Evolution: A Lizard's Tale

by Jonathan B. Losos

On some islands in the Caribbean, evolution seems to have taken the same turn—over and over and over again

Anole lizards can be found everywhere on the islands of the Greater Antilles: in the tops of trees, along their trunks, down among the leaf litter, on fence posts, near flowers. They come in all forms: short, long, blue, brown, green or gray, strong jumpers, poor jumpers, big and brazen, creeping and cautious. This incredible diversity makes the anoles, members of the genus *Anolis,* fascinating creatures to study. For hidden in their myriad forms and dwelling places is the key to an important biological mystery: What drives a creature's evolution to take one path instead of another?

Any visitor to the islands will quickly see that the kinds of anoles that occur together—that is, sympatrically—differ in the habitat they occupy. One species, for example, will be found only in the grass, another only on twigs, a third nearby on the base of tree trunks, sometimes venturing onto the ground. These three species also differ in their morphology. The grass dweller is slender with a long tail, the twig dweller is also thin but with relatively stubby legs, and the tree lizard is stocky with long legs.

What is striking about these lizards is not just that coexisting species differ in morphology and how they use their habitat. Such differences are actually the norm among closely related, sympatric species: Darwin's finches on the Galápagos Islands and the lemurs of Madagascar

ANOLE LIZARDS of the Caribbean islands are a diverse bunch. In the Greater Antilles, about 110 species have evolved to fill nearly every ecological niche, from the crown giant that lives in tree canopies to the long-tailed grass-dwelling anole.

ROBERTO OSTI

provide two famous examples of animals that adapted into every available niche. What is unusual about the Caribbean anoles is that the same types of habitat specialists occur on each island. If a visitor goes to Puerto Rico and observes the twig species that lives there, he can then travel to each of the other Greater Antillean islands of Cuba, Hispaniola (which encompasses Haiti and the Dominican Republic) and Jamaica, and find a species that looks nearly identical, lives in the same type of habitat and behaves in much the same manner. All four islands also have a base-of-tree specialist, an arboreal specialist and a tree-canopy giant. In addition, grass specialists occur on three islands, and trunk specialists (which have flatter bodies and shorter tails than do base-of-tree lizards) on two.

Biologists are accustomed to finding similar species in similar ecological niches in different parts of the world. The marsupial cat and marsupial wolf of Australia are morphologically and ecologically similar to their feline and canine counterparts on other continents. But convergence of entire communities is an entirely different matter. Although communities in different areas often bear some resemblance to one another, the occurrence of communities composed of the same set of ecological specialists is virtually unparalleled.

Once Was Not Enough

The existence of such communities implies that some deterministic process is responsible for shaping their structure—that something drives the lizards' evolution to take the same course again and again. My colleagues and I have been testing this idea, which has meant testing the three assumptions it is based on: that the specialists evolved independently on each island, that the lizards are indeed adapted for their particular ecological niches and that similar ecological and evolutionary processes operate on each island. In the past 20 years the arsenal of tools available to evolutionary biologists has expanded enormously, allowing us to draw on many disciplines to answer our questions. Using fossil records, field observations, experiments and DNA sequencing, we have begun to figure out what is happening with the anoles of the Greater Antilles.

The presence of similar species on different islands could be explained in several ways. An ancestral species might have adapted to exploit a particular ecological niche on one island and then made its way over water—perhaps by raft or hurricane—to colonize other islands. Or this ancestral specialist might have evolved at a time when the islands were connected, which some of the Caribbean islands may have been. After the islands separated, the isolated lizard populations would have become distinct species, while also retaining the adaptations of their ancestors. Both of these scenarios imply that specialization to each niche occurred only once. Alternatively, each specialist could have arisen independently—or convergently—on each of the Greater Antilles.

