Current Biology
Magazine

Quick guide

Colour polymorphism

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What is colour polymorphism? Colour polymorphism refers to the occurrence of multiple discrete colour phenotypes within populations that result directly from genetic variation. Direct genetic causality distinguishes colour polymorphism from polyphenism, whereby identical genotypes possess the ability to express varied phenotypes depending upon the environment. This definition also excludes ontogenetic and reversible colour change. Colour polymorphism may be limited to the presence of just two discrete morphs (dichromatism). Cases involving multiple morphs are not uncommon, however, and are particularly well documented for colour polymorphism. Dramatic examples include the exuberantly polymorphic happy-face spider (*Theridion grallator*) that exhibits 12 different morphs across four Hawaiian Islands, or poison strawberry frogs (*Oophaga pumilio*) with at least 20 true-breeding morphs across their Central American distribution (Figure 1).

Figure 1. Colour polymorphism in nature.
(A,B) Both morphs of the spiny spider *Gasteracantha fornicata*, whose conspicuous colour patterns visually lure prey (Photos: Thomas White). (C,D) Colour and pattern variation in the highly polymorphic land snail *Cepaea nemoralis* (Photos: Ettore Balocchi). (E,F) Two of approximately 20 morphs of the aposematic poison frog *Dendrobates pumilio* (Photos: Justin Lawrence).

How does colour polymorphism develop? Colour in nature is almost exclusively due to pigments that absorb light or physical structures that reflect it. Both properties may be highly sensitive to genetic variation. In some cases, starkly divergent colour patterns may result from allelic variation in one or a few genes. Cichlid fish of the genus *Amphilophus*, for example, exhibit a dark-versus-gold polymorphism that is entirely due to alleles at a single pigment-controlling locus. Likewise, human eye colour is largely determined by the outcome of dominant and epistatic allelic interactions at two primary loci. In more complex cases, polymorphisms may result from variation across multiple genes that segregate together. This linkage across loci can enable discrete yet highly complex colour phenotypes while precluding less fit intermediates.

Is colour polymorphism common? Colour polymorphism occurs across a breadth of taxa and ecological contexts. Cases are documented for most major metazoan animal groups (Figure 1), across gymnosperm and angiosperm plants, and for species residing in terrestrial and aquatic habitats. Among animals, the incidence of colour polymorphism appears over-represented (if not over-reported) in taxa such as birds, anurans and lepidopterans. Functionally, polymorphism has been documented for colour traits involved in sexual signalling, crypsis, thermoregulation, mutualism, aposematism and in various forms of deceptive signaling including Batesian and Müllerian mimicry.

How is colour polymorphism maintained? Stable polymorphism is thought to require some form of balancing selection to maintain equivalent average fitness among colour morphs. One obvious candidate is negative frequency dependent selection, which arises when rarity confers a selective advantage. This is particular well established in the context of predation, as in the classic case of polymorphic grove snails (Figure 1C,D), and is referred to as ‘apostatic selection’. Visually guided predators, such as birds, often memorize and form ‘search images’ of locally abundant prey. Rare prey morphs therefore benefit from reduced recognition and hence suffer less predation, up until the point at which they become the more common variety. The predators' search image is then switched to the newly abundant morph, and the cycle begins again.

Other examples for negative frequency-dependent selection come from sexual competition. Mate choice, for example, may levy selection of this nature by favouring novel or rare colour phenotypes, as hypothesized for male guppies. For intra-sexual selection, a notable example is the side-blotched lizard *Uta stansburiana*. Males of this species exhibit three throat-colour morphs – blue, orange and yellow – that signal distinct male-competitive strategies. Importantly, each morph is capable of out-competing only one of the others. This creates a dynamic akin to a 'rock–paper–scissors' game, in which no single morph can dominate, so their relatives abundance shifts perpetually.

Variation in selection across space and time is frequently associated with variation in colour phenotypes. This can favour genetic polymorphism, as in the African swallowtail butterfly *Papilio dardanus*. This species exhibits a stark, female-limited colour polymorphism, wherein alternative morphs are considered Batesian mimics of various distasteful model species. The relative abundance of each model varies in a manner that defines discrete 'zones' of sympatry within the broader range of *P. dardanus*. Different female morphs are honed to accurately match their most locally abundant model, which generates the disruptive selection necessary to maintain polymorphism. Interestingly, males are monomorphic across their entire range, as a putative result of stabilizing sexual selection, and additional female morphs exist that cannot easily be explained by mimicry.

Despite select examples, however, it is unclear whether and when colour polymorphism can be maintained by ecological variation alone. Where such variation generates more subtle or stochastic gradients of selection, stable polymorphisms may require additional processes such as sexual or frequency-dependent selection. It is also well established that where an element of environmental predictability exists, as in seasonality, phenotypic plasticity is readily favoured as an adaptive regulator of colour variation.

What are the consequences of colour polymorphism? With respect to evolution, one ultimate consequence is the potential for speciation. This could occur via several pathways. First, reproductive isolation in sympatry can arise when disruptive selection acts on a phenotypic trait that also mediates assortative mating. Colour polymorphisms offer excellent candidates for such so-called 'magic traits' because visual signaling often plays a key role in mate selection. Although considered rare in nature, putative magic traits have been identified in *Heliconius* butterflies and in fishes such as cichlids and sticklebacks. Second, any geographic basis to polymorphism raises potential to influence allo- and parapatric speciation. Clinal variation in morph frequency typifies many colour polymorphisms, and may result from geographic gradients of selection. Although countered by gene flow, such scenarios may promote reproductive isolation at a level ultimately necessary for speciation. Notably, some 20 % of polymorphic birds exhibit clinal morph variation, and colour polymorphism has been linked to accelerated rates of both phenotypic evolution and speciation in these systems.

Where can I find out more?

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