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The Adaptive Radiation and Convergent Evolution of *Anolis* Lizards

In the West Indies, there are numerous species of anole lizards that have undergone adaptive radiation on each island, much like Darwin's finches on the Galapagos islands. These anoles are iguanian lizards of the genus *Anolis* and family *Dactyloidae* with over 400 species throughout the West Indies, Central America, the northern half of South America, and southeastern United States. They "are primarily but not exclusively arboreal, are exclusively dinural, and include both thermorregulators and thermoconformers, that is, species that bask and those that do not bask" (Williams 1983). What is remarkable about these anole lizards, specifically the island anoles, is that despite inhabiting separate islands with little to no relation to one another, they have convergently evolved to have similar morphological characteristics with others of the same ecological environment. The distinct ecological and morphological similarities amongst convergently evolved anoles are what characterize different ecomorph classes found throughout islands of the West Indies. In this paper, to examine in more detail the phenomenon of adaptive radiation and convergent evolution, it will focus on these occurrences in the evolution of *Anolis* lizards on the islands of the West Indies.

In each of the islands of the West Indies, speciation of *Anolis* lizards has, for the most part, been due to adaptive radiation. Adaptive radiation refers to the phenomenon of when an ancestral species diversifies and produces offsprings that are adapted to a wide variety of different ecological niches. This phenomenon is produced when competition among species exists which causes species to shift in their habitat use to reduce overlap in resources and thus each species adapts to the new conditions of their habitat. This same pattern is seen in island anoles.

Competition amongst anole species on the same island exists when they are ecologically similar. Being ecologically similar means, they are of the same ecomorph class and thermal microenvironment. In Palaca and Roughgarden (1985), competition amongst ecologically similar anoles is shown in the competition effects of decreased growth rates, decreased reproduction, decreased total volume of prey, increased perch height, and decreased mean prey size in *A. gingivinus* when *A. wattsi pogus* was present in the same enclosure in comparison to when *A. gingivinus* was by itself because these two species are ecologically similar. On the other hand, no competition effects were observed between *A. bimaculatus* and *A. wattsi schwartzi* when they were together in an enclosure because these two species are not ecologically similar (Palaca and Roughgarden 1985). The reason why competition exists only in ecologically similar anole species is because those anoles will tend to overlap in structural environment, thermal climate, and prey which will lead to competition and partitioning of those resources (Palaca and Roughgarden 1985).

As a result of competition between ecologically similar species, the competing species will shift their habitat use to reduce overlap in resources. This is called resource partitioning, and it involves not only the structural environment but also climatic environment and prey. There is much evidence of resource partitioning shown in both experimental research or observational studies like in Palaca and Roughgarden (1985) where increased perch height was shown in *A. gingivinus* when *A. wattsi pogus* was present in the same enclosure or in Losos et al (1993) where a comparison to previous studies to when it was initially introduced in Grand Cayman showed that *A. sagrei* have shifted up in habitat use. From these papers, it is known that competing species tend to shift their habitat use, however, that is only when there are niches available for the introduced species to occupy. In Williams (1972), there was the *A. cuvieri* (a giant anole), *A. occultus* (a dwarf), and *A. evermanni* (a green tree anole) that occupied the tree crown niche in Puerto Rico. The tree crown niche has three subdivisions: a twig or dwarf niche (the peripheral parts of the crown), a giant niche (central crown), and a trunk-crown niche (trunk-crown) which are continuous but they do not broadly overlap (Williams 1972). With the three anoles, all the subdivisions of the crown niche were filled, the crown is full, so when *A. gunlachi* was added, instead of going to the full crown, it goes to the available trunk-ground niche (Williams 1972). This shows that competing species only shift their habitat use when there are available niches for them to occupy. In a review of the results of species of anole lizards being first introduced to an island, when niches are not available, the introduced species tend to become extinct (Losos et al, 1993). When there are available niches for competing species to occupy, they will shift into that niche and will then adapt to their new environment.

After competing species have shifted in their habitat use, they will then adapt to their new environment which often results in morphological changes. Evidence pertaining to this hypothesis comes mostly from comparisons of populations of a species that differ in habitat use. In Williams (1972), one example is shown in a comparison of the body sizes of *A. cuvieri* (a crown giant anole), *A. occultus* (a twig anole), and *A. evermanni* (a trunk-crown anole) that inhabit the uppermost canopy of tall trees, the twigs of canopies, and the upper trunk and canopy of trees, respectively. They were described as large, small, and intermediate, respectively (Williams 1972). The reason for this variation in size is because the structural environment of the niches puts selective pressure on certain morphological traits of the anoles to optimize their performance abilities within the environment. An example of this is demonstrated in the locomotion of anoles. The structural environment anoles inhabit has three properties: perch diameters, perch lengths, and distances between perches (Moermond 1979). These properties affect locomotion in anole lizards because different combinations of these properties require different methods of locomotion to traverse the environment. Moermond (1979) found evidence of this in his observations of anoles and the perches they regularly used. He found that *A. semilineatus*, *A. koopmani*, and *A. hendersoni*, who occupy dense clusters of perches with small diameters, jump often; *A.* coelestinus, who occupy intermediate conditions where perches may frequently be too far apart to jump between and too narrow for rapid movement, crawl more; and *A. distichus* and *A.* cybotes, who occupy wide, separated surfaces, run more. This shows how because of the structure of their environment, anoles must adjust their movement performance to better traverse it. And, to optimally move in the structural environment of their niches, the morphology of anoles is adapted to do so as well. In an examination of the morphology of *Anolis* lizards related to locomotion in runners (*A. distichus* and *A. cybotes*), crawlers (*A. coelestinus)*, and jumpers, (*A. semilineatus, A. koopmani,* and *A. hendersoni*), Moermond (1979) determined that: (1) jumpers and runners have longer hind limbs that aid in rapid acceleration; (2) crawlers have lower tibia:femur ratio to grip narrow perches; (3) runners and crawlers have relatively more equally proportioned fore and hind limbs than the jumpers who have longer hind limbs to provide the necessary rapid thrust; and (4) jumpers have longer tails for balance during jumps. For each of the different movements in anoles examined, the evidence shows that there is selection for certain morphological traits that aid in the movement of the anoles. The anoles are morphologically becoming specialized to their environment. Thus, competing anole species, who shifted in their habitat use, adapt to their new habitat through the properties of the structural environment that select certain morphological characteristics to aid in the performance ability of the anoles in that environment. This is how anoles have adaptively radiated on individual islands of the West Indies. What is more interesting about island anoles is how the same pattern of adaptive radiation on one island has been observed in multiple other islands through convergent evolution.

