



# Prevalence and potential evolutionary significance of color variants in freshwater crayfishes (Decapoda: Astacidea)

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## ABSTRACT

Mutations may lead to the evolution and diversification of color phenotypes in animals. Much of the research on this topic, however, has been conducted on vertebrates. I compile here records of color variants in freshwater crayfishes (Decapoda: Astacidea). I found color variants to be surprisingly common, with 115 documented occurrences. The overwhelming majority of these variants were blue-colored (71.3%), although there are records of document red and orange variants, among others. Whether these variants are all due to mutations or can lead to adaptive evolution in crayfishes is unknown. Some crayfish species exhibit conspicuous colors like blue, orange, and red in nature. Many of these conspicuously colored species are also semi-terrestrial burrowers, which have limited migration potential, smaller population sizes, and thus reduced gene flow compared to aquatic burrowing crayfishes. I speculate that in at least some species, conspicuous colors may be a neutral color trait that faces little to no selective pressure. This is one potential explanation as to why semi-terrestrial burrowing species are more likely to be conspicuously colored. Genetic studies and behavioral experiments are required to test this hypothesis.

**KEY WORDS:** color abnormalities, color morphs, Crustacea, mutants, pigments

Every few years, news outlets report the discovery of a conspicuously colored blue lobster (*Homarus* sp.), which is presumed to be the result of a one in two or one in three million chance mutation (although the sources of these reported odds are unknown and not scientifically validated). This phenomenon has been reported over a dozen times throughout the range of the two species of *Homarus* (Aiken & Waddy, 1995; Beale *et al.*, 1998). White, yellow, orange; and in rare cases, bilateral phenotypes and unique mottled patterns have also been reported in lobsters. Similar color mutations are reported in other decapods, like freshwater crayfishes (Momot & Gall, 1971; Fitzpatrick, 1995; Secker, 2013; Stubbs *et al.*, 2023), sand crabs (Faulkes, 2017; Nasir & Faulkes, 2011), and spiny lobsters (Landa-Jaime *et al.*, 2018).

Mutations are thought to play a dominant role in the evolution of color phenotypes across all animal groups (Bennett & Lamoreux, 2003; Rosenblum *et al.*, 2004; Hoekstra, 2006), although most of this research has been conducted on vertebrates. In many cases, a single mutation can lead to a drastic change in color (Orteu & Jiggins, 2020). For example, mutations that alter melanin production (both pheomelanin and eumelanin) in vertebrates such as rodents have been studied for decades. There are over 800 alleles known to influence color in mice, with many of these alleles having been cloned or sequenced (Bennett

& Lamoreux, 2003). In some cases, mutations or mutation loci are initially identified in laboratory populations and then investigated in natural systems. For example, in the deer mouse (*Peromyscus polionotus* Wagner, 1843), a single amino acid mutation in the melanocortin-1 receptor *Mc1r* generates a lighter coat color, which aids in crypsis in some populations of this species (Hoekstra *et al.*, 2006). Research on vertebrates demonstrates the benefits of documenting color mutations, as this can allow researchers to understand how mutations can result in phenotypic change in natural populations (Orteu & Jiggins, 2020). Although the prevalence and potential evolutionary significance of color mutations is well studied in model animals like rodents, research on this topic in other groups, like crustaceans, is sparse.

I compiled records of color variations which are putative genetic mutations throughout freshwater crayfishes (Decapoda: Astacidea). I chose to focus on freshwater crayfishes for several reasons. First, crayfishes are present on all continents aside from Antarctica and mainland Africa (Longshaw & Stebbing, 2016), where they are among the most abundant freshwater macroinvertebrates (Momot, 1978, 1995). Second, natural colors in crayfishes varies widely both within and between species. Although crayfishes are most often associated with cryptic colors (i.e., brown, tan) that presumably aid in crypsis, with over 700 species, crayfishes possess a range of conspicuous colors

and patterns, with many species naturally exhibiting blue, red, orange, or purple phenotypes (Schuster, 2020). Lastly, color variations and color mutations appear to be relatively common in crayfishes, with many reports of these mutations scattered throughout the literature (Momot & Gall, 1971; Fitzpatrick, 1995; Secker, 2013; Hamr *et al.*, 2019 (Fig. 1). A comprehensive list of these variants and a discussion of their potential evolutionary significance in crayfishes, however, had yet to be conducted.

