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Part I

Sex ratio theory

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Chapter 1

Models of sex ratio evolution

Jon Seger & J. William Stubblefield

1.1 Summary

Our understanding of sex ratio evolution depends strongly on models that identify: (1) constraints on the production of male and female offspring, and (2) fitness consequences entailed by the production of different attainable brood sex ratios. Verbal and mathematical arguments by, among others, Darwin, Düsing, Fisher, and Shaw and Mohler established the fundamental principle that members of the minority sex tend to have higher fitness than members of the majority sex. They also outlined how various ecological, demographic and genetic variables might affect the details of sex-allocation strategies by modifying both the constraints and the fitness functions. Modern sex-allocation research is devoted largely to the exploration of such effects, which connect sex ratios to many other aspects of the biologies of many species. The models used in this work are of two general kinds: (1) expected-future-fitness or tracer-gene models that ask how a given sex allocation will affect the future frequencies of neutral genes carried by the allocating parent, and (2) explicit population-genetic models that consider the dynamics of alleles that determine alternative parental sex allocation phenotypes. Each kind of model has different strengths and weaknesses, and both are often essential to the full elucidation of a given problem.

1.2 Introduction

Males and females are produced in approximately equal numbers in most species with separate sexes, regardless of the mechanism of sex determination, and in most hermaphroditic species individuals expend approximately equal effort on male and female reproductive functions. Why should this be so? Sex allocation is a frequency-dependent evolutionary game (Charnov 1982, Maynard Smith 1982, Bulmer 1994). The basic principle that explains why balanced sex ratios evolve so often was described in a limited and tentative way by Darwin (1871), further developed by Karl Düsing (1883, 1884) and several early twentieth century authors, and then summarized concisely by RA Fisher in *The Genetical Theory of Natural Selection* (1930) (Edwards 1998, 2000). Subsequent work has generalized the principle and extended it to cover a great variety of special circumstances to which Fisher's elegant but elementary account does not apply.

Sex allocation is now remarkably well understood, and this understanding is often hailed as a triumph of evolutionary theory. However, to say that the fundamentals may be well understood is not to say that all of the interesting and important discoveries have been made. Despite its focus on a seemingly simple and singular phenomenon, sex-allocation research has become a rich and diverse enterprise that makes contact

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with many aspects of biology in a wide range of taxa. The field has continued to yield surprising phenomena and novel insights, and the pace of discovery shows no signs of slowing. The book you are now holding illustrates the field's amazing richness and describes many of the current research frontiers. But because the field is so large, not even a multi-authored volume can cover it all. Reviews of varying emphasis and scope have been provided by Williams (1979), Charnov (1982, 1993), Trivers (1985), Clutton-Brock (1986, 1991), Clutton-Brock and Iason (1986), Karlin and Lessard (1986), Nonacs (1986), Bull and Charnov (1988), Frank (1990, 1998), Wrensch and Ebbert (1993), Bulmer (1994), Godfray (1994), Bourke and Franks (1995), Crozier and Pamilo (1996), Herre *et al.* (1997), Klinkhamer *et al.* (1997), Hewison and Gaillard (1999) and West *et al.* (2000), among many other authors.

In this chapter we introduce the central principle of sex ratio evolution and some of the techniques used to model it. We emphasize basic concepts and issues that appear (at least implicitly) in all models, and we attempt to place these ideas in their historical context.

1.3 Models have always been central

Mathematical models are, and always have been, central to the study of sex ratios. Indeed, it is hard to think of any biological field, associated with specific phenotypes, that is more thoroughly model-driven. Population genetics is also model-driven in this sense, of course, but its models concern genes *in general*; the genes of population genetics are abstracted, intentionally, from any particular class of phenotypic effects.

The sex ratio, by contrast, could hardly be more concrete. This is sometimes forgotten, because every sexual species has a sex ratio (or at least allocation to male and female functions). But in fact the phenotype at issue (the relative numbers of two reproductive morphs) is in many ways an extremely particular and mundane fact of life. Even so, biologists from Darwin to the present have sensed an underlying generality of principle. They have spoken of 'the' sex ratio (singular), as if to understand the sex ratio of any *one* species would be (obviously) to understand the sex ratios of many *others*. Today we have good reasons to view 'the' sex ratio in this way, but most of these were unknown to Darwin. Nonetheless, he initiated the modern discussion of sex ratios, in *The Descent of Man and Selection in Relation to Sex* (1871), by describing the outlines of a quantitative, dynamical model that includes most of the essential features of everything that would follow. Formal mathematical analysis came later, as did direct connections to genetics, and these developments gave rise to a richness that Darwin could not have anticipated. Even so, he saw that there must be a simple underlying principle to be elucidated and then (by implication) applied to a broad diversity of special cases. We still see the subject in this way.

