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Book Review

***The Flexible Phenotype: A Body-Centred Integration of Ecology, Physiology, and Behaviour.* By Theunis Piersma & Jan A. van Gils. Oxford: Oxford University Press (2011). Pp. 238. Price \$52.95 paperback.**

Organisms are complex systems, organized in a strongly hierarchical (and often modular) fashion. Behaviour is at or near the top of this hierarchy and, of course, notoriously flexible. Hence, the title of *The Flexible Phenotype* should immediately attract readers of this journal. Physiology, too, can be highly variable within an individual (e.g. Iberall 1984 and countless documented instances of metabolic acclimation or acclimatization), and this book is written by ecological physiologists/behavioural ecologists who are well positioned to see the similarities between physiology and behaviour with respect to their flexibility (or plasticity). The back cover of the book states that it attempts a synthesis of physiology, behaviour, and ecology in the context of 'the rapidly growing synthesis in evolutionary biology that incorporates developmental processes, self-organization, and the multiple dimensions of inheritance'. Further, the 'text is aimed at graduate level students and researchers in the fields of physiology, behavioural ecology, and evolutionary biology'. This book could be the basis for a lively graduate seminar in any of those areas, and indeed it would be a good focal point for bringing together graduate students from those disparate areas, who still far too often avoid each other's seminars and courses, at least in U.S. universities.

The authors work primarily on migrant shorebirds, which they encountered from early ages in their native Netherlands. They use these animals to illustrate basic principles throughout the volume, generally to great effect. Although I don't know shorebirds from Shinola, I was able to understand the application of principles to them because the prose is accessible and generally easy to read, often using a conversational style. Many examples involve the red knot, *Calidris canutus*, 'as a focal species in which to evaluate the energetic consequences of [variable] intercontinental migration behaviour' (page 1).

Following an introductory Chapter 1, Chapter 2 provides a concise encapsulation of classic information from animal physiological ecology (e.g. energy, heat, water balance; effects of body size), with emphasis on birds and mammals, and relevant historical context. Some may not be thrilled to find an entire Chapter 3 devoted to 'symmorphosis', a concept that I and others have criticized in print (e.g. Garland & Carter 1994). Piersma & van Gils do reference several published critiques of symmorphosis, but only in passing. Many would disagree with their statements in the synopsis that symmorphosis 'is now widely accepted as a useful, heuristic design principle' and that it is, per se, 'a useful null hypothesis' (page 49).

Chapter 4 on metabolic ceilings presents, among other examples, information on amazing feats of human energetic endurance, such as during expeditions to the poles of the earth. The narrative

includes illuminating historical touches. However, Box 3 on basal metabolic rate (BMR) would have benefited from a more reductionist perspective (e.g. Hulbert & Else 2004 and references therein). Further, readers should be aware that the use of ratios to resting or basal metabolic rate to quantify such feats should not be done without due caution. On the other hand, I strongly agree with Piersma & van Gils' statement that 'BMR may be too much of an epiphenomenon to be a good trait for natural selection to work on' (page 78).

Chapter 5 considers how phenotypic plasticity helps organisms to match phenotypes with environmental demands. The authors suggest that when we fail to find organisms (species) that are good at doing two things, rather than one or the other, this means that some sort of trade-off must be at work (page 98). This perspective ignores an alternative explanation that selection has not yet favoured organisms that could do both things well (or, one might say, such a niche has not existed). In some organisms, these kinds of hypotheses can be tested directly via selection experiments (Garland & Rose 2009).

Chapters 6 and 7 take optimal foraging theory as their framework. Chapter 8 brings disease and predation into the mix, noting that the immune system is one of the most flexible aspects of the phenotype. Chapter 9 is timely in that it considers rapid global change and phenotypic flexibility in relation to conservation biology and management issues, with emphasis on shorebirds.

The final Chapter 10 struggles with 'evolution in five dimensions', referring to a scenario presented by M. J. West-Eberhard (e.g. West-Eberhard 1989, 2007). Within this context, the authors consider whether behaviour has primacy in evolution. They admit that 'The writing of this final chapter on evolutionary implications was difficult' (page 7). Strong conclusions are not forthcoming, nor should they be at this stage in our understanding of organismal evolution. Much work remains to be done, and this chapter makes that clear.

I learned quite a lot in reading this volume, particularly with respect to interesting biological facts and cases of phenotypic flexibility or plasticity. For instance, male ptarmigan soil themselves, apparently to improve camouflage, a clear example of behaviour allowing rapid compensation for a seasonally disadvantageous morphology. Some barnacles lose their penises outside of the mating season. Many of the examples used to illustrate particular points, and a number of the accompanying illustrations, would be very useful for constructing undergraduate lectures on such material.

The authors sometimes refer to 'animals' when offering general summary statements, but the information on which the conclusions are based pertain solely or largely to birds and/or mammals. Vertebrate ectotherms, let alone nonvertebrates, are often quite different, even at the level of some fundamental physiological functions and basic biochemical pathways (Hochachka & Somero 2002). Comparative physiologists would be aware of this, but those who focus on animal behaviour may not be. Readers should also be

aware that some of the comparative studies cited as evidence for or against a particular point either involved few species (sometimes only two) or were not analysed with modern phylogenetic statistical methods, and hence may be misleading (Garland & Carter 1994). Indeed, the word 'phylogeny' does not appear in the index.

No single volume on such a broad topic could possibly cite all of the relevant literature, and readers with different backgrounds and experiences will inevitably find favourite examples that miss mention. As a case in point, the interesting sections on 'The evolution of laziness' (pp. 68–69) and 'Better lazy than tired' (pp. 114–115) reminded me of Herbers' (1981) classic paper. To be fair, the authors do cite a more recent publication by Jeschke (2007) that cites Herbers' paper. I would also have hoped for more on the genetics of plasticity, e.g. some discussion of successful selection experiments that have directly targeted plasticity in various traits (Scheiner 2002). Although many relevant references are cited in somewhat different contexts, this area does not receive direct coverage.

A strength of the book is its few typographic or editorial errors, such as cited references missing from the references section. In the areas I know best, I noted relatively few misstatements. The book also looks good, and has enough figures and tables to encourage thumbing through it to find sections of particular interest or just places to stop because they catch the eye. It is also possible to get much from the book by skipping around; you don't need to read it from beginning to end.

A weakness of the book is that it does not include bulleted chapter summaries. Each chapter does end with a synopsis, but the synopses don't always capture the 'take-home messages' in an efficient way. Because the chapters themselves are written in an engaging and story-telling form of narrative, the essential points are sometimes not easy to grasp by the end, and we do not benefit from bold font or some other device to highlight key points. On the other hand, this lack of spoon-feeding means that an obvious mode of operation for a graduate seminar course would be to ask students to prepare a careful summary for any chapter they covered.

Small shortcomings aside, this is a very good book, and one that I can strongly recommend to ethologists and others interested in

how animal behaviour interfaces with life history, physiology, and morphology. The price seems a bit steep, but perhaps it is necessitated by the rather high production values. Piersma & van Gils successfully integrate a massive amount of information without being either encyclopedic (in the negative sense) or soporific. Readers will be entertained and enlightened, and likely to be inspired to read more from the primary literature and also from other books on this and related subjects. I found myself frequently flipping back to the reference section to see the title of a cited paper that was not familiar. But for those with limited time to delve further, the present treatment is sufficiently comprehensive, and it is accessible to nonspecialists.

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