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EDITORIAL

SPECIAL ISSUE

DEVELOPMENTAL PLASTICITY: FROM MECHANISMS TO EVOLUTIONARY PROCESSES

Diversity drives discovery in developmental plasticity

Patricia A. Wright[1,*] and Kathleen M. Gilmour[2]

Understanding the effects of the environment on animal physiology and biomechanics is at the core of Journal of Experimental Biology. Environmental factors such as temperature, food availability, sound or the presence of predators can profoundly shape how an animal grows and matures into an adult. In this Special Issue, we take a close look at developmental plasticity, which is the influence of conditions experienced during early development on an animal's phenotype. In her classic book of 20 years ago, 'Developmental Plasticity and Evolution', Mary Jane West-Eberhard proposed that 'alternative phenotypes' that arise in organisms under different early life conditions play a critical role in moulding animal evolution and diversification (West-Eberhard, 2003). The ensuing years have seen increasing attention on how developmental plasticity may contribute to evolution. Given this, coupled with the explosion of new information on the epigenetic mechanisms underlying developmental plasticity, the growing number of submissions to JEB in this area, and the fact that an earlier special issue on 'Phenotypic Plasticity' (Hoppeler et al., 2006) is now 18 years old, the time seemed right for a special issue on developmental plasticity. In the current issue, we have capitalized on the diversity of animal models under study, from worms to dung beetles and lizards to mice, to assemble a strong comparative approach to the topic. We also aimed to bring together researchers considering developmental plasticity from diverse angles, from molecular and cellular biology to whole animal physiology, ecology and evolution, to more fully understand and integrate new approaches and research findings.

Developmental plasticity is defined by the rearing environment, from nutrition to social conditions, which provides critical information that developing animals use to shape the maturation process and resultant adult behaviour and physiology. Such context-dependent plasticity during development is often considered to be both widespread and adaptive, although the extent to which this is the case remains unclear (Sánchez-Tójar et al., 2020). It is also important to recognize that conditions such as resource limitations or exposure to environmental contaminants can result in damaged phenotypes that are clearly not adaptive. In this Special Issue, Metcalfe (2024) discusses a third possibility – that variation in early conditions need not always result in obvious adult changes, but may alter developmental trajectories in ways that have more nuanced consequences over longer periods of time. Other articles in this Special Issue focus on identifying critical environmental factors that serve as cues for developmental adjustments, and how these, in turn, are transduced within the developing animal. For example, information transmission may be mediated by parental behaviour (e.g. Mariette, 2024) or indirectly via provisioning of the egg. Hotter temperatures, food scarcity or stress (e.g. from predators) experienced by a parent provide anticipatory cues to developing animals that may prepare them for similar stressors in later life. Food availability or nutrition, in particular, appears to be of fundamental importance in an animal's developmental trajectory, to the point where we may ask whether it is a 'master' regulator of development. Understanding the mechanisms involved in nutritional effects on development is a critically important area for future research.

Signals about the rearing environment are transduced into phenotypic changes via neuroendocrine, cellular and molecular pathways, and characterizing these proximate mechanisms likewise constitutes a critical and active area of research. In particular, recognition of the role played by epigenetic mechanisms in determining how genomic DNA is expressed has opened the door to a deeper understanding of how developmental plasticity is enabled. Although much remains to be learned, DNA methylation, histone acetylation and non-coding RNAs such as microRNAs have all been implicated in context-dependent adjustment of growth and differentiation. Indeed, the possible involvement of the same or similar molecular mechanisms in mediating responses to disparate environmental factors raises questions about whether there are 'generalized' responses that underpin aspects of developmental plasticity (e.g. Potticary and Duckworth, 2020).

Understanding the molecular mechanisms of developmental plasticity requires good model species to study, something that experimental biologists are familiar with as the Krogh principle (Krogh, 1929). From this perspective, *Caenorhabditis elegans* is particularly useful for studies of developmental plasticity, because the developmental fate of every cell in this organism has been mapped (Jarriault and Gally, 2024). At the same time, the identification of specific epigenetic markers that may be associated with developmental plasticity allows these markers to be investigated across a broad range of species and/or a broad range of environmental factors. For this reason, epigenetic markers may be useful in a conservation context, for example in understanding the ecological or evolutionary history of wild populations.

