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Book Review

**Integration of Ecology and Endocrinology in Avian Reproduction: A New Synthesis. Edited by J. C. Wingfield, M. E. Visser & T. D. Williams (2008). *Philosophical Transactions of the Royal Society, B,* 363, 1579–1723. Price £59.50, paperback.**

Modern biology is split into many disciplines that approach the study of life at different levels of analysis, from molecules to cells, systems, organisms, populations and communities. With the smashing amount of information being published every day in the biological sciences, biologists working at different levels of organization of the living world have problems keeping informed on other areas of research and very seldom ignore the progress being made outside their field. Therefore, roughly two research communities have emerged within the biological sciences, which use specific research methodologies, have their own theoretical constructs and use their own jargon: those that study biology below the skin (cellular and molecular processes and physiology) and those that study it above the skin (behaviour, ecology and evolution). These two communities did not talk to each other for a long time, and finding biologists working at the interface was not very common. This scenario has changed in the last decade, and an increasing number of labs are adopting an integrative and multidisciplinary approach to their research. The present volume is an excellent example of this effort to integrate the study of proximate causes with that of ecological consequences and evolutionary context.

This thematic issue emerged from the activities of a joint European–North American (U.S.A. and Canada) research network on function between 2003 and 2006 (E-BIRD: Adaptation and Constraints in Avian Reproduction: Integrating Ecology and Endocrinology: E-BIRD Europe: http://e-bird.cefe.cnrs.fr/; E-BIRD U.S.A: http://depts.washington.edu/ebirdusa/; E-BIRD Canada: http://www.sfu.ca/biology/faculty/williams/ebird/). The main aim of this network was to assess the potential impact of large-scale climate changes on bird populations by studying the decision-making mechanisms involved in bird reproduction (e.g. laying date, clutch size) from an integrative perspective. This topic translates into two major questions: (1) how have physiological mechanisms underlying these decisions evolved and how might they change because of current selection; (2) what are the proximate causes involved in the decision-making processes, and particularly what is the role of hormones.

The answers to these two questions fall within the domains of ecology and endocrinology, respectively, so the Network aimed to gather researchers from both fields and to foster the exchange of knowledge on different methodologies and conceptual frameworks between these two fields. For this purpose, three thematic workshops were held: 'Trade-offs and constraints' in 2004, 'Maternal effects' in 2005 and 'Individual variation' in 2006. The current volume is organized along the lines of these workshops.

The volume opens with an introductory paper by the editors, explaining the context for this issue and the key issues that arose from each contribution. In this introduction the editors also group the different contributions into three main clusters, each corresponding to one of the main topics of the Network identified above. This organization provides the reader with an overall appreciation of the whole volume, and with the option to read it from cover to cover with internal coherence, where one paper follows from the previous one, instead of using it as a collection of stand-alone papers.

The topic of trade-offs and constraints in avian life histories is addressed in the first four papers. The contribution by Lessels questions the role of neuroendocrine mechanisms in shaping phenotypic plasticity of life-history traits. She argues that there are two situations in which the neuroendocrine system may constrain the evolution of reaction norms. One is when the architecture of the system is not able to provide the best solution because it creates constraints (e.g. trade-offs that emerge from pleiotropic-like effects of hormones on multiple target tissues in the organism). The second situation is when costs are associated with the neuroendocrine system itself (e.g. cost of hormone synthesis, toxicity of certain hormones, increased metabolic rate, immune suppression). This is a conceptual paper that will prompt a number of us to rethink our views on the role of costs and constraints on the evolution of phenotypic plasticity. In the second paper, Adkins-Regan discusses whether hormonal control systems may impose evolutionary constraints. To assess this possibility, she analyses three systems, the HPG axis, the activational role of steroids on mating behaviour and sexual differentiation, and concludes that only in the last case is there potential for the hormonal system to contribute to evolutionary inertia.