I compiled reports of color variants in crayfishes by searching the literature and other relevant sources. I only collected data from color variants which I deemed to be conspicuous and verifiably different than wild-type coloration. Further, because crayfishes are able to change color within and between molt cycles (Thacker *et al.*, 1993), small differences from wild-type color (i.e., brown *vs.* rusty brown) were not included in this dataset. For literature searches, I performed Google Scholar searches using the keyword “crayfish” combined one additional keyword, including: “color,” “mutation,” “morph,” “phase,” “phenotype,” “variant,” “blue,” “orange,” “red,” “white,” “lucetic,” and “albino.” Literature searches were performed in March 2023. I also compiled records of color variants on the citizen science platform iNaturalist using the same search keywords as above within Infraorder Astacidea (excluding family Nephropidae). I also searched throughout crayfish-specific literature, including the journal *Freshwater Crayfish* and the associated newsletter for the International Association of Astacology, *Crayfish News*. Lastly, I searched Google, Google Images and Flickr. I identified all crayfishes with color variations down to the lowest taxonomic level possible. Photographs were excluded if there was any evidence of recent molting or if the crayfish was not alive and therefore prone to color degradation. I also excluded cases when the photographed crayfish was suspected to have been bred in captivity or purchased from the pet trade. Crayfish photographs suspected from the pet trade were removed as conspicuous colors are sought after and intentionally bred by

aquarists. These variations may not represent phenotypes that naturally occur and persist in wild populations. Many unusual color phenotypes are nevertheless bred and sold in the pet trade, all of which are worthy of future investigation. A complete list of the data I collected are presented in [Supplementary material Data S1](#), which contains references and sources for all photographs included in the study.

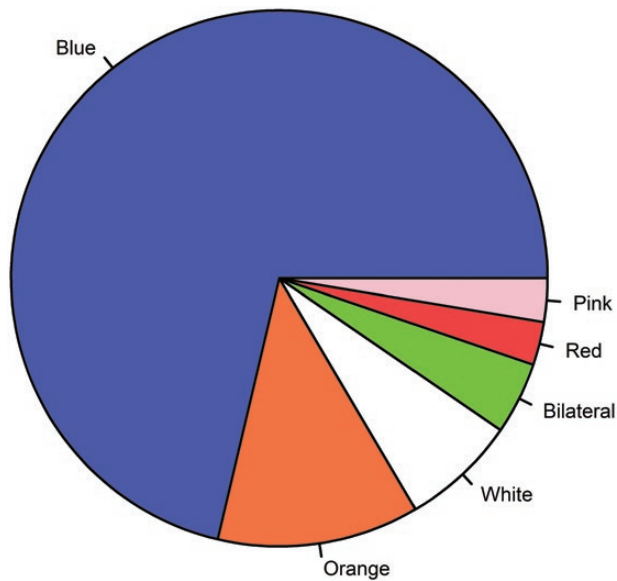
In total, I recorded 115 conspicuous color variants (Figs. 1, 2). Of these, 20 (17.39%) were obtained from the scientific literature, 68 (59.13%) were found from iNaturalist, whereas the remaining 27 (23.47%) were found from other sources, such as the Crayfish News Newsletter. Ninety-six (83.47%) observations were identified down to the species level, the remaining 19 (16.52%) were identified to genus level. All four extant crayfish families were recorded, with a majority of observations being from Cambaridae (88; 76.52%), followed by Astacidae (16; 13.91%), Parastacidae (10; 8.69%), and Cambaroididae (1; < 1%).

