the head relative to the much larger movements of their bodies. Films and videos of flying heavier birds, such as geese and swans, show that while there is an upward thrust of their bodies produced with each downward wing-beat their heads maintain a nearly perfect level path.

Is the visual system specialized for this type of image stabilization?

Experimental observations on many species have shown that smooth motion of a very large image over an animal's visual field produces optokinetic response of the eye, head and body, where the gaze follows the moving stimulus for a while and then makes a fast resetting movement (saccade), and then another stimulus following movement occurs. These following movements, or pursuit movements as they a usually called, are performing the same task as the head stabilization seen in birds; that is, they are stabilizing the gaze. Not surprisingly there are specialized neurons in the visual system of invertebrates and vertebrates that specifically detect slow motion over very large areas of the visual field, and in birds (and most likely other vertebrate species also) they even have their own special ganglion cells in the retina that begin to carry out this task. These specialized retinal ganglion cells then forward this information to an area of the brain called the accessory optic system, which ultimately connects up with information from the vestibular system or sense of balance, which also plays a role in stabilizing the gaze. Interestingly, birds such as humming birds, kestrels and kingfishers that have remarkably good head stabilization while hovering have an accessory optic system that is relatively several times larger than most other birds.

Where can I find out more about bird head stabilization?

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Anolis lizards

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What is an anole? Anoles comprise one of the most diverse vertebrate genera, with nearly 400 species known and more being discovered every year. They have become a textbook example of adaptive radiation and have contributed greatly to our understanding of evolution, ecology and organismal function. About 150 species occur on islands in the Caribbean; the rest are found in Central and northern South America. Only one species is native to the southeastern United States.

Often quite beautiful, anoles are captivating lizards with a rich behavioral repertoire and extensive variation among species. Most anoles are green, grey or brown; they are generally 35–85 mm in body length and 1–10 g in mass, though some can be substantially larger. They have a generalized lizard body form with robust limbs and a moderately long tail, though there is significant variation among species. The two primary traits that characterize anoles (with a very few exceptions) are possession of expanded toepads and an extensible colorful flap of skin, the *dewlap*, which is attached to the throat.

How much ecological and evolutionary diversity do they exhibit? Studies of anoles have been central to the development of key concepts in ecology and evolution. Two important patterns of diversity have generated substantial ecological and evolutionary research on anoles. First, on each of the islands of the Greater Antilles — Cuba, Hispaniola, Jamaica, and Puerto Rico — sympatric species differ in habitat use, behavior and morphology. For example, species that use broad tree trunks near the ground tend to have long hindlimbs, which they use to run quickly and jump great distances. In contrast, species that use narrow twigs high in the trees have very short legs and tend to creep very slowly to capture prey and escape detection by predators. Species that use the vegetation high in the tree have very large toepads and are green in color. In all, six types of habitat specialists, termed *ecomorphs*, have been defined.

The second important insight from studies of anoles in the Greater Antilles is that, with a few exceptions, the same set of habitat specialists has evolved independently on each island. Phylogenetic analysis indicates that distinct species occupying the same habitat specialist category on the different islands are not closely related.

These anole communities served as a model system for the development of ecological theory in the 1960s and 1970s, and important early work on interspecific competition, niche variation, character displacement and other phenomena were conducted on anoles.

Convergent evolution has long been taken as evidence of adaptation. A hypothesis of adaptation can be further tested by demonstrating that the convergent features are beneficial in the environment in which they occur. Work on anoles was instrumental in developing the idea that ecological adaptation must be studied by examining measures of whole organism performance. These studies indicated that the morphological and physiological variation among species leads to differences in capabilities that are appropriate to the different habitats that species occupy (Figure 1), thus strongly supporting the hypothesis that adaptive radiation has occurred.

What drives evolutionary diversification of anoles? The classic idea of adaptive radiation is that it results from interspecific competition driving initially similar species to diverge in resource use and adapt to new habitats. These predictions are strongly supported for anoles. A wide variety of research— including behavioral observations, comparisons across study sites and experimental manipulations— indicates that anole species interact strongly and that interspecific competition for resources is likely the cause of their adaptive divergence. Moreover, shifts in habitat use as a result of the presence of other species are well-documented, and comparisons across populations demonstrate corresponding adaptive changes in morphology.

These ideas can further be tested directly by measuring natural selection

in natural or experimental settings. Such work is just beginning, but studies to date indicate that strong selection often occurs in anole populations and that the addition of a larger predatory lizard (not an anole) can drive both shifts in habitat and changes in patterns of selection.

How do new species arise?

Speciation in anoles is not yet well understood. For some reason, cladogenetic speciation (one species splitting into two) has occurred only on islands the size of Puerto Rico or larger. Many of the bigger islands in the Lesser Antilles, such as Guadeloupe, harbor only a single anole species, despite having extensive vegetational diversity within and between localities. According to molecular systematic studies, the anoles on these islands have been present for long periods of time, and they appear to have the appropriate niche space to maintain all of the habitat specialists found in the Greater Antilles. The lack of speciation to produce such specialists suggests that sympatric and parapatric speciation are not important phenomena in anole evolutionary diversification. Presumably, geographic isolation within the larger islands of the Greater Antilles, or isolation on nearby islets, has allowed speciation to occur on larger islands.

