

Sex Allocation

Stuart West

Sex Allocation

MONOGRAPHS IN POPULATION BIOLOGY
EDITED BY SIMON A. LEVIN AND HENRY S. HORN

Complete series list follows the index

Sex Allocation

STUART A. WEST

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*To my parents,
John and Gloria*

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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).

CHAPTER 2

The Düsing-Fisher Theory of Equal Investment

R. A. Fisher (1930) clearly was the pathbreaker in sex ratio theory.

—*Charnov 1982, p. 13*

Fisher's theory of equal investment provides the basic null model for sex allocation theory, but it is also the foundation for all subsequent theoretical developments. This theory has firm theoretical foundations, established both before and after Fisher's influential work. However, attempts to test Fisher's prediction of equal investment in the sexes will usually be in vain, because the conditions required for this are likely to be extremely rare. Instead, it is more productive to test the frequency-dependent nature of Fisher's theory by perturbing the population sex ratio and then examining whether it evolves back toward equal investment. Some species with unusual life histories also provide useful opportunities for testing Fisher's theory.

2.1 INTRODUCTION

Fisher (1930) provided an explanation for why males and females should be produced in approximately equal numbers, as is observed in many animal species. However, it has recently been shown that this theory was probably widely accepted at the time and had been developed previously by others (Edwards 1998, 2000). In particular, Darwin (1871) had provided a related verbal explanation, and Düsing (1883, 1884a, 1884b) had provided a formal mathematic model.

In the next section of this chapter, I describe the theory for equal investment in the sexes as presented by Fisher. Although Fisher may not have been the first to solve this problem, his treatment was, typically, extremely succinct and, perhaps atypically, very clear, grasping the importance of reproductive value, and it has been highly influential in the field of evolutionary biology in general. I then briefly consider the formal development of this theory, both before and

TABLE 2.1. A Simple Numerical Illustration of Fisher's Theory

<i>Population Sex Ratio</i>	<i>Number in Population</i>	<i>Reproductive Value Per Individual</i>	<i>Selection Favors Individuals Who Produce a/an</i>
Male biased			
Males	200	$100/200 = 0.5$	Female biased sex ratio
Females	100	1	
Female biased			
Males	100	$200/100 = 2$	Male biased sex ratio
Females	200	1	
Unbiased			
Males	150	$150/150 = 1$	Unbiased sex ratio
Females	150	1	

The relative reproductive values of male and female offspring are given for situations where the population sex ratio is biased toward males or females or is unbiased. The mean reproductive value of females is assumed to be 1.0, and the mean reproductive value of males is given by the average number of matings they will obtain multiplied by the mean reproductive value of females, which is given by (number of females/number of males) \times 1.0.

after Fisher's treatment (section 2.3), and the consequences of when mortality rates vary between the sexes (section 2.4). Last, I review empirical tests of Fisher's theory (section 2.5).

2.2 FISHER'S THEORY OF EQUAL INVESTMENT

Fisher's (1930) argument was that, all else being equal, natural selection favors equal investment into the two sexes. He argued that this follows from the fact that each offspring has one mother and one father, so the total reproductive value (genetic contribution to the next generation) of all the males in a generation must equal the total reproductive value of all the females. Consider the case where males and females are equally costly to produce. If there were an excess of males, they would on average obtain less than one mate, and so the average reproductive value of females would be greater, favoring parents that produced a relative excess of female offspring (table 2.1). In contrast, if there were an excess of females, males would on average obtain more than one mate, and so the average reproductive value of males would be greater, favoring parents that produced a relative excess of male offspring (table 2.1). Consequently, the average reproductive value of males and females is equal only when equal numbers of the two sexes are produced (a sex ratio of 0.5).

Fisher's argument also applies more generally, when males and females are not equally costly to produce. In this case, the argument must be phrased in terms of the resources invested into each sex, and the evolutionary stable strategy (ESS) is to invest equal amounts of resources into male and female offspring. For example, if sons are twice as costly to produce as daughters, then we would expect twice as many daughters to be produced as sons (a sex ratio of 0.33).

Fisherian investment could be reached in two ways. Assuming that sons and daughters are equally costly to produce, one way is if all individuals invested equally in sons and daughters, producing a sex ratio of 50% sons. The other way is if different individuals produced different sex ratios, some male biased and some female biased, with the overall average being 50% sons. Verner (1965) showed that natural selection would favor the former, with all individuals producing 50% sons. This stabilizing selection on the sex ratio arises because, for example, an individual who produces a male biased sex ratio would lose more when the population sex ratio is male biased than it would gain when the population sex ratio is female biased (Verner 1965; Taylor and Sauer 1980). However, the strength of stabilizing selection declines as the sex ratio approaches 50% male and the population size increases (Taylor and Sauer 1980).

Fisher's argument is important for two reasons, which are often muddled. First, it makes a specific prediction for the population sex ratio (proportion male) and overall sex investment (proportion of resources invested in the production of sons). This prediction of equal investment in the sexes provides the null model (or *neutral theory*) for sex allocation theory. If we observe biased sex allocation, then this suggests that something interesting is going on to cause this deviation from Fisher's prediction.

Second, it demonstrates the frequency-dependent nature of selection on the sex ratio or sex allocation. As the sex ratio becomes biased toward one sex, this increases the relative reproductive value of members of the other sex. This Fisherian frequency-dependent selection provides the fundamental foundation for all of sex allocation theory. Indeed, one way of conceptualizing the different areas of sex allocation that are discussed in this book is that each represents the consequences of when one of the implicit assumptions in Fisher's theory is relaxed (table 2.2; Bull and Charnov 1988; Charnov 1993).