The principle emerges from an analysis of the reproductive consequences of an elementary but generic model of reproduction. The principle is then applied and extended by specifying details that may be left vague in the generic model, which is to say by modifying various implicit and explicit assumptions of the model.

Sex ratio modelling has been an extremely successful enterprise. This success can be attributed to three features of the relationship between the models and reality. First, the relevant biological factors can be specified and represented appropriately in simple mathematical expressions. Second, these factors can be observed and measured in nature, and many of them vary both within and among species in ways that are predicted to change the sex ratios produced by different individuals or species. Third, the fitness differences arising from sex ratio behaviours are often large, so real organisms are expected to show sex ratio modifications at least qualitatively like those predicted by theory, and in fact they often do. In this chapter we focus mainly on the first of these three features of sex ratio research: how biology is represented in models, and how the models are then analysed to uncover

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predictions that might (at least in principle) be tested in nature. Other chapters more thoroughly explore the variations that have been incorporated into sex ratio models, and the ways in which experimental and observational data have been used to test these models.

1.4 Darwin's argument

As its title implies, *The Descent of Man and Selection in Relation to Sex* (1871) is really two books merged into one. The book on human origins begins with Chapter I, 'The Evidence of the Descent of Man from some Lower Form', and the book on sexual selection begins with Chapter VIII, 'Principles of Sexual Selection'. Darwin opens the chapter by explaining that sexual selection is 'that kind of selection' that 'depends on the advantage which certain individuals have over other individuals of the same sex and species, in exclusive relation to reproduction' (page 256). Sexual selection is about *relative* advantage in the competition for mates, not about survival or absolute competence to reproduce.

> When the two sexes follow exactly the same habits of life, and the male has more highly developed sense or locomotive organs than the female, it may be that these in their perfected state are indispensable to the male for finding the female; but in the vast majority of cases, they serve only to give one male an advantage over another, for the less well-endowed males, if time were allowed them, would succeed in pairing with the females; and they would in all other respects, judging from the structure of the female, be equally well adapted for their ordinary habits of life.
>
> *(page 257)*

Darwin then describes several kinds of sex differences that seem to make sense on this principle; for example, the generally earlier emergence of male insects. He notes that the intensity of the competition for mates will be a function of the sex ratio and then opens a section titled 'Numerical Proportion of the Two Sexes' (page 263).

> I have remarked that sexual selection would be a simple affair if the males considerably exceeded in number the females. Hence I was led to investigate, as far as I could, the proportions between the two sexes of as many animals as possible; but the materials are scanty. I will here give only a brief abstract of the results, retaining the details for a supplementary discussion, so as not to interfere with the course of my argument. Domesticated animals alone afford the opportunity of ascertaining the proportional numbers at birth; but no records have been specially kept for this purpose. By indirect means, however, I have collected a considerable body of statistical data, from which it appears that with most of our domestic animals the sexes are nearly equal at birth.

Darwin's numbers show rough equality or modest male excesses at birth for various domestic species and for humans. He then points out that 'we are concerned with the proportion of the sexes, not at birth, but at maturity,' because that is when the competition for mates will occur. His data here are less definite, but they suggest greater male mortality and thus a relative *deficit* of males at maturity. However, 'The practice of polygamy leads to the same results as . . . an actual inequality . . . for if each male secures two or more females, many males will not be able to pair; and the latter assuredly will be the weaker or less attractive individuals.' Pages 266–279 then review patterns of polygamy and sexual dimorphism, and pages 279–300 discuss the 'laws of inheritance' of secondary sexual characters.

The chapter then returns to the problem of the sex ratio. Pages 300–315 present a detailed 'Supplement on the proportional numbers of the two sexes in animals belonging to various classes' (humans, horses, sheep, birds, fish and insects). A final short section 'On the Power of Natural Selection to regulate the proportional Numbers of the Sexes, and General Fertility' (pages 315–320) lays out the evolutionary argument. Its second paragraph (page 316) begins 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 equalized through natural selection? We may feel sure, from all characters being variable, that certain pairs

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> 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 the 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 equalization 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.