By examining an evolutionary tree, termed a phylogeny, for Caribbean anoles, we can determine which of these possibilities occurred. If each type of specialist evolved just once, then similar specialists on different islands would be closely related. Conversely, if the specialists evolved independently on each island, then similar specialists on different islands would not be closely related. In the latter case, a specialist on one island would be more closely related to other types of lizards on the same island—regardless of their ecological niche—than it would be to similar niche-users on different islands. So a twig dweller on Jamaica would be more closely related to the Jamaican canopy or tree-base lizards than it would be to a Cuban twig dweller.

By comparing DNA sequences for the same gene or genes in different species, biologists can draw inferences about how species are related evolutionarily. Although controversy exists about the best method of deducing phylogenetic relationships from DNA comparisons, researchers agree that species that have more similar DNA are, in most cases, more closely related to each other than to another species whose DNA is less similar. Thus, humans and chimps, which share a great deal of their DNA, had a common ancestor much more recently than did humans and baboons, which share less.

Using this approach, a team including Todd R. Jackman (now at Villanova University), Allan Larson of Washington University and Kevin de Queiroz of the Smithsonian Institution sequenced several genes from more than 50 species of anoles. The data are clear-cut: habitat specialists on one island are not closely related to the same habitat specialists elsewhere. Our findings indicate that specialists evolved independently on each island and that similar communities evolved independently on each island.

The fossil record can often provide another form of evidence for such conclusions. Unfortunately, except for specimens from only the past few thousand years, anole fossils are extremely rare. Perhaps a dozen exist, all of them encased in amber. Presumably these lizards became stuck in the oozing resin of ancient trees that later fell to the ground and became fossilized. Given

GREATER ANTILLES islands, which consist of Cuba, Hispaniola (Haiti and the Dominican Republic), Puerto Rico and Jamaica, each have an anole that has evolved to live primarily on twigs.

ROBERTO OSTI (map); JONATHAN B. LOSOS (photographs)

the popularity of *Jurassic Park*, most of the amber fossils quickly find their way into private hands and remain unavailable for study. Nevertheless, we have examined two specimens found on Hispaniola, dating from the Miocene period, approximately 20 million years ago. These specimens are virtually indistinguishable from the tree-canopy habitat specialists living today and make clear that the phenomenon of anole habitat specialization is an ancient one.

Convergent evolution in similar situations suggests that features have evolved in response to similar problems posed by the environment. Testing this possibility requires understanding why a particular feature may be favored in certain circumstances. Take leg length as an example. As I mentioned above, Caribbean anoles that live on twigs have very short legs, whereas those occupying lower tree trunks have very long legs. To see whether leg length evolved as a response to differences in the diameter of the surface, we need two kinds of information. We have to discover what the functional consequences of differences in leg length are, and we have to gather data on the relevance of such differences to the behavior and habitat use of the species.

To obtain such information we had to combine laboratory and field approaches. In the laboratory, we investigated functional capabilities by focusing on ecologically relevant measures, such as how fast a lizard can run or how well it can cling. Some of these studies required sophisticated electronic equipment. To record how fast a lizard runs, for example, we built a lizard racetrack—a narrow route two meters in length with infrared beams and detectors positioned every quarter of a meter. Lizards placed at one end of the track usually sprint rapidly toward the dark bag at the opposite end. To determine clinging ability, we placed lizards on a vertical, highly sensitive plate that measures the force their toe pads generate as the lizards attempt to maintain their position while being pulled downward by the experimenter.

Other equipment is not nearly so technologically advanced. To measure maximum jumping capabilities, we put lizards on a flat board 30 centimeters above the ground and induced them to jump by tapping them on the tail. We then measured how far they had jumped.

These various studies have confirmed much of what one would expect. When the effects of the differences in body size are factored out, both running and jumping ability are related to relative hind-limb length. This finding is predictable because long-legged lizards take longer strides and attain higher velocities during jump takeoff. Similarly, larger toe pads confer greater clinging ability.

