Preface

While the majority of flowering plant species are hermaphroditic, gender dimorphism, or the occurrence of two sexual morphs, has, nevertheless, evolved on repeated occasions. Gender dimorphism is found in nearly half of all angiosperm families and in approximately 10% of flowering plant species. Where plants are dimorphic in gender, they can also be dimorphic in secondary sex characters. We refer to dimorphism of the latter kind as sexual dimorphism, in keeping with the term's usage by most zoologists. This book is about the evolution of both forms of dimorphism – hence the book's lengthy title.

Gender dimorphism in plants has been an active topic of research from theoretical and empirical perspectives, and has been the focus of several recent reviews and book chapters. By contrast, sexual dimorphism in plants is much less widely appreciated. Indeed, the last comprehensive review of the subject dates back to Lloyd and Webb's 1977 paper on "Secondary Sex Characters in Plants." In addition, when we first spoke of editing a book on sexual dimorphism in plants, some people doubted that there was enough material to justify the effort. We hope that this book not only provides an update to Lloyd and Webb's seminal work but also dispels doubts about the widespread nature of sexual dimorphism in plants. We decided to combine reviews of both gender and sexual dimorphism in a single book, because each form of dimorphism can provide the evolutionary impetus for the other. Thus, once gender dimorphism evolves, the sexual types may be selected to diverge in secondary sex traits. Likewise, selection for ecological or reproductive specialization may promote the evolution of separate sexes.

The book has three sections: the first on Gender Dimorphism deals with the prevalence and evolution of dimorphic sexual systems; the second on Sexual Dimorphism addresses the evolution of dimorphism in secondary sex characters; and the third on Genetics of Dimorphism covers the genetic basis of dimorphism in gender and in secondary sex characters. Authors of each chapter summarize the present state of knowledge in the relevant subject areas and suggest directions for future research. In Chapter 1, Ann Sakai and Steve Weller review the phylogenetic and biogeographic patterns in the occurrence of dioecy (a breeding system in which there are two sexes – pure females and pure males), and examine the ecological correlates of this breeding system. They also provide an extremely valuable review of the terminology on plant breeding systems. If you have ever been confused about the plethora of terms that describe how male and female gametes are com-

bined or separated in and among flowers, you will want to read this chapter. Sakai and Weller make it clear that the "troublesome" terminology is not a product of mischievous or sadistic tendencies by botanists. Rather, the terminology reflects the tremendous variety of breeding systems in plants *and* the variety of research perspectives on these systems. Read this chapter and you will be able to speak in terms such as cosex and gynodioecy like an expert. To make matters easier for the reader, all of the book's contributing authors use the terms as they are defined in Chapter 1.

In Chapter 2, Deborah Charlesworth explains theoretical work on the evolution of gender dimorphism from monomorphism. Gender dimorphism is generally modelled as the invasion and spread of unisexual mutants in a hermaphroditic (or monoecious) population. In the case of dioecy, a two step process is envisioned: the invasion of a hermaphroditic population by one unisexual mutant, followed by the conversion of hermaphrodites to the other unisex. The focus of the models is on the factors that allow for the invasion and spread of unisexual mutants. Charlesworth examines the role of three such factors – the genetics of gender, inbreeding, and resource reallocation – in the evolution of gender dimorphism, and explains how these factors affect the likelihood of alternative pathways to dioecy (e.g., gynodioecy vs. androdioecy).

Charlesworth's chapter is followed by Colin Webb's review of empirical evidence of the evolution of gender dimorphism. In an especially comprehensive treatment, Webb documents five evolutionary pathways to gender dimorphism from monomorphism. He deals extensively with gynodioecious species, because the hermaphrodite-gyndioecy-dioecy pathway appears to be particularly common and is the best documented. Other pathways are less well understood, in part because they may be more transitional. Webb's evaluation of theory's predictions dovetails nicely with a discussion of ecological perspectives on dioecy from the empirical literature.

The middle section of the book consists of five chapters that are devoted to sexual dimorphism. In the first of these (Chap. 4), Monica Geber reviews theoretical models on the evolution of sexual dimorphism via natural and sexual selection. She considers models in which sexual dimorphism arises secondarily to gender dimorphism as well as models in which selection for ecological and reproductive specialization promote the evolution of separate genders. Because the evolutionary dynamics of sexual dimorphism depend on the relationship between phenotype and fitness, Geber explores three biological circumstances with different fitness relationships: in the first, direct selection within each sex favors different phenotypes between the sexes; in the second, intra- and intersexual competition for limiting resources drives divergence through a form of intersexual character displacement; and in the third, intersexual selection or mate choice promotes sexual dimorphism. All three forms of selection have been proposed as causes of sexual dimorphism. In Chapter 5, Vince Eckhart examines the myriad of floral and inflorescence characters that differ among hermaphroditic, female and male

plants, including perianth and inflorescence size, nectar production, flower longevity, and primary sex characters. He first summarizes the patterns of dimorphism in reproductive characters, and then discusses their possible adaptive andnon-adaptive causes. The principal adaptive cause is thought to be sex differences in the importance of mate limitation vs. resource limitation to reproductive success (Bateman's principle). For flower and inflorescence size – traits for which the data are most complete – the direction and degree of dimorphism vary with pollination mode and biogeographic origin. Eckhart urges that, for these characters at least, we move beyond the stage of describing dimorphism and into the arena of explaining quantitative variation in dimorphism. This will require careful evaluation of the costs and benefits of floral traits.

