

COPYRIGHT NOTICE:

Stuart West: Sex Allocation

is published by Princeton University Press and copyrighted, © 2009, by Princeton University Press. All rights reserved. No part of this book may be reproduced in any form by any electronic or mechanical means (including photocopying, recording, or information storage and retrieval) without permission in writing from the publisher, except for reading and browsing via the World Wide Web. Users are not permitted to mount this file on any network servers.

Follow links for Class Use and other Permissions. For more information send email to: permissions@press.princeton.edu

CHAPTER 1

Sex Allocation

I would regard the problem of sex ratio as solved (see pp. 146–156).

—Williams 1966, p. 272

In this chapter, I describe my reasons for writing this book. In order to provide some context, I start by presenting the problems of sex allocation and a short, potted history of the field. I then provide a discussion of why I hope this book will prove useful, a description of the book contents, and tips on how to read it.

1.1 WHAT IS SEX ALLOCATION?

Sex allocation is the allocation of resources to male versus female reproduction in sexual species (Charnov 1979c, 1982). Sex allocation depends on the breeding system of a species, as well as on how reproduction is carried out within each breeding system. Breeding systems can be categorized as *dioecious*, in which individuals are either male or female for their entire lifetime (e.g., birds and mammals), or *hermaphroditic*, in which the same individual can produce both male and female gametes. Hermaphrodites can be either *sequential* or *simultaneous*. Sequential hermaphrodites, or sex changers, function as one sex early in their life and then switch to the other (e.g., some reef fish such as angelfish and some invertebrates such as Pandalid shrimps). Simultaneous hermaphrodites are capable of both female and male reproduction at the same time (e.g., most flowering plants).

Given the preceding scheme, the six fundamental problems of sex allocation are as follows (Charnov 1979c, 1982):

- Under what conditions are sequential hermaphroditism, simultaneous hermaphroditism, or dioecy evolutionarily stable (ES)? When is a mixture of sexual types stable, such as in gynodioecious plant populations, which contain both simultaneous hermaphrodites and females?

- For a dioecious species, should the sex of the offspring be determined by the mother, the environment (*environmental sex determination*), or randomly (*chromosomal sex determination*)?
- Given dioecy, what is the ES offspring sex ratio to produce, defined as the proportion of males in a brood?
- For a sequential hermaphrodite, what is the ES sex order (male or female first) and time of sex change?
- For a simultaneous hermaphrodite, what is the equilibrium allocation of resources to male and female reproduction?
- For all breeding systems, when does selection favor the ability of an individual to alter its allocation to male versus female function in response to particular environmental conditions?

1.2 A POTTED HISTORY

In this section, I give a brief and oversimplified history of the development of the field of sex allocation. I divide the history into pre- and post-Charnov's (1982) monograph, as most historical accounts usually cover only up to 1982.

1.2.1 PRE-CHARNOV

Darwin (1871, 1874) realized that the preponderance of unbiased sex ratios posed a problem for his theory of natural selection. He made a start at developing possible explanations but was unsatisfied and left the problem for future generations (see section 2.3). This problem was solved decisively by Fisher (1930), who showed that selection for an unbiased sex ratio follows from the fact that each offspring has a mother and father, and so males and females make equal genetic contributions to the next generation (section 2.2). Importantly, Fisher clarified the frequency-dependent nature of selection on sex allocation that is at the center of all subsequent developments.

Modern research on sex allocation began with Hamilton (1967), who made five pivotal contributions to the field of sex allocation and to evolutionary biology more generally. First, Hamilton showed how competition between relatives can select for biased sex allocation. When populations are structured such that brothers compete for mates, this leads to selection for a female biased sex allocation by a process that Hamilton termed *local mate competition* (LMC). This insight has led to one of the most productive areas of evolutionary biology (chapters 3 to 5). Second, Hamilton showed how the sex ratio can be modeled

