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***An Introduction to Behavioural Ecology*. 4th edn. By Nicholas B. Davies, John R. Krebs & Stuart A. West (Eds.). Wiley-Blackwell, Chichester (2012). Pp. xiii + 506. Price £34.99 paperback**

The evolutionary biologist David Reznick once memorably, if unflatteringly, described behavioural ecology as 'the soft underbelly of evolutionary biology' (Owens 2006, page 358). However, as this new, fourth, edition of *An Introduction to Behavioural Ecology* (hereafter *AIBE*) admirably illustrates, behavioural ecology appears to be remarkably robust for a 'soft underbelly'.

The central principles of behavioural ecology, outlined in the first edition of *AIBE*, remain the same: a 'gene's eye', reductionist, cost–benefit approach to behaviour that uses optimality/game theory to consider how trade-offs and conflicts of interest are resolved by selection. However, this is not to say that the subject has not developed. In fact, since the last edition of *AIBE* almost 20 years ago (in 1993) behavioural ecology has changed considerably, in particular becoming much more interdisciplinary (Danchin et al. 2008). This ability to forge exciting new links with other disciplines, as Davies, Krebs & West put it, allied to the robustness of its core principles over time, indicate a field of study that is coming of age, able to adapt through becoming more interdisciplinary while maintaining its functional integrity (somewhat analogous to the 'plasticity' and 'robustness' of development itself; Bateson & Gluckman 2011).

Although behavioural ecology has its roots in the classic work by Hamilton, Maynard Price, Parker, Trivers and Williams, among others, in the 1960s and 1970s it was the publication of the first edited volume of *Behavioural Ecology* by Krebs & Davies in 1978 and subsequently the first edition of *AIBE* in 1981 that led to the conceptual unification of the field (Owens 2006). So a new edition of the textbook that has introduced generations of undergraduates (and postgraduates) to the delights of behavioural ecology, inspiring many (myself included) to take up the discipline professionally, is a rare treat. So what has changed since the third edition?

Incidental details aside (Krebs and Davies are now both FRS and one of them is also a Baron) one of the fundamental changes is the addition of a third author, Stuart West, from the University of Oxford. As explained in the preface, the authors represent 'three (short!) academic generations', with Krebs having supervised Davies at Oxford and Davies having lectured to West at Cambridge. This certainly appears to have helped maintain the integrity of the fourth edition of *AIBE*, and the addition of West as a coauthor has undoubtedly enhanced the text, not least through the addition of a terrific new chapter on sex allocation, a subject that has flourished over the last 20 years. All the chapters have been heavily revised/reorganized to incorporate new concepts and new studies, resulting in a sizeable increase in the size of the book from 420 to 506 pages.

The first four chapters have largely been revised rather than reorganized, and cover key concepts and hypothesis testing in behavioural ecology (Chapters 1 and 2), the cost–benefit/optimality approach (Chapter 3; including a new section on the evolution of cognition) and evolutionary arms races (Chapter 4; including updates on aposematism and cuckoo–host coevolution). Chapter 5, on competing for resources, has been heavily reorganized and rewritten, and now contains information on fighting and assessment and alternative breeding systems, both of which topics were given their own, independent chapters in the third edition, and, slightly curiously for a chapter on competing for resources, personalities. There follows a revised chapter on living in groups (Chapter 6), now including a section on reproductive skew, before three chapters on topics relating to various conflicts. This is an area that has expanded rapidly since the early 1990s. Chapter 7 introduces the link between sexual selection and parental investment and the evidence for sexual selection before reviewing the huge number of studies on sexual conflict over mating and postmating (sperm competition) that demonstrate the antagonistic coevolution of traits between males and females. This chapter is followed by a new chapter (Chapter 8) that considers how conflicts of interest among family members shape patterns of parental care, another recent growth area in behavioural ecology, while Chapter 9 provides a restructured review of mating systems, emphasizing the importance of life history constraints, ecology and social conflicts.

