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# The right tools for the job: regulating polyphenic morph development in insects

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Polyphenism is a form of developmental plasticity in which organisms respond to environmental cues by producing adaptive, discrete, alternative phenotypes known as morphs. The phenomenon is common and important as both a form of adaptation and a source of variation for natural selection. Understanding the evolution of polyphenism will require understanding the proximate factors that regulate alternative morph production. Renewed interest and technological advances have fueled multiple approaches to the latter, including hormone manipulation studies, targeted transcriptomic studies, and epigenetic profiling. We review these studies and suggest that integration of multilayered approaches will be necessary to understand the complex mechanisms involved in regulating alternative morphologies.

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## Introduction

Many organisms have evolved the ability to respond to changing environmental conditions by altering development to produce adaptive phenotypes. Such developmental plasticity can be a decisive boon, allowing individuals within populations to adapt to changing environmental circumstances on short, non-evolutionary time scales. If, in addition to being adaptive, the developmental response is discrete and stable, then the phenomenon is referred to as a *polyphenism*, with alternative phenotypes, referred to as *morphs*, typically exhibiting correlated suites of traits [1–3]. The production of alternative phenotypes by the same genetic material is inherently a regulatory process: external cues are perceived by the organism and then converted into a molecular signal or signals that specify development of the appropriate morph (Figure 1). Once morph identity is specified, alternative morphs develop by proceeding down different ontogenies.

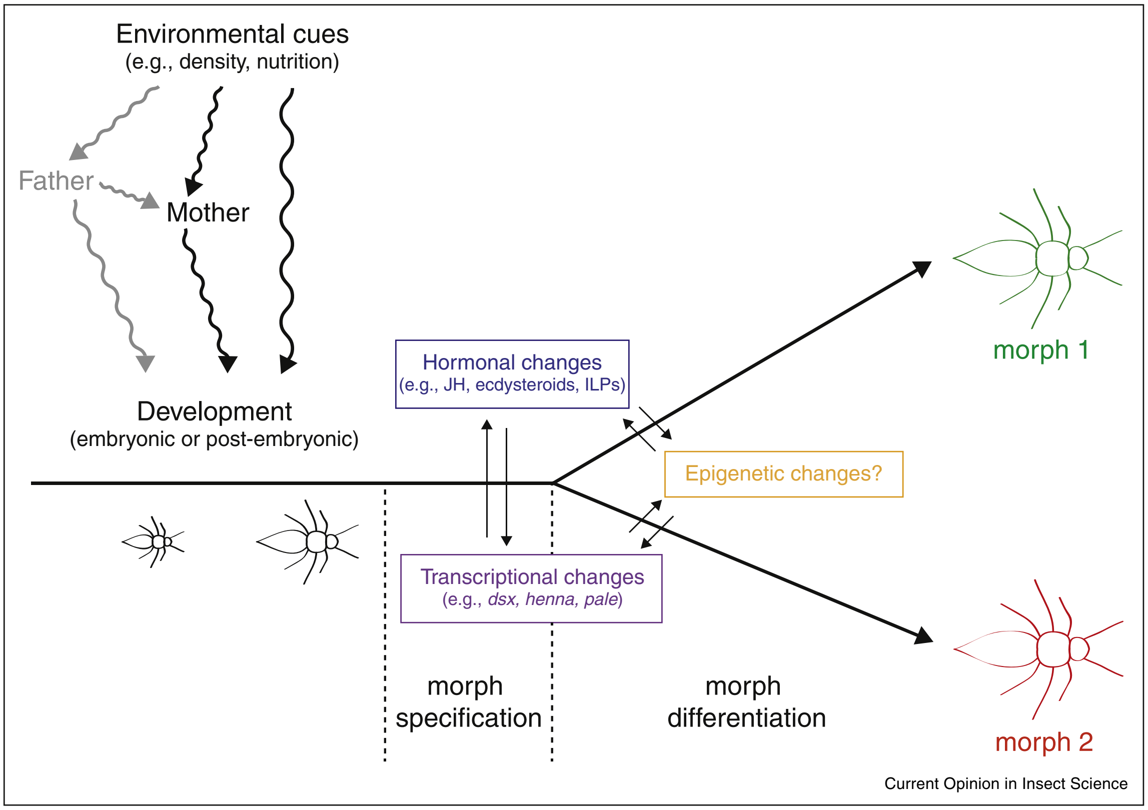
Evolutionary studies of polyphenism typically aim to understand how polyphenic responses evolve and how such plasticity can, in turn, affect the course of evolution. Answers to both of these questions will undoubtedly be informed by a deeper understanding of the proximate mechanisms of polyphenism, in particular its underlying genetics, epigenetics, and development. Fortunately, renewed interest in phenotypic plasticity, combined with technological advances, has provided insights into this area. Here we review recent contributions to the regulation of polyphenic morph development in insects with an eye toward identifying common themes in how these alternative phenotypes are regulated.