2.3 DARWIN TO TODAY

Up until just before the end of the twentieth century, it was widely assumed that Fisher developed his theory of equal investment independently. However,

TABLE 2.2. The Relation between the Implicit Assumptions of Fisher's Theory and the Different Parts of This Book

<i>Underlying Assumption</i>	<i>Chapters in which the Consequences of Relaxing that Assumption are Examined</i>
No cooperative or competitive interactions between relatives	Chapters 3–5
Environmental conditions do not have differential consequences for male and female fitness	Chapters 6 and 7
Stable age distribution	Chapter 8
Parental control of the sex ratio	Chapter 9
Mendelian segregation of alleles influencing sex allocation	Chapter 10

Edwards (1998) has since argued that this theory was already well known in the early decades of the twentieth century. He suggested that this is the reason Fisher felt no need to attribute the theory to particular sources, alongside the fact that Fisher was not very systematic with references, as was customary at the time (Edwards 1998, 2000; Seger and Stubblefield 2002).

Darwin provided an argument for equal investment in the sexes that was remarkably close to Fisher's in the first edition of his book *The Descent of Man and Selection in Relation to Sex* (1871). However, he removed this statement from the second edition published three years later (1874), replacing it with his famous quote that left the problem for future generations to solve (Bulmer 1986c; Edwards 1998; Seger and Stubblefield 2002). Darwin's near success in this area was ignored because the second and later editions of this book were more widely read. Frank (2002, pp. 2562–2563) has suggested that the reason for Darwin's retraction is that he was assuming monogamy and realized that his argument for an equal sex ratio relied on maximizing the number of monogamous mated pairs, which is a species selection argument. The relevant extracts are as follows:

Let us now take the case of a species producing . . . an excess of one sex—we will say of males—these being superfluous and useless, or nearly useless. Could the sexes be equalised through natural selection? We may feel sure, from all characters being variable, that certain pairs would produce a somewhat less excess of males over females than other pairs. The former, supposing the actual number of the offspring to remain constant, would

necessarily produce more females, and would therefore be more productive. On the doctrine of chances a greater number of offspring of the more productive pairs would survive; and these would inherit a tendency to procreate fewer males and more females. Thus a tendency towards the equalisation of the sexes would be brought about. . . . The same train of reasoning is applicable . . . if we assume that females instead of males are produced in excess, for such females from not uniting with males would be superfluous and useless.

(Darwin 1871, p. 316)

In no case, as far as we can see, would an inherited tendency to produce both sexes in equal numbers or to produce one sex in excess, be a direct advantage or disadvantage to certain individuals more than to others; for instance, an individual with a tendency to produce more males than females would not succeed better in the battle for life than an individual with an opposite tendency; and therefore a tendency of this kind could not be gained through natural selection. . . . I formerly thought that when a tendency to produce the two sexes in equal number was advantageous to the species, it would follow from natural selection, but I now see that the whole problem is so intricate that it is safer to leave its solution for the future.

(Darwin 1874)

The first general mathematical treatment of the theory for equal investment in the sexes was provided by Düsing. He published this in German, in his doctoral thesis (1883), a paper (1884b), and a book (1884a), the last of which has recently had the relevant extract translated into English (Edwards 2000). Fisher was likely to have been aware of this work, as it was quite well known, being included in the principal books on the subject around the turn of the century as well as in the *Encyclopedia Britannica*. Düsing's treatment is actually identical except for notation to that later provided by Shaw and Mohler (1953)—a paper that has acquired much fame as the first mathematical treatment of Fisher's theory and sex allocation in general. More generally, this rediscovery of Düsing's work by Edwards places it as one of the earliest examples of mathematical argument in evolutionary biology. Darwin and Düsing's discussions also stand as a clear contrast to the earlier claim that unbiased sex ratios were due to "divine providence," because "polygamy is contrary to the law of nature and justice" (Arbuthnott 1710, pp. 186 and 189).

There have since been a large number of theoretical papers formalizing Fisher's principle of equal investment in the sexes (e.g., Shaw and Mohler 1953; MacArthur 1965; Hamilton 1967; Leigh 1970; Charnov 1982; Leigh et al. 1985; Grafen 1986; Karlin and Lessard 1986; Boomsma and Grafen 1991;

Pamilo 1991; Frank 1998b; Pen and Weissing 2002). These papers have obtained the same result utilizing both population genetic and phenotypic (ESS or optimality) approaches. While all these different approaches agree on the prediction of equal investment, the evolutionary dynamics by which equal investment is reached can be influenced by genetic details such as epistasis, linkage, and recombination (Lessard 1987; Feldman and Otto 1989; Liberman et al. 1990; Feldman et al. 1991). Mesterson-Gibbons and Hardy (2001) have suggested that Fisher's theory will not hold if one parent controls offspring sex, but this result appears to be due to an incorrect calculation of reproductive value (I. Pen, personal communication). Another complication is that if the variance in reproductive value differs between the sexes, then a bias toward the sex with lower variance is favored as a form of bet hedging (Yanega 1996; Proulx 2000), but this effect is negligible except in very small or subdivided populations (A. Gardner, unpublished).

2.4 DIFFERENTIAL MORTALITY

The consequences of random differential mortality between the sexes for sex allocation within the context of Fisher's theory are frequently misunderstood. A crucial distinction here is whether the mortality takes place before or after the period of parental investment. If mortality takes place after the period of parental investment, then it has no influence on the ESS sex ratio (Fisher 1930; Leigh 1970). Suppose that mortality was higher in adult males compared with adult females. This reduces the likelihood of any male reproducing, and so it is often assumed that this selects for a female biased sex ratio. However, this also leads to the reproductive success of any survival male being greater. Provided that the mortality is random with respect to parental character, these effects cancel out exactly, leading to the mortality rate having no influence on the average fitness of a male, and so there is no effect on the ESS sex allocation (Leigh 1970). That is to say, the primary sex ratio is expected to be 50% males, even when adult mortality leads to skew in the tertiary sex ratio.

In contrast, when differential mortality occurs before the period of parental investment, it does select for biased sex allocation (Fisher 1930). Suppose that sons and daughters that survive to the end of the period of parental investment are equally costly to produce, but that sons are more likely to die during the period of parental investment. In this case, the average cost of each son born is less than the average cost of each daughter born. This favors a sex ratio bias toward sons in the primary sex ratio. However, the higher mortality of males leads to the sex ratio being biased toward daughters by the end of the period of

parental expenditure. The exact sex ratio favored is that which leads to the total investment in sons and daughters over the whole period being equal.

