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# Developmental and evolutionary mechanisms shaping butterfly eyespots

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Butterfly eyespots are visually compelling models to study the reciprocal interactions between evolutionary and developmental processes that shape phenotypic variation. They are evolutionarily diversified, ecologically relevant, and developmentally tractable, and have made key contributions to linking genotype, development, phenotype and fitness. Advances in the availability of analytical tools (e.g. gene editing and visualization techniques) and resources (e.g. genomic and transcriptomic data) are boosting the detailed dissection of the mechanisms underlying eyespot development and evolution. Here, we review current knowledge on the ecology, development, and evolution of butterfly eyespots, with focus on recent advances. We also highlight a number of unsolved mysteries in our understanding of the patterns and processes underlying the diversification of these structures.

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Phenotypic diversity results from a balance between the developmental processes that translate genotype into phenotype, and the evolutionary forces that sort phenotypic variation in natural populations. Both development and evolution are shaped by interactions between organisms and their environment. The integration of concepts and approaches from ecology, evolutionary biology and developmental biology (eco-evo-devo) is, therefore, essential for a more complete understanding of the proximate and ultimate mechanisms shaping the evolution of adaptive traits. In recent years, a number of study systems have emerged in this quest, including traits from various insect groups (this issue); both in classical laboratory models (e.g. *Drosophila* wing spots and sex combs) and also in less studied species with exciting ecology (e.g. beetle horns, water strider legs, and butterfly wing patterns). Despite much progress, general principles are

yet to be established about the types of changes in genotype that affect development to produce the natural phenotypic variation that fuels adaptive evolution and phenotypic diversification. To establish such principles, the eco-evo-devo community needs a broad representation of phylogenetic and morphological diversity [1,2], and the integration of detailed studies of various systems [3].

The color patterns on butterfly wings have provided much fascination and important insight. They have emerged as valuable systems for linking variation in genotypes, development, phenotypes, and fitness because they are evolutionarily diversified, ecologically relevant, and experimentally tractable [4,5]. In addition, they are a powerful tool for promoting the public understanding and appreciation of science, as well as for science education. Some butterfly species have become text-book examples of various important topics in eco-evo-devo, including mimicry and convergent evolution in *Heliconius* [6], and plasticity, constraint, and novelty in *Bicyclus* [7]. The increasing availability of genomic resources (e.g. transcriptome and whole genome sequences) and analytical tools (e.g. for visualization and testing gene function) for these and other lepidopterans are finally making it possible to properly probe the mechanisms behind these and other examples of the ‘endless forms most beautiful’ that so inspired Darwin and generations of biologists after him.

## Butterfly eyespots and eyespot patterns

Butterfly wings are covered with partly overlapping, monochromatic scales whose spatial arrangement can form exquisitely sophisticated color patterns. These scales, which inspired the name of the order of insects that includes butterflies and moths (Lepidoptera), have unique morphological and ultrastructural properties and continue to attract the attention of researchers interested in a complete understanding of butterfly wing patterns. Recent examples include the characterization of the relationship between scale size and color [8], and of scale development [9].

The arrangement of colored scales produce distinct types of pattern elements, including eyespots. Eyespots are made up of rings of contrasting colors and are one of the pattern elements described in the Nymphalid Ground Plan (NGP) [4]. The NGP is a representation of the relationships among color pattern elements on the wings of Nymphalid butterflies. It describes different groups of serially repeated pattern elements, including the eyespots

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or border ocelli, a designation that reflects their location (along the margin of the wings) and morphology (eye-like rings of color). While the NGP has been immensely useful and continues to guide comparative analyses of wing patterns between distantly and closely related species [10,11], researchers recognize some limitations. These include it being difficult to apply to diverged color patterns such as those of *Heliconius* butterflies, as well as the need for revision [12] and for caution with its interpretation [13\*\*]. There is documented variation for many aspects of eyespot morphology, including their number, color, size, and shape, with differences between species (examples in Figure 1a-b) and within species (geographical, seasonal, and sexual; examples in Figure 1c-d). There are also differences between wing surfaces of the same individual, and between individual eyespots on one wing surface. The spectacular diversity in butterfly eyespots is thought to be shaped by natural and sexual selection [14], and eyespot development has been characterized in different species, with focus on species such as *Junonia coenia*, *Vanessa cardui*, and *Bicyclus anynana* (Figure 1). Importantly, eyespots represent eco-evo-devo case studies for traits that are novel, serially repeated, and developmentally plastic. Here, we review our current understanding of ecological interactions eyespots play a role in, how they develop, and about their evolution.