## The classic approach: hormone manipulation studies

Although technological advances promise continued progress in understanding the proximate basis of polyphenism, important insights can still be gained through the classic technique of hormone manipulation. As polyphenisms often involve manifold changes throughout the organism, it is not surprising that hormones have long been known to coordinate the development of alternative morphs. In insects, two classes of hormones, ecdysteroids and juvenile hormones (JH), underlie the developmental decisions inherent in many polyphenisms [4,5].

Two studies highlight the power of this technique and the insights they can provide. First, at least two species of the ant genus *Pheidole* possess a 'supersoldier' subcaste that is affected by nutritional state and mediated by JH. In several *Pheidole* species that do not normally produce supersoldiers, application of a JH analog can induce supersoldiers. This result suggests that there is an ancestral developmental potential for this plastic response and that activating this latent response likely facilitated parallel evolution of the supersoldier subcaste in multiple *Pheidole* species [6]. Second, a hormonal approach has linked seasonal changes to color and life history adaptation in the butterfly *Bicyclus anynana*. In this species, wet season or dry season morphs are induced depending on the temperature that larvae and pupae experience during development [7]. A recent study has functionally confirmed what had long been

**Figure 1**



The process of morph specification and differentiation during development involves a branching ontogeny influenced by hormonal, transcriptional and epigenetic changes, all of which may influence each other. Although images of post-embryonic development are shown, specification and differentiation can just as easily take place during embryonic development. These can influence development directly, or be mediated by a mother, who may receive the cue and transmit this information on to her progeny as a maternal effect. Although less supported and less investigated, paternal mediation (shown in gray) is also possible [55], either in combination with or independently of the mother.

suspected about this polyphenism based on titer correlations: ecdysteroids act as part of the switch that controls progression down developmental pathways leading to alternative life histories [8•]. This latter study is also one of the first to examine carefully whether each member of the suite of ecologically relevant traits that characterize the alternative morphs is affected by ecdysteroids.

In general, hormonal manipulation studies are most informative when combined with attempts to correlate morph development with direct measurements of hormone titer, with differential expression of hormone regulators, and with correlated changes of morph-specific downstream genes (reviewed in [9]). These two examples and a myriad of hormonal investigations in other polyphenic insects (reviewed in [5]) reveal a common theme: hormonal signaling is a critical aspect of regulating polyphenisms. That said, polyphenic ontogenies involve much more than hormones and recent technological advances are revealing some of these additional regulators.

## Transcriptomic approaches

The establishment of model systems for studying plasticity and advances in our ability to describe transcriptomes have fueled rapid progress toward understanding the details of alternative developmental trajectories and the nature of environmentally controlled developmental switches (sensu [10]). In a number of polyphenisms, for example, transcriptomic approaches have identified a large number of gene expression differences between morphs (e.g., [11–14]), indicating that different genes from a shared genome contribute to each phenotype. Although most of these studies have focused on the differentiation of adult phenotypes, long after morph identity has been specified, a few have used transcriptomics to identify differences in gene expression that regulate alternative morph specification by precise temporal profiling of the transcriptome in response to inducing cues [15–18]. Even with these more targeted studies, however, it can be challenging to identify the changes in gene expression that are indeed responsible for morph specification because often there are numerous correlated changes in gene expression.