Mortality rates can also have an influence on sex allocation when other assumptions of Fisher's theory are broken—i.e., when other factors are influencing the ESS sex allocation strategy. These cases are discussed elsewhere, when considering local mate competition (section 5.9) or when the population age distribution is perturbed (chapter 8).

2.5 TESTING FISHER'S THEORY

In this section, I review the three ways in which Fisher's theory has been tested. In section 2.5.1, I consider static tests, which determine whether equal investment is placed into male and female offspring at the level of the population. In section 2.5.2, I consider dynamic tests, where the population investment or sex ratio is experimentally perturbed from 50% male and then followed to examine whether it evolves back toward 50% male. In section 2.5.3, I consider some species with unusual life histories that allow Fisher's theory to be tested in novel ways. Last, in section 2.5.4, I consider the consequences of when some individuals are constrained to produce offspring of only one sex.

2.5.1 STATIC TESTS OF FISHER'S THEORY

A large number of animals produce approximately equal numbers of sons and daughters, especially birds and mammals (Williams 1979; Charnov 1982; Clutton-Brock 1986; Clutton-Brock and Iason 1986). It has sometimes been suggested that this provides support for Fisher's theory. However, several workers have pointed out that many animals, particularly those that are large and conspicuous such as birds and mammals, have chromosomal (genetic) sex determination, and so it could be argued that they are constrained to produce 50% males (but see section 11.3.3). Another problem here is that this uses the observation (unbiased sex ratios) that Fisher set out to explain as evidence to support his theory, which is completely circular! An alternative view is that Fisher's theory explains why a form of sex determination that leads to 50% males has been favored. Another possible response is that many birds and mammals have been shown to adjust their offspring sex ratio in response to environmental conditions and that there is a lack of quantitative evidence that chromosomal sex determination prevents offspring sex ratios (section 11.3.3; West et al. 2005).

The latter point raises the fundamental issue that if parents are adjusting their offspring sex ratio in response to environmental conditions, then Fisher's theory is not expected to hold (see section 7.2.1). Instead, the sex and investment ratios can be biased in either direction; the degree of bias and even the direction are likely to be very hard to predict. A failure to appreciate this point is one of the most common errors in the field of sex allocation. This problem is possibly confounded by the fact that although a 50% investment into sons is not expected, the frequency-dependent selection that is at the heart of Fisher's theory leads to the expected and observed deviations from 50% not being too great, and so it looks like Fisher's theory holds even when it does not apply (see also Boomsma and Grafen 1991).

Several workers have attempted to test Fisher's theory by examining the pattern of sex allocation in haplodiploid species where mothers can control the sex of their offspring. The earliest work to use this method was that of Noonan (1978) and Metcalf (1980) on one and two species of *Polistes* wasps, respectively. These are social species, but it was argued that confounding factors such as worker control of sex allocation (chapter 8) and local mate competition (chapter 4) were unimportant. In all three species, female and male offspring were significantly different in size (males larger in two species; females larger in the other), but the overall population sex ratio was biased in the other direction (female bias in two species; male bias in the other), leading to an overall investment ratio that was not significantly different from 50% male (Noonan 1978; Metcalf 1980).

However, the same problem arises with these studies, which is that the biology appears to not match the assumptions of Fisher's theory. Specifically, mothers are investing different amounts of resources into sons and daughters, suggesting that the relationship between resources invested and offspring fitness differ between males and females (see chapter 7). In this case, the overall investment ratio is not necessarily expected to be 50% male, as is also the case when mothers adjust their offspring sex ratio in response to environmental conditions (section 7.2.1). Another issue is that it is often not clear as to what exactly the currency of investment (most limiting resource) really is. Consequently, it appears that there is a lack of wholly theoretically appropriate tests of Fisher's theory. An appropriate test would need to be carried out on a species where mothers had control of the offspring sex ratio, equal investment is made into sons and daughters, and mothers do not adjust their offspring sex ratio in response to environmental conditions. The extent to which this occurs is a matter of debate, without even considering the problem of demonstrating it—although cyclically parthenogenetic species, especially haplodiploids, may

prove useful in this respect (Aparici et al. 1998; Calsina et al. 2000; Aparici et al. 2002; McGovern 2002).

Fisher's theory predicts that when individuals of one sex are more costly to produce, then the sex ratio should be biased toward the cheaper sex, such that the overall investment in the sexes is equal. In principle, this could be tested with a comparative approach across species, examining whether the sex ratio was correlated with the investment ratio in the two sexes. Various authors have suggested or attempted to do this by looking at whether the offspring sex ratio correlates with the degree of sexual size dimorphism, based on the assumption that there will be a greater sex difference in investment in more dimorphic species (Trivers and Hare 1976; Clutton-Brock et al. 1985; Boomsma 1989; Pen 2000; Benito and González-Solís 2007; Magrath et al. 2007). Across bird species, there is a trend in the predicted direction, with a tendency to produce a higher proportion of sons in species where females are relatively larger (Benito and González-Solís 2007). However, this trend is weak, and it is not significant when other life history variables such as plumage dichromatism, developmental mode, and age at first breeding are also included in the analysis. In addition, the same problem occurs here, that if different amounts are being invested in the sexes, then there is not an equal fitness return on investment in the two sexes, and so conditional sex allocation may be occurring, in which case, Fisher's theory does not hold (section 7.2.1; Frank 1987b). Consequently, in such cases, it is more useful to develop specific models that can be applied to those taxa (section 7.2.2; Frank 1995b). The assumptions of Fisher's theory do not hold, and so the aim is not to test Fisher's theory. Furthermore, and equally fundamentally, another problem with testing Fisher's theory with such a comparative approach in vertebrates, such as birds and mammals, is that differences in the mortality rate between males and females are expected to be correlated with the extent of sexual size dimorphism (Clutton-Brock et al. 1985; Benito and González-Solís 2007; Desfor et al. 2007). Such differential mortality will lead to higher proportion of daughters in species where males are relatively larger, in the absence of any sex ratio adjustment.