Chapter 10 covers sex allocation, a topic that was embedded in the chapter on sexual conflict in the third edition, before three, heavily revised chapters on altruism/cooperation. These superbly written chapters on altruism between relatives (Chapter 11), cooperation (Chapter 12) and altruism/conflict in social insects (Chapter 13) perhaps illustrate most clearly how behavioural ecology has matured, moving on from asking questions about whether altruism/cooperation is genetically selfish or not to considering common mechanisms for the evolution of cooperation across taxa (Owens 2006) and overturning established ideas (e.g. about the central importance of haplodiploidy in the evolution of eusociality; Chapter 13). The book ends with an excellent chapter on signalling (Chapter 14) that has a wealth of new material and some superb examples and a final chapter that considers how plausible the central premises of the book are, including a robust defence of the phenotypic gambit and a brief mention of some of the new areas behavioural ecology has expanded into.

It is difficult to criticize this edition of *AIBE*, especially since the text was already a classic, but it could be argued that in some respects the current edition is not as representative of the state of behavioural ecology as it once was, perhaps because of the new interdisciplinary nature of the field. It seems surprising, for example, that maternal effects receive so little coverage, or that some of the more functional aspects of behavioural ecology, such as the underlying genetic or physiological mechanisms, are so sparingly considered. However, this is splitting hairs. Behavioural ecology is, fundamentally, modern-day natural history and there is no clearer written, more inspiringly enthusiastic guide to the subject on the market. Just read the description of the studies of blackcap migration on page 9, coadaptation of nestling and parent great tits on page 247 or spiteful wasps on page 327: it would be difficult not to be gripped by the vivid enthusiasm of Davies, Krebs and West. This book sets the gold standard for behavioural ecology and animal behaviour textbooks which will no doubt continue to inform and delight students and researchers in equal measure for many years to come.

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Physiological Adaptations for Breeding in Birds, By Tony D. Williams. Princeton University Press, Princeton, New Jersey (2012). Pp. xviii + 368. Price $69.50

Understanding the causes of variation in biological fitness among individuals in a population remains one of the most important questions facing biologists. One therefore might assume that this question is a key focus of investigators in fields related to the study of reproduction. Differential reproductive success is, after all, the currency of evolution. However, this question is often not the focus of reproductive biologists, as Tony Williams argues in his important new book. The book's goal is to summarize what is known about the physiological mechanisms that might explain the extensive diversity in breeding strategies of members of the approximately 10 000 extant species of birds. Although the book focuses on proximate mechanisms, it considers them from an evolutionary perspective. Williams wants to understand how physiological mechanisms are shaped by natural selection to optimize reproductive success in the context of periodic breeding. Birds are theoretically an ideal taxon for such an endeavour. Ecological studies of breeding strategies have a long history, starting with the seminal work of David Lack (1968) and continuing to contemporary investigations in the tradition initiated by Lack (e.g. Bennett & Owens 2002). Research on the mechanisms regulating breeding cycles in birds also has a long history. The phenomenon of photoperiodism, for example, was first discovered in vertebrate animals based on pioneering studies in juncos by Rowan (1925), and work on this topic has now been completed in a variety of species (e.g. Farner 1986).

