax et al. 2005). Examination of the record of anole introductions revealed a stark contrast: In cases in which an ecologically similar anole was not already present, 7 of 11 introductions 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 (Losos et al. 1993).

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 (Gerber and Echternacht 2000). 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. Photograph: Jonathan B. Losos.

Hypothesis 2: Anole species shift habitat use in the presence of other species. Evidence for habitat shifts is widespread and occurs at the individual and landscape levels. On one hand, observations of individual lizards have revealed that they will move away when individuals of a second species appear (Jenssen 1973). Experimental studies such as those described in the last section reveal a similar population-level response; in the experiments on St. Maarten, for example, *A. gingivinus* perches much higher in the tree in enclosures containing a second species than in those in which it occurs alone (Pacala and Roughgarden 1985). Similar shifts are documented in the presence of an introduced species (Salzburg 1984, Losos et al. 1993). Lastly, comparisons of populations of a species throughout its geographic range show consistent changes in habitat use depending on whether other anole species are present (Schoener 1975).

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. On the basis of 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 that use narrower surfaces should evolve shorter limbs, and species that become more arboreal should evolve more highly developed toe pads. Comparisons of populations of several species have confirmed these predictions (Lister 1976, Losos et al. 1994).

The occurrence of introduced species provides the opportunity to test these predictions over a shorter timescale. For example, *A. sagrei* was introduced into southern Florida some time in the latter half of the 19th century (Williams 1969, Kolbe et al. 2004). As this species continues its spread throughout the southeastern United States, its ecological and evolutionary effects on the native green anole (*Anolis carolinensis*) should prove a fascinating subject for research. Surprisingly, such studies have not yet been conducted.

Overall, the extensive data on anoles, which I have only briefly skimmed 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 that its workings would be evident only after thousands of years. This view persisted for more than a century, and led to the widespread notion that evolution could be studied only through the lens of a historian.

Recent years, however, have revealed that Darwin got this one wrong: Given strong enough selection, evolution can occur extremely rapidly, not only over the course of a scientist's career but even over the course of a few years (Reznick et al. 1997, Grant and Grant 2002). Consequently, not only is evolution observable as it occurs, but 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 (Endler 1980).

In a series of experiments, my collaborators, Thomas Schoener and David Spiller, and I have attempted to experimentally test ideas fundamental to the adaptive radiation hypothesis. 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 illustrate the perils and pitfalls of fieldwork in evolutionary biology.

Our first experiment examined the ecological and evolutionary consequences of interspecific interactions between *A. smaragdinus* and *A. sagrei.* The experiment clearly indicated the negative affect of *A. sagrei* on *A. smaragdinus;* the densities of *A. smaragdinus* populations sympatric with *A. sagrei* were consistently lower than the densities of allopatric *A. smaragdinus* populations. Moreover, *A. smaragdinus* perched

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

higher on the sympatric islands than on the allopatric ones, evidence that they were shifting up into the vegetation in the presence of the more terrestrial *A. sagrei* (Losos and Spiller 1999). Unfortunately, before we had a chance to detect evolutionary changes in morphology, populations of *A. smaragdinus* on all islands crashed, presumably because of 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 before 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 islands unoccupied [Spiller et al. 1998]).

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 6 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 (Schoener et al. 1982), we did not know 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 mean perch height skyrocketed; the surviving lizards were moving up into the bushes to avoid the terrestrial predators (figure 11; Schoener et al. 2002). *A. 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 (Losos et al. 2003). Thus, even though all lizards were washed off our islands, the 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 already have been 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, we did something new in round 2: We measured and individually marked *A. sagrei* before the start of the

Figure 10. A curly-tailed lizard **(Leiocephalus carinatus)*****. Photograph: Jonathan B. Losos.***

experiment. Our prediction was that, in the first generation, predation by curly-tailed lizards would favor those lizards with the longest legs, because they would be faster and thus better 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 the *A. sagrei* became more arboreal, we predicted that selection would reverse its course and favor the shorter legs suitable for using narrow, arboreal perches.

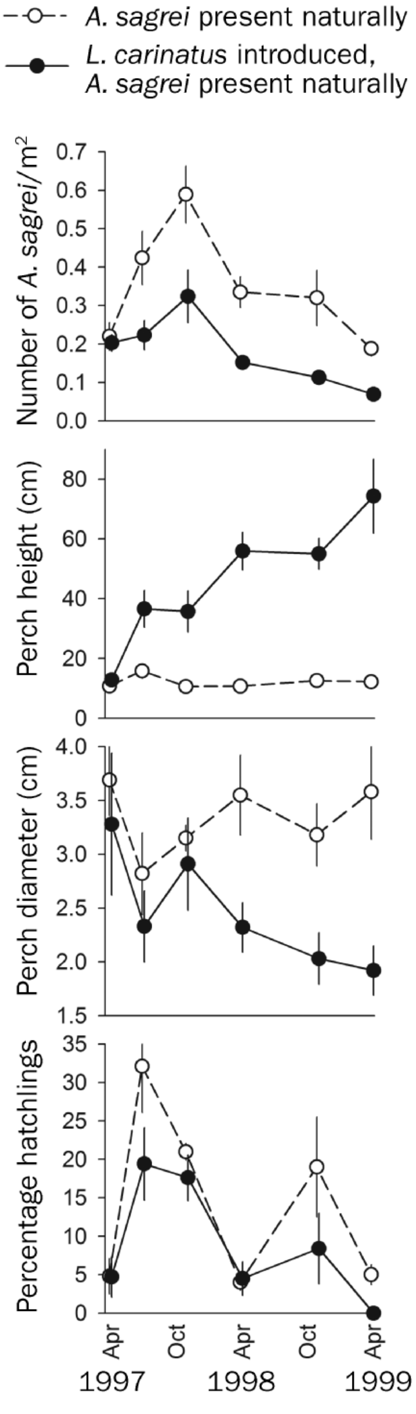

*Figure 11. Effect of introduction of predatory lizards (***Leiocephalus carinatus***) on* **Anolis sagrei** *populations, in terms of (a) population density, (b) perch height, (c) perch diameter, and (d) percentage of lizards observed that were hatchlings. Modified from Schoener and colleagues (2002).*

By going back after 6 and 12 months, we could determine which lizards had survived and which had not. By examining the measurements we took at the start of the experiment, we could ask whether survival was related to limb length. In other words, we were looking for evidence of whether natural selection had occurred, and whether its form differed between experimental and control islands.