Another way to test Fisher's theory would be to examine whether the primary sex ratio is correlated with mortality rates during the period of parental investment (section 2.4). For example, in species where the mortality rate was greater for males, we would expect a more female biased primary sex ratio. Trivers (1985, p. 276) refers to a manuscript by Seger et al. showing that primary sex ratios are correlated with mortality rates during the period of parental investment in whales. This paper was never published because the whaling data used could lead to this correlation as an artifact, through sexing errors that get worse and more male biased as fetuses get smaller (younger) and the

censoring of the data at smaller sizes (J. Seger, personal communication). However, this problem could be addressed with recent techniques that allow the sex to be measured at earlier stages during pregnancy and hence allow better estimates of both the primary sex ratio and developmental mortality rates. A higher mortality rate in males during the development period is often given as the reason for the slight male bias in the human sex ratio at birth, although a multitude of other possible explanations could be given (see chapter 7).

2.5.2 DYNAMIC TESTS OF FISHER'S THEORY

Fisher's theory has also been tested in a number of species experimentally, by perturbing the sex ratio away from approximately 50% male and then examining whether it evolves back toward this point. An advantage of this method is that it tests the fundamental frequency-dependent nature of Fisher's theory, and not necessarily whether a sex allocation of exactly 50% male is favored. Consequently, this method can still provide qualitative tests of theory even in cases such as those discussed earlier (section 2.5.1), where we are unable to predict what the overall sex or investment ratio should be but expect it to be near 50% male.

Dynamic tests of Fisher's theory require a method to perturb the population sex or investment ratio away from 50% male. To date, four such studies have been published, each on a species where sons and daughters appear to be equally costly to produce, and each using a different method to perturb the population sex ratio. Specifically, the population sex ratio was skewed by (1) keeping populations at extreme temperatures in the fish *Menedia menidia*, where sex is determined by temperature (Conover and van Voorhees 1990; Conover et al. 1992; for further details on this species see section 6.7.2); (2) manipulating the genotype frequency in the southern platyfish *Xiphophorus maculatus*, where sex is determined by a single locus with three sex alleles, with three female genotypes (WX, WY, XX) and two male genotypes (YY, XY) (Basolo 1994, 2001); (3) a naturally occurring X–Y meiotic drive system called *sex ratio* in *Drosophila mediopunctata* (Carvalho et al. 1998); and (4) generating hybrids between two *Drosophila species* (Blows et al. 1999). Ideally, populations should be replicated and used as independent data points in such selection experiments to avoid the problem of pseudoreplication (Hurlbert 1984). In practice, the different experiments used from 4 to 30 independent populations.

In all experiments, the sex ratio evolved in the predicted direction, toward 50% males. However, there was considerable variation across experiments in the rate at which 50% males was approached. In *X. maculatus* and *M. menidia*, the

sex ratio (proportion male) reached approximately 0.5 in only 1 to 4 generations from sex ratios as biased as 0.05 and 0.7. The sex ratio change in the *Drosophila* hybrids was also quite fast, changing from 0 to 0.75 to approximately 0.5 over 16 generations (Blows et al. 1999). In contrast, the observed rate of change was much slower in *D. mediopunctata*, changing from 0.16 to 0.32 over 49 generations, with an estimated 330 generations to reach 0.5 (Carvalho et al. 1998).

Why should there be such variation across species? If sex is determined by sex chromosomes with large effects, then rapid evolution is predicted (Karlin and Lessard 1986; Basolo 1994). This can explain the pattern in *X. maculatus* and *M. menidia*, where sex is determined by sex chromosomes and by major sex-determining genes that behave like sex chromosomes, respectively. Indeed, the sex ratio dynamics in *X. maculatus* showed reasonably quantitative agreement with a specific population genetic model (Basolo 1994). In contrast, if the sex ratio is a quantitative trait determined by many loci, then the rate of sex ratio change is predicted to be much slower, and positively correlated to the heritability of sex ratio (Bulmer and Bull 1982; Carvalho et al. 1998). The rate of change in *D. mediopunctata* showed a close fit to the prediction of theory, given the observed heritability (Carvalho et al. 1998). In this experiment, the heritability of sex ratio was much higher than is commonly observed (e.g., Bull et al. 1982; Toro and Charlesworth 1982; Orzack and Gladstone 1994), emphasizing that Fisherian selection will often be a slow process by the standard of modern experimental evolution studies.

Another prediction from theory is that because Fisherian selection is frequency dependent, it should weaken as the sex ratio approaches 50% males. This pattern was found in *D. mediopunctata* (Toro and Charlesworth 1982). An alternative explanation for this pattern is exhaustion of genetic variability, and although this was not specifically controlled for, there are a number of lines of evidence that suggest this was not the driving factor. The same pattern was not tested for in the experiment with *Drosophila* hybrids (Blows et al. 1999). Future analyses of this issue will need to control for spurious correlations due to the problem of “regression to the mean,” whereby successive trait measurements will, on average, tend to be closer to the mean on the second measurement (Kelly and Price 2005).

2.5.3 UNUSUAL LIFE HISTORIES AND FISHER’S THEORY—HETERONOMOUS PARASITOID WASPS

Fisher’s theory predicts that the resource limiting reproduction be invested equally in sons and daughters. In some organisms, the limiting resource that is

invested in offspring varies with environmental conditions, providing some novel opportunities for testing Fisher's theory. In this section, I consider some parasitoid wasps that have attracted attention for this reason. *Parasitoids* are insects whose larvae develop by feeding on the bodies of other arthropods, usually insects, but also spiders and centipedes (Godfray 1994).

In most parasitoid wasps, male and female offspring are laid in the same type of host. An exception to this occurs in many species of the chalcidoid family Aphelinidae, where males and females are obligatorily restricted to develop on different types of hosts (Hunter and Woolley 2001). In most of these species, female offspring develop as normal parasitoids on homopteran hosts, such as whitefly, mealybugs, or scale insects (the *primary host*). In contrast, males develop as parasitoids of parasitoids (termed *hyperparasitoids*), attacking females of their own or another species of parasitoid (the *secondary host*) within homopteran hosts. In all cases, only one wasp develops per host (termed *solitary parasitoids*). These species are termed *heteronomous hyperparasitoids*, or more specifically *autoparasitoids*, when their secondary host range includes conspecific females. The reasons for this unusual life history are not clear.

