

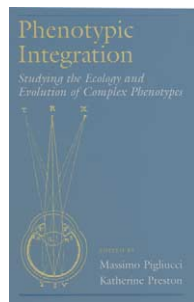


# Understanding organisms: the architectural imperative

**Phenotypic Integration. Studying the Ecology and Evolution of Complex Phenotypes** edited by Massimo Pigliucci and Katherine Preston, Oxford University Press, 2004. £35.00 hbk (443 pages) ISBN 0195160436

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There is much drive, ambition and hope in the editors of, and contributors to, this intellectually overwhelmingly rich volume about 'phenotypic integration'. As suggested early in *Phenotypic Integration*, many 'subtle and interesting research programmes' in ecology and evolution run the risk of degenerating into '*nothing more* than parameterization of single-trait optimality models' [italics are mine] if they

do not consider the adaptation and constraints that are implicit in the evolution of any complex phenotype. Although this might be true, it comes close to stating that many historic and current research efforts in (behavioural) ecology are somewhat trivial. *TREE* readers take note! I was interested to see what an evolutionary or behavioural ecologist, particularly someone who is interested in (particular aspects of) the phenotype of his or her favourite organism(s), would get from this book.

Reflecting the lack of coherence in this volume, one encounters various definitions of 'phenotypic integration'. According to the opening words, Olsson and Miller dedicated a 1958 treatise to develop the concept of integration as the 'complex aspects of an organism's phenotype' [1]. Although this is rather unhelpful, on the next page we see 'integration' (defined here as 'increased genetic and functional relationship among traits') contrasted with 'parcellation' ('decrease in integration by decoupling of formerly related traits to form quasi-independent modules'). However, on pp. 155–156, co-editor Pigliucci gives his personal definition of integration as 'simply... whatever set of evolutionary and developmental processes result in an observable network of multivariate relationships among phenotypic traits that define the morphology and life history of a living organism'. Again referring to Olsson and Miller [1], Merilä and Björklund define phenotypic integration in more statistical terms as 'a pattern and magnitude of covariation among a set of traits'. This is enough to give us a flavour of what phenotypic integration is all about. As Pigliucci points out, even concepts that elude exact definition (such as that of a 'species') can nevertheless have immense heuristic value (we are reminded of the insightful work on 'speciation').

For me, the heuristic value of an integrative approach to the phenotype came most alive in the chapter by

Badyaev about the integration and modularity of sexual ornaments. Badyaev describes the 'cute' paradox of an 'ideal sexual ornament'. On the one hand, ornaments such as extravagant feathering in birds, antlers in deer and horns in beetles should be under strong directional selection for greater expression, and this would favour reduced integration with other bodily functions; on the other hand, such sexually selected traits should indicate health and vigour, favouring tight integration with other organismal functions. Viewing ornaments as reflecting the evolutionary tradeoff between the selection pressure on males to develop the showiest ornaments at the lowest costs (acting to reduce integration) and the selection pressure on the choosy sex (usually females) to maintain the condition dependence and honesty of the ornament by restoring the costs and enhance integration, provides a sophisticated yet insightful way to make sense of the bewildering variety of ornaments within and among species and the extent to which they should reflect integrative processes within the organisms. It also illustrates why ornamental traits that are affected by few genetic factors and developmental pathways (e.g. colour variants) should show higher evolutionary lability than should complex and highly integrated ornamental traits, such as nuptial displays.

Badyaev's is one of five chapters in the section about adaptation and constraints. The remaining chapters are presented in sections ranging from phenotypic plasticity and integration, to genetics and molecular biology of phenotypic integration, to macroevolutionary patterns in phenotypic integration, to theory and analysis of phenotypic integration. In addition, there is a brief historic overview of the diversity of complexity. This eclectic mix of subjects illustrates aspects of phenotypic integration from ecological, developmental, (population-) genetical, morphological, paleontological, statistical and philosophical perspectives. I found myself moving back and forth through the book, somewhat bewildered by the variety of perspectives and the intricacies of some of the arguments, but always intrigued. In spite of the lack of integration in the phenotype of the book itself, the editors have done a good job in introducing, summarizing and aligning the chapters in brief introductions to the various sections.

As testified by recent books about organismal evolution and the phenotype [2,3], there blows a fresh wind in biology, an attitude that is characterized by a real 'willingness to grapple with problems of complexity and multidirectional interactions'. Although the busy

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(behavioural) ecologist might be irritated by the implications of trying to come to grips with the architecture of his or her favourite organism, such attempts will yield results: sexually selected trait variation within and among species might begin to make sense and so might the use of various anti-predator strategies by prey in different predatory contexts. I commend the editors, authors and publishers for taking on this by no means small task.

#### References

- 1 Olsson, E.C. and Miller, R.L. (1958) *Morphological Integration*, University of Chicago Press
- 2 Schlichting, C.D. and Pigliucci, M. (1998) *Phenotypic Evolution: A Reaction Norm Perspective*, Sinauer
- 3 West-Eberhard, M.J. (2003) *Developmental Plasticity and Evolution*, Oxford University Press