

IS THERE A UNIFYING THEORY OF SEX ALLOCATION?

Suzanne H. Alonzo^{1,2}

¹*Department of Ecology and Evolutionary Biology, Yale University*

²*E-mail: Suzanne.Alonzo@Yale.edu*

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Within evolutionary biology, the field of sex allocation is often heralded as one of the great successes, where simple and elegant theory can explain and predict the patterns we observe in the natural world. Perhaps even more impressive is the accumulated evidence that organisms from parasitic flatworms to red deer exhibit subtle patterns of sex allocation, biasing their relative production of gametes or sons and daughters in response to a variety of environmental variables and individual conditions. For those of us who watch the field closely, however, we know that lurking beyond that true sense of achievement there is also a plaguing amount of overlooked biological complexity and unexplained empirical variation. As such, I recently found myself wondering aloud whether there was or ever could be a unifying theory of sex allocation? I do not mean to imply that we do not know a great deal about sex allocation in terms of both theoretical expectations and empirical patterns. Instead, what I would argue is that we have a lot of really wonderful, but slightly myopic, understanding of observed patterns and that research often sets out to examine overlapping hypotheses without a clear sense of how (or whether) we can truly distinguish between them, independent of any specific set of results. This means that we end up being both a little bit right and a little bit wrong most of the time. To be fair, this problem is not limited to our understanding of sex allocation. The question is whether this is the inevitable outcome of biological complexity or whether one might actually hope for

a general theory of sex allocation or at least some testable and mutually exclusive hypotheses that apply as well to plants as they do to mammals. I may be an optimist, but I was personally hoping for the latter as I sat down to read Stuart West's recent book titled "Sex Allocation" (2009). I also could not help but compare it with Charnov's (1982) book on "The Theory of Sex Allocation." In my defense, in case you are thinking these were unrealistically high expectations for any one book, it is precisely the need to update Charnov (1982) and a desire to unify this large but fractured field that Stuart West gives as his reasons for "Why this book is needed" (p. 8, West 2009).

Putting aside those lofty goals for the moment, there is a lot to like about this book. First, I found it surprisingly easy and interesting to read. It is serious and rigorous, yet interspersed with just enough humor and personal notes to be enjoyable without being cute. My personal favorites were the suggested reading plans for (among others) "those already familiar with sex allocation and aged >30" (Table 1.1, which for the record I ignored) and the assertion that "only a loony would use a multilocus model to solve a sex allocation problem that could be addressed with ESS theory" (page 360–361, which you may admittedly have to be a game theorist to appreciate). Each chapter includes a rigorous presentation of key theoretical and empirical results, and the book represents an impressive synthesis of what is a large and complex field. For those new to the subject, they will likely find certain explanations incomplete and will need to go to the primary literature for enlightenment. This task should, however, be relatively easy as the text is well-referenced throughout (though those

individuals not new to the field could certainly quibble over what is or is not included). In sum, this book will provide an invaluable entry point for graduate students and early researchers. Numerous potential thesis topics are contained within the “Conclusions and Future Directions” sections at the end of each chapter and the final section of the book on “Outstanding Problems.” New graduate students interested in sex allocation could do much worse than to read these sections carefully for inspiration. Returning to the comparison with Charnov (1982), although the earlier chapters might appear superficially to serve as an update, the final chapters are synthetic and move well beyond what Charnov already covered, and the amount of new research and individual insights makes this text much more than a simple update of that earlier and now classic text (though in my opinion students should be sternly told to read both). An interesting side note is that both Charnov and West set out to write their books with coauthors, before being left with the large task of writing a synthetic and comprehensive review of sex allocation on their own.

The text also provides a comprehensive history of sex allocation research. I especially appreciated the first chapter’s pre- and post-Charnov history of the field and the explanation of the role that Darwin’s writings on sex-ratio evolution and the mathematical theory of Düsing likely played in shaping Fisher’s now famous verbal arguments regarding the evolution of equal primary sex ratios. Those that falsely think these ideas originated with Fisher should read Edwards (1998) and (p. 14–15, West 2009). Although the presentation of the various arguments for a biased primary sex ratio are presented in a relatively traditional manner, I found the social evolution and kin selection insights the author brought to these otherwise traditional theories added new insights and greater generality. For example, Chapter 3 is, on the surface, simply a review of local resource competition, but I found the presentation of classic sex-allocation theory in terms of the balance between competition and cooperation among relatives extremely intuitive, general, and powerful. This was one of my favorite chapters of the book. In addition, you cannot read the theory and empirical results summarized here without being impressed by the depth of theory and data that can be brought to bear on the relatively simple question of how organisms allocate between male and female function. What sex-allocation research has discovered about organisms is truly amazing.