using game theory. His approach for determining the “unbeatable strategy” was very similar to and laid the foundation for the technically superior *evolutionary stable strategy* (ESS) approach that was later formalized by Maynard Smith and Price (1973). Third, he showed that simple mathematical models could be used to make comparative predictions that could be easily tested (section 11.3.4.2). His specific example was to show that selection favors more female biased sex ratios when less females lay eggs on a patch and that this could be tested either by comparing across species or by looking at how individuals vary their behavior under different conditions (chapter 4). The use of comparative predictions is taken for granted today because these predictions form the daily bread of evolutionary and behavioral ecology research programs. However, it should be remembered just how astounding this was at the time, to suggest that a few lines of simple maths could make testable predictions about how organisms should behave (Frank 2002). Fourth, he showed how different genes within a genome can be selected to pursue their own selfish interests, to the detriment of other members of the genome, and the way in which meiotic drive fitted into this framework. Fifth, by emphasizing the costliness of male production and the evolution of parthenogenesis, he helped to initiate the debate over the adaptive function of sex (Hamilton 1996).

The next major step was made by Trivers and Willard (1973), who showed that individuals could be selected to adjust the sex of their offspring in response to environmental conditions. They discussed their prediction in the context of mammals such as caribou, and why offspring sex ratios might be adjusted in response to maternal condition. Charnov and colleagues built upon this work by showing how the same principle could be applied more widely to a huge range of issues in both dioecious and hermaphroditic species (chapters 6 and 7)—for example, whether host size should influence offspring sex ratios in parasitoid wasps, the age and direction of sex change in sequential hermaphrodites, and when different breeding systems such as simultaneous hermaphroditism or *environmental sex determination* (ESD) should be favored (Warner et al. 1975; Charnov et al. 1976; Leigh et al. 1976; Charnov and Bull 1977; Charnov et al. 1978; Charnov 1979c; Charnov et al. 1981; Charnov 1982). Importantly, these predictions clearly lend themselves to empirical testing, which has helped make the Trivers and Willard hypothesis and its various extensions one of the two most productive areas of sex allocation, alongside LMC theory.

Another major strand of sex allocation research was initiated when Trivers and Hare (1976) examined conflict over sex allocation in the social hymenoptera (ants, bees, and wasps). This paper made two key contributions. First, it combined Fisher’s (1930) theory of equal investment with Hamilton’s (1964) inclusive fitness theory to show how the ES sex allocation differed from the

point of view of the queens and their workers. Research on sex allocation conflict within the social hymenoptera has since become the third most productive area in the field of sex allocation (chapter 9). Second, they showed how parent–offspring conflict and inclusive fitness (kin selection) theory could generate predictions that could be tested with empirical data. This was at a time when these topics were still contentious, and to this day, sex allocation still provides some of the clearest support for inclusive fitness theory (sections 9.7.1 and 11.3.1).

Charnov's (1982) monograph, *The Theory of Sex Allocation*, brought all this together, providing a masterly synthesis of theoretical and empirical work. He unified the different areas of sex allocation research into a single field. From a theoretical perspective, Charnov showed how the same underlying concepts and similar mathematical models could be applied to all of the problems of sex allocation. From an empirical perspective, Charnov's monograph showed the power of *selection thinking* and simple models to make predictions that could be tested with empirical data, and it led to a surge of interest in sex allocation that continues to this day (Frank 2002; Hardy 2002). The increase in interest in this area is demonstrated by the increasing number of citations per year—comparing 2007 with 1982, the number of citations produced by a Web of Knowledge search on the phrase “sex allocation” has increased 50-fold, and the number of citations produced by a search on the phrases “sex allocation” or “sex ratio” has doubled (subject areas: zoology, genetics and heredity, evolutionary biology, behavioral sciences, plant biology). Charnov's monograph also contained a wealth of leads to potentially useful biological systems that remain underexploited to this day.