In order to examine how Fisher's theory would apply to this life history, it is necessary to consider the cost of reproduction (Godfray and Waage 1990; Godfray and Hunter 1992). In parasitoid wasps, the most important factors limiting reproduction are likely to be the availability of either hosts or eggs (Godfray 1994). If a female's reproductive success is limited by the number of hosts that she can locate, then she is termed *host limited* (or *time limited*). In contrast, if a female's reproductive success is limited by the number of eggs she carries or the rate at which she can mature eggs, she is termed *egg limited*. These represent two end points of a continuum, and females can be anywhere between, in which case, they would be partially host limited and partially egg limited.

Consider first when females encounter fewer hosts than they have eggs to lay and so are host limited (Godfray and Waage 1990). In this case, hosts, or the time spent looking for hosts, represents the cost of reproduction, and so Fisher's principle suggests that females should spend equal amounts of time searching for male and female hosts. If male and female hosts are in different locations, then this would mean equal time searching in the different areas and laying an appropriate (fertilized or unfertilized) egg in all hosts found. This would lead to a sex ratio that would be biased according to the relative encounter rate with hosts suitable for male and female offspring. Similarly, if male and female hosts occur in the same habitat, then females are predicted to lay an appropriate egg in all hosts encountered, with the sex ratio depending on the relative rate at which male and female hosts are encountered.

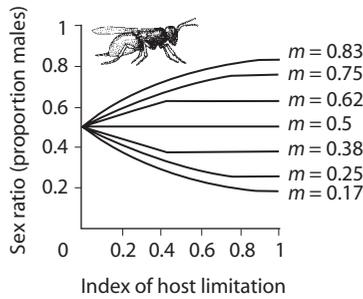


FIGURE 2.1. The population sex ratio for autoparasitoids whose reproductive success can be egg or time limited (redrawn from Hunter and Godfray 1995). The different lines show the predictions for different proportions of hosts suitable for males (m). As the extent of host limitation increases (less egg limitation), the population sex ratio moves from 0.5 toward the proportion of hosts suitable for males.

Consider now the situation where females encounter more hosts than they have eggs to lay and so are egg limited (Godfray and Waage 1990). In this case, eggs are the cost of reproduction, and so Fisher's principle predicts that females should lay equal numbers of male and female eggs. This would lead to females preferentially ovipositing on the less abundant host type and avoiding the more abundant host type. The preceding verbal arguments consider the extreme cases. However, the situation has been modeled formally for the entire continuum from extreme host to extreme egg limitation (Hunter and Godfray 1995). This confirms the predictions for extreme host and egg limitation but also shows how wasps move between these extremes in intermediate situations (figure 2.1). A primary determinant of the extent to which females are egg or host limited under field conditions will be host density, with lower host densities leading to host limitation being most important (and egg limitation being less important).

Hunter and Godfray (1995) tested the predictions of theory experimentally with the species *Encarsia tricolor*. They manipulated (1) host density, to produce situations that would lead to variable extents of host limitation, and (2) the proportion of hosts suitable for males (secondary hosts), to produce situations where there is a bias toward either primary or secondary hosts. Their experiment provided qualitative support for the predictions of theory. At low host densities, females biased their sex ratio toward the sex where more suitable hosts were available—a female biased sex ratio when primary hosts were more abundant, and a male biased sex ratio when secondary hosts were more abundant (figure 2.2). As host density increased, a higher proportion of the

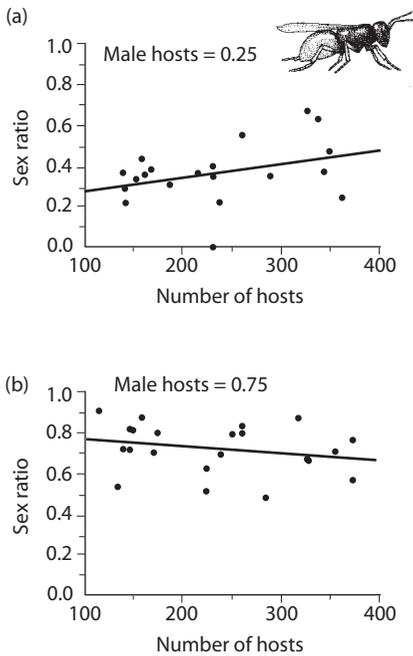


FIGURE 2.2. The relationship between sex ratio and host density (number of hosts per arena) when the proportion of hosts that were suitable for males was either (a) <0.5 (proportion = 0.25) or (b) >0.5 (proportion = 0.75) (redrawn from Hunter and Godfray 1995).

rarer host type was utilized, leading to less biased sex ratios, as would be expected if higher host densities led to egg limitation being more important.

The available field data are also consistent with the predictions of theory, although they do not provide an explicit test (Hunter and Godfray 1995). Several field studies have shown that the sex ratio is largely influenced by the proportion of secondary hosts, in the predicted direction (Donaldson and Walter 1991; Hunter 1993). This would be expected if females are host limited or are somewhere between the extremes of host and egg limitation (i.e., anywhere but extreme egg limitation). Although little is known about the extent to which individuals are host or egg limited under field conditions, theory suggests that individuals would be expected to be at an intermediate or a host limited end of the continuum (Rosenheim 1996; Sevenster et al. 1998; Rosenheim 1999; Ellers et al. 2000). In addition, one study showed a marked preference for the less abundant secondary hosts, as would also be expected under intermediate host and egg limitation (Hunter 1993).

