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Evolutionary Diversification of Caribbean *Anolis* Lizards

16.1 Introduction

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The diversification of the lizard genus *Anolis* on Caribbean islands surely represents one of the best-studied cases of adaptive radiation in evolutionary biology. Over the course of the past four decades, researchers have studied almost every aspect of anole evolutionary ecology. These include systematics; community, physiological, and behavioral ecology; functional morphology; ethology; and demography. Studies have been conducted in the laboratory and in the field, and have included basic natural history, geographic and temporal comparisons of populations, and a wide variety of experimental approaches to the study of phenotypic plasticity, ethology, ecology, and evolution [recent reviews include Losos (1994) and Roughgarden (1995)]. The result is an unusually broad and detailed understanding of the factors that promote and sustain evolutionary diversification and species coexistence.

Speciation and adaptation in anoles

Two conclusions from the current body of work are obvious. First, the genus *Anolis* has experienced extensive speciation. With more than 400 described species, and more being described every year, *Anolis* is the largest amniote genus, exceeded among tetrapods only by the potentially para- or polyphyletic frog genus *Eleutherodactylus*. The nearly 150 Caribbean species are descendants from as few as two initial colonizing species from the mainland (Jackman *et al.* 1997). Hence, the diversity of Caribbean species results almost entirely from speciation, rather than from repeated colonization.

Second, adaptive diversification has been rampant. Within assemblages of anoles, species are clearly specialized to occupy different niches. Physiological and functional studies have revealed evidence for adaptation to particular microclimatic and structural habitats. Moreover, intraspecific comparisons indicate that populations adapt to their particular environmental conditions (reviewed in Malhotra and Thorpe 2000).

Given the extensive adaptation and speciation exhibited by Caribbean anoles, one might wonder whether the two processes are linked. Can adaptive speciation – the topic of this volume and the theory that as a population diverges under the pressure of disruptive selection, speciation ultimately ensues – explain the evolutionary radiation of anoles? Alternatively, are adaptation and speciation in anoles largely unrelated, perhaps influencing each other to some extent (speciation making adaptation more likely, or vice versa), but not necessarily linked?

The anole radiations

Anoles are small, insectivorous, and primarily arboreal lizards found throughout the Caribbean, Central America, northern South America, and the southeastern United States. Two morphological features characterize anoles. First is the possession of expanded subdigital toe pads. These toe pads are composed of laterally expanded scales, termed lamellae. Each lamella is covered with millions of microscopic hair-like structures, called setae. These setae allow anoles to adhere to smooth surfaces by the forces that form between electrons on the setae and electrons on the surface (Irschick *et al.* 1996 and references therein; see also Autumn *et al.* 2000). Very similar structures have evolved independently in two other groups of lizards, the geckos and prasinohaemid skinks (Williams and Peterson 1982).

The second morphological structure that characterizes anoles is the presence of a gular throat fan, termed a dewlap. This structure, possessed by males of almost all species and females of many, is deployed in a variety of different contexts, including encounters with territorial rivals, potential mates, and predators. The color and pattern of the dewlap, as well as the specific pattern of head movements, is species specific and is used in species recognition (Rand and Williams 1970; Jenssen 1978; Losos 1985).

The closest relative of *Anolis* is the genus *Polychrus*, which contains five species in Central and South America (Frost and Etheridge 1989). Based on estimates from immunological studies, *Anolis* evolved at least 40 million years ago (Shochat and Dessauer 1981). Although the fossil record is sparse, several amber specimens from the Dominican Republic date to the Oligocene or Miocene (de Queiroz *et al.* 1998). Phylogenetic studies (reviewed in Jackman *et al.* 1997) indicate that *Anolis* originated in Central or South America and invaded the Caribbean twice. One lineage gave rise to the *roquet* group, which occupies the southern Lesser Antilles, whereas the second lineage gave rise to all other Caribbean anoles. In turn, the extensive radiation of the beta, or *Norops*, group on the mainland, composed of more than 150 species, appears to descend from a single colonist from the Caribbean back to the mainland.

As many as 11 species of anoles can occur sympatrically in the Caribbean; assemblages nearly as large are known from the mainland. Comparisons of sympatric species indicate that species are almost invariably differentiated from sympatric congeners in some aspect of habitat use and either morphology or physiology, or both. On Caribbean islands, interspecific competition appears to be a potent force in the regulation of assemblage structure (reviewed in Losos 1994); on the mainland, both competition and predation may be important (Andrews 1976, 1979; Guyer 1988).

The following two sections focus in turn on anole radiation in the Lesser Antilles (Section 16.2) and in the Greater Antilles (Section 16.3).

16.2 Adaptation and Speciation in Lesser Antillean Anoles

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The Lesser Antilles archipelago is composed of an older outer arc and a younger inner arc, with some islands (e.g., Martinique) being composed of elements of both (Figure 16.1). Younger islands tend to have a high elevation (e.g., Dominica), that in turn results in pronounced ecological (both biotic and physical) altitudinal and longitudinal zonation. These islands are occupied by two nonoverlapping series of anoles. The northern islands, down to and including Dominica, are occupied by anoles from the *bimaculatus* series and the southern islands, up to and including Martinique, are occupied by anoles from the *roquet* series (Figure 16.1; Underwood 1959). No major island is unoccupied and, naturally, an island has either one or two species. The far northern and southern islands tend to have two species, even if the islands are small and ecologically homogeneous, while central, large, ecologically heterogeneous islands have only a single species (Figure 16.1). As these islands may have been colonized from the northern and southern extremities (Gorman and Atkins 1969), the number of species that occupy an island may be related to the temporal opportunity for two successful colonizations rather than to ecological complexity of the habitat. In any event, these communities are characterized by less congeneric competition than the Greater Antillean anole communities, in which many species may live in sympatry (Section 16.3).

While the number of sympatric species within a community is low, there are numerous allopatric species in this system. Here we attempt to elucidate the relative importance of adaptation in this system, the frequency and pattern of speciation, and the evidence for adaptive speciation.

Evidence for adaptation by natural selection

Evidence for the relative importance of adaptation in this system comes from three classes of study:

- Correlations between phenotype and habitat over space;
- Common-garden experiments;
- Natural selection experiments.

Correlational evidence. Geographic variations in the phenotype of anoles from mountainous, single-species islands (Montserrat, Basse Terre, Dominica, Martinique, and St Lucia) have been investigated (Malhotra and Thorpe 1991a, 1997a, 1997b; Thorpe and Malhotra 1996). These islands tend to have rather similar ecological zonation with windswept littoral woodland on at least part of the Atlantic coast, xeric woodland on the Caribbean coast, and rainforest (giving way to elfin woodland) at higher elevations. The anoles tend to adapt to these