### Ecology of butterfly eyespots: predators, mates, and plasticity

Insect pigmentation provides many visually compelling examples of adaptive evolution. Body pigmentation plays roles in thermal regulation, crypsis, and in different forms of visual communication with partners from the same or different species. Butterfly eyespots, in particular, are classically thought of as eye mimics that serve to avoid predation by either scaring off or confusing predators. There is experimental evidence consistent with both an ‘intimidation’ [15–17] and a ‘deflection’ [18,19,20\*\*] role. To fully distinguish between these alternative anti-predatory strategies, studies need to consider the eyespot pattern phenotype together with the species’ eyespot-display behavior. For example, otherwise-hidden pairs of eyespots flashed upon predator attack can startle and scare off predators, while series of marginal eyespots displayed in resting individuals might effectively attract the predators’ attention to the wing margin and away from the butterfly’s more vulnerable body. Experiments with manipulated eyespot phenotypes continue to shed light onto what aspects of eyespot patterns render them effective anti-predatory traits: eye mimicry or general conspicuousness [15], pairedness or different aspects of eyespot morphology [21\*,22]. It is also important to consider that eyespots in different species and different wing surfaces of the same species, and possibly even different eyespots on the same wing surface, might be shaped by different selection agents. This seems to be the case for the eyespots of *B. anynana*. While the ventral eyespots displayed

in resting butterflies serve as anti-predation distractions, those on the dorsal surface are displayed during courtship and the UV reflectance of their centers play a role in mate choice [14,23], by either females or males [24].

The eyespot phenotype not only affects an individual’s performance in relation to its environment, but is itself affected by the environmental conditions individuals are exposed to during development. Wing pattern formation depends on external abiotic factors such as photoperiod and temperature, which underlie striking examples of seasonal polyphenism described for different butterflies [4,25]. This type of developmental plasticity, whereby the same genotype can result in distinct phenotypes better suited to the environmental conditions adults live in, provides means for organisms to cope with environmental heterogeneity [26]. The physiological regulation of this phenomenon has been described for a number of species. In *B. anynana*, for example, it has been shown that temperature-induced changes in ecdysone dynamics affect different aspects of eyespot development. Manipulations of ecdysone levels during the larval wandering stage affects the size and brightness of eyespot foci [27\*], while manipulations during early pupal life affect the size of eyespot color rings [28\*]. Despite recent advances and ongoing efforts, important questions about the environmental regulation of eyespot formation remain unresolved. We do not know how changes in temperature affect ecdysone dynamics and how ecdysone dynamics affect eyespot development genes. We also know little about the evolution of plasticity in eyespot development. Studies characterizing the wing transcriptome for individuals developing in different conditions [29] can help with the former, and studies of plasticity in closely related species [30] or in differently plastic populations of the same species [31] can help with the latter.

### Development of butterfly eyespots: cellular and molecular underpinnings

Eyespots are arguably the wing pattern elements whose development is best understood. Classical experiments with manipulation of developing wings established that eyespot centers, or foci, are able to induce the production of rings of different colors around them. Destroying or transplanting the presumptive eyespot centers in early pupae respectively eliminates or displaces the corresponding eyespots [4]. Different successive stages in eyespot development can be recognized: 1) establishment of eyespot foci in late larval wings (Figure 2a), presumably involving signals from wing veins and the wing margin, 2) establishment of color rings in early pupae (Figure 2b), presumably involving focus-derived signals which commit surrounding cells to different color fates, and 3) pigment synthesis in late pupae, with light bright colors typically appearing before dark colors (Figure 2c).

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