

Temperature-dependent Sex Determination in Vertebrates. Nicole Valenzuela and Valentine A. Lance (eds). Smithsonian Books, Washington 2004. 194 pages. Price: US \$69.95.

Of all the inborn differences that distinguish individual organisms (including humans) from each other, an individual's sex exerts the most far-reaching effects. It is thus not surprising that sex, and especially the factors that determine sex, have been debated for more than 3000 years¹. Although sex determination is an intensively-studied topic, variation in sex-determining systems remains a subject of much debate and uncertainty². In vertebrates, the sex of an individual is known to be influenced by a surprising variety of mechanisms³. These are generally classified into two major modes: genetic sex determination (GSD) and environmental sex determination (ESD). The idea that an offspring's sex can be affected by external conditions as well as by its genes has been around for a long time, perhaps more than a century¹. But, during that time the most decisive of the external conditions was thought to be nutrition, with temperature exerting a secondary effect. Although temperature-dependent sex determination (TSD) was first described in vertebrates by Madelaine Charnier⁴, based on her work on African lizards, her work was largely ignored for more than a decade. The widespread scepticism concerning vertebrate TSD lasted until the late 1970s, when studies on turtles provided strong confirmation. As this book shows, the field of TSD has come a long way since then. A vast amount of information related to this mechanism has been gathered from a variety of disciplines, and the present volume is dedicated exclusively to this fascinating subject.

This volume encompasses a series of reviews about the ecological, physiological, molecular and evolutionary aspects of TSD. The book is organized into four thematic sections, i.e. (i) prevalence of temperature-dependent sex determination in vertebrates, (ii) thermal effects, ecology, and interactions, (iii) evolutionary considerations and (iv) conclusions: missing links and future directions. All these sections correspond to basic questions about TSD; what species possess TSD? How does it work? When and why did it evolve, and how is it maintained by evolutionary forces? What do we still need to learn about it?

In chapter 1, James J. Bull provides a historical account of TSD based on his experience under the title 'Perspective on sex determination: past and future'. He is a pioneer in this field, and he provides a brief historical account of TSD starting from Bull's undergraduate days, Ohno's legacy on sex chromosomes and sex-linked genes, scepticism about TSD in earlier days and attempts to disprove it. For instance, he recalls how in 1976, he had assured Eric Charnov that the published reports of TSD in turtles were bogus – that the phenomenon was due to differential mortality or to lab artefacts. Only a year later, Bull and Charnov published their theory of the adaptive significance of environmental sex determination – a model that still remains among the most popular today. Although Bull's chapter offers important insights, it is deprived of several details of long history of sex determination in vertebrates. To me, a better representation of past literature regarding history of ESD (especially, presented in Mittwoch¹) could have improved this chapter. I recommend the paper by Mittwoch¹ as an insight into those broader ESD historical issues.

In chapter 2, David Conover provides a well-illustrated account of definitions and methodology for recognizing TSD, along with a summary of the incidence of TSD as well as thermal sex ratio distortions in fishes. The chapter 'temperature-dependent sex determination in fishes' provides detailed information regarding how to discriminate between ESD and anomalous GSD. These systems can be difficult to distinguish in practice, and this useful discussion is one of the highlights of this well-written chapter.

Chapter 3, 'Turtle sex-determining modes and TSD patterns, and some TSD pattern correlates' by the late Michael Ewert and collaborators, provides an exhaustive account of TSD in turtles with the addition of new data on previously unexamined species. This chapter is well compiled and provides excellent information regarding the diversity in TSD patterns, phenotypic vs genetic distance and TSD, estimating pivotal temperature, functional transitions, geographic trends, environmental correlates, etc. Ewert's recent death represents the loss of one of the most productive and influential figures in studies of turtle reproduction and especially, sex-determining systems.

In chapter 4, Denis Deeming presents an account of TSD in each of the cro-

codilian species under the title 'Prevalence of TSD in crocodylians'. All living crocodylians apparently exhibit TSD, and Deeming ably highlights the similarities and differences in TSD systems among these taxa. The chapter also includes details of thermally induced phenotypic effects other than sex, including thermally induced modifications of morphology, behaviour and physiology.

In chapter 5, Peter S. Harlow reviews the occurrence of TSD in lizards. Despite the fact that TSD was first described in lizards, studies on squamates have lagged behind those on turtles and crocodylians. Harlow provides extensive new data and greatly expands the number of TSD cases in lizards. His unpublished data on several Australian species are welcome, and change our view of the distribution and frequency of TSD in this group. Strikingly, there appear to have been multiple evolutionary shifts in sex-determining systems within the Australian dragons. Harlow speculates on potential evolutionary explanations for the presence of TSD, but the lack of detailed information on tropical TSD species inevitably makes it difficult to reach any firm conclusions. Researchers in tropical countries have an enormous research opportunity in this respect, because they can obtain the critical information to test evolutionary theories about the ecological correlates of sex-determining systems such as TSD.

Chapter 6 'Temperature-dependent sex determination in tuatara' by Nicola Nelson *et al.*, summarizes the extensive information available on the two extant tuatara species, based on not only laboratory data but also on data from natural nests. In chapter 7, Dominique Chardard *et al.*, under the title 'thermal sex reversal in amphibians' present a detailed review on sex determination in amphibians. Current research in amphibians suggests only a single major mode of sex determination (GSD) but with some species being susceptible for thermal sex reversal. The chapter identifies gaps (e.g. lack of information on the Gymnophiona) and future directions for research to understand amphibian sex determination in greater detail.

Chapter 8 'General effects of temperature on animal biology' by Marshall McCue is an attempt to introduce readers to general thermal biology, including definitions for commonly used terminology, thermal limits, thermal sensitivity, and chronic and acute thermal effects on animals. A well-compiled table for commonly

used terminology and a couple of schematic diagrams are highlights of this chapter.