One factor that may be important in the great species-richness of anoles is the possession of a dewlap, used not only in intraspecific courtship and territorial contexts, but also for species-recognition. Sympatric species invariably differ in the color, patterning or size of their dewlaps, and experimental studies suggest that anoles use their dewlaps, as well as their species-specific head-bobbing patterns, to distinguish conspecifics from non-conspecifics. The importance of these signals for both intraspecific and interspecific communication suggests one means by which speciation might occur: a population isolated in a new environment, perhaps darker or windier than the ancestral habitat, might evolve a different dewlap or head-bobbing pattern to maximize intra-specific communication effectiveness. An incidental by-product of such adaptive evolution, however, might be that

Figure 1. *Anolis* habitat specialists.
Anoles have adapted to use different parts of the environment, including: tree trunks near the ground (*A. cybotes*, Hispaniola, top left and *A. lineatopus*, Jamaica, top right, with dewlap extended), twigs (*A. valencienni*, Jamaica, bottom left) and tree canopies (*A. chlorocyanus*, Hispaniola, bottom right). Photo credits: top right, bottom left: L. Mahler; bottom right: M. Losos.

premating reproductive isolation evolves between the population and the rest of its species.

What about anoles on the mainland?

The anoles of Central and South America, though more numerous in species and equally diverse in ecology and morphology, have been studied substantially less than island anoles. Despite this relative lack of study, it is clear that most mainland species do not belong to one of the habitat specialist types from the Greater Antilles. Why anole evolution on the mainland has

proceeded in different directions than in the islands is unclear, but the much greater diversity of predators on the mainland is one possible explanation.

Traditional ecological wisdom is that competition, predation and other biotic interactions are much more intense in mainland settings, and thus that colonization between mainlands and islands is unidirectional from the former to the latter. Anoles present one of a number of recent challenges to this idea. The majority of mainland anoles belong to a clade nested deeply within the Caribbean radiation, and thus they must have resulted from

a back-colonization from the islands to the mainland.

How have anoles evolved such diverse morphologies? This is an exciting time in anole biology because recently the genome of the green anole, *Anolis carolinensis*, was completely sequenced (http://www.broad.mit.edu/models/anole/). The completion of an anole genome opened a new avenue of research into the genetic changes that accompany adaptive radiation. Researchers would like to know how many, and which, genes are involved in adaptive change, what is the magnitude of their effects on phenotype, and whether there is variation in those genes in existing populations on which natural selection can act. Of particular interest are the genetic changes underlying phenotypic evolution in ecologically important characteristics such as color, limb and digit morphology, and cranial morphology. Given that anoles have convergently evolved similar morphologies, an obvious question arises...

Have similar morphologies evolved through the same kinds of genetic changes in different species? It is early days in the analysis of the genetics of adaptive radiation in anoles, but studies on the developmental genetics of limb and cranial morphology are underway. Studies of developing embryos have shown that differences in limb morphology among species are established during the earliest stages of bone formation during limb development. This is important because now we can identify genes that determine limb growth and differentiation at the stage when differences among species are established. Comparing the DNA sequences and patterns of expression of those genes among species should allow researchers to determine if similar changes in gene sequence and expression are involved in the convergent evolution of limb morphology. A similar approach is being applied to understand the genetic basis of cranial development and variation. Having the genome of *Anolis carolinensis* as a reference greatly facilitates the identification and mapping of genes that may be important in adaptive evolution.

Anoles are colorful animals and color and pattern play important roles in social communication and predator avoidance. In particular, the dewlap is a colorful signal that has important roles in social communication and predator deterrence, as discussed above. As with other aspects of morphology, similar colors (both body and dewlap) have evolved repeatedly among species of anoles. Studies on the genetics of coloration are underway and genes that are known to produce pigments in other organisms are being examined within and among anole species to determine how color patterns are produced and if similar genetic mechanisms underlie similar phenotypes among distantly related species.

How else is the* Anolis carolinensis *genome being used? All of the comparative studies among species discussed above rely on an estimate of the evolutionary relationships among species (a phylogenetic tree). The *Anolis carolinensis* genome has proved a great resource from which to develop a large number of genetic markers that can be used to infer the evolutionary relationships among species. This is a massive undertaking, given the great number of anole species, but the resulting data will provide a hypothesis of relationships among species that can be used to trace the evolution of genes, phenotypes, behavior and ecology. As with nearly all such analyses, the results are likely to generate more questions than they answer and anole biology promises to be a fruitful field of research for years to come.

Where can I find out more?

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Dinosaurs

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Every two weeks, a new species of dinosaur is named from somewhere in the world, and the fact is reported in newspapers worldwide. This astonishing statistic makes one ask how evolutionary biologists might be able to look behind the intense public fascination to understand the real importance of the dinosaurs.

Dinosaurs were hugely successful animals that existed for over 160 million years, and in one way or another shaped the terrestrial ecosystems of the Mesozoic Era. Dinosaurs originated in the Triassic, some 230 million years ago, rising to substantial positions in terrestrial ecosystems through the Jurassic and Cretaceous, and dying out at the end of the Cretaceous 65 million years ago. Dinosaurs are divided into several major groups (Figure 1) that came and went variously through their long existence, and these groups may track changing aspects of their environment.

Dinosaurs arose in the Middle or Late Triassic from among the archosaurs, the wider group that includes birds and crocodilians today. The Archosauria split into the Crurotarsi (the 'crocodile line') and the Avemetatarsalia or Ornithodira (the 'bird line'), and these two groups continued through the Triassic at equal levels of diversity. Basal avemetatarsalians were all bipedal and small, and they branched into the flying pterosaurs and the ground-based dinosauromorphs. One or two intriguing little dinosauromorphs from the Middle and Late Triassic show us that the first dinosaurs were less than 1 metre long, bipedal, and flesh eating. Quadrupedalism evolved independently several times among dinosaurs, presumably as their body masses increased.

The fundamental split of dinosaurs into Saurischia and Ornithischia occurred soon after their origin (Figures 1 and 2). Saurischians retain the generalised reptilian hip bones, and they share several unique features of the skull and forelimb. This clade includes the long-necked, plant-eating sauropodomorphs, sometimes divided into prosauropods (Late Triassic to