But the studies also provided some surprises. Most notably, the relation between limb length and sprint speed depends on the surface on which the lizard is running. As surface diameter diminishes, so does the advantage of longer limbs. The long-legged Puerto Rican base-of-trunk specialist *Anolis gundlachi* can run twice as fast as the short-legged Jamaican twig species *A. valencienni* on flat surfaces. But *A. gundlachi*'s speed declines markedly with diminishing surface diameter. On narrow surfaces that are one centimeter in diameter, the species run equally slowly, despite the differences in the lengths of their legs. But whereas the twig anole is very sure-footed on surfaces of all widths, the longer-legged species trips or falls more often than not on narrow surfaces.

This variation in functional capability supports the contention that morphological differences have indeed evolved as adaptations to different environmental niches. But only by examining what animals actually do in nature can we determine whether these capabilities really confer any advantage. Painstaking field studies, conducted primarily by Duncan Irschick, now at Tulane University, reveal that anoles almost always jump distances considerably shorter than the maximum capabilities observed in the laboratory. Therefore, the evolution of long legs is unlikely to have resulted as a response to selection for jumping ability.

In contrast, anoles often do run at top speed—especially when trying to avoid predators. The species that run most frequently are those with the greatest sprinting abilities and the longest legs. Short-legged species rarely run: whether stalking prey or eluding predators, they take the opposite approach, moving stealthily to avoid detection. Given their lack of speed, surefootedness is particularly important, as a stumbling lizard is more likely to attract attention and, once detected, is less likely to escape.

Of Plasticity and Natural Selection

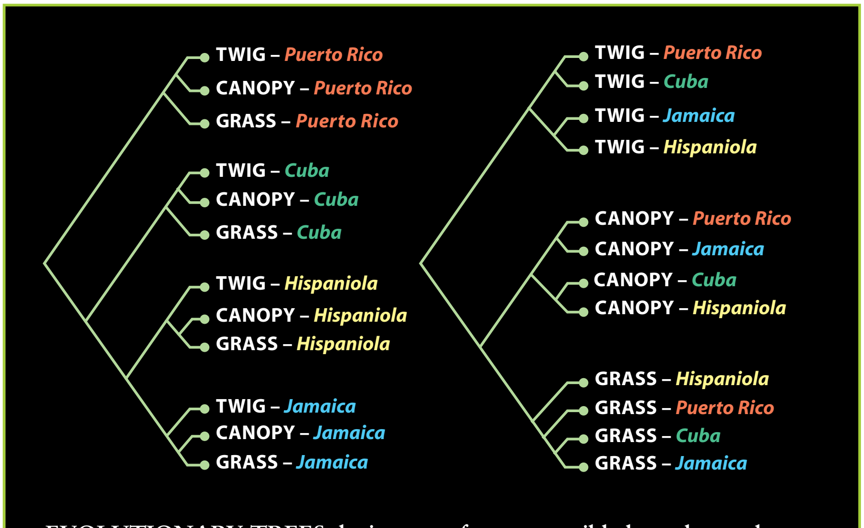
Seeing natural selection at work—that is, seeing a creature adapt to a new habitat and develop a specialization such as short-legged surefootedness—is a rare privilege. Evolution most often occurs over timescales humans cannot experience. But an experiment initiated in the late 1970s by Thomas and Amy Schoener of the University of California at Davis has allowed us a tiny window onto this process. Noticing that certain very small islands in the Bahamas do not naturally harbor anoles, the Schoeners introduced the brown anole, *A. sagrei*, to 20 islands to study the process of extinction. To their surprise, the Schoeners found that the populations survived and even flourished on all but the smallest islands. (The Schoeners' conclusion that the absence of lizards results from the occasional hurricane was verified in 1996 when Hurricane Lili wiped out lizard populations on many small islands.)

Because the islands differ in vegetation—some have broad tree trunks and others only scraggly bushes—the Schoeners' introduced lizards gave us the chance in 1991 to see whether they had adapted to the different circumstances in which they found themselves. Based on our studies of the anoles of the Greater Antilles, we could make predictions: lizard populations on islands with broad surfaces should have longer legs than do those on islands with only narrow perching surfaces. Our findings corroborated these predictions, indicating that populations had rapidly adapted to environmental differences in just the way we expected. We found that lizards with wider substrates had legs that were several millimeters longer than those raised on narrower surfaces.