1.2.2 POST-CHARNOV

In the 1980s, our theoretical understanding of LMC leaped forward. At a very general level, the reasons for the female biased sex ratio were clarified, disentangling the separate effects of competition between males, the availability of mates for those males, and inbreeding (section 4.2; Taylor 1981a; Frank 1985b; Herre 1985; Frank 1986a). In addition to settling a long-running controversy, this work solved the debate over the level at which selection operates (Frank 1986a), which sadly still persists in other areas (section 11.3.1.2). At a more specific level, a number of workers began extending LMC theory to fit the biology of specific systems (Werren 1980a; Green et al. 1982; Werren 1984a; Frank 1985b; Herre 1985; Yamaguchi 1985). This generated a slew of new predictions, which allowed for some of the most elegant tests of LMC

theory in a wide range of organisms, and such work is still extremely active today (chapter 5).

Following Charnov's monograph, there was a profusion of empirical studies testing the various forms of Trivers and Willard's (1973) hypothesis. The most famous of these was the work of Clutton-Brock and colleagues on red deer, which provided support for both the assumptions and the predictions of Trivers and Willard's hypothesis in response to maternal quality (Clutton-Brock et al. 1984, 1986). This work has inspired many researchers over the years, and an extensive literature on sex allocation in ungulates has accumulated (section 6.4; Sheldon and West 2004). Equally impressive were two long-term studies on species with ESD, one by Conover and colleagues on a fish (section 6.7.2; Conover and Kynard 1981; Conover 1984; Conover and Heins 1987a) and one by Adams and colleagues on a shrimp (section 6.7.1; Naylor et al. 1988a; Naylor et al. 1988b; Watt and Adams 1994; McCabe and Dunn 1997; Dunn et al. 2005). These studies showed the pattern of ESD, the fitness consequences, and why the pattern of ESD should vary across populations.

Our understanding of selfish sex ratio distorters was revolutionized in the 1980s and 1990s (chapter 10). Relatively little was known about distorters at the time of Charnov's (1982) monograph; they were assumed to be rare aberrations. Appreciation of their importance started to emerge, however, with Werren and Skinner's discovery that three different sex ratio distorters occurred in the parasitoid wasp *Nasonia vitripennis* (Werren et al. 1981; Skinner 1982, 1985). This discovery was shocking because *Nasonia* had been intensively studied as a model species for understanding LMC and had provided some of the best evidence that individuals adjust offspring sex ratios in response to environmental conditions (Werren 1980a, 1983). The next major jump into the sex allocation limelight for sex ratio distorters was the discovery that endosymbiotic bacteria such as *Wolbachia* and *Cardinium* were responsible for many cases of sex ratio distortion and that these endosymbionts were extremely widespread (chapter 9; Rousset et al. 1992; Stouthamer et al. 1993; Werren et al. 1995; Weeks et al. 2003). There is now an extensive literature on sex ratio distorters, with recent work by G. Hurst and colleagues demonstrating how we can even follow their spread and suppression in natural populations (section 10.3.3).

The other major development of the 1980s was an understanding of the population-level consequences of individual-level sex ratio adjustment (section 7.2). Frank (see Frank 1987b; Frank and Swingland 1988; Frank 1990) showed that Trivers and Willard-type sex ratio adjustment can lead to a bias in the population sex ratio or the overall population investment ratio. He also showed that the direction and magnitude of this bias could be hard to predict, depending on biological details that could be hard or impossible to assess.

A consequence of this, which is still rarely appreciated, is that population-level patterns will often be useless for testing whether sex allocation is being adjusted facultatively in response to local conditions. Frank, Charnov, and Bull also showed that an important exception to this is in sex changing organisms, where we can make and test predictions about the population sex ratio (section 7.2.3; Frank and Swingland 1988; Charnov 1989; Charnov and Bull 1989a, 1989b; Charnov 1993; Allsop and West 2004b).