Developmental plasticity is a product of evolution by natural selection, allowing animals to respond adaptively to environmental changes by altering their morphology, physiology or behaviour. However, it may also contribute to evolutionary processes by generating diverse phenotypes that differ in their ability to survive and reproduce in a given environment. It was this thesis, i.e. that developmental plasticity can contribute to adaptive evolution by shaping phenotypic variation visible to natural selection, including the emergence of novel trait variants, which formed the basis of West-Eberhard's influential book. Twenty years later, with a deeper understanding of the proximate mechanisms through which environmentally induced phenotypes arise, Uller et al. (2024) take the opportunity to revisit West-Eberhard's seminal publication in considering how the role of plasticity in evolution can be tested through experimental biology.

[1]JEB Deputy Editor-in-Chief at the University of Guelph, Guelph, ON, Canada N1G 2W1. [2]JEB Monitoring Editor at the University of Ottawa, Ottawa, ON, Canada K1N 6T2.

*Author for correspondence (patwrigh@uoguelph.ca)

P.A.W., 0000-0003-4041-8885; K.M.G., 0000-0001-9056-4704

At least three research themes emerge from the collection of reviews in this Special Issue. First, there is still a need to identify which aspects of the environment matter as well as how these critical environmental cues are transmitted to the developing animal. Second, there is still much to learn about the proximate mechanisms that transduce environmental signals into developmental changes. Finally, although it is now clear that developmental plasticity is both a product and a cause of evolution, the exact mechanisms mediating innovation and the emergence of novel phenotypes remain to be elucidated. We hope readers will find stimulating ideas for future research within this Special Issue. In particular, we hope that comparative physiologists and those studying comparative biomechanics will use these papers to think more about developmental plasticity as a mechanism that helps shape the adult phenotype and how it responds to the environment. More generally, understanding the significance of plasticity in development and evolution is increasingly urgent, as animal taxa are confronting environmental change at a pace much faster than ever before in their evolutionary history.

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References
Hoppeler, H., Flück, M., Lukowiak, K. and Garland, T., Jr. (eds) (2006). *Phenotypic Plasticity*. *J. Exp. Biol.* **209**, 2239-2383. https://journals.biologists.com/jeb/issue/209/12

Jarriault, S. and Gally, C. (2024). Developmental plasticity, a worm's eye view. *J. Exp. Biol.* **227 (Suppl. 1)**, jeb246546. doi:10.1242/jeb.246546

Krogh, A. (1929). The progress of physiology. *Am. J. Physiol.* **90**, 243-251. doi:10.1152/ajplegacy.1929.90.2.243

Mariette, M. M. (2024). Developmental programming by prenatal sounds: insights into possible mechanisms. *J. Exp. Biol.* **227**, jeb246696. doi:10.1242/jeb.246696

Metcalfe, N. B. (2024). How important is hidden phenotypic plasticity arising from alternative but converging developmental trajectories, and what limits it? *J. Exp. Biol.* **227 (Suppl. 1)**, jeb246010. doi:10.1242/jeb.246010

Potticary, A. L. and Duckworth, R. A. (2020). Multiple environmental stressors induce an adaptive maternal effect. *Am. Nat.* **196**, 487-500. doi:10.1086/710210

Sánchez-Tójar, A., Lagisz, M., Moran, N. P., Nakagawa, S., Noble, D. W. A. and Reinhold, K. (2020). The jury is still out regarding the generality of adaptive 'transgenerational' effects. *Ecol. Lett.* **23**, 1715-1718. doi:10.1111/ele.13479

Uller, T., Milocco, L., Isanta-Navarro, J., Cornwallis, C. K. and Feiner, N. (2024). Twenty years on from *Developmental Plasticity and Evolution*: middle-range theories and how to test them. *J. Exp. Biol.* **227 (Suppl. 1)**, jeb246375. doi:10.1242/jeb.246375

West-Eberhard, M. J. (2003). *Developmental Plasticity and Evolution*. New York: Oxford University Press.