Parents that produce an excess of the minority sex will be 'more productive' because fewer of their offspring will be 'superfluous'. The paragraph says more of these offspring will 'survive', but this is illogical. Perhaps Darwin meant 'reproduce', or perhaps he was confused about the cause of the differential productivity. The paragraph asserts that parents of the minority sex will enjoy a productivity advantage, no matter which sex is 'produced in excess', and it indicates that the sex in excess will suffer increased failure to mate ('not uniting'). But does the paragraph show *how* these effects modulate parental fitness? It certainly contains all the elements and reaches the right conclusion, but it does not clearly explain why, or in what sense, parents of the minority sex are 'more productive'. In retrospect it comes extremely close (see Sober 1984, Bulmer 1994, Edwards 1998), but it does not explain what will happen in the generation of the parents' grandprogeny.

The next paragraph (pp. 317–318) presents both an advance and a retreat. The advance is an overt anticipation of the concept of parental expenditure or investment (as 'force'). In the previous paragraph, Darwin had explicitly noted the trade-off between numbers of male and numbers of female offspring; in this paragraph he explicitly notes the trade-off between offspring number and offspring quality. Parents that produce fewer 'superfluous males' but 'an equal number of productive females' would probably benefit, as a consequence, from 'larger and finer' ova or embryos, and 'their young [would be] better nurtured in the womb and afterwards.' In support of this idea, Darwin notes that inverse relationships between seed number and seed size can be seen both among and within species of plants. 'Hence the offspring of the parents which had wasted least force in producing superfluous males would be the most likely to survive, and would inherit the same tendency not to produce superfluous males, whilst retaining their full fertility in the production of females. So it would be with the converse case of [an excess of] the female sex.'

The retreat is a muddled explanation of the disadvantages experienced by 'superfluous' offspring. For purposes of argument, Darwin had begun the paragraph assuming that there was an excess of males, and that some parents produced fewer of them but a typical number of females. 'When the offspring from the more and the less male-productive parents were all mingled together, none would have any direct advantage over the others.' This is not true in the sense that he seems to intend. The offspring might be equivalent *individually* (leaving aside the 'indirect' benefits noted above), but not *collectively*; parents that produced more males would have more descendants *through males* than those that produced fewer males, given that the offspring 'were all mingled together'. In this sense sons are not 'superfluous' even when produced in excess. Darwin seems to be imagining that parents that contribute to the male excess will have no more grandoffspring through their sons (collectively) than those parents that refrain from producing excess males.

In the second edition of the *Descent* (1874), most of Chapter VIII is similar to that of the first edition, but the final section is completely different. It is renamed 'The proportion of the sexes in relation to natural selection', and it consists mainly of an inconclusive discussion of the relationship between sex-biased infanticide and the primary sex ratio. It concludes:

> 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

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> 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 numbers 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.

Why did Darwin abandon his own previous argument which was close to the 'solution' and clearly moving in the right direction? On one reading of the 1874 retraction, he considers the 1871 argument to be flawed by a reliance on species-benefit reasoning. Consistent with such an interpretation, the paragraph laying out the evolutionary argument (1871, p 316) includes an extraneous and confused aside on the adjustment of fertility, which we deleted from our earlier quotation.

> . . . But our supposed species would by this process be rendered, as just remarked, more productive; and this would in many cases be far from an advantage; for whenever the limit to the numbers which exist, depends, not on destruction by enemies, but on the amount of food, increased fertility will lead to severer competition and to most of the survivors being badly fed. In this case, if the sexes were equalized by an increase in the number of the females, a simultaneous decrease in the total number of the offspring would be beneficial, or even necessary, for the existence of the species; and this, I believe, could be effected through natural selection in the manner hereafter to be described.

Why Darwin should invoke, here, the concept of species' benefit (or need!) seems baffling. Two pages later, as promised, he describes in two paragraphs how reduced fertility (offspring number) could evolve by ordinary natural selection, given trade-offs between maintenance and reproduction, and between offspring number and quality. These two paragraphs end the chapter and brilliantly anticipate late-twentieth-century developments in life-history theory. They contain no species-benefit reasoning that we can detect. Darwin credits Herbert Spencer's *Principles of Biology* (1867) for inspiration on this subject.

