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Colour Polymorphism – A Nature's Puzzle

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Introduction

Colouration mediates the relationship between an organism and its environment in different ways *viz*., social signaling, antipredator defenses, thermoregulation, parasitic exploitation and protection from microbes, ultraviolet light and abrasion. Colour polymorphism refers to the occurrence of multiple discrete colour phenotypes within populations that result from genetic variation. Direct genetic causality distinguishes colour polymorphism from polyphenism, whereby the identical genotypes possess the ability to express varied phenotypes depending upon the environment. This definition excludes reversible and ontogenetic colour change. Colour polymorphism sometimes limited to the presence of just two discrete colour morphs (dichromatism). Colour polymorphism occurs across a breadth of taxa and ecological contexts. Stable polymorphism is thought to require some form of balancing selection to maintain equal average fitness among the colour morphs. Colour polymorphism is widely distributed among cryptic prey species and involved in prey-predator interactions through mimicry, aposematism (colours that warn) and crypsis (camouflage).

The classic work of Edward Poulton's an evolutionary biologist, *The Colours of Animals* (1890), provided the first evolutionary account of cryptic coloration, focusing mainly on woodland moths that adopt the colour patterns of twigs, leaves, and bark. Poulton noticed that these insects were often colour polymorphic, occurring in multiple distinctive pattern variants, and proposed that this served to reduce the search efficiency of predators.

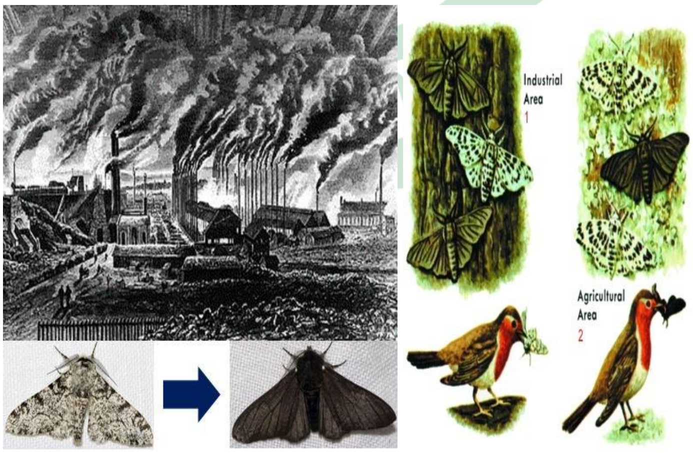
Evolution of colour polymorphism

Maintaining colour polymorphisms within populations is usually believed to require some form of balancing selection. Natural selection was presumed to operate on colour polymorphisms. For example, one of themost classic colour polymorphism studies is on the peppered moth. Colour polymorphisms may play a prominent role as visual signals in sexual selection and mate choice and as targets of selection for avoidance of matings with individuals of other species. Sexual selection, where members of one sex choose to mate with suitably coloured members of the other sex, thus driving the development of such colour morphs appears to be bitter-tasting or dangerous gives natural selection.

The recent advance in genome-wide sequencing methods has shown that various colour loci cluster with functionally unrelated genes to form supergenes. Most of the genes have more than one effect on the phenotype of an organism (pleiotropism). Epistasis occurs when the expression of one gene is modified by another gene and the supergenes consist of several tightly linked genes on a single chromosome.

Evolutionary change

Classical example of microevolutionary change - peppered moth (*Biston betularia*) is a temperate species of night-flying moth. Peppered moth evolution is an example of population genetics and natural selection. However, due to widespread pollution during the Industrial Revolution in England, many of the lichens died out, and the trees which peppered moths rested on became blackened by soot, causing most of the light coloured moths, or *typica*, to die off due to predation. On the same time, the dark-coloured, or melanic, moths, *carbonaria*, flourished because they could hide on the darkened trees. Since then, with improved environmental standards, light coloured peppered moths have again become common, and the dramatic change in the peppered moth's population has remained a subject of much interest and study.



This has led to the coining of the term "industrial melanism" to refer to the genetic darkening of species in responses to pollutants. As a result of relatively simple and easy-to-understand circumstances of the adaptation, the peppered moth has become a common example used in explaining or demonstrating natural selection. This evolution is mainly responsible for survival, reproduction, dispersal and defence.