Research on sex allocation conflict between individuals really took off in the 1990s (section 9.6). Trivers and Hare's (1976) paper had attracted much interest, but there are limitations on the testability of their predictions using population-level data. Boomsma and Grafen (see Boomsma and Grafen 1990; Boomsma 1991; Boomsma and Grafen 1991) solved this by showing that a range of more specific predictions could be made for how sex allocation should vary between colonies, within a population. In particular, they predicted that if workers were in control of sex ratio in a colony, we should observe split sex ratios, with some colonies producing predominantly male reproductives and others predominantly female (section 9.6.2). Stunning support for their predictions rapidly followed from both observational and experimental studies (section 9.6.3; Mueller 1991; Sundstrom 1994; Evans 1995). Since then, an impressive level of understanding has been obtained in this area by looking at the underlying mechanisms, finer levels of within-colony adjustment, mistakes, and situations where the workers do not win (sections 9.6.4–6; Sundstrom et al. 1996; Sundstrom and Boomsma 2000; Passera et al. 2001; Boomsma et al. 2003). A new area of research on conflict was also opened up by the work of Strand and colleagues showing the potential for sex allocation conflict in polyembryonic wasps and how this might lead to the evolution of a sterile worker caste (section 9.5; Grbic et al. 1992; Giron et al. 2004; Gardner et al. 2007a).

The 1990s saw the conventional wisdom on sex ratio adjustment in vertebrates overturned. It had long been assumed that chromosomal (genetic) sex determination (CSD) in vertebrates such as birds and mammals would prevent adaptive control of offspring sex ratios (Williams 1979). This conception was clearly blown out of the water by a number of studies, primarily on birds. Komdeur and colleagues showed that Seychelles warblers were capable of adjusting the proportion of males in a clutch from between 10% and 90%, depending on environmental conditions (section 3.3.1.1; Komdeur 1996; Komdeur et al. 1997; Komdeur 1998; Komdeur and Pen 2002). Sex allocation is adjusted in the Seychelles warbler in response to cooperation and competition with offspring. Another area of sex ratio adjustment in birds was opened up by Sheldon and colleagues, who showed that females in species such as collared flycatchers and blue tits can adjust the sex of their offspring in response to mate quality,

with females producing a higher proportion of sons when they mated with more attractive males (section 6.6; Ellegren et al. 1996; Sheldon et al. 1999). This work was built upon previous findings by Burley (1981) that were so revolutionary in their time that they had been effectively ignored for 15 years. The patterns of sex ratio adjustment in response to helping and male attractiveness have since been shown to be repeatable within and across species, proving clear evidence for control of offspring sex ratios in species with CSD (section 6.6; West and Sheldon 2002).

The final major development of the 1990s was Frank's (1998b) reunification of sex allocation theory, in his monograph *Foundations of Social Evolution*. Our understanding of sex allocation theory increased enormously during the 1980s and 1990s, thanks largely to the work of Taylor and Frank (see Taylor 1981a; Frank 1986a, 1986b, 1987b; Taylor 1988, 1990b, 1996a; Taylor and Frank 1996; Frank 1997b, 1998b). They clarified the underlying reasons for adjustment of sex allocation, linked different areas of research, and developed new methods for constructing theory that were both simpler to apply and more general. Frank brought all this together in his 1998 monograph, which provided a guide on how to model sex allocation as well as a unification of existing work. Taylor and Frank's work was part of a more general program on how to model inclusive fitness and social evolution, in which sex allocation theory has played a pivotal role (section 11.3.1).

The major development this millennium has been the attempt to explain broad taxonomic variation in the extent of sex ratio adjustment. This has united work in different conceptual areas on different taxa. One consequence has been to determine when vertebrates, with supposedly constraining CSD, really do show consistent patterns of sex ratio adjustment in the predicted direction. For example, birds adjust their offspring sex ratios in response to mate quality and the number of helpers on their patch (West and Sheldon 2002; West et al. 2005), but primates show no consistent pattern with maternal quality (Brown and Silk 2002). The other consequence of this work has been to show how variation in the extent of sex ratio adjustment across species can be explained by variation in the strength of selection. For example, birds show greater shifts of sex ratio in response to the number of helpers on their patch when helpers provide greater benefits (section 3.3.1.1; Griffin et al. 2005), and wasps show greater shifts of sex ratio in response to host size when host size better correlates with the resources that will be available for their offspring (section 6.3.1; West and Sheldon 2002). This work has emphasized not only that cases in which vertebrates show little or no sex ratio adjustment may simply reflect a lack of selection rather than the constraints of CSD, but also how sex allocation can be used to address very general issues on how adaptation may be limited (section 11.3.3).