The third paper, by McGlothin & Ketterson, continues the theme of constraint versus adaptation by analysing suites of correlated traits linked by hormonal systems that may act either as evolutionary facilitators or as constraints. The authors apply methods and concepts of quantitative genetics that have been developed for the study of the evolution of correlated traits to hormone-mediated traits, and make the parallel between genetic and hormonal correlations. This is an inspiring new approach with a high potential to provide new insights into the dual role of hormone-mediated suites as both adaptations and evolutionary constraints. Dawson then gives an informative overview of the extrinsic and intrinsic factors controlling the annual cycle in birds. Photoperiod is identified as the main cue used by birds to time each life-history stage of their annual cycle, but he emphasizes the role of supplementary nonphotoperiodic cues, such as temperature and food availability, in fine-tuning the transitions between stages. His contribution stresses the need to understand these species-specific mechanisms that allow for quick adjustments to environmental changes in order to predict how well different species will respond to anthropogenic environmental changes, such as climate change.


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The second set of papers changes the subject to maternal effects and includes four contributions. Monaghan makes a good starting point by showing how phenotypic development is orchestrated not only by the organism's current developmental environment but also by the adult environment faced by the parents, and how early developmental conditions interact with the quality of the adult environment to influence the fitness of the individuals. Groothuis & Schwabl follow, giving a thorough introduction to the hormonal mechanisms of maternal effects. They focus on three aspects essential for the understanding of these mechanisms: (1) how maternal hormones are transferred to the yolk, and if females can actively control the amount of hormones allocated to each egg; (2) how the embryos use maternal steroids (i.e. are metabolizing enzymes and receptors present in the embryo at early stages of development?); (3) what are the mechanisms through which maternal hormones influence the developing phenotype of their offspring. By answering these questions, the authors provide a framework for studying the mechanisms underlying the effects of maternal steroids on offspring development that have been so much studied at the functional level. This chapter is nicely followed by the only research paper in this issue, in which Martin & Schwabl analyse a data set on developmental rates, parental investment and yolk hormone levels in 83 species of temperate and tropical bird species from the American continent. They conclude not only that mothers can influence the duration of incubation periods and concomitantly offspring quality, but also that the patterns of adult and offspring mortality impose a selective pressure on the strategies of maternal investment. Moreover, they show that the yolk of tropical species contains lower levels of androgens therefore allowing the adjustment of developmental rates according the environmental demands. This pioneering work sets the stage for further comparative field studies. Rutkowska & Badyaev close the topic of maternal effects with a timely and thorough review on the proximate mechanisms allowing for sex-ratio adjustment.

The third and final set of papers addresses the topic of individual variation. In many areas of evolutionary ecology, individual-based models are widely used because heritable variation within populations is needed for an evolutionary framework. In contrast, endocrinologists tend to ignore individual variation and to focus on commonalities in an effort to find general processes. This set of papers is a call against this 'tyranny of the golden mean', as Williams puts it. Williams' contribution emphasises the added value of a focus on interindividual variation in endocrine systems, in terms of both a re-evaluation of unsolved issues (e.g. structure-function relationships between hormones, binding globulins and receptors) and contributing solid mechanisms to key questions in evolutionary biology. The contribution by Ball & Balthazart is a continuation of the topic, with a focus on the cellular and molecular mechanisms involved in the neuroendocrine regulation of behaviour. The authors go beyond hormone levels and provide a very informative picture of properties of the endocrine target tissues that might contribute to individual differences in the hormonal regulation of behaviour. Again, this is a thorough review both in terms of depth and topics covered. The final chapter, by Kempenaers et al. provides a case study of the patterns of interindividual variation of testosterone levels in a well-studied, free-living bird, the blue tit. The authors stress the importance of understanding the source of within- and between-individual variation in hormone titres and argue that it is often difficult to disentangle intrinsic (e.g. genetic or maternal effects) from extrinsic (e.g. time of day, territorial status) factors that contribute to these variations. This distinction would be of the utmost importance given the central role proposed for hormones such as testosterone in behavioural ecology theory, for example, honest signalling and life-history trade-offs.

In summary, this volume is a timely contribution to the area of integrative and comparative biology, and although it is focused on avian physiology and behaviour, the principles presented here can certainly be extended to other vertebrates. Thus, this publication is better seen not only as a final output of the Research Network that prompted it, but also as a steppingstone that will promote future research in the interface between ecology and endocrinology.

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