The preceding discussion shows that Fisher's theory coupled with an unusual life history can lead to the prediction of biased sex ratios and that this prediction is supported. However, there has been only limited attention to this area, and there are a number of further complexities that remain to be explored. One complexity is that females sometimes feed on primary hosts, whereas they do not feed on secondary hosts (Hunter and Godfray 1995). This host feeding is destructive, and so a female faces the additional decision of whether to use a primary host for feeding or oviposition. The relative advantage of feeding is also likely to vary with the extent of host limitation because resources from host feeding are used to mature eggs (Rivero and West 2005). A possible role of host feeding is supported by the fact that the extent of host feeding and the sex ratio both vary dependent on whether the different host types occur in the same or different patches (Hunter and Godfray 1995; Ode and Hunter 2002). Another possible complication is that if the female developing in a secondary host is the daughter of the foraging female, then she is selected to be less likely to lay a male egg (Colgan and Taylor 1981). Although females cannot tell the difference between their offspring and those of a conspecific, this is unlikely to be of general importance under natural conditions (Williams 1996; Ode and Hunter 2002). Another area worth pursuing is heteronomous parasitoids with different life cycles to the autoparasitoid species described earlier. In *indirect autoparasitoids*, male eggs are sometimes laid in unparasitized hosts, in anticipation of later parasitism (Godfray and Waage 1990; Ode and Hunter 2002). In heterotrophic parasitoids, males develop in different host species, as primary parasitoids of lepidopteran eggs (Ode and Hunter 2002). Last, very similar issues arise, with the extent of host or egg limitation influencing sex allocation, in parasitoid wasps that produce single-sex broods (Godfray 1994; West et al. 1999a, 2001a).

2.5.4 VIRGINITY AND CONSTRAINED SEX ALLOCATION IN HAPLODIPLOIDS

Fisher's principle predicts equal investment in the sexes at the population level. Consequently, if some individuals are constrained to produce a biased sex allocation, the other individuals in the population can be selected to bias their sex allocation in the opposite direction to make up for this. A clear example of this is provided by virginity and constrained sex allocation in haplodiploid species. In haplodiploids, males develop from unfertilized eggs, and females from fertilized eggs (Cook 1993b). This means that females who are unmated (virgins) or constrained from fertilizing their eggs for another reason (e.g., sperm depletion, lack of sperm transfer during copulation, and so on) are still able to

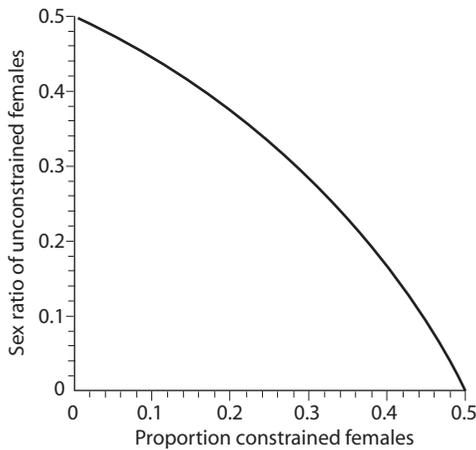


FIGURE 2.3. The ESS sex ratio for unconstrained females in a population with panmictic mating as a function of the proportion of females in the population that are producing only male offspring (redrawn from Godfray 1990).

produce males. The presence of constrained females skews the population sex ratio toward males. This decreases the average mating success of males and hence selects for mated females to lay a higher proportion of daughters (Metcalfe 1980; Taylor 1981b; Godfray 1990). Specifically, if a proportion p of females is constrained to produce only males, then the ESS sex ratio for unconstrained females (r^*) is given by (Godfray 1990):

$$r^* = \frac{1-2p}{2(1-p)}. \quad (2.1)$$

This result is plotted in figure 2.3 and shows that the ESS sex ratio for unconstrained females becomes progressively more female biased until, when $p = 0.5$, they should produce only daughters. A female bias is favored because the excess of males leads to a decrease in the average mating success of males. The ESS sex ratio for unconstrained females is that which leads to the overall population sex ratio being 0.5 (unless $p > 0.5$), at which point, the reproductive value of males and females is equal. This means that the unconstrained females exactly compensate for the excess of males produced by the constrained females (when $p \leq 0.5$).

Individuals could be expected to adjust their offspring sex ratios in response to the presence of constrained females in two ways (Godfray 1990). First, they might have a fixed strategy, adjusting their offspring sex ratios as predicted by equation 2.1 in response to the mean prevalence of constrained females over evolutionary time. Second, they might have a variable or facultative strategy if

TABLE 2.3. Data on the Estimated Prevalence of Virgin Females Constrained to Produce Only Sons, Sex Ratio, and Predicted Sex Ratio (from Equation 2.1), for Four Haplodiploid Species

<i>Species</i>	<i>Proportion Virgin (p)</i>	<i>Predicted Sex Ratio</i>	<i>Observed Sex Ratio</i>
Gall thrip <i>Kladothrips rugosus</i>	0.24	0.34	0.36 ± 0.02
Western flower thrip <i>Frankliniella occidentalis</i>	0.21–0.25	0.33–0.37	0.26
Parasitoid wasp <i>Bracon hebetor</i>	0.17–0.20	0.38–0.40	0.34–0.36
Social wasp <i>Polistes metricus</i>	0.26	0.32	0.38

(Metcalf 1980; Antolin and Strand 1992; Guertin et al. 1996; Ode et al. 1997; Kranz et al. 2000.)

they can assess the current level of constrained females. The extent of sex ratio adjustment will depend on the frequency of constrained oviposition, which has been estimated in a large number of hymenopteran species, especially parasitoid wasps, fig wasps, and to a lesser extent thrips (Metcalf 1980; Godfray 1988; Hardy and Godfray 1990; Higgins and Myers 1992; Godfray and Hardy 1993; Morgan and Cook 1994; Hardy and Cook 1995; West et al. 1997; Hardy et al. 1998; West et al. 1998a; Otsuka and Koshio 1999; Kranz et al. 2000). The estimated proportion of constrained females ranges from 0 to 35%. However, the majority of studies indicate low (<5%) frequencies of constrained oviposition in natural populations, and so it is not of widespread importance. In addition, the instances with a high proportion of constrained females tend to be in species subject to extreme LMC (chapters 4 and 5), where the sex ratio strategy is not expected to be adjusted in response to the presence of virgins (see section 5.9.4).