Another key strength of this book is the almost relentless connection between theory and data. Not only are the general predictions of key theories presented but the book also deals with the complexities of developing and testing theory and they need to interpret support for these theories cautiously. In fact, I would recommend this book to anyone who thinks deeply about how we test theory in evolutionary biology because the specific treatment of this more general theme is a key strength of this book. I was

also happy to see that the book included some explanation of where some of the key predictions come from, even if claiming to leave the full treatment of theory to others. However, I would also argue (as I expect would the author) that it cannot and should not replace Charnov (1982) or Frank (1998), where the conceptual background behind the mathematical theory is more complete. This book also will not replace Hardy (2002) regarding important methodological issues that arise when studying sex ratios. At times, I found the discussion of the caveats and complexities of testing sex-allocation theory daunting. This was not necessarily because of any fault of the book, but because the point is made throughout that important caveats exist regarding even the most powerful theoretical predictions and their best supporting evidence. Yet without hopelessly complex theory (and even less feasible tests of theory), it is not clear these limitations are solvable. In the end, the book gives some clear directions forward and identifies specific gaps that need filling. It is not a unifying theory of sex allocation, but it is a step in the right direction. However, it is not clear from the book how we would move forward to do a better job of developing and testing general theory. It is argued that this is needed, but it is not clear how it can or should be done. I think this is a key question for our field: How do we develop general and useful conceptual frameworks that help us understand and predict empirical patterns but that are not hopelessly complex or impossible to test?

My major complaint would be that I found the presentation of sex-allocation bias in the production of sons versus daughters more satisfying than the treatment of sex allocation in hermaphrodites or the presentation of research on plants and other organisms with systems other than two separate sexes. The relative separation between the discussion of sex allocation between sons and daughters in separate-sexed species and the allocation between male and female function in hermaphroditic species also clearly demonstrates the above-mentioned absence of a unifying framework. I was also surprised that I found no description of the Shaw–Mohler equation (Shaw and Mohler 1953), which is often presented as a general and unifying theory of sex allocation (e.g., Charnov 1982). I would have been curious to at least know why this equation was not included amongst the many others. On another picky note, as someone with a long interest in state-dependence and a weakness for fish, I would have presented Ghiselin’s size-advantage model as a precursor to the later, albeit more general, Trivers–Willard arguments about how individual or environmental state affect sex-allocation patterns. I believe it is fair to say this book is more about the relative allocation to sons versus daughters than other forms of sex allocation. Although the synthesis within topics and sections was impressive, synthesis across chapters was less prevalent. To be fair, I fully accept that it may be too much to expect one book and author to do what a field of researchers has not.

On a more general note, a strong case is made for the relevance of sex-allocation research to evolutionary biology throughout the book. Though not always discussed explicitly, it becomes clear when reading the entire book that an understanding of sex allocation is relevant to sexual conflict, social evolution, and a wide variety of other areas of research. For me this was the most satisfying but subtle message of the book. Sex allocation research may seem to be asking a relatively simple question. However, what we understand (and do not understand) about sex allocation hinges on and has the potential to influence our knowledge of a variety of other topics within evolutionary biology, from how resources and relatedness interact to shape social systems to how the mechanistic details of what it means to be male or female (or both) may influence evolutionary conflict or cooperation. The final chapter is also worth reading if you need a boost of enthusiasm about being an evolutionary biologist because it both shows how exciting the past work has been and yet how much more exciting work there is to be done. I would further argue that many of the points made in the final section on “Outstanding Problems” are relevant to anyone interested in trait evolution. For example, improving our ability to understand reproductive patterns may require thinking about how multiple selective forces interact and how underlying mechanisms affect the evolution and expression of traits, whether the patterns under study are sex allocation, seminal fluids, or parental effort.

Reading this book also raises key and basic questions about the way we do science and what is and what is not possible, which are worth thinking about no matter what your field. In the end, I would have liked him to take a stronger stand on where the field should be going and what the big questions and directions should be. Stuart West has not been shy about what he thinks about the levels of selection debate and what the field of social evolution does and does not need (West et al. 2007a,b), and I was hoping for a little more of that kind of argument in this book. The strongest

opinions come through in the sections relevant to social evolution, and I would have like to see more of this elsewhere (though some would certainly disagree with me on this). If nothing else, this might more strongly motivate discussion that could move the field toward more generality and synthesis. In the end, my hope for a unifying and elegant conceptual framework for understanding the evolution and expression of sex allocation was not realized. However, the author’s obvious enthusiasm for the subject should inspire another generation of sex-allocation researchers which may bring us closer to that goal or at least generate discussion about whether such a thing is even possible or useful. In my opinion, this book is worth taking the time to read and think about whether you are new to the field of sex allocation, think you know it all already, or are mainly interested in the evolution of other social and reproductive traits. It might influence the way you think about your own research and if nothing else you will learn some cool facts about the impressive subtleties of sex allocation in the natural world.

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