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Evolution: Poison frogs changing colors while island hopping

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Evolutionary theory predicts that poisonous species that have evolved warning signals should have minimal variation in these signals among individuals. However, strawberry poison frogs in Bocas del Toro, Panama defy this theory. A new study begins to solve this paradox.

Many poisonous prey species have evolved warning signals (also known as aposematism) that serve as cues for predators to learn — or even evolve — to avoid[1]. If predators learn or evolve to avoid a poisonous species based on how it looks, it stands to reason that they may avoid individuals that look different less strongly. Accordingly, evolutionary theory predicts that members of an aposematic species should have minimal variation in the warning signals. Therefore, it would be surprising if aposematic species qualitatively changed the warning signals they have already evolved. Yet, this is precisely what has happened with strawberry poison frogs (*Oophaga pumilio*). While most strawberry poison frogs in mainland Central America are bright red, in the peninsula and islands of Bocas del Toro in Panama the frogs are red, yellow, orange, green, and blue (Figure 1)[2–4]. Most of the islands host strawberry poison frogs of a given color, whereas one island is inhabited by both red and yellow frogs. What are the evolutionary forces and the genetic variants shaping the colors of these frogs and how can we explain the turnover in warning coloration?

Genome sequencing, combined with advanced statistical approaches, can be used to characterize the genetic bases of color variation among these frogs, to infer when the color variants arose and if their prevalence is shaped by selection or merely by chance. However, this approach has not yet been adopted, largely because the genome of these frogs is huge: at 6.7 billion base pairs, it is more than twice the size of the human genome[5]. Because answering these questions with enough confidence requires sequencing many frogs of each color from each location, the cost can be quite high. In a new study in this issue of *Current Biology*, Diana Aguilar-Gómez and colleagues[6] produced a specialized reagent to sequence only the genes and not the rest of the genome of these frogs. This allowed them to focus on the ∼1% of the genome that might yield the most promising results and not waste sequencing effort on the rest. Still, because genetic variants are inherited in chunks across generations, this 1% of the genome is still informative of regions that were not sequenced.

Using this approach, Aguilar-Gómez and colleagues[6] sequenced 347 frogs from across Bocas del Toro. By comparing their genomes, they found that each of the colors is not caused by genetic variants in a single gene but rather in at least three. However, their results indicate that some of the genetic variants have outsized effects (Figure 1). For blue coloration, variants in the *kit* gene are particularly important. For red and yellow, it is variants in *ttc39b*. And for green, which is a combination of yellow pigments with structural blue coloration, it is *ttc39b* and *bco1*; these explain the yellow component but the variants that lead to the blue component remain to be properly described.

These genes are well known for their developmental and metabolic role in coloration and for harboring variation affecting the color of other animals. *kit* encodes a receptor for kit ligand and this ligand–receptor pair is crucial for pigment cell development and migration[7]. Variation in these genes affects coloration in humans and other mammals, and in fish[8–10]. *ttc39b* promotes the conversion of dietary yellow carotenoids into red carotenoids and its variation is associated with yellow-orange-red coloration in fish and birds[11,12]. *bco1* is also involved in the

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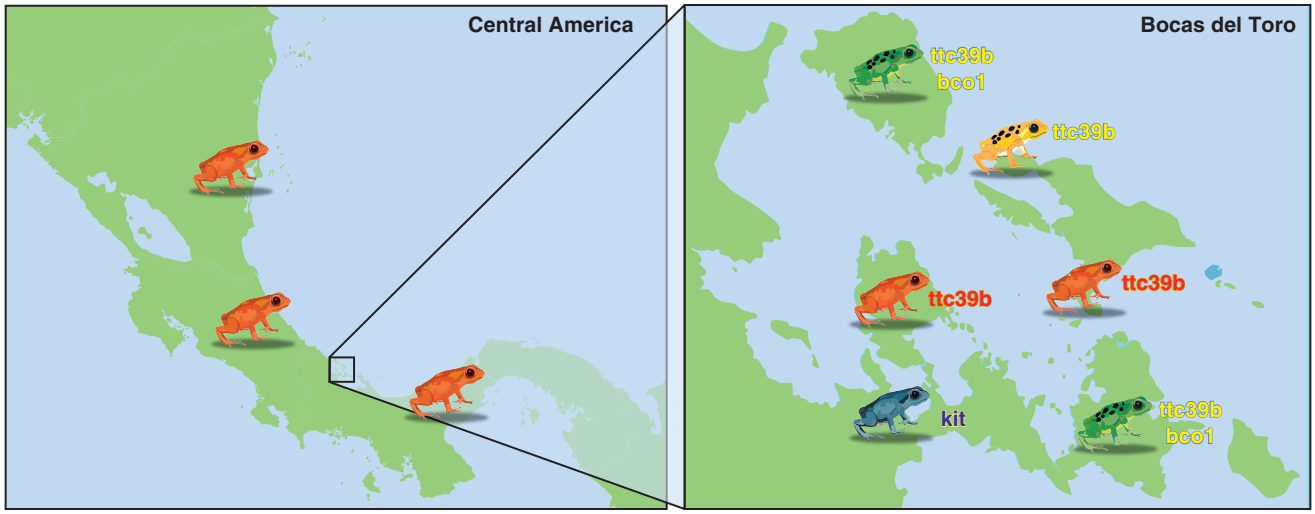