Blue was the most common color variant, with 82 occurrences (Fig. 2). Fourteen orange variants were documented also, whereas there were eight white and three red variants (Fig. 2). I recorded five accounts of bilateral color phenotypes, with different color patterns split down the center line of their carapace (Fig. 2). Pink variants were recorded three times (Fig. 2). I presumed these color variations are the result of pigment-related mutations (Black, 1976; Walker *et al.*, 2000), although I acknowledge that diet or other environmental factors could influence color (Wenner, 1972; Barnard *et al.*, 2012; Wade *et al.*, 2012; Stevens *et al.*, 2015;).

Because of their prevalence, much of my discussion focuses on blue variants, although the same arguments and rationale I discuss below could equally apply to other color variants. For example, the genes responsible for blue-color mutations in crayfishes are unknown, but inheritance studies have been conducted on blue phenotypes in two species: *Cherax destructor* Clark, 1936, and *Procambarus alleni* Faxon, 1884. Despite being from separate families, blue mutations in both species are the result of a



**Figure 1.** Color variants throughout freshwater crayfishes. Orange phenotype in *Faxonius nana* (A) and *Cambarus bartonii* (B). Blue-color phenotypes in *Faxonius rusticus* (C), *Pacifastacus leniusculus* (D), and *Spinastacoides inermis* (E). White-color mutation in *Faxonius propinquus* (F). Red-color phenotype in *Cambarus asperimanus* (G). All species presented below are typically cryptic colored (i.e., brown, tan, etc.). Photo credits: A, Dustin Lynch, Arkansas Natural Heritage Commission; B, Emilio Concari; C, Wisconsin Department of Natural Resources; D, John Schaefer; E, Alex2713 on iNaturalist; F, Premek Hamr; G, Benjamin Lowe.



**Figure 2.** Distribution in color of color variants across freshwater crayfishes. Colors are coded based on the observed phenotypes, aside from bilateral color phenotypes, which are coded as green. One hundred-and-fifteen occurrences of color phenotypes were used to create this figure. Blue is overwhelmingly the most common color phenotype recorded.

single autosomal recessive mutation (Black, 1976; Walker *et al.*, 2000). The simple Mendelian inheritance of these mutations allows for the phenotype to spread rapidly, as these species are produced for the pet trade and aquaculture industry (Churchill, 2013; Faulkes, 2015). Although speculative, both blue mutations could be the result of mutations to the same loci, as has been reported throughout other animals (Martin & Orgogozo, 2013). Repeat mutations on the same loci, resulting in similar phenotypes are well known in other taxa (Martin & Orgogozo, 2013). The prevalence of blue mutations in crayfishes I recorded throughout the literature could be the result from mutations repeatedly occurring on the same loci, resulting in commonality of blue color across distantly related species. Genetic studies are nevertheless required to substantiate these claims. Luckily, pigment-altering candidate genes from other crustaceans make the testing the hypothesis of repeated occurrence of blue mutations possible (Huang *et al.*, 2022; Lin *et al.*, 2022).

The physiological mechanisms that control decapod pigmentation are well understood (Fox, 1973; Wade *et al.*, 2015). Decapod coloration results from the expression of carotenoid pigments (i.e., astaxanthin) and carotenoid-protein complexes (crustochrin, A-crustacyanin,  $\beta$ -crustacyanin; Cianci *et al.*, 2002; Tlusty & Hyland, 2005; Begum *et al.*, 2015). Each pigment has its own spectral properties that relate to specific reflectance of light. For example, astaxanthin reflects red wavelengths, whereas  $\alpha$ -crustacyanin reflects blue wavelengths (Tlusty & Hyland, 2005). Since these pigments are expressed in different layers of the cuticle and epidermis, their layering can result in a diversity of color phenotypes (Tlusty & Hyland, 2005). The combined reflectance of all pigments in a cryptic-colored species generally relates to cryptic colors, whereas there is a presumed under- or over-expression of a pigment or carotenoid-pigment in color mutants (Gaeta *et al.*, 2021). Individuals carrying blue-color

mutations are likely to express blue coloration from some mechanisms that either upregulates the expression of  $\alpha$ -crustacyanin, or downregulates the expression of other non- $\alpha$ -crustacyanin pigments (Gaeta *et al.*, 2021). The same logic can be applied to other color mutations, such as red variations that either result in the over-expression of astaxanthin, or the under-expression of other pigments. Future physiological studies should confirm these hypotheses and can also explore whether blue-mutant crayfishes are the result of the same or different mechanisms (Hsiung *et al.*, 2015).

