

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 environmental background. This definition also excludes ontogenetic and reversible colour change. Polymorphism is ultimately supported when allelic variation is known to code faithfully for discrete morphs regardless of environment, or when a heritable basis to such phenotypes can be isolated via pedigree experiments.

Polymorphism may be limited to the presence of just two discrete morphs. Dualisms of this nature are termed dimorphism, or dichromatism where they deal specifically with colour phenotype. 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, and poison strawberry frogs (*Oophaga pumilio*) with at least 20 true-breeding morphs across their Central American distribution (Figure 1).

How do they develop?

Colour in nature exists almost exclusively as the combined product of pigments that absorb light and physical structures that reflect it. In phenotypes, both properties are highly sensitive to variation in biochemistry and/or surface morphology, and are therefore malleable via subtle alteration of protein-coding and regulatory genes. In some cases, starkly divergent colour schemes may result from allelic variation at single loci. Cichlid fish of the genus *Amphilophus*, for example, exhibit a dark-versus-gold polymorphism that is entirely due to alternate alleles at a single pigment-controlling locus. Likewise, variation in 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 polygenic variation segregating in the manner of unified “supergenes” (also known as quantitative trait loci, QTLs). Physical linkage across loci is thought to mediate the development of discrete yet complex colour phenotypes while precluding less fit intermediates. This is particularly well documented in co-mimetic *Heliconius* butterflies. In *H. numata*, for example, seven discrete morphs have been traced to allelic variation at a single locus in a manner superficially analogous to the earlier cichlid example. However, closer examination has revealed this locus as an operand for large-scale chromosomal rearrangement, regulating the gene expression responsible for complex differences in colour phenotypes.

Is polymorphism common?

Although rare in absolute terms, colour polymorphism occurs across a breadth of taxa and ecological con-

texts. 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 mullerian mimicry.

Why are colour polymorphisms puzzling?

Phenotypic color pattern is subject to selection in many biotic and abiotic contexts. Divergence among species is naively expected by virtue of differences in ecological niche, if not due to intraspecific selection dedicated to driving divergence (such as selection for mate recognition or appraisal). Some degree of within-species variation is also anticipated for many traits. In adaptive terms, however, the maintenance of discrete and highly divergent phenotypes raises intriguing questions. Given that all individuals of a species draw upon a single gene pool, the most fundamental question is why selection does not ultimately favour a single optimal phenotype? This raises questions regarding the selective factors that serve to maintain alternative discrete phenotypes. A further broad area of intrigue concerns the ecological circumstances and/or evolutionary processes that favour discrete polymorphism over phenotypic plasticity. These are fundamental questions in evolutionary theory, and colour polymorphism has featured prominently in empirical efforts to test them.

So how is polymorphism maintained?

Stable polymorphism is thought to require some form of balancing selection to maintain equivalent fitness (on average) among morphs. One obvious candidate is negative frequency dependent selection, which arises when rarity confers a selective advantage. Specifically, this refers to an increase in marginal fitness that is proportional to the rarity of a phenotype in the broader population. Empiricists have explored this particularly in regard to natural selection due to predation, prompted intuitively from how predators develop visual search images for abundant or profitable prey. Selection arising from such foraging biases – referred to as “apostatic selection” – is levied in a negative frequency-dependent manner. Support for how this may engender colour polymorphism is strong, and traces to classic studies such as Clarke’s work on polymorphic grove snails (Figure 1C-D).

Other avenues for negative frequency-dependence are offered in the realm of sexual competition. Mate choice, for example, may levy inter-sexual selection of this nature by favouring novel or rare colour phenotypes, as hypothesized for guppies. For intra-sexual selection, a notable paradigm has arisen from studies of the side-blotched lizard *Uta stansburiana*. Males of this species exhibit three throat colour morphs – blue, orange and

yellow – that in-turn map onto distinct male-competitive strategies. Importantly, each morph is capable of out-competing only one of its alternatives, thereby generating a population dynamic akin to a “rock-paper-scissors” game. No single morph can exert net dominance, and all three are maintained in perpetuity due to the increase in marginal fitness associated with rarity. Game theoretic modelling has successfully predicted short-scale temporal oscillations in morph frequencies, thereby supporting this three-morph system as an evolutionarily stable state.

An alternative source of balancing selection is given by heterozygote advantage; that is, where heterozygotes (at one locus or across multiple loci) experience fitness advantages over their homozygotic counterparts. This is a well-established driver of allelic and phenotypic polymorphism, with a prominent heritage regarding the sickle-cell locus in human populations sympatric with malarial blood parasites. Accordingly, heterozygote advantage has long been considered a primary candidate for the maintenance of colour polymorphism. The sum of empirical work has nevertheless produced little direct support for this hypothesis, casting doubt on its broader role in such variation.

Variation in selection across space and time is frequently associated with variation in colour phenotypes. This can engender genetic polymorphism, as shown compellingly 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. Importantly, 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 evidently honed to accurately match the phenotype of 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. Nevertheless, *P. dardanus* presents compelling evidence for how ecological and/or geographic variation can favour evolutionary stability in colour polymorphism.

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, less discrete, or more stochastic gradients of selection, evolutionarily 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.

Ultimately, polymorphism may be promoted in populations due to a suite of adaptive and/or neutral drivers. As noted above, ecological, frequency-dependent and disruptive selection need not necessarily act in a mu-

tually exclusive fashion. Furthermore, processes due to hybridization, secondary contact, gene-flow, non-random mating, and genetic drift have all been implicated in colour polymorphism. Defining and partitioning the causality of polymorphism therefore presents an ongoing challenge. Paradigms offered by systems such as Anolis lizards and Papilio butterflies have proven greatly informative, yet likely understate the causal complexity of polymorphism as it occurs more broadly.