It seems odd that Darwin should have lost his nerve and failed to correct confusions that were probably no worse than hundreds that he must have surmounted in other contexts. His decision to remove the entire argument from the second edition of the *Descent* (1874) can be taken to support the view that he never really understood the principle as well as a generous reading might suggest he did at the time he wrote it. He sees a close connection between sexual selection and the sex ratio: as the number of males competing for each productive mating increases, their average reproductive success must decrease. But he does not seem to recognize that he should directly compare the average fitnesses of males and females, and that he should evaluate the fitnesses of parents by counting their grandprogeny. In any case, his decision to remove the evolutionary argument from the second edition undoubtedly changed the history of behavioural ecology. The second edition was reprinted far more extensively than the first and became the edition read by almost everyone, including RA Fisher (Edwards 1998).

The recognition that sex ratios evolve through negatively frequency-dependent selection on the relative reproductive success of male and female offspring is traditionally attributed to Fisher (1930). His two-page verbal argument is informed by a knowledge of genes and it is far more lucid than Darwin's, but otherwise it is very similar in spirit. Why does Fisher not credit Darwin? One explanation is that, like most of his contemporaries, Fisher had read the second edition of the *Descent* and understandably failed to see any reason to persue Darwin's hint about what he 'formerly thought'. Edwards (1998) has shown that Darwin's initial lead was picked up by Düsing and several early twentieth century authors who further clarified the argument, and that Fisher was almost certainly aware of at least some of these later works. Why does Fisher not cite them either? Edwards suggests that Fisher understood his own account of the principle to be derived from these sources, that he assumed his interested contemporaries also would have been aware of them, and that standards of scholarly attribution were not as strict in 1930 as they are today. These factors could

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explain why Fisher (1930) presents the principle so casually.

1.5 The elements of a sex ratio model

A fully specified model of evolutionary adaptation can be viewed as a proposal showing how certain biological circumstances will give rise to a *fitness function* and a set of *constraints*. These relations are typically referred to as the *assumptions*, because the modeller is free, in principle, to change them in arbitrary ways. Models based on relatively 'realistic' assumptions are often considered more scientifically 'interesting' than those based on unrealistic assumptions, but, as Fisher himself points out in the preface to *The Genetical Theory of Natural Selection* (1930), models cannot really illuminate the natural world without also illuminating unnatural worlds. 'No practical biologist interested in sexual reproduction would be led to work out the detailed consequences experienced by organisms having three or more sexes; yet what else should he do if he wishes to understand why the sexes are, in fact, always two?' A model becomes explicitly mathematical when it embodies its assumptions ('three sexes', for example) in a set of formal quantitative relations that can be evaluated to reveal expected evolutionary outcomes. These deductions, following from the assumptions, can be interpreted as predictions about what would be expected to happen if the world actually worked as the assumptions propose it does. Such a derivation of expected consequences of the assumptions is often referred to as an *analysis* of the model.

There are two distinctive but complementary approaches to setting up and analysing explicit sex ratio models. The older, more intuitive and more expressive approach employs 'expected-future-fitness' calculations similar in spirit to those used in many inclusive-fitness and quantitative-genetic models. In this approach, sex-allocation strategies are evaluated with respect to the expected future frequencies of selectively neutral genes (tracers of descent) carried by an individual parent that exhibits a given sex ratio phenotype. The younger, more rigorous but less transparent approach employs dynamical population-genetic models to ask under what circumstances an allele that determines a specific parental sex ratio phenotype can invade (or fix) against an allele that determines a different phenotype. Both kinds of models can vary widely in sophistication and complexity. Neither is inherently 'better'; the choice of approach is largely a matter of taste and the nature of the problem being considered (see Bulmer 1994). We will illustrate both approaches.

Even in its original verbal form, the Darwin–Fisher argument is a legitimate (if primitive) sex ratio model. It is only marginally mathematical, but that does not disqualify it as a model. The relevant assumptions are clearly identified, most importantly: (1) that sex-specific fitness differences arise from an inevitable 'competition' for mates, which implies a *fitness function*, and (2) that parents that produce more sons (or daughters) must necessarily produce fewer daughters (or sons), which implies a *constraint*. The implicitly quantitative analysis proceeds as follows. Parents that overproduce the minority sex will have offspring that enjoy greater than average reproductive success, on average. Therefore, any heritable variants that tend to cause overproduction of the minority sex will increase in frequency, and as they do so the sex ratio imbalance will decrease. Because this is true no matter which sex is currently under-represented, there must be a stable evolutionary equilibrium at which male and female offspring are produced in approximately equal numbers. If all parents were to produce equal numbers of females and males, then no other sex ratio phenotype could increase under selection. Today we would call this unbeatable phenotype an 'evolutionarily stable strategy' or ESS (Maynard Smith & Price 1973).

1.6 Düsing's model

The first general mathematical treatment of sