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## Physiology Underlying Phenotypic Plasticity and Polyphenisms: Introduction to the Symposium<sup>1</sup>

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71 Among the most important events in the development of an individual animal are the commitments to major life-history transitions (*e.g.*, metamorphosis, sex determination, reproduction). In many cases, these commitments are accompanied by a switch from plastic (=environmentally sensitive) to canalized (=environmentally insensitive) development (West-Eberhard, 2003) for a given trait (*e.g.*, the next developmental stage, gender). At this moment, individuals can move toward growing horns or lacking horns (beetles, Emlen and Nijhout, 1997), undergoing metamorphosis or growing to a larger larvae (toads, Denver, 1997; moths, Nijhout and Williams, 1974), developing wings with large or small eyespots (butterflies, Brakefield *et al.*, 1998), becoming a queen or a worker (ants, Wheeler, 1991), or laying eggs or continuing to accumulate reserves (grasshoppers, Hatle *et al.*, 2000; Moehrlin and Juliano, 1998). Before this transition, individuals are plastic and can adjust a given phenotype developmentally in response to environmental conditions. After the transition, individuals are canalized, with limited potential for adjusting the phenotype in response to environmental conditions. Because the phenotypes that result from these developmental trajectories can be drastically different, these transitions are critical points in animal life-histories (Crews, 2003; Nijhout, 1999). This symposium focuses on the physiological and endocrinological mechanisms that regulate such life-history transitions. These mechanisms are crucial links between the molecular biology of gene expression and life-history. The symposium includes papers on both continuous plasticity (the production of multiple phenotypes from one genotype) and discrete plasticity (*a.k.a.*, polyphenisms; the production of two or more discrete phenotypes from one genotype). A major goal of the symposium is to reveal common patterns among the mechanisms that produce phenotypic canalization in a broad range of animals and for a variety of life-history transitions.

How are drastically different phenotypes produced from genetically similar individuals? The answer may always involve hormones. Hormones control many important developmental events and probably control most environmentally sensitive life-history transitions (Ketterson and Nolan, 1992; Nijhout, 2003; Stearns, 1992; Zera and Harshman, 2001). Slight variations in

the titer or temporal pattern of hormones can result in large differences in ultimate phenotype. For example, in the butterfly *Bicyclus anynana*, pupae with high ecdysteroid levels develop into adults with large eyespots on their wings. Pupae with low ecdysteroid levels develop into adults with small eyespots on their wings (Brakefield *et al.*, 1998). Further, interactions among hormones may have important effects on life-history transitions. For example, in the development of larval insects, ecdysteroids determine the time of molting but juvenile hormones determine what the next developmental stage will be (*i.e.*, larger larvae or pupae or adult; Nijhout, 1994).

Perhaps most important, mechanistic study could reveal general patterns across taxa. An appropriate focus could be on the initiation of life-history transitions. For example, are peptide hormones that release steroid hormones typically the signals that initiate animal metamorphosis? This discovery of general patterns could reveal how endocrinological mechanisms influence the degree of flexibility. Are gene-regulating hormones that act slowly always involved in the cascade of steps underlying inflexible phases? Hence, the mechanisms underlying life-history transitions are of interest to endocrinologists concerned with the regulation, interaction, and mechanism of action of hormones.

The regulation of life-histories, especially crucial developmental transitions, is also of evolutionary interest (Garland and Carter, 1994; Zera and Harshman, 2001). Comparative study of mechanisms can shed light on the evolution of plasticity. Phenotypic variability within a species (the crux of natural selection) can come from either plasticity in development or from genetic variation. By comparing *how* plasticity produces different phenotypes and *how* genotypic variation produces different phenotypes, one can address the evolution of plasticity. If the mechanisms by which plasticity produces phenotypic variability (from similar genotypes) are different from the mechanisms by which different genotypes produce phenotypic variability, then those mechanisms are likely of separate evolutionary origins (*i.e.*, evolutionary convergence; Hodin, 2000; Hodin and Riddiford, 2000). If the mechanisms behind plastic and genetic variation are the same, they may have the same evolutionary origin.

Trade-offs exist when two physiological demands (*e.g.*, growth and reproduction) are limited by the same resource (*e.g.*, protein in phytophagous insects). An unresolved issue in the study of trade-offs is the relative importance of resource acquisition *vs.* regulatory constraints. Which of these is most important in lim-

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iting the range of phenotypes that can result from a single genotype? The mechanisms by which developmental trajectories become canalized can reveal information about regulatory constraints. Therefore, these mechanisms of canalization may be just as important as the mechanisms that retain plasticity, but canalization largely has been overlooked. It is probable that canalization sometimes constrains adaptative evolution. These putative constraints on evolutionary change are the product of constraints on the development of an individual. Physiological canalization may limit the number of phenotypes (*i.e.*, developmental trajectories) that can be produced in response to environmental variation. Extant endocrine systems have inherent, physiological limitations, such as the speed with which they respond to environmental changes or the limited number of responses that are possible. These limits can result in the inability to respond adaptively to environmental perturbations (Schlichting and Pigliucci, 1998). Certainly, the biochemical processes underlying this developmental inflexibility can evolve, but because selection acts on the phenotype of the whole organism and not directly on the biochemical processes, this selection might be sluggish. Study of the mechanisms underlying these canalized phases, likely controlled by hormones, can give insight on putative constraints of regulation (Zera and Harshman, 2001). Hence, mechanisms of canalization are important to the study of evolutionary trade-offs.

Last but not least, these mechanisms underlying plasticity are also of interest to developmental biologists. In fact, the present symposium on the physiology underlying plasticity builds on a previous Society for Integrative and Comparative Biology symposium titled Ecological Developmental Biology (see Gilbert and Bolker, 2003). The present symposium extends this by focusing on the regulation of non-embryonic life-history transitions, and how these transitions are affected by the environment.

*Goals of the symposium*

The first goal of the symposium was to stimulate the search for common mechanisms underlying putative switches from plastic to canalized phases of development of specific traits. To address this, the symposium encompassed numerous animal taxa and types of life-history events. This goal was addressed by bringing together workers from diverse fields, but that were linked by an interest in the control of developmental switches in their study animals.

Second, the symposium emphasized the importance of studying the physiological and endocrinological mechanisms of relatively inflexible phases. These inflexible phases represent a developmental period in which the number of possible phenotypes is limited,

and this may partially constrain adaptative evolution. Understanding the physiology underlying these phases may shed light on limits of adaptations.

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