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Book Review

Toward an integrated concept of the phenotype

The Flexible Phenotype: A Body-Centred Integration of Ecology, Physiology, and Behaviour by Theunis Piersma and Jan A. van Gils. Oxford University Press, 2010. US$117.00/£65.00 hbk; US$52.95/£29.95 pbk (248 pages) ISBN13: 978 0 19 923372 4/ 978 0 19 959724 6.

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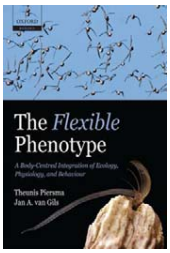

A major problem that transcends the boundaries of biological disciplines is reconciliation of phenotypic change and stability. On the one hand, individual organisms are extraordinarily plastic, responding to life-stage transitions, seasonal cues and environmental change. Some of these changes are permanent and some are reversible, occurring thousands of times during a single lifetime. On the other hand, phenotypic stability is equally evident, enabling reliable recognition of individuals and their assignment into morphs, populations and species. An integrated concept of the phenotype must include both its changeability and stability; yet, such integration has been slow in coming. Nowhere is this more evident than in the focus of different biological disciplines on distinct aspects of phenotypic changeability; behavioral ecologists and physiologists focus on externally and internally flexible components of the phenotype, developmental biologists on ontogenetic changes, and evolutionary biologists on intergenerational changes. As a result, these fields have different concepts of the phenotype, which hinders a truly integrative view of organismal form, function and evolution.

Recent decades, however, have witnessed an expansion of the view of the phenotype by each of these disciplines. In evolutionary biology, a renewed focus on developmental plasticity balances an overemphasis on stable components of the phenotype (i.e. genes). In behavioral and physiological ecology, a recent emphasis on personalities and coping styles counters an imbalance in the opposite direction by acknowledging that, even for the most reactive of traits, there are limits to flexibility. Although such expansion of outlook has proved highly beneficial within disciplines, true integration across fields remains elusive. *The Flexible Phenotype* is a major accomplishment in such integration and a timely reminder that phenotypically flexible traits are not limited to behavior and physiology but instead span the entire spectrum of characters, including those morphological traits at the center of many evolutionary studies. It is also a reminder that even the most flexible aspects of the phenotype are limited by physical laws and the demands of performance.

The first part of the book discusses limits to organismal design: the authors make a case for the existence of metabolic ceilings and for the principle of symmorphosis, which states that optimal body design should avoid excess capacity. The authors' masterful use of examples from both the human and animal physiology literature establishes that limits to performance are evolutionary outcomes and these can only be interpreted in light of ecological context and life-history constraints. These chapters provide an overview of basic concepts in physiology and energetics and, at first, they seem unrelated to the title of the book as phenotypic plasticity is not explicitly discussed until Chapter 5. In hindsight, however, it makes sense to describe limits to phenotypic flexibility before delving into the seemingly unlimited ways that organisms respond to their environment; my only criticism is that the authors could have incorporated the concept of phenotypic flexibility more clearly into these early chapters.

From this point on, the authors focus on linking phenotypic change and ecology using a multitude of fascinating examples of flexible phenotypes, from the immense reorganization of the internal organs of a snake within minutes of swallowing prey to the rapid loss of bone density in zero gravity. The latter example is a reminder that interaction with the environment is as important for maintaining phenotypic stability as it is for inducing plasticity. Throughout, the authors return to their own comprehensive research on red knots (*Calidris canutus*) to show how this species flexibly adjusts its physiology, morphology and behavior to breeding, wintering and traveling through vastly different ecosystems, from the high Arctic to southern Africa. Threading the story of the red knot through the book provides a strong continuity and illustrates how *a priori* integration of ecology, physiology and behavior into research design can lead to novel insights into form and function. A main theme that emerges is that, because adaptations involve flexible phenotypes that respond to their environments, ecological context is crucial to understanding adaptation. The authors also emphasize that, despite the importance of phenotypic flexibility for adaptation, it has largely been ignored in evolutionary studies, which tend to focus on irreversible developmental plasticity.

Evolution and adaptation are themes that run in the background of *The Flexible Phenotype*, but are not explicitly discussed until the last chapter, where the authors argue that, because organisms are constantly reacting to and actively modifying their environments, there are reciprocal feedback loops between flexible phenotypes and evolutionary change. Readers should not expect to

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find an answer to how such reciprocal interactions evolve as the authors' focus is not evolutionary mechanisms; instead, they provide an engaging synopsis of how we arrived at our current concept of the phenotype, where genes are internal factors that influence organismal form separately from an external factor, the environment. By establishing phenotypic flexibility as a ubiquitous component of adaptation and a key factor in evolutionary change, the entire book is a convincing argument against such a dichotomy.

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