As predicted, selection favoring longer limbs was stronger on experimental islands than on controls over the first six months (Losos et al. 2004). Further, and again as predicted, selection reversed course and began to favor shorter legs (figure 12; Losos et al. 2006). However, that reversal occurred in the second six-month period, much faster than we had expected.

Because selection on the experimental islands first had 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. The *A. sagrei* populations are again recovering, and we hope to initiate round 3 of the experiment before too long. One silver lining is that what we learn in each experiment allows us to modify what we do the next time around. We hope that in the future, we

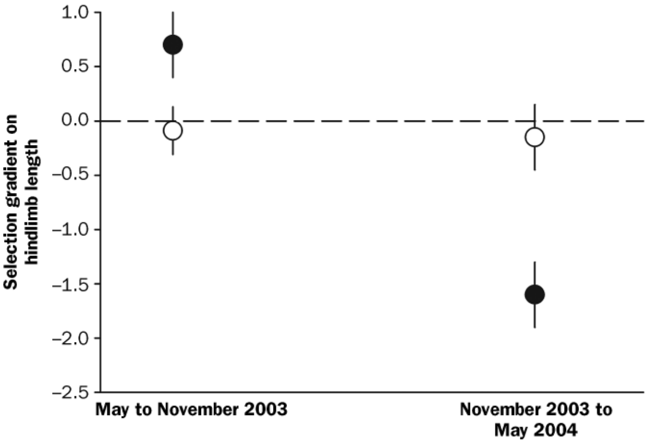

Figure 12. Reversal of natural selection. In the first six-month period, natural selection favored longer legs (as indicated by positive selection gradients) in populations on islands with the curly-tailed lizard, whereas in the second six-month period, selection favored shorter legs in those populations. Source: Losos et al. 2006.

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); and (3) variation among individuals must have a hereditary basis such that offspring tend to resemble their parents.

Anoles meet the first two of these conditions, but studies of 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 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 (Calsbeek et al. 2006, Calsbeek and Smith 2007).

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 the phenomenon of phenotypic plasticity, in which a single genotype can produce different phenotypes in different environments. 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, evidence for plasticity in animals has increased greatly in recent years (DeWitt and Scheiner 2004). Because of phenotypic plasticity, scientists need to be cautious in interpreting variations they see within and among populations, which, rather than reflecting genetic differences, may result from the different environment in which organisms developed.

The potential significance of phenotypic plasticity in anoles was driven home years ago in a study on limb-length variation in *A. sagrei.* Tired of botanists pestering me with questions after seminars, I conducted an experiment at the Saint Louis Zoo along with a number of colleagues, raising 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 (Losos et al. 2000, 2001). A subsequent study on *A. carolinensis* yielded the same result (Kolbe and Losos 2005).

The existence of plasticity in anoles has two major 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. Although some of the *A. sagrei* in our study grew up on surfaces approximating tree trunks (broad and flat) and others on surfaces resembling twigs, the differences in limb length between lizards in the two treatments were quite minor compared with the differences that characterize species adapted to living on tree trunks and twigs. These much more substantial differences between species surely are the result of genetic change. Moreover, in the only study to examine the genetic basis of differences among populations, Thorpe and colleagues (2005) raised baby Dominican anoles (*Anolis oculatus*) from different populations 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 for the most part persisted, suggesting an underlying genetic basis (although further studies are needed to rule out "maternal effects" in which environmentally induced, nongenetic differences among mothers are passed on to their offspring; Roach and Wulff 1987).

More generally, evolutionary biologists are paying increasing attention to phenotypic plasticity as a process that could accelerate evolutionary diversification (Schlichting and Pigliucci 1988, DeWitt and Scheiner 2004). Although variation among individual anoles may not have a genetic basis, plasticity itself is a genetically based trait that can be selected upon and can evolve. Thus, species that tend to occur in highly variable populations may evolve a great capacity for plasticity to produce phenotypes 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 evolve enhanced phenotypic adaptations through genetic means, as beneficial mutations occur and are favored by natural selection (West-Eberhard 2003).

A discussion of anole genetics would not be complete without mention of the impending genomic tidal wave. The genome of *A. carolinensis* is currently being sequenced at the Broad Institute in Cambridge, Massachusetts. Once the sequencing effort is completed, some time next year, 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 (Storz and Hoekstra 2007). The developmental genetics of some traits of particular significance in anoles, such as limb or head dimensions, have been extensively studied in other vertebrates (Niswander 2002, Tickle 2002, Abzhanov et al. 2004, 2006, Stopper and Wagner 2005). Many genes are evolutionarily conservative (Carroll et al. 2005); 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 phenotypic traits such as limb length has been accomplished through convergent changes at the DNA level (cf. Colosimo et al. 2005).

A lot of hard work stands between obtaining a genome sequence and actually finding the alleles 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 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 article. First, evolutionary biology is inherently multidisciplinary and synthetic. To study what happened in the past, researchers 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 synthesized, these approaches can be mutually illuminating, allowing scientists 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 will 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.

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