The possibility of fixed strategies has been tested in a small number of species, giving mixed support for equation 2.1 (table 2.3). The observed sex ratio appears to be not significantly different from that predicted in two species (gall thrips *Kladothrips rugosus* and parasitoid wasp *Bracon hebetor*), significantly higher in one species (social wasp *Polistes metricus*), and significantly lower in the other (western flower thrip *Frankliniella occidentalis*). However, there are a number of limitations with the predictions given in table 2.3. In *F. occidentalis*, females can become rapidly sperm depleted, depending on how many times

they mate, and older females produced less female biased sex ratios, suggesting that the proportion of constrained females (p) may be higher than that suggested, which would explain why the observed sex ratio is more female biased. In *B. hebetor*, local mate competition (chapters 4 and 5) may occur, which would also predict a female biased sex ratio (Ode et al. 1995, 1998). In *P. metricus*, the virgin females are unmated workers in orphaned nests. Consequently, the predicted sex ratio is extremely tentative, as it would be influenced by the relative productivity of different nest types, and there is the potential problem of differential investment in sons and daughters (chapters 6 and 7) and parent-offspring conflict over the sex ratio (chapter 9). The last two examples stress the general point that it can be hard to test equation 2.1 quantitatively with data from a single species, because multiple factors can influence sex allocation, analogous to the stated problem with static tests of Fisher's theory. A possibly more powerful way to test theory would be to compare the predicted and observed sex ratio across a number of species where the prevalence of virginity varies. An experimental evolution study in which the proportion of virgins was manipulated would be another possibility.

The possibility of facultative strategies has been tested by examining whether females adjust their offspring sex ratio in response to delays between reaching maturity and mating. Godfray (1990) argued that if virginity was a major cause of constrained reproduction, then longer delays before mating would suggest a higher proportion of similarly constrained females. Consequently, females would be predicted to produce a more female biased sex ratio after mating, when mating is delayed. He also pointed out that such a pattern has been observed in two parasitoid wasp species, one of which was *B. hebetor* (Hoelscher and Vinson 1971; Rotary and Gerling 1973; Godfray 1990). Since then, the same pattern has also been found with the parasitoid wasp *Aphelinus asychis* (Fauverge et al. 1998), but not with the sawfly *Strongylogaster osmundae* (Otsuka and Koshio 1999). It is worth noting that this predicted consequence of mating delay in haplodiploids is in the opposite direction to that predicted by Werren and Charnov's (1978) perturbation model (section 8.2.1), although Godfray's prediction can possibly be made more unambiguously, as it can arise due to a lack of males or low population density (the Werren and Charnov model requires the former).

2.6 CONCLUSIONS AND FUTURE DIRECTIONS

Fisher's theory predicts equal investment in male and female offspring. However, as I have touched upon here and will discuss in detail in section 7.2, the

conditions required for this are likely to be rare. Consequently, static tests of Fisher's theory that look for equal investment in the sexes are rarely likely to be appropriate. Instead, it is more useful to test the frequency dependence involved in Fisher's theory by perturbing the population sex ratio and then following the subsequent evolution. Another useful way of testing Fisher's theory is to couple it with unusual life histories to make novel predictions. Other useful cases, not discussed here, include thrips, where males are produced by viviparity and females are produced by oviparity (Crespi 1989, 1993), and brittle stars, where males are more likely to divide than females (McGovern 2002).

To conclude this chapter, what should we call Fisher's theory (or principle) of equal investment, given recent evidence that he was not the first to develop it? One option is to still call it Fisher's theory, as (1) this is its well-established name, and (2) Fisher's treatment was particularly clear and provided the key role in stimulating interest in this area. Another option is to call it the Düsing-Fisher theory of equal investment, to acknowledge both Düsing's precedence and Fisher's importance. For simplicity and continuity, I will take the first option in this book, although I see no problems with the latter option.

CHAPTER 3

Interactions between Relatives I: Cooperation and Competition

If members of one sex perform more altruistic acts toward kin of the opposite sex than the other way around, then one can show that parents will be selected to invest, on the average, more than 50 percent of their resources in producing offspring of the more altruistic sex.

—Trivers and Willard 1973, p. 179, n. 21

Biased sex allocation can be favored when relatives compete or cooperate over a very wide range of biological circumstances. Cooperation or competition between relatives has been suggested as an explanation for biased sex allocation in a variety of organisms, including birds, mammals, reptiles, insects, mealybugs, and plants. In some cases, there is strong empirical support for the predictions of theory. However, much of the work in this area is still at the suggestive phase. Previous empirical research has frequently (1) focused on overall population sex ratios, where unambiguous predictions can rarely be made, and (2) described biases in sex allocation, but without evidence demonstrating the fitness benefit of these biases—competition and cooperation are far too often assumed rather than being demonstrated. In addition, there is a lack of theory that can be applied to specific systems.

3.1 INTRODUCTION

Fisher's theory of equal investment in the sexes implicitly assumes that there are no competitive or cooperative (enhancing) interactions between relatives. If such interactions do occur, then biased sex allocation can be favored (Hamilton 1967). These situations can be broadly lumped into two categories: *local resource competition* (LRC) and *local resource enhancement* (LRE).

LRC occurs when production of one sex leads to relatively more competition between relatives for limiting resources (Clark 1978). In this case, selection favors overproduction of the sex that leads to less competition (Bulmer

and Taylor 1980a; Taylor 1981a). This possibility was first discussed by Hamilton (1967), who showed that when related males (brothers) compete for mates, a female biased sex allocation is favored. He called this process *local mate competition* (LMC) and argued that it could explain extremely female biased sex ratios in insects and mites. Since then it has been realized that LMC is just a special case of LRC, and that LRC can occur for a variety of reasons, favoring sex allocation biased toward either sex. For example, if daughters compete with their mothers for resources, then a male biased sex allocation can be favored, as has been argued to occur in some primates (Clark 1978).

LRE is the opposite situation, when production of one sex has a relatively enhancing effect on the fitness of relatives. In this case, selection favors an overproduction of that sex (Trivers and Willard 1973; Taylor 1981a). This possibility was first discussed by Trivers (Trivers and Willard 1973, p. 92, n. 21), who pointed out that when individuals of one sex are more altruistic to relatives, then selection could favor an overproduction of that sex. For example, in cooperatively breeding species, when individuals of one sex are more likely to stay and help raise other offspring, then selection could favor an overproduction of the helping sex (Trivers and Hare 1976, p. 262, n. 63).