Factors involved in maintaining colour polymorphism

1. **Genetic polymorphism** - the phenotype of each individual is genetically determined. Genetic polymorphism is the occurrence in the same population of two or more alleles at one locus, each with appreciable frequency. Gautier *et al*. (2018) conducted an experiment to identify colour pattern locus and the mechanisms underlying discrete colour pattern variation in the distinct colour forms of harlequin ladybird, *Harmonia axyridis*. The study showed that variation was controlled by the transcription factor *pannier* (*pnr*) and highly variable discrete colour forms could arise in natural populations through cis-regulatory allelic variation of a single gene.
2. **Environmental factors -** includes both biotic and abiotic factors. Ahsaei *et al*. (2013) studied the differential accumulation of energy by the two distinct colour morphs (red and green) of pea aphid, *Acyrthosiphon pisum* and their adaptive response to environmental factors. The study proved that different colour morphs were physiologically specialized to adjust their energy reserves relative to their specific ecological adaptations and maximize their fitness in form of dispersal, reproduction, defense and survival.
3. **Sexual selection -** colour polymorphism may be produced and maintained by female preference for conspicuous morphs and by predation pressure in favour of cryptic morphs (Reuther *et al*., 2013).
4. **Predator - prey interaction -** colour polymorphism is distributed amongst cryptic prey species and often involved in prey-predator interactions through mimicry, aposematism (colours that warn) and crypsis (camouflage). Interaction between the two has a net benefit in maintaining colour polymorphism and can reduce detection rate of camouflaged prey individuals and population.

Functions of colour polymorphism

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1. **Sexual signalling** - colour as a clue to sexual identity. The dyeing dart frog (*Dendrobates tinctorius*) is highly conspicuous and poisonous but also sexually dichromatic species, showing sexually selected colouration for the mate choice.
2. **Crypsis** - Some colour displays are behaviourally triggered and only displayed when a predator is very near *eg.*, katydids (deimatic displays). Spotted lanternfly (*Lycorma delicatula*) is a cryptic toxic plant hopper at rest, with wings folded vertically, but displays conspicuous red hindwings during flight.
3. **Thermoregulation** - the process by which organisms regulate their body temperature within an optimal range *eg.*, Honey bees. By selectively absorbing and reflecting solar radiation, coloured tissue can directly affect the body temperature.
4. **Aposematism** (warning colouration) - the larvae of Wood tiger moth (*Parasemia plantaginis*) are aposematic *i.e.*, individuals found in more northern latitudes are darker. Paper wasps (*Polistes dominulus*) signal dominance by the extant of black portion on the yellow of their heads and characteristic yellow and black aposematic integument.
5. **Deceptive signaling** - includes batesian and mullerian mimicry. The African mocker swallowtail, *Papilio dardanus* displays female limited batesian mimicry of different unpalatable models and males are undefended non mimics.

Consequences of colour polymorphism

Compared with non-variable populations, populations exhibiting color polymorphism should be associated with (1) utilization of a larger diversity of environmental resources (broader niches); (2) reduced intraspecific competition; (3) decreased vulnerability to environmental change; (4) lower variability in population size; (5) higher evolvability (increased adaptability); (6) increased probability of successful dispersal, colonization, and establishment in novel environments; (7) larger distribution ranges; (8) lower rates of extinction; and (9) higher rates of speciation.

Other consequences

1. **Speciation**

Comeault *et al.* (2015) showed the differences in selection acting on traits can interact with genetics to constrain speciation. They show how melanistic stick insects that are maintained by selection are able to act as a ‘‘genetic bridge’’ between populations. Their results provide a mechanistic example of phenotypic variation constraining speciation.

2. **Species misidentificaton**

Precision in identification of an organism formulates the fundamental step for most aspects of biological science. *Acletoxenus* is a predator belonging to Drosophilidae with only four described species (*Acletoxenus formosus, A. indicus, A. meijerei* and *A. quadristriatus*) that are closely associated with whiteflies. Unfortunately, a confident species identification of the Singapore *Acletoxenus* population to species level was not possible because species identification and description in the genus overemphasize colouration characters of the mesonotum which are shown to be unsuitable. The Singapore population has flies with colouration patterns matching three of the four described species. Based on morphology and DNA sequences, the *Acletoxenus* population from Singapore is tentatively assigned to *Acletoxenus indicus* or a closely related species. But unsuccessful to identify the population of *Acletoxenus* based on their mesonotum colouration pattern.

Colour polymorphism in red palm weevil (Jones *et al.*, 2013)

The red palm weevil (RPW) is a major threat for palms and extreme forms of colour polymorphism in adult specimens are observed in red palm weevil, *Rhynchophorus ferrugineus. Rhynchophorus ferrugineus* (Olivier), RPW displays remarkable colour variation across its range, and consequently has a taxonomic history littered with new species descriptions and synonymization. Jones *et al.* (2013) compared DNA sequences of the mitochondrial cytochrome oxidase subunit I (COI) gene from RPW populations. Molecular data presented here confirms that these specimens in fact represent at least two species, *R. ferrugineus* and *R. vulneratus.* The present study confirms *Rhynchophorus vulneratus* (Panzer, 1798) as a valid species distinct from *R. ferrugineus* (Olivier, 1790).

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Conclusion

Occurrence of two or more alternative colour morphs with associated trait-value combinations may influence the ecological success and evolutionary dynamics of polymorphic populations and species. Colour polymorphism plays a crucial role in mate selection, deterring predators, regulating body temperature and habitat selection. These colour variations are possibly the result of phenotypic plasticity, nutritional status, bacterial symbionts, genetic factors or combination of two or more of the above factors. Colour polymorphic species provide an invaluable insight on intraspecific variation.

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