What are the consequences of colour polymorphism?

In regard to evolution, one ultimate consequence of polymorphism 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 serves to broker 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, promising avenues 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 has been either established or interpreted to 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. Given that suites of fitness-related traits tend to associate via genetic linkage or pleiotropy, discrete colour morphs should be expected to diverge in broader aspects of their biology. Indeed, alternative morphs are well known for correlated variation in life history, behaviour, physiology, and morphology. Here it is often unclear whether polymorphism arises from adaption driven principally by colour variation per se, or as a correlated response to selection. In reality this will often be a question of causal extent, given that selection operates upon phenotypes directly and then upon gene frequencies/genetic architecture as an indirect consequence. Selection for polymorphic variation may therefore often influence colour phenotypes in ways not easily partitioned at the level of individual traits. Irrespective of causality, discrete colour variation nevertheless indicates the presence of non-neutral genetic diversity. Such diversity may mediate range expansion, habitat colonization, and enable populations to persist despite environmental variation. These are core tenets of population and ecological genetics, with great relevance for biodiversity conservation, yet feature rarely as a motivation to examine colour polymorphism.

Where can I find more?

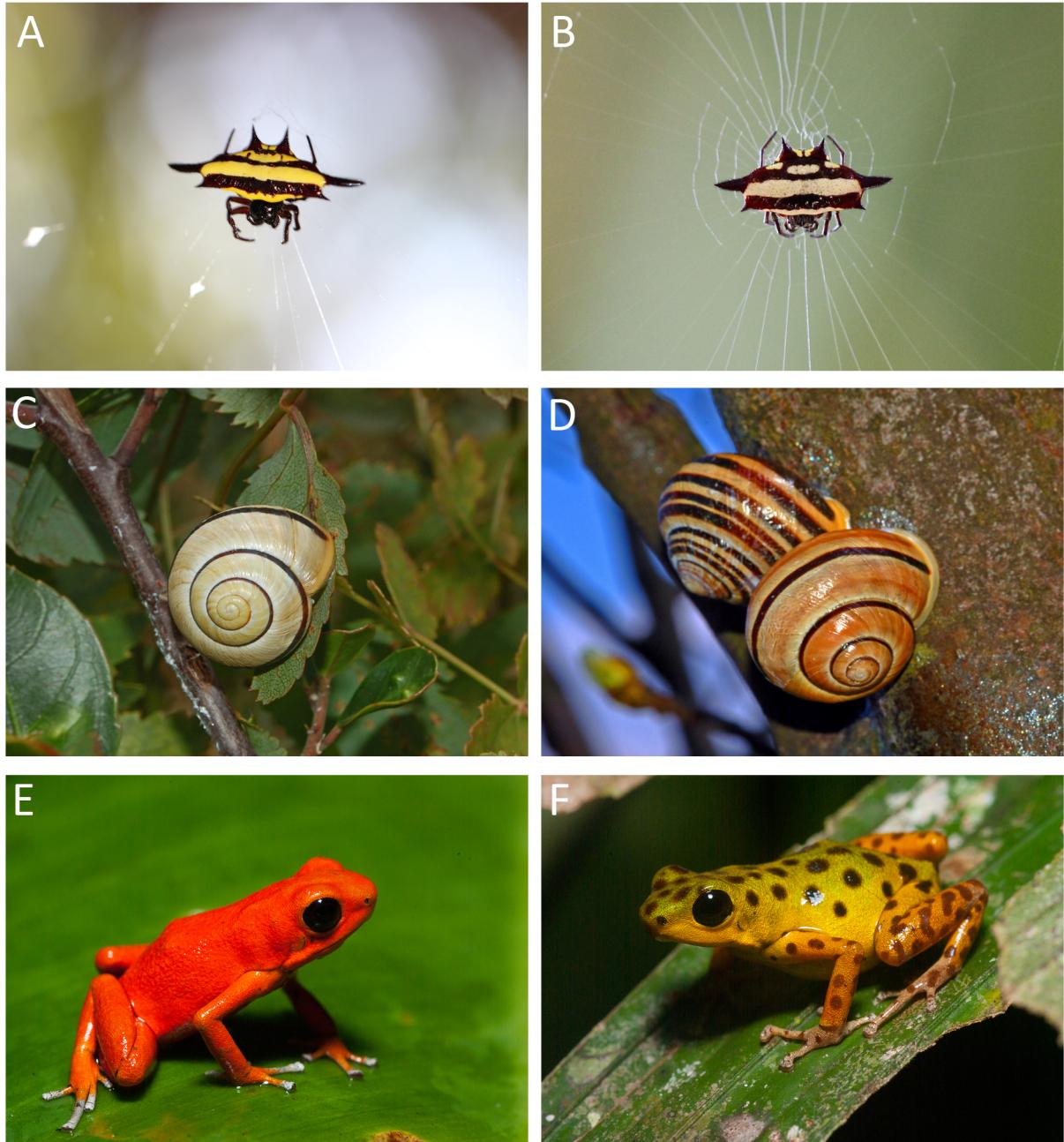


Figure 1: Colour polymorphism in nature. (a, b) Both morphs of the spiny spider *Gasteracantha fornicata*, whose conspicuous colour patterns visually lure prey (Photos: Thomas White). (c, d) Colour and pattern variation in the highly polymorphic land snail *Cepaea nemoralis* (Photos: Ettore Balocchi). (e, f) Two of approximately 20 morphs of the aposematic poison frog *Dendrobates pumilio* (photos: Justin Lawrence).

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