

Guppies and Goldilocks:  
Models and Evidence of Two Types of Speciation

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Determining how a given species has arisen is a central question for any field biologist. There are two competing models of speciation: allopatric and sympatric. In 1859, Charles Darwin<sup>1</sup> asserted that speciation could be sympatric, saying, "I believe that many perfectly defined species have been formed on strictly continuous areas." One hundred years later, Ernst Mayr<sup>2</sup> contested Darwin's assertion, saying, "All the evidence that has accumulated since Darwin indicates that this assumption [that species have been formed on strictly continuous areas] is unwarranted as far as higher animals are concerned." Was Mayr right to condemn Darwin for failing to assess correctly the lessons of nature that he observed in the Galapagos archipelago? The difficulty of determining the provenance of a species—whether it arose through sympatric or allopatric speciation—lies in knowing what to look for. And while recent research employing computer simulations<sup>3</sup> suggests a solution to the problem by providing a set of criteria necessary for sympatric speciation, the results predicted by those simulations did not actually arise in the field study that provides the most comprehensive data available to test the model. Rather than invalidating the model, however, this research points to the challenges that complex natural environments pose to the isolation of observable criteria for distinguishing the two types of speciation.

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#### Allopatric and Sympatric: Conditions and Examples

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The two types of speciation differ in their view of what conditions are crucial in determining whether speciation can occur. Allopatric speciation, which Mayr<sup>2</sup> championed, explains the divergence of species by physical isolation, as when a population of

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some species becomes divided or isolated by geological barriers long enough for the individuals involved to grow far enough apart that they lose the capacity to successfully reproduce with each other if, or when, the barrier is removed<sup>4</sup>. The speciation evident in the diversity of species among the islands of Galapagos is commonly regarded as an example of this because of the distances that separate the islands<sup>5</sup>.

A specific case of allopatric speciation is provided in the work of John Endler in his guppy studies<sup>6</sup>. Endler observed two populations of the guppies that live in the streams of Trinidad, *Poecilia reticulata*. These populations are divided between the highlands and the lowlands. The crucial difference between the two populations is the presence of the predatory cichlid fish *Crenicichla alta*, which hunts the *P. reticulata*. In those lowland areas in which *P. reticulata* and *C. alta* live, the guppies have drab, mottled markings that function as camouflage. Meanwhile, in those highland streams where *C. alta* is absent, the *P. reticulata* markings are bright orange, yellow, and blue.

Endler theorized that two selective pressures were working together to create the two distinct guppy populations he observed. The first was that the pressure of the cichlid predators on lowland populations had selected for those mottled and dull appearances, that worked best as camouflage. The second selective pressure was sexual selection by female guppies, which resulted in the bright colorful displays of the highland guppies. Given time, and the right circumstances, these two opposing pressures would push apart the two populations to the point where, even upon a

Genus and species names italicized; genus abbreviated in subsequent references.

chance reunion, they would not be able to interbreed or raise successful progeny<sup>7</sup>.

But the guppies aren't diverging on their own; what is causing the populations to differ is the presence or absence of *C. alta*, and its presence is dictated by whether there are any waterfalls around too high for *C. alta* to jump. In this case of allopatric speciation, the physical environment that creates a barrier to gene flow between populations is the waterfall. In contrast, sympatric speciation achieves divergence without this physical separation.

The most popular explanation of how sympatric speciation could occur comes from John Maynard Smith<sup>8</sup>, who set up a hypothetical model in which selection favored individuals located at the extremes of some phenotypic continuum. For example, imagine that out of a population of porridge-eaters like Goldilocks, a range of temperature preferences could be found: some like it cold, and some like it hot—and others, children of cold parents and hot parents, prefer to eat porridge of middling temperature. Like the Goldilocks of the story, these individuals refuse to eat anything but what they prefer. This separation of food preference works fine in times of plenty when all three options of porridge are available and there is no reason for a cold-porridge-loving individual not to mate with a hot-porridge-loving individual and have warm-porridge-loving offspring. But if for some reason the warm porridge were removed from the environment entirely, then there would be a reason for cold-porridge lovers to spurn hot-porridge-loving mates: a mating between the two extremes would

produce children that were much more likely to starve to death. In this scenario, the adaptations of the extremes drive the populations away from each other while the unfit mixed-parentage offspring are selected against and die out.

It is difficult to give an actual example of sympatric speciation, however, because almost anyone who points to such a potential example encounters objections from detractors; it is very difficult to show, conclusively, that what is claimed as sympatric speciation isn't simply allopatric speciation in disguise. Because allopatric speciation is widely regarded as the default model for speciation, much more persuasive, concrete evidence is required to support the validity of a claim for sympatric speciation.