Previous attempts to summarize this body of work in birds include, most notably, *Avian Breeding Cycles* (Murton & Westwood 1977). Bronson (1989) wrote a similar book, but with a focus on mammals. However, the current volume by Williams is very different from either of these books. Murton & Westwood's book reads more like an encyclopedia of research in a specialized subfield. Bronson's *Mammalian Reproductive Biology*, although more integrative than *Avian Breeding Cycles*, still has a textbook feel to it. *Physiological Adaptations for Breeding in Birds*, on the other hand, takes a clear theoretical stance and unapologetically advocates for certain research approaches. For example, according to Williams, despite extensive research on the physiological mechanisms regulating seasonal breeding in birds, in general the 'right' questions tend not to be asked. From the perspective of an evolutionary physiologist, the 'right' questions are related to how breeding strategies can be adjusted to maximize fitness. Williams proposes three types of questions. First, he strongly argues that research should focus on the sources of individual variation in reproductive traits, so that one can understand the mechanistic basis of trait variation that might be directly related to fitness variation. He also emphasizes the importance of focusing on female rather than male subjects, because females make the key reproductive decision in that they actually lay the eggs. Finally, Williams is concerned that much recent work on how environmental cues regulate reproduction in birds has assumed that central nervous system mechanisms are paramount, and that scientists interested in these questions have not investigated sufficiently how peripheral physiological signals may work in concert with neural processes.

These valuable points are worth stressing. First, most physiological studies do tend to look for general principles rather than assess causes of individual variation. Williams does not explain this focus on group effects, but a key reason is obvious to anyone working in the field of biomedicine. Mechanistic studies in biomedicine are generally funded by government agencies to elucidate the workings of animal 'model systems', in which a reductionist approach to the investigation of physiological questions is aimed at revealing principles generally applicable to all species, including humans. Studies of intraspecific variation related to adaptive significance, although important, are much harder to garner support for in this climate.

Second, the bias towards studying male subjects has been discussed extensively in the biomedical community and is also a concern for those studying mammals as well as birds (Beery & Zucker 2011). For example, the field of avian photoperiodism settled on studying males because wild-caught males provide such a clear readout of testis growth in captive conditions in response to photoperiod; wild-caught female birds, however, often do not show the exponential phase of ovarian growth needed for ovulation under laboratory conditions. This focus on males has paid off with the development of many principles of general value to ecophysiologists (e.g. Farner & Follett 1979), but Williams is correct in advocating for more attention to females to tackle questions underlying the evolution of physiological mechanisms regulating reproduction.

Regarding Williams' third issue, the excessive research focus on brain mechanisms mediating the processing of cues as opposed to peripheral signals, I agree with the need to understand how central systems, such as the gonadotrophin-releasing hormone (GnRH) neuronal system, work in concert with a wide range of peripheral signals, but I fear that Williams is throwing the proverbial baby out with the bathwater. Ovulation requires a surge in luteinizing hormone (LH), stimulated by positive feedback effects on the GnRH system. This poorly understood process that mediates ovulation would be a critical component of any overall theory about the regulation of reproduction that focuses on females, yet Williams does not mention this as an important future research goal. In general, the book gives too little attention to recent research on how environmental cues can regulate GnRH and the related neuropeptide, gonadotrophin inhibiting hormone (GnIH), in male and female birds and mediate the integration of environmental cues (reviews by Ubuka & Bentley 2011; Stevenson et al. 2012).

Given the theoretical stance adopted by Williams, the chapter topics are not surprising; they include the physiological and hormonal control of egg laying, the timing of breeding, the control of egg size and quality, the regulation of clutch size and the physiological basis of parental care. A final data chapter considers trade-offs between investments in breeding and pre- and postbreeding activities, and the book ends with a summary and conclusion. Williams not only provides an excellent overview of the state of each of these specialized fields, but he also identifies questions that must be addressed to understand these topics in ecological and evolutionary contexts. Of particular interest is his critical evaluation of supplementary feeding studies and investigations of variation in egg quality, as assessed by the measurement of yolk hormones as well as egg immunoglobulins, antimicrobial proteins and antioxidants. The discussion of parental care mechanisms is also valuable; again, Williams points out both the well-documented variation in the amount of parental care allocated within bird populations and our lack of knowledge of the physiological factors regulating this variation. For example, an extensive literature on hormones and the transition from courtship to incubation and nestling care in birds (e.g. Buntin 1996) has stressed the importance of steroid hormones and prolactin. However, this work does not explain the extensive variation in parental effort that, as Williams documents,