It is unknown whether color mutations in crayfishes can lead to adaptive evolution in natural populations, as is it known in other taxa (Bennett & Lamoreux, 2003; Rosenblum *et al.*, 2004; Hoekstra, 2006). Natural color variation in crayfishes is surprisingly understudied, with no evidence regarding the adaptive value of conspicuous colors in these species (Schuster, 2020). Paradoxically, many of the conspicuously colored crayfish are also semi-terrestrial burrowing species (Schuster, 2020), which are nocturnal and reside within burrows (i.e., primary and secondary burrowers; Hobbs, 1981; Bearden *et al.*, 2021). Although future research may show that conspicuous color in these species is adaptive, an alternative to this hypothesis is that color in these species may be neutral. Caro (2021) has speculated that the red/blue color polymorphism in coconut crabs, *Birgus latro* Linnaeus, 1767, is non-adaptive and may be a neutral color trait that has arisen from mutations. The neutral color hypothesis could be similarly applied to conspicuous colors in semi-terrestrial burrowing crayfishes, as there is no evidence to suggest that these colors serve a particular function (Schuster, 2020). This idea is further supported by the data presented herein, as color mutations appear to be relatively common in crayfishes. If a color mutation appears in a semi-terrestrial burrowing species that rarely leaves their burrows, the trait may not be selected against, and remain evolutionary neutral. Most semi-terrestrial burrowing crayfishes have small geographic ranges due to poor dispersal abilities over land, resulting in lower population sizes, genetic diversity, and gene flow compared to aquatic burrowing crayfishes (Ponniiah & Hughes, 2004; Stern *et al.*, 2017; Hurt *et al.*, 2019). Because in at least blue-color mutations can result from simple genetic mutations (Black, 1976; Walker *et al.*, 2000), once a mutation arises, it may quickly spread throughout the population. The neutral hypothesis of the evolution of color remains poorly tested. Crayfishes may be an ideal group to pursue this provocative, but potentially informative hypothesis.

Despite documenting commonality in crayfish color variants, several limitations are worth highlighting. For example, a majority of the presented data comes from sources that may be deemed “unscientific and unvalidated” (i.e., iNaturalist, Google Images). Citizen science, however, remains a valuable source of ecological data (Adler *et al.* &, 2020; Dickinson *et al.*, 2010), especially in instances such as the current study, as it increases the amount of data available. Moreover, it would be acknowledged that human perception of color may present biases based on our visual system or inherent preferences for certain colors. Analysis in birds nevertheless suggests that human assessments of color correlate the quantitative analyses of color (Bergeron & Fuller, 2018). Lastly, blue colors specifically may be overrepresented in such studies based on the conspicuousness of this color to humans, although accounting for this bias is difficult. Taking

these limitations into account, future studies should undoubtedly attempt to collect quantitative color data (Johnsen, 2016; Stevens et al. 2007).

The documentation of the widespread occurrence and commonality of color mutations across crayfishes will stimulate research on both mechanistic and evolutionary studies of coloration throughout crayfishes and other crustaceans. Such research should pursue the genetic architecture of color in crayfishes, as well as studies that test for the adaptive value (or lack thereof) of conspicuous color in semi-terrestrial burrowing species.

## SUPPLEMENTARY MATERIAL

Supplementary material is available at *Journal of Crustacean Biology* online.

S1 Data. Raw data containing the taxonomy, color variant type, and source of each specific photographed included within the current study.

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