In section 3.2, I describe the theoretical models that illustrate the basic features of LRC and LRE. A general point is that while predictions can sometimes be made about how offspring sex ratios should vary across the broods of different individuals, it can be much harder to predict overall population sex ratios (Wild and West 2007). In sections 3.3 and 3.4, I describe specific examples of LRC and LRE, respectively. A recurring issue in these areas is that specific models are often required to make predictions for specific cases; hence, I describe all relevant theory as we go along. There has been an enormous amount of work on LMC, and so I describe this separately, in chapters 4 and 5.

3.2 BASIC THEORY

In this section, I first discuss general models of how LRC and LRE can lead to biased sex allocation (section 3.2.1). I then go on to consider when split sex ratios should be expected (section 3.2.2) and the special case of LRE in cooperative breeding species (section 3.2.3).

3.2.1 GENERAL MODELS

Taylor (1981a) was the first to show how LRC and LRE could be united in a single theoretical framework. Consider the simplest case of a diploid species

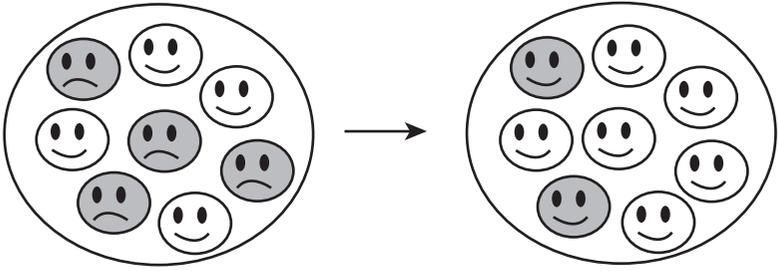
with nonoverlapping generations in which siblings can interact. In this case, the fitness of a female is given by the number of daughters that she produces multiplied by their reproductive value, plus the number of sons that she produces multiplied by their reproductive value. Reproductive value measures the genetic contribution of individuals to future generations (Fisher 1930; Grafen 2006a). Interactions between siblings can favor biased sex allocation because they cause the reproductive value of sons or daughters to depend on the number of sons and daughters produced, and hence the sex ratio.

For example, if daughters compete for resources (LRC), then the average reproductive value of a daughter will be negatively correlated with the number of daughters produced (Taylor 1981a). This favors the production of a male biased sex ratio to lessen competition between daughters and hence increase the average reproductive value of daughters (figure 3.1; Taylor 1981a; Charnov 1982; Frank 1986a). In contrast, if daughters cooperate (LRE), then the average fitness of a daughter will be positively correlated with the number of daughters produced. This would favor a female biased sex ratio to increase the number of daughters that can cooperate, and hence increase the average reproductive value of daughters (figure 3.1).

In all these cases, the evolutionary stable strategy (ESS) sex ratio will be determined by the effects of these interactions between relatives and the Fisherian frequency-dependent selection that provides a fitness advantage to the rarer sex (chapter 2). For example, consider the case where daughters cooperate, favoring a female biased sex ratio. As the sex ratio becomes increasingly female biased, this will increase the mating success of males. The ESS sex ratio will be that at which these two forces are balanced, and the marginal fitness gains from the production of sons and daughters are equal (Charnov 1982; Frank 1998b).

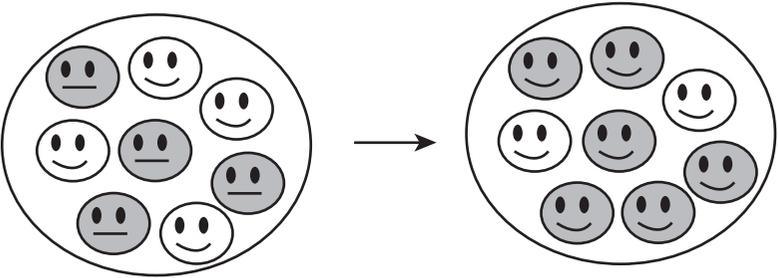
The preceding description focuses on the simplest possible case in order to illustrate the main principles. However, the ideas can be applied much more generally (Taylor 1981a). One particularly important point is that the preceding description considers only interactions between relatives within generations. Some cases of LRE and LRC will include more complicated interactions between relatives from different generations. For example, in primates, daughters may compete with mothers for reproductive resources (space, food; LRC, section 3.4.1), or in birds, sons may help their mothers rear additional offspring (LRE, section 3.3.1). The same general principles will apply in these cases, with a biased sex allocation favored to reduce competition or increase cooperation. A further complication arises with sex determination mechanisms such as haplodiploidy, which can cause mothers to be differently related to sons and daughters.

(A) LRC



Moving from an unbiased to a male-biased sex ratio
reduces LRC between females

(B) LRE



Moving from an unbiased to a female-biased sex ratio
increases the amount of cooperation between females

FIGURE 3.1. LRC and LRE. (a) LRC between females. If daughters (shaded; sons are unshaded) compete with each other for resources, then the reproductive value of daughters has a negative correlation with the number (or proportion) of daughters. Consequently, a male biased offspring sex ratio decreases this competition and increases the reproductive value of daughters. (b) LRE between females. If daughters cooperate with each other, then the reproductive value of daughters has a positive correlation with the number of daughters. A female biased offspring sex ratio takes advantage of this.

Another general point is that the prediction of biased sex ratios due to LRE and LRC do not rely on the population being split into groups, subgroups, or demes (see also sections 4.2.1 and 4.4.6). This has been most clearly demonstrated with LRC, where biased sex ratios can be shown to evolve in models that assume a specific multidimensional geographic structure without groups, and in which the amount of competition between relatives is varied by the average dispersal distances of the two sexes (Bulmer and Taylor 1980a; Taylor 1994b; de Jong et al. 2002). The general principle that arises from these models is that sex allocation will be biased toward the sex that competes less (Taylor 1981a; Wild and Taylor 2004). In many cases, the degree of competition will