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Getting the temperature right for sex

Temperature-Dependent Sex Determination in Vertebrates

Edited by Nicole Valenzuela and Valentine A Lance Smithsonian Books, WW Norton & Company, New York, NY, USA; 2004. 194 pp. £37.00, hardback. ISBN 1588342034.

Heredity (2006) 96, 273-274. doi:10.1038/sj.hdy.6800799

Reviewed by SD Sarre

Sex, or rather how it is determined in vertebrates, has become a topic of mainstream interest; that's if the number of books generated in recent years is any indication. Since 2001, five substantial volumes dealing with topics ranging from the genes and mechanisms of sex determination (Scherer and Schmid, 2001) through to the influence of sex determination and other processes on population sex ratios (Hardy, 2002) have been published. This productivity compares markedly with the spasmodic offerings of the 18 years that followed Bull's (1983) seminal publication on the evolution of sex-determining mechanisms. Much of this recent productivity has undoubtedly been fuelled by the genomic revolution that is providing unparalleled opportunities for investigations into the molecular basis for sex determination. The decision by Valenzuela and Lance to focus this most recent book on temperature-dependent sex determination (TSD; where the sex of offspring is determined by the temperature of incubation) clearly sets this book apart from its contemporaries, which have tended to focus on genetic sex determination (GSD), particularly in mammals and birds.

Like most of its recent cohort of publications, the edited-collection style of *Temperature-Dependent Sex Determination in Vertebrates* makes for some unevenness in presentation. However, the editors have made a concerted effort to compile a logical and cohesive set of papers that divide nicely into three broad parts: (1) the prevalence of TSD in vertebrates; (2) thermal effects, ecology and interactions; and (3) evolutionary considerations. They have also gathered together many of the leading researchers in this field and even managed to extract an illuminating, and in his own words, 'biased' historical perspective on the field from James Bull (Chapter 1).

The last two decades have seen much work in many taxonomic groups, and this update gives a much clearer picture of how TSD is distributed among taxa and how robust is our knowledge of that distribution. It also makes clear that much basic work is still required to really get a handle on the distribution of TSD among taxa and that our understanding of TSD mechanisms is still very shallow. Part 1 provides an excellent update on the distribution and expression of TSD among species within the vertebrate groups with separate chapters on fish, amphibians, and the four reptile groups for which TSD has been recorded (turtles, crocodilians, lizards, and tuatara). It also serves to highlight the differences between the six groups, with a preponderance of GSD in fish and amphibians and considerably higher numbers of TSD species among the reptiles. Most authors stick fairly closely to the task of defining the limits of TSD in their taxa, and I found myself wishing for a bit more analysis on some of the broader methodological and evolutionary issues that were touched upon.

A common theme in many of the chapters was the absence of really good field data to test the ecological relevance of laboratory incubation experiments. Conover (Chapter 2) makes the point that the Atlantic silverside is the only species of fish for which TSD has been definitively demonstrated in the wild. While the situation is considerably better among reptiles (particularly crocodilians and some turtles), the exploration of the significance of TSD in nature is in its infancy. Georges and co-authors (Chapter 9) make headway here with their 'degree hour' approach to find equivalence between laboratory and field incubations and point at the necessity for incorporating nonlinear and aperiodic processes in future field studies. The subsequent chapters on the phenotypic effects of incubation temperature (Rhen and Lang; Chapter 10), the molecular biology of TSD (Place and Lance; Chapter 11), and the potential role of yolk steroid hormones (Elf; Chapter 12) provide solid reviews of the state of knowledge in these areas and serve not only to reinforce how little is really known about the mechanisms of TSD, but also to emphasize the huge complexity of transferring knowledge gained in the laboratory to the broader ecological and evolutionary context.

It is in considering evolution that we see how cautious we should be in drawing conclusions from current knowledge. While Janzen and Krenz (Chapter 13) boldly declare that, on the basis of parsimony analysis, 'GSD came first!', Valenzuela (Chapter 14) treads a more cautious line in her evaluation of the role of the many adaptive and neutral hypotheses that abound as explanations for the evolution of TSD. She makes headway by reframing some of the postulated mechanisms as testable predictions and suggests a greater emphasis on the falsification of neutral hypotheses rather than just the current focus on adaptive explanations. I watch with interest to see how TSD/GSD distributions unfold in the future, and for the light that they may shed on transitions from one mode to the other.

The focus of the book on TSD is both its strength and its weakness. As the first compendium to concentrate solely on TSD in vertebrates, this book holds important insights into TSD and should therefore be essential reading to all interested in sex determination. In particular, it brings together in the one place, an up-todate overview of the disparate taxonomic groups that exhibit TSD and provides an excellent platform for future investigations into the evolution of TSD. However, within the broader context of sex determination, the focus on TSD tends to obscure the potential interplay between temperature-dependent and genetic sex determination mechanisms (Kraak and Pen, 2002; Sarre et al, 2004), which must surely be among the most fruitful of areas in which to expand on our understanding of how interactions and transitions occur between these mechanisms. The awkwardness of this dichotomous perspective is most evident in the fascinating chapter on amphibians (Chardard et al, Chapter 7). Probably all amphibians





exhibit GSD characteristics, yet sex reversal through exposure to high or low temperatures is observed in several species in the lab and, based on laboratory experiments, temperature-induced sex reversal in the wild could occur in at least one species. When it is considered that <0.2% of amphibian species have been examined for their response to incubation temperature, it is not hard to believe that there are many surprises in store for sex determination among amphibians and indeed among all vertebrates.

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