In the last three chapters of this section, coverage is given to plant traits that many people may not think of as being dimorphic. For example, in Chapter 6, Lynda Delph examines dimorphism in life history traits (e.g., age and size at first reproduction, frequency of reproduction, growth rate, and longevity) in > 40 dioecious species. Her chapter is the first comprehensive review of the subject since Lloyd and Webb's 1977 paper. In Chapter 7, Todd Dawson and Monica Geber present the first review of dimorphism in physiology and vegetative morphology. In Chapter 8, Jon Ågren and colleagues consider evidence and hypotheses on dimorphism in biotic interactions. The premise of all three chapters is that sexual differences in the resource costs of reproduction (with females typically having higher costs) can have consequences for, and indeed can select for, dimorphism in other ecologically important traits. The data are most compelling for life history traits. Delph finds strong evidence both in support of sex differential resource costs and for dimorphism in the demographic costs of reproduction. She points out, however, that there can be mitigating factors that ameliorate the life history costs of high reproductive investments in females. In their chapter on physiology and morphology, Dawson and Geber outline expected differences in resource acquisition between the sexes of dioecious plants (females have higher resource intake than males), and then examine the data in light of these expectations. They find that some species conform to predictions, while others do not. Furthermore, clear patterns of dimorphism in physiology and morphology have yet to emerge, perhaps because evolutionary studies in this area are of relatively recent vintage and are few in number. At the same time, studies of dimorphism in physiology have yielded important insights on the causes of spatial variation in the sex ratio in dioecious species. Ågren and colleagues examine the hypothesis that sex differences in the timing and amount of resource expenditure on reproduction lead to dimorphism in competitive ability and in plants' susceptibility to herbivores and pathogens. They encounter some difficulty in testing the predictions because of the uneven nature of the data. In particular, there is virtually no information on competitive ability in dioecious plants. Dimorphism in herbivore damage has been documented repeatedly, however, but the link between susceptibil-

ity and defense levels is more elusive. Susceptibility to pathogens appears to depend as much on the mode of pathogen transmission as on sex. Ågren and coworkers also examine the consequences of dimorphism in biotic interactions for plant demography and evolution.

In Chapter 9, the first of the book's final section, Sarah Grant discusses the diversity of genetic mechanisms by which hermaphroditic flowers are converted into unisexual flowers. This diversity reflects the fact that unisexuality has evolved independently on multiple occasions. Grant also reviews work on sex chromosomes in plants, and it may surprise some readers to learn that the male (or Y) chromosome is larger than the autosomes in some plant species. Throughout the chapter, Grant makes interesting and valuable comparisons between mechanisms of sex determination in plants and animals. We hope that Grant's chapter serves to bring the molecular biology of gender to the attention of evolutionary biologists, and conversely that molecular biologists will be drawn to the book because of its coverage of evolutionary aspects of gender. In the final chapter of the book, Tom Meagher focuses on the genetics of secondary sex characters. He presents a quantitative genetic analysis of variation in flower size and number in the dioecious white campion, *Silene latifolia*, which he then uses to perform a retrospective analysis of selection on the traits. The goal of a retrospective analysis of selection is to determine the strength and form of past selection that would have been required to produced current-day levels of dimorphism While speculative in nature, this sort of retrospective analysis can lead to testable hypotheses on patterns of selection, past and present.

This book is intended for anyone interested in the evolution of dimorphism, whether in plants or in animals. As evolutionary biologists, we consider flowering plants to be excellent subjects for studies of gender and sexual dimorphism. Because both forms of dimorphism have arisen multiple times at the species or generic level, there is ample fodder for comparative studies on the factors that contribute to their evolution. In addition, variation often exists among and within populations in the degree of gender specialization and in levels of sexual dimorphism. This variation is the spice of life for evolutionary studies and should be the focus of future work. We hope that the book fosters further research by providing readers with the theoretical, experimental, and analytical tools to study the evolutionary pathways to dimorphism. We concur with many of the book's authors in advocating the integration of genetic, physiological, ecological, and comparative approaches in order to better understand how and when dimorphism evolves.

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