



Speciation: Frog Mimics Prefer Their Own

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Speciation: lethal frog mimicry and courtship

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Ranitomeya poison frogs in the Peruvian Amazon mimic one another, a rare example of Müllerian mimicry in vertebrates. In *Ranitomeya imitator*, courtship is more likely between same-coloured mimics than between differently coloured mimics. Divergence in mimicry may therefore play a role in the origin of new species.

Had they been alive today, Henry Walter Bates and Charles Darwin would have enjoyed a recent finding that natural selection for mimicry in poison frogs (Fig. 1) is involved in the origin of species, or speciation [1].



Fig. 1. Top row, the mimic *Ranitomeya imitator*: left, "Varadero" blotched morph; right, striped morph. Bottom row, the models: left, the aptly named *R. fantastica*; right, *R. variabilis*. Photos courtesy of Evan Twomey.

To understand why the new result is both a novelty to us and also would have intrigued early Darwinians requires a little history. Darwin's 'Origin' [2] was long on logic and evidence for evolution, but short on convincing evidence for natural selection [3]. Henry Walter Bates supplied a key example: Batesian mimicry was

the best and arguably the first clear case of natural selection [3]. Bates argued that edible butterflies in the Brazilian Amazon 'mimicked' the colour patterns of inedible 'model' species avoided by predators. The patterns of both mimic and model switched every few hundred km or so. The multiple convergences and rapid spatial turnover in mimetic colour schemes argued for natural selection on signalling rather than mere chance or inheritance from a common ancestor [4]. Müller later showed how mimicry among unpalatable butterflies could be explained: convergent species benefit by sharing the costs of educating predators [5]. Mimicry between unpalatable species is today termed Müllerian mimicry.

Neither Bates nor Müller noticed that on the mossy floors of the rainforests they knew so well there were tiny jewel-like dendrobatid frogs playing the same Müllerian games as the butterflies. Dendrobatid frogs are often known as poison arrow frogs or poison dart frogs due to their extreme toxicity. Extracts of some species are used by Amazon peoples on the tips of blowpipe darts to kill prey. When I first visited the Amazon of Eastern Peru in search of contact zones between mimicry races of butterflies, Rainer Schulte, a resident of Tarapoto, astonished me by demonstrating a rare case of Müllerian mimicry in a frog he had just described. His new species, the dendrobatid *Ranitomeya imitator* [6] mimics various other *Ranitomeya* (at that time these mimics and models were included in the genus *Dendrobates*). Some *Ranitomeya*, according to Schulte, are so toxic that a single whiff can lead to a headache. As in butterflies, mimetic frogs in different places switch colour morphs in concert. In contrast to Bates' butterflies, however, these mimicry switches take place over tens instead of hundreds of kilometres. The narrower spatial scale of dendrobatid colour switching is simply explained: butterflies fly further than frogs hop.

Evan Twomey et al. [1] followed up Schulte's work. They found that local mimicry switches by *Ranitomeya* correlate with behaviour. Near Tarapoto, five distinct colour morphs of *R. imitator* are known, each mimicking a different model species in a different location. Two of these *R. imitator* morphs meet in a narrow zone of contact near the village of Varadero: a blotched "Varadero" morph mimicking *Ranitomeya fantastica* and a striped morph mimicking *R. variabilis*. Striped *R. imitator* from near the contact zone prefer to court fellow striped morphs than blotched morphs. Blotched morphs, meanwhile, as well as striped morphs from further away, fail to show clear preference [1]. This partial courtship preference suggests an early and still incomplete form of reproductive isolation. A break in molecular genetic markers is highly concordant with the colour pattern, showing that gene flow across the contact is limited [1]. Naturally selected divergence in mimicry therefore seems to catalyze the beginnings of so-called pre-mating reproductive isolation.

That natural selection is driving speciation in poison frogs might not seem particularly novel at first sight: Darwin's 155 year-old book (Darwin 1859) was after all entitled "On the Origin of Species by Means of Natural Selection ..."

However, theories of the origins of species have since then largely sidelined natural selection. By the 1890s, although most biologists accepted evolution, the "Eclipse of Darwinism" was beginning [7]. Alfred Russel Wallace eloquently defended his and Darwin's ideas [8]. However, by then natural selection was almost universally rejected as a major cause of evolution in favour of a plethora of ideas now best forgotten [7]. Natural selection was also, in this environment, likewise dismissed as a cause of the origin of species. The eclipse of natural selection lasted until the 1920s and 1930s, when Mendelian inheritance was found to be consistent with Darwinian evolution by natural selection [9].