#### Sympatric Criteria Based on Computer Simulations

A clearer definition of what constitutes concrete evidence of sympatric speciation would help mitigate this problem. Recently, some researchers have attempted to clarify the situation through computer simulations of both models. The simulations recently completed by van Doorn et al.<sup>3</sup> suggest that a sympatric speciation event is possible when sexual selection aligns with other local selection pressures. In Endler's<sup>6</sup> allopatric guppies, the sexual selection was in opposition to predation pressure; van Doorn<sup>3</sup> suggests that we should find the opposite to be true in species undergoing sympatric speciation. Consider again the Goldilocks example: if a hot-porridge-eating individual mated with a cold-porridge-eating individual during a time of scarcity for warm porridge, their unfortunate warm-porridge-eating offspring would be selected against. If all porridge-eaters are identical in appearance,

neither extreme (hot nor cold) is able to identify mates with whom it would produce the most viable offspring. If, however, there is an observable difference in appearance between extremes—hot-eaters are red and cold-eaters are blue, for example—then this appearance trait would enable individuals on each extreme to easily pick the most advantageous mate. In these cases, sexual selection is “self-selection”<sup>8</sup>; of the available types of mate, you choose the one closest to yourself. By sexually selecting along these lines, the two extremes can diverge into two separate species even without the presence of the physical barrier dictated by the allopatric speciation model.

#### Simulation Criteria and the Galapagos Finches

Do field studies bear out the predictions of the simulation by van Doorn et al.<sup>3</sup> that sympatric species will have these condition-dependent sexually selected traits? The most comprehensive field research that provides data to test this model is that of the Grants<sup>5</sup> and other researchers, who have studied Darwin’s finches in the Galapagos for six months of every year since 1973. In studies originally reported over thirty years ago, populations of finches were observed selecting mates based on bird song and the bird songs themselves were directly tied to the birds’ beak morphology. In the original paper, the Grants argued that they were observing sympatric speciation in progress; since different seeds can be best exploited by specialized beaks, any sexual selection of those who share beak morphology would increase the rate of divergence. The reduction in competition between the two morphologies as each settled into its own niche would drive the two populations apart, leading them to become fully separated species. Given that the

First author's name followed by et al. used for work by three or more authors.

original research was conducted over thirty years ago, the van Doorn et al.<sup>3</sup> model would predict that by now the populations might have diverged into two distinct daughter species.

Unfortunately, that prediction did not come true. In *The Beak of the Finch*<sup>7</sup>, Weiner details how the finch song patterns and the sexual selection based on them decayed not long after the Grants' first paper<sup>5</sup> was published and that the songs never seemed to reassert themselves even over the decades of continued observation. But this negative result is not, I would argue, the failure of the van Doorn et al.<sup>3</sup> prediction but rather the result of poor timing. Indeed, the absence of two daughter species may be the exception that proves the rule.

The sexual selection that might otherwise have occurred between the finch populations may have been cut short by changes in the natural conditions—specifically, the weather. The Galapagos Islands are unique in that they experience variable seasons. This yearly cycle is occasionally interrupted by the large-scale Pacific weather patterns La Niña and El Niño. The oscillating month-long downpours and year-long droughts caused by these climate patterns invariably upset the course by which the finch populations were separating<sup>9</sup>. Published in 1979, the Grants' original paper<sup>5</sup> reflected the environmental conditions of a prolonged drought, already at that time two years old and that would last until 1983<sup>7</sup>. It was during these adverse drought conditions that the finch populations began separating by songs. Since the drought had created a scarcity of food that the mid-size-beak finches depended on, the songs became a means by which mating pairs could determine which

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mates would produce self-similar (and more highly fit) offspring. But in 1983, torrential downpours reversed the drought conditions in a matter of days. Along with the rain came the removal of the selective pressure that had first initiated the speciation: the food supply for mid-size-beak finches was no longer scarce.

So the absence of evidence that corroborates the predictions from van Doorn et al.<sup>3</sup> does not necessarily invalidate that model. Indeed, it could be argued that it was the removal of van Doorn's second criterion, other local selection pressures, that made the finches' sexual selection unnecessary. Or, as the Grants said in the final line of their paper, paraphrasing John Maynard Smith, "establishment of a stable polymorphism in a heterogeneous environment is a crucial step in sympatric speciation"<sup>5,8</sup>.

The simulations by van Doorn et al.<sup>3</sup> are invaluable for their effort to identify observable criteria for sympatric speciation and thereby resolve the question of whether, in contrast to Mayr, Darwin correctly identified the trends he observed in nature<sup>1,2,3</sup>. Ideal evidence of the model's validity would entail a population in which the conditions that van Doorn et al.<sup>3</sup> outline led directly and unequivocally to the divergence of species. But as the Galapagos finches demonstrate, the complexity of natural environments and the variability of conditions over time may make such ideal evidence hard to come by. Further assessment of available data from field studies is necessary in order to investigate fully the utility of van Doorn's criteria in explaining speciation mechanisms; the challenge of such assessment will be in accounting for the multiple environmental variables that affect natural populations.



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