Figure 1. Color variation in strawberry poison frogs (*Oophaga pumilio*).
Strawberry poison frogs are red throughout their range in Central America but have different colors in the Bocas del Toro islands and peninsula region of Panama. The genes whose variation makes the most important contribution to shaping the colors of these frogs are noted next to each color. Red frogs have one version of the gene *ttc39b*, whereas yellow and green frogs have a different version of that gene (frog drawings courtesy of Diana Aguilar-Gómez).

metabolism of carotenoids, by cleaving them into two molecules of retinal (vitamin A)[13].

Identifying the genetic variants with the strongest effects on coloration allowed the authors to combine that information with the mutation rate of frogs (1 in a billion base pairs per year) to estimate when the variants arose. Notably, the *kit*, *ttc39b*, and *bco1* variants appear to have evolved 700,000 to 3,000,000 years ago — much longer ago than the age of the islands, which formed only in the last 9,000 years. This suggests that the blue, orange, yellow and green colors of the Bocas del Toro frogs existed before the islands.

Why are frogs from these non-red colors found essentially exclusively in Bocas del Toro? There are three main possibilities: first, the genetic variants that give rise to these colors may have been isolated in different frogs in the mainland, and their effects become visible only after they combined and co-occurred in individuals; second, the color variants may have existed outside Bocas del Toro but went extinct; lastly, the variants might still exist outside Bocas del Toro but at much lower frequencies, suggesting that non-red strawberry poison frogs might be found elsewhere. Extensive frog sampling and genotyping outside Bocas del Toro would help settle this question.

The color variants could occur at different frequencies in the mainland and the islands because they are selected against (purifying selection) in the mainland — as aposematism evolutionary theory predicts — since predators may not avoid them as strongly. Notably, evidence suggests that bird predators avoid bright frogs of any color, rather than avoiding just one specific color, minimizing the potential negative consequences for frogs evolving a new color[14]. Alternatively, color variants might occur at higher frequencies in the islands because they are selected for (positive selection). Indeed, the authors find strong molecular signatures of positive selection for the color variants in the island populations, suggesting these colors are beneficial, rather than detrimental. How can that be? One intriguing possibility is that the Bocas del Toro color variants are positively selected not because they deter predators more effectively, but rather because they make frogs more attractive mates and because they modulate competition with other strawberry poison frogs. Mate choice and intrasexual competition are both types of sexual selection. Indeed, there is evidence that animal colors have dual roles in aposematism and sexual selection and that strawberry poison frogs prefer to mate with and compete more with frogs of specific colors[15–19].

Sexual selection, in synergy with founder effects during colonization of new places, could lead to colors that are rare in the source population becoming the predominant one in the destination. In this scenario, colonization of an island by a small number of frogs that are predominantly of a particular color would make that color the most frequent one in the island; its spread would be accelerated because it is preferred by potential mates of the same color. More behavioral and genetic work will help answer this question and determine the extent to which color preferences during mate choice and competition behaviors are genetic or learned. Intriguingly, one of the genetic variants at high frequency in green frogs is in a gene (*dscaml1*) involved in vision, suggesting a potential mechanism by which vision in green frogs might be shaped to prefer other green frogs.

Altogether, the work of Aguilar-Gómez and colleagues[6] leapfrogs over the challenges of working with huge genomes by generating a reagent that focuses on genes, then uses this reagent to map the genetic basis of aposematism in one of the paradigmatic species and finishes by tracing the evolutionary history of these variants. Notably, the genetic variants that lead to the diverse colors of poison frogs in Bocas del Toro show evidence of positive selection,

suggesting the colors are adaptive, rather than detrimental, as evolutionary theory of aposematism predicts. Furthermore, these genetic variants are much older than the islands in which these frogs live, suggesting that aposematic coloration was variable outside Bocas del Toro and might still be variable, but infrequently. More work on the role of strawberry poison frog coloration on sexual selection and its interaction with demographic events during the colonization and migration through the islands will help understand how these color variants established in this region. Like other significant advances, the work answers many long-standing questions in the field and opens new ones that can be tested using the new molecular tools developed by the authors or with further technical advances and more colorful fieldwork.

DECLARATION OF INTERESTS

The author declares no competing interests.

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Tissue morphogenesis: Regional differences in basement membrane mechanics influence epithelial geometry

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A new study dissects the forces shaping the peripodial region of *Drosophila* wing discs and identifies the stress-free mechanical state of its basement membrane as a key determinant of the squamous morphology of its central region.

Explaining how organs are shaped ultimately requires identifying the multiple forces at play. Research into the molecular mechanisms of cellular force generation have yielded a detailed picture of how actomyosin contractility,

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