Even after natural selection was again understood to be important in evolution, speciation lingered on in eclipse phase. Natural selection was regarded by many, perhaps most, biologists as unlikely to play a major role in speciation. Speciation was believed instead to require Lamarckian adaptation to local environments (especially in France and Germany) or special *deus ex machina* intervention, such as macromutation [10], or geographic isolation [11]. Ernst Mayr, first writing in the 1940s on speciation, famously promoted the latter view, and by the 1960s, the majority of evolutionary biologists appeared to agree with Mayr and Dobzhansky that geographic and reproductive isolation were the keys to speciation, rather than natural selection. As late as 1999, Mayr put it thus: "... the crucial process in speciation is not selection, which is always present in evolution even when there is no speciation, but *isolation*"[12]: xix.

Mimicry was implicated in the origin of species from the earliest days of Darwinism, by Bates himself. Divergent natural selection, as Darwin knew well, could be reversed by "intercrossing" [2]. According to Bates, butterflies of the genera *Mechanitis*, *Hyposcada* and *Heliconius* displayed mimicry forms in the process of diverging into species. In these genera, different colour forms tended to mate assortatively, "coexisting in the same locality without intercrossing" (p. 501) as a result of which further divergence of the forms into species would be ensured [4]. The often sceptical Darwin was effusive in his praise of Bates. Not only had Bates found the clearest ever example of natural selection causing divergence, but he was now showing how the same kind of natural selection could lead to increased separation, due to reduced "intercrossing." Darwin was desperate to get his hands on more information, and criticised Bates for not providing the detailed evidence on which his assertions about the absence of intercrossing rested [13]. Unfortunately, by this time Bates was back in England, never to return to the Amazon. No further data on the topic was forthcoming in Darwin's lifetime.

By the 1930s, mimicry had become a premier example of natural selection, albeit without the early implications for speciation [9]. Much later, courtship behaviour was found to depend directly on divergent mimicry in *Heliconius* butterflies [14, 15]. Males were more likely to court females of their own colour pattern rather than divergent patterns. The response was similar with coloured paper models,

so this preference depended directly on colour pattern. Here at last was the result Darwin required. Mimicry can be a 'magic' trait that contributes to species separation as well as to survival.

The recent evidence with poison frogs is similar. Mating between adjacent forms considered members of the same species, but with different mimicry affiliations, follows colour pattern [1]. Colour pattern is known to be used in mate choice in some dendrobatids [16, 17], so preference might here also depend directly on mimicry signals. I'd guess that many more such cases will be found among mimetic butterflies, frogs and other species. In any case, taxa occupying different ecological niches are today well known to diverge in mating behaviour. Space does not permit citations of original papers on ecological speciation: insects that switch host plants, cuckoos and other birds that parasitize multiple bird host species, cichlid fish with divergent sexually selected colour patterns, and the famous Darwin's Finches feeding on different seed species in the Galápagos islands. As a result of this recent work, the role of natural selection in speciation has been rehabilitated (with or without geographic isolation) [18, 19] in strong contrast to the beliefs of a couple of decades ago.

Our current capitulation to Darwin, it seems to me, still misses an important insight the great man had. A hundred and sixty years later, we still struggle to tune in to Darwin's wavelength. In his "principle of divergence," Darwin argued that intermediates become rarer because they are selected against, out-reproduced in the "struggle for existence" [2]. Hybrid sterility and avoidance of cross-mating (pre- and post-mating isolation) are usually cited as the main components of reproductive isolation, but disruptive or divergent natural selection, on mimicry for example, will yield, on outcrossing, some poorly adapted intermediates. Any divergent selection therefore automatically leads to a form of reproductive isolation. Ecological genetic divergence may indeed often be enhanced by hybrid sterility or inviability, or by reinforcement of divergence through selective mating. But reproductive isolation also results more directly as a simple consequence of all ecological divergence -- in mimicry, for example.

Mimetic poison frogs in the rainforests of the Amazon basin, with their extraordinarily diverse and colourful mimetic patterns, demonstrate not just natural selection but also the very essence of speciation.

*Interesting fact: Over 70% of *Ranitomeya* were described in the last (recent) 10 years (1990-2010) fide Brown, Twomey et al 2011.*

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