A second scenario could also explain these results. The legs of lizards growing up on broader surfaces might simply grow longer than the legs of lizards on narrower surfaces. Such a phenomenon, termed phenotypic plasticity, could even result in individuals that are genetically identical. Studies on bone growth, conducted on mammals and birds, indicate that the bones of individuals experiencing different stresses and strains during growth develop differently. For example, the serving arms of professional tennis players are longer than their nonserving arms. Given that professional tennis players spend hours smashing tennis balls, day after day, during their childhood, these results clearly indicate how differences in activity patterns can lead to differences in limb length.

It is a long way, however, from professional tennis players to lizards growing up on islands with different kinds of vegetation. To see if experience could alter the limb length of the lizards, a number of colleagues and I raised baby *A. sagrei* at the St. Louis Zoo in two environments: on narrow 0.7-centimeter-wide wooden dowels and on broad eight-centimeter-wide boards. What we found, to our surprise, is that the lizards that grew up on the broad surface developed longer limbs than those that grew up on the narrow surfaces—although the differences were not as great as those found between twig users and base-of-tree users in the Greater Antilles.

These findings suggest that the differences observed among the introduced Bahamian populations might result from phenotypic plasticity. To verify this conclusion, we will need to raise lizards from populations with different limb lengths under similar, controlled conditions. If the observed differences in nature are the result of phenotypic plasticity, then differences in limb length should not appear among individuals raised in captivity under identical conditions.



EVOLUTIONARY TREES depict two of many possible hypotheses about the anole lizards' genetic relatedness. At one extreme, each kind of specialist evolved again and again, on different islands (*left*). At the other extreme, each specialist evolved only once and then ended up on various islands (*right*). DNA analysis suggests that a situation similar to the first scenario is more likely.

LAURIE GRACE

In recent years scientists have begun to consider the possibility that phenotypic plasticity may play an important role in adaptive evolution. By producing morphologies suited to different environments, phenotypic plasticity may allow a population to utilize a habitat in which it otherwise could not survive. Such differences, of course, are not genetically based and do not reflect evolutionary change. But eventually mutations will occur, by chance, in these populations, making the individuals even better adapted to this new habitat. These changes, being genetically based, would lead to evolutionary change. Given enough time, mutation and natural selection could produce species substantially different, and better adapted, than the ancestral form. In this way, phenotypic plasticity could be an important means by which major evolutionary changes are initiated. This hypothesis—first put forth more than 50 years ago but only now receiving serious attention—merits further investigation.

An Island Is an Island Is an Island

The last piece of the puzzle that we needed to look at is why specializations evolved in the first place. One explanation posits that two ancestral, unspecialized species became sympatric, perhaps because one colonized an island occupied by the other. Because most species of anoles are quite generalized in their diets, eating a wide variety of different kinds of insects as well as, in some cases, fruits and small vertebrates, two such species are likely to have competed for food. By utilizing different habitats and eating different prey, they could minimize competitive interactions. Natural selection would favor the evolution of features that made each species well adapted to its habitat, producing the specialized species we now see.

Although it is not possible to determine whether, in fact, competition among ancestral anoles led to specialization, we can ascertain whether competition occurs among species today. A large body of work implies that it does. Comparisons of populations of *A. sagrei* in the Bahamas reveal that in areas where the species occurs by itself, it perches higher and uses a broader range of perching sites than it does in areas where other species of anoles are present. Competition with other, more arboreal species seems to force the brown anole to alter

PHENOTYPIC PLASTICITY is evident when *Anolis sagrei* is raised from hatching to adulthood on different substrates. Lizards growing up on thin dowels develop slightly shorter hind limbs (by a few millimeters) than do those growing up on wider boards. (Drawings are not to scale.)

its habitat use. But there are other explanations for this behavior as well. Maybe the habitat differs in places with and without other species.