Across numerous islands of the West Indies, there are similar sets of specializations in anoles inhabiting similar environments on each island. This is because of convergent evolution. Convergent evolution refers to the phenomenon of when species unrelated genetically have evolved similar morphological characteristics independently. Island anole lizards are known to have undergone convergent evolution because of comparative analysis done on the morphological characteristics of anoles from each of the islands of the Greater Antilles (Cuba, Hispaniola, Jamaica, and Puerto Rico). The analysis by Losos et al (1998) indicated that "members of an ecomorph class were more similar to other members of that class than they are to members of different ecomorph classes from their own island," while phylogenetic analysis based on mitochondrial DNA sequences indicated that "members of the same ecomorph class from different islands are not closely related." According to the definition of convergent evolution, island anole lizards have indeed convergently evolved. They have convergently evolved towards specific sets of traits designated as ecomorph classes that gives them certain advantages performance-wise depending on the specific niche these lizards occupy.

The word ecomorph, first termed by Edward Williams (1972), refers to "species with the same structural habitat/niche, similar in morphology and behavior, but not necessarily close phyletically." There are several distinct ecomorph classes for island anole lizards that are classified based on the similar niches they occupy and the morphological similarities that evolved because of the similar niches. In an analysis of six morphometric characteristics linked to habitat use in island anole lizards, Losos et al (1998) determined six distinct ecomorph classes: crown giant, trunk-crown, trunk, trunk-ground, twig, and brush-grass. Why this phenomenon is occurring is because of two factors: adaptive radiation is occurring on anole populations on each island of the West Indies and each island has similar niches for the anoles to occupy.

One reason why adaptive radiation is able to occur on each island of the West Indies is because of the lack of predation that is present on the islands. Compared to the mainland that has various predatorial mammals, birds, and other lizards to the anole populations, the islands do not. This difference in predation alone affects whether adaptive radiation occurs as shown in Calsbeek and Cox (2010) where they experimented on several replicate island populations of *A. sagrei* given 3 different treatments (no predators, bird predators only, bird and snake predators) to determine the significance of predation in *Anolis* populations. What they found was that "terrestrial predators increased lizard mortality and altered habitat use, but these changes did not alter patterns of phenotypic selection" (Calsbeek & Cox, 2010). Additionally, they gave the treatments across a range of low to high population densities to determine the significance of competition on these populations (Calsbeek & Cox, 2010). What they found was that "increased population leads to strong selection on these traits, whereas reduced competition relaxes this selection pressure and may lower trait values" (Calsbeek & Cox, 2010). While comparing the relative importance of predation and competition, they determined that the "results strongly implicate competition as the central driver of viability selection on island populations," while the effects of predation was "clearly weak relative to those of competition" (Calsbeek & Cox 2010). From this research paper, it can be deduced that because of the presence of predators in mainland populations the lizard population decreased which lowered the competition among anole lizard populations, and thus, caused a weaker selection of traits contributing to why adaptive radiation does not occur in the mainland anole populations. On the other hand, because the islands of the West Indies lack predators, the anole populations would likely increase in population leading to an increase in competition and thus the occurrence of adaptive radiation. With anoles being primarily arboreal, as long as the islands have available crown giant, trunk-crown, trunk, trunk-ground, twig, and/or brush-grass niches in the trees and surrounding area, then convergent evolution for the respective ecomorph classes is likely to occur. This is seen in how specific ecomorphs are described like how "trunk-ground species are stocky, with long forelegs, hindlegs, and tails, whereas twig anoles are elongate, with short forelegs, hindlegs, and tails" (Losos, 1990). So, as anoles on separate islands undergo adaptive radiation attributed to the lack of predation present, they evolve adaptations to similar niches in their environment causing them to convergently evolve.

In summary, lizards of the genus *Anolis* on the islands of the West Indies are able to miraculously undergo both adaptive radiation and convergent evolution due to a number of ecological factors. For adaptive radiation, the presence of competition amongst anole populations is essential as it leads to the partitioning of resources including the structural environment. This leads the anoles to shift into non-overlapping niches and adapt specific morphological characteristics to aid in their performance abilities in their specific niches. As a result, on islands, anoles have diversified and evolved to occupy a variety of niches. With convergent evolution, the phenomenon of adaptive radiation occurs on multiple islands thanks to the lack of predation. In combination with the similarities of niches in these islands, separate anole populations are able to adapt similar morphological characteristics called ecomorphs to aid in their performance ability in their specific niches. Through the study of these phenomenons in island anoles, we are able to learn the finer details of adaptive radiation and convergent evolution including the process and necessary factors for them to occur. With this, this information can be used to examine the adaptive radiation or convergent evolution in other species and may even predict such phenomenons in different environments.

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