1.3 WHY IS THIS BOOK NEEDED?

The first reason for this book is to unify the field, bringing together the empirical and theoretical work that has accumulated since Charnov's (1982) monograph almost 30 years ago. The explosion of sex allocation research, stimulated by Charnov's book, has become fragmented and taxonomically focused. Workers in one area often do not know the relevant theory or realize the conceptual links with other areas. This leads to reinvention of the wheel, broad links being missed, and mistakes being made. In addition, the empirical and theoretical literature have become disjointed, leading to empirical work and conclusions that can be misleading. To give specific examples, studies on LMC make mistakes when they do not take account of the various ways in which LMC theory has been extended (chapter 5), and studies on the Trivers and Willard (1973) hypothesis frequently make mistakes about the direction of sex ratio adjustment (sections 3.4.1.2 and 6.4.2) and the population-level consequences (section 7.2).

The second reason for this book is to emphasize the excellent opportunities that sex allocation offers for examining more general questions in biology. It is generally accepted that sex allocation theory is one of the great success stories of evolutionary biology (section 11.2). Given this, sex allocation theory can be exploited to address very general issues of widespread importance (section 11.3). In the past, this has led to sex allocation playing a pivotal role in areas such as social evolution, parent-offspring conflict, and genomic conflict (sections 9.7.1, 10.2 and 11.3.1), as well as fundamental issues such as how we should develop and test evolutionary models (sections 11.3.2 and 11.3.4). There is considerable potential for future work to address similarly big issues, such as the relative importance of different possible constraints on evolution (11.3.3). However, the broader insights made with sex allocation research are often missed, even within the field of sex allocation, let alone more generally.

1.4 WHAT IS IN THIS BOOK

In chapters 2 through 10 of this book, I unify the theoretical and empirical sex allocation literature. My aim is to provide a theoretical overview and to critically assess how well the empirical literature matches the predictions of theory. I emphasize when sex allocation theory has been successful, as well as when it has not, and hopefully dispel several common misconceptions.

In chapter 2, I consider Fisher's theory for equal investment in the sexes. I describe the basic theory, its historical development, how it forms the founda-

tion for all subsequent areas of sex allocation research, and the various ways in which it can be tested.

In chapters 3 to 5, I examine the consequences of competitive or cooperative interactions between relatives. In chapter 3, I show how competitive (*local resource competition*, or LRC) and cooperative (*local resource enhancement*, or LRE) interactions between relatives can favor biased sex allocation. LRC and LRE have been argued to be important in a range of taxa, including cooperative breeding birds and mammals, primates, marsupials, ungulates, rodents, plants, social insects, primitively social bees, and other insects. In chapter 4, I describe Hamilton's basic theory of local mate competition (LMC), and in chapter 5, I describe the various ways in which the theory has been extended. LMC theory has been applied to a huge range of taxa, including insects, arachnids, snakes, and protozoan parasites such as malaria, worms, and plants.

In chapters 6 and 7, I describe Trivers and Willard's (1973) theory and the various ways in which it has been applied. In chapter 6, I show how this theory has been applied to explain (1) conditional adjustment of offspring sex ratios in groups such as parasitoid wasps, ungulates, and other mammals and birds; (2) environmental sex determination (ESD), especially in fish and shrimps; and (3) sex change in a variety of taxa, especially shrimps and fish. In chapter 7, I first consider the population-level consequences of conditionally adjusting sex allocation in terms of the population sex ratio and the overall investment ratio. It is often hard to make clear predictions at the population level, with the exception of in sex changers. I then go on to consider some of the complications that can occur with sex change and ESD, such as alternative life history strategies (early maturers or bidirectional sex change), intersexes, and the confusion surrounding reptiles.

In chapter 8, I consider the consequences of population perturbations in species where generations overlap. Such perturbations can occur unpredictably, due to periods of exceptional mortality or recruitment, or predictably, due to cyclical (seasonal) variation in the amount of overlap between generations. This theory has been applied with relatively little success, especially to bees, wasps, and lizards.