In chapter 9, Arthur Georges *et al.* describe mathematical and other models for TSD under the title 'Thermal models of TSD under laboratory and field conditions'. This is the one of the important chapters of the book for field biologists. It contains information regarding the mode of action of temperature on development, and sex ratio under both laboratory and field conditions. Also, information for the prediction of embryonic development trajectories, thermo-sensitive periods and ultimately sexual outcome from nest temperature data are well presented. Details of the 'degree-hour approach' and 'constant temperature equivalent' (CTE) methods, which attempt to reconcile results from controlled laboratory experiments and variable temperature regimes by focusing on development rather than absolute time, are highlights of this chapter. However, the explicit mathematical models may distract or confuse some readers of this well-written chapter.

Chapter 10 'Phenotypic effects of incubation temperature in reptiles' by Turk Rhen and Jeffrey Lang provides a detailed review of the effect of incubation temperature on phenotypic traits other than sex in both TSD and GSD taxa, particularly in relation to fitness. This chapter addresses issues that are slightly deviated from the main theme of the book, but relevant to evolutionary interpretations for the adaptive significance of TSD. It provides a wealth of information for reptilian biologists.

In chapter 11 'The temperature-dependent sex determination drama: same cast, different stars' Allen Place and Valentine Lance review current knowledge about the molecular mechanisms associated with sex determination in vertebrates, starting with the best studied orders with GSD (i.e. mammals followed by birds) and then comparing this information with TSD reptiles. A detailed description of genes, their location on chromosomes, family, putative functions, etc. are well presented. However, this chapter (like many others) is already out-of-date following recent work by Ursula Mittwoch⁵ revealing some exceptional examples in mammals (for GSD) that prove the rule and link mammalian system with non-mammalian vertebrates.

Chapter 12 by Pamela Elf is again restricted to reptiles and explores the rela-

tionship between yolk steroid hormones and sex determination. Hypotheses about mode of action, published and unpublished observations of the dynamics of yolk hormones during development in TSD taxa are discussed. This field is likely to become a major research theme within the next few years, so a review is timely indeed.

Chapters 13–15 present a new phylogenetic analysis exploring the ancestry of sex-determining mechanisms in vertebrates (i.e. 'which was first, TSD or GSD?' by Fredric Janzen and James Krenz), and review hypotheses regarding TSD's past and present evolution (by Nicole Valenzuela), as well as interactions among TSD, offspring sex-ratio, population dynamics, and some conservation issues (by Mark Girondot *et al.*). In the last section, Nicole Valenzuela presents an overall view, conclusions, and attempts to identify missing links and future directions on TSD research. Her own focus on turtles and her opinions about the needs for careful definitions to distinguish between processes such as TSD vs thermally-induced sex reversal, come through very clearly. Time will tell whether this attempt to rigorously define different sex-determining systems is premature, given the strong conservatism in genetic mechanisms underlying both TSD and GSD⁵, and the apparently high frequency of evolutionary shifts between the two systems. I suspect that we may need to know more about the diversity of sex-determining systems before we can generate robust classification systems.

One of the best things about this book is that it brings together, for the first time, the diversity of information and issues related to TSD from various perspectives. The volume also has a few shortcomings. The title appears too broad; TSD is not known in one major class of vertebrates, i.e. mammals. Depending on definitions, one might also conclude that TSD does not occur in birds and amphibians either – so that we are left with the apparent restriction of TSD to one vertebrate class only – the reptiles. So why not call the book 'TSD in reptiles'?

The price US \$70 (Rs 3150) seems to me beyond the reach of many researchers and especially students. The book will be soon out-of-date simply because sex-determining systems are attracting such intense attention, and new results are appearing so rapidly. For example, we now have the first report of a thermal effect

on offspring sex ratios in a bird (a mound-building megapode)⁵.

Overall this volume will be useful for students, biology teachers, general biologists and anyone who is interested in sex determination mechanisms. Especially, it is a crucial reference source for budding researchers who want to undertake research in sex determination. I hope that all institutional libraries will have copies of this volume. Further, I hope the book stimulates young minds to undertake more detailed research using non-mammalian as well as mammalian systems to tackle the long-standing question 'what determines the sex of a newborn animal?'. Sex determination will be one of the most fascinating areas of biology in the 21st century, as evidence accumulates that epigenetic as well as genetic factors play a critical role in sex determination – even in mammals. Thus, there are many opportunities for rich rewards for young investigators who attack this exciting field of research.

-
1. Mittwoch, U., *Cytogenetics Cell Genet.*, 2000, **91**, 186–191.
 2. Hardy, I. C. W., *Appl. Anim. Behav. Sci.*, 1997, **51**, 217–241.
 3. Western, P. S. and Sinclair, A. H., *J. Exp. Zool.*, 2001, **290**, 624–631.
 4. Charnier, M., *C. R. Seances Soc. Biol. L'ouest Afr.*, 1966, **160**, 620–622.
 5. Goth, A. and Booth, D. T., *Biol. Lett.*, 2005, **1**, 31–33.
-

RAJKUMAR S. RADDER

*The School of Biological Sciences A08,
University Sydney,
NSW 2006, Australia
e-mail: rajju@mail.usyd.edu.au*

Sneaking a Look at God's Cards. Giancarlo Ghirardi. Princeton University Press, 41 William Street, Princeton, NJ 08540, USA. 488 pp. Price: \$ 22.95.

Ever since its conception in the beginning of the twentieth century, quantum theory has profoundly influenced not only science and technology, but also humankind's thinking and philosophy. Debates about fundamental issues in quantum mechanics such as nonlocality and the measurement paradox, that sprang up almost as soon as the theory was formulated, have