Fortunately, field experiments can help settle this question. In the Puerto Rican rain forest, graduate students Manuel Leal and Javier A. Rodríguez-Robles (now, respectively, at Union College and the University of California at Berkeley) and I captured and removed all individuals of *A. gundlachi*—the long-legged lizard that lives at the base of the tree—from three 20-by-20-meter plots. We then monitored the population densities of a second species, the Evermann's tree-canopy anole, or *A. evermanni.* Three similar plots in which *A. gundlachi* was not removed served as controls. After eight weeks, population densities of *A. evermanni* were significantly higher in the plots without *A. gundlachi* than they were in the controls.

Similar results were obtained in studies that David Spiller of the University of California at Davis and I conducted on some tiny islands in the Bahamas. We introduced populations of the green anole, *A. carolinensis,* which lives in the canopy, to some of the uninhabited sites. We then compared how they did alone versus how they did on islands where they coexisted with *A. sagrei*. We found that *A. carolinensis* was doing much better when it did not have to compete with *A. sagrei.* These findings and others strongly support the argument that sympatric species of anoles negatively affect one another. Although other processes are possible—such as predation by one anole species on another—competition for resources is by far the most likely explanation. Experiments by Joan Roughgarden and her colleagues at Stanford University indicate that the more ecologically and morphologically similar species are, the stronger the effect they will have on each other. Consequently, it is very plausible that competition was the process leading to habitat specialization.

Unraveling the secrets of evolution is truly like a detective story. Clues exist, but none are definitive. And in the case of the Caribbean lizards, we are still left with the big question: Why did evolutionary diversification lead to such similar outcomes? One possibility is that the islands are relatively biologically impoverished—that is, they have many fewer other species of lizards, birds and other animals than do nearby Central American regions. As a result, anoles have been able to radiate into relatively open ecosystems, unfettered by much competition or predation. Because few other creatures influence the course of evolution and because the environment of each island is quite similar, evolution might take the same course. Indeed, this is seen in the repeated radiation of cichlid fish in different East African lakes [see "Cichlids of the Rift Lakes," by Melanie Stiassny; SCIENTIFIC AMERICAN, February 1999].

But as far as we can tell, replicated adaptive radiation is not the rule but the exception. Only by keeping an open mind and following the data, wherever they lead, can we ultimately hope to solve this mystery of natural history.

The Author

JONATHAN B. LOSOS examines the causes and consequences of evolutionary diversification. An associate professor of biology at Washington University and director of the Tyson Research Center there, Losos has focused his studies on lizards because they are well suited for the kinds of multidisciplinary questions he wants to answer. Between his travels around the world looking for lizards, he likes to play ice hockey.

Further Information

Adaptive Differentiation Following Experimental Island Colonization in *Anolis* Lizards. Jonathan B. Losos, Kenneth I. Warheit and Thomas W. Schoener in *Nature,* Vol. 387, pages 70–73; May 1, 1997.

A Comparative Analysis of the Ecological Significance of Maximal Locomotor Performance in Caribbean *Anolis* Lizards. Duncan J. Irschick and Jonathan B. Losos in *Evolution,* Vol. 52, No. 1, pages 219–226; February 1998.

Contingency and Determinism in Replicated Adaptive Radiations of Island Lizards. Jonathan B. Losos, Todd R. Jackman, Allan Larson, Kevin de Queiroz and Lourdes Rodríguez Schettino in *Science,* Vol. 279, pages 2115–2118; March 27, 1998.

An Experimental Study of Interspecific Interactions between Two Puerto Rican *Anolis* Lizards. Manuel Leal, Javier A. Rodríguez-Robles and Jonathan B. Losos in *Oecologia,* Vol. 117, No. 1/2, pages 273–278; November 17, 1998.

Jonathan B. Losos maintains a Web site at http://biosgi.wustl.edu/~lososlab/

ROBERTO OSTI