In chapters 9 and 10, I describe situations where there is conflict over sex allocation. In chapter 9, I show how conflict can occur between individuals. The major part of this chapter focuses on conflict within hymenopteran social insect colonies, but conflict can also occur in a variety of other situations, most notably polyembryonic parasitoid wasps. In chapter 10, I show how conflict can occur between different genes within an individual. A range of nuclear genes and cytoplasmic elements, including endosymbionts, has been shown to distort sex allocation to these elements' own advantage. I discuss the factors

that influence the prevalence of these selfish elements and the consequences for the evolution of their hosts.

In chapter 11, I consider the more general implications of sex allocation research. I exploit the fact that, as chapters 2 to 10 show, sex allocation is one of the most successful areas of evolutionary biology. Given this, I use sex allocation as a tool to address general issues about adaptation and how to study it. I consider specific topics, such as the evolution of social traits, levels of selection, the importance of possible constraints that may limit adaptation, and the applied implications of sex allocation. I then show how sex allocation provides an extremely illuminating test case of how to study adaptation. In particular, I consider the use of the different possible approaches for modeling evolution, such as phenotypic versus genotypic, and the interplay between the development of theoretical and empirical work. This chapter addresses the possible issue of why, given that we understand sex allocation so well, we should bother working on it anymore. My response to this is that in cases where we have a relatively good understanding of sex allocation, this opens up the territory for a range of more detailed studies that allow very general questions of the evolutionary process to be addressed.

1.5 WHAT IS NOT IN THIS BOOK

In this book, I have focused on how natural selection shapes sex allocation for given sex determination systems. Consequently, I have avoided a detailed coverage of how and when different sex determination systems will be favored (the first of the six problems of sex allocation given in section 1.1), except for when it overlaps with my aims in chapters 6, 7, and 10. I have avoided this topic for two reasons: Charnov's (1982) monograph still provides an excellent overview of the topic, and this book is plenty long enough anyway. Recent advances in this area, especially in plants, are reviewed elsewhere (e.g., Charlesworth and Morgan 1991; Barrett and Harder 1996; Campbell 2000; Barrett 2002; Pannell 2002; Vamosi et al. 2003; Delph and Wolf 2005). I have also not gone into the rapidly advancing research on the mechanisms by which vertebrates with chromosomal sex determination are able to control their offspring sex ratios (Krackow 1995; Pike and Petrie 2003; Rutkowska and Badyaev 2008). I am happy to simply accept that sex ratios can be adjusted, although when enough information is available on the mechanism of sex determination, it would be useful to add any constraints that this imposes back into sex allocation theory (section 11.3.3; Pen and Weissing 2002; Uller 2003).

I have organized and written this book from a conceptual and theoretical perspective, blending theory and data, to give an overview of sex allocation theory and how different areas may be applied to different organisms. Consequently, while I have avoided the use of mathematics, to make the book more accessible to empirical workers, I have also addressed the existing theoretical problems. I have not gone into details of how to model sex allocation theory because (1) this has recently been done in detail elsewhere by Frank (1998b) and (2) to give the theory enough coverage to do it justice would require too much space in an already too large book. Readers interested in the development of sex allocation theory are directed elsewhere for an overview of earlier techniques based around the Shaw-Mohler equation (Charnov 1982) or for more modern and powerful techniques based on inclusive fitness theory and how it can be implemented with the direct fitness method (Taylor and Frank 1996; Frank 1998b; Pen and Weissing 2002; Taylor et al. 2007). The direct fitness method for constructing theoretical models has been an extremely important development, allowing more general models to be constructed more simply and led by the biology (Taylor and Frank 1996).

In addition, while I have linked areas, I have not provided specific taxonomic overviews, as the book is conceptually organized, and a given taxon can therefore appear in multiple chapters. Numerous taxonomically based reviews are already available (e.g., see chapters in Wrensch and Ebbert 1993; Godfray 1994; Hardy 2002). I have tried to give a balanced coverage of different organisms but have probably not given enough attention to plants. Last, I would like to point readers toward Hardy's (2002) book, which provides a thorough introduction to the practical methods that are required to study sex allocation, from how to work with different organisms to data analysis.

1.6 HOW TO READ THIS BOOK

I appreciate that this is a big book, but sex allocation is a big field of research. To help the reader, I have tried to write it in such a way that the different chapters, and even sections within chapters, can stand alone. Within each chapter, I start with a general introduction to the theoretical issues before discussing specific empirical cases and then finishing with a discussion of general issues and future directions. In principle, readers should be able to jump from the general theory section to the cases that interest them. In the longer chapters, such as chapters 5 and 6, I have created tables to provide a road map to guide readers to specific cases. I provide some suggested reading plans in table 1.1.

TABLE 1.1. Some Suggested Reading Plans for Different Readers

<i>Interests of the Reader</i>	<i>Suggested Chapters and Sections</i>
Basic introduction to sex allocation	Chapters 2 (except sections 2.5.3 and 2.5.4), 3, 4 (except 4.2.3), 6, and 11; sections 5.3, 7.2, 9.6, 10.1, and 10.2
Basic introduction to sex allocation theory	Sections 2.2, 3.2, 4.2, 6.2, 7.2, 9.6.1, 9.6.2, 10.2.1.1, and 10.2.2.1–3
Sex allocation in vertebrates	Chapters 2 (except sections 2.5.3 and 2.5.4), 3, 6 and 11; section 7.2
Sex allocation in parasitoids	Chapters 2, 4–6, 10, and 11; sections 7.2, 7.5, and 9.5
Sex allocation in social insects	Chapters 2, 3, 4, 5, 6, 10, and 11; section 9.6
Sex allocation in plants	Chapters 2 (except section 2.5.3 and 2.5.4), 3 (except 3.3), 4, 6, 10, and 11; sections 5.3, 5.5, 5.11, 7.2, 7.6
Reader already familiar with sex allocation and aged >30	Chapter 11

The suggestion for readers aged over 30 is based on the assumption that no one over 30 reads books, they just review them (S. A. Frank, personal communication).

1.7 LANGUAGE AND SEX RATIOS

Before going on to the main parts of this book, it is useful to clarify my use of language. At a general level, as is done by most evolutionary researchers, I will use an informal shorthand and write things such as “individuals are selected to maximize their reproductive success.” This does not mean that I think animals are consciously maximizing their reproductive success or that they are consciously aware of the links between various behaviors and reproductive success and the consequences of natural selection. I use such phrases to avoid the constant repetition of long and tedious sentences detailing precisely how natural selection works—e.g., individuals who have a greater reproductive success provide a greater genetic contribution to the next generation, and hence natural selection will favor genes that lead to individuals behaving in a way that maximizes their reproductive success (Grafen 2007b).

At a more specific level, the *sex ratio* is usually defined as the proportion of males in a population, and the *sex allocation* as the proportion of resources allocated to the production of males (an important exception is with the social insects). It is useful to define the stage at which the sex ratio is measured, with

the *primary sex ratio* being the ratio at the time of conception, the *secondary sex ratio* as the ratio at birth, and the *tertiary sex ratio* as the ratio of mature (adult) organisms. These will differ if the sexes differ in their mortality rates at various stages in their development. For example, if developmental mortality rates are greater for males, then an unbiased primary sex ratio would become a female biased secondary sex ratio. From here on, unless I state otherwise, it should be assumed that the predictions of sex allocation theory are for the primary sex ratio (section 2.4), and that empirical data are attempting to measure as close to this as possible, but that they usually measure the secondary sex ratio (although methodological advances have moved observations closer to the primary sex ratio; Ellegren and Sheldon 1997; Griffiths et al. 1998; Stehlik et al. 2007). This emphasizes that differential mortality between the sexes should always be considered as a possible explanation for biases in the secondary sex ratio of a given population. The possibility of differential mortality also illustrates the advantage of making comparative predictions for how the sex ratio should vary across individuals or populations, rather than making absolute predictions for the overall population sex ratio (see also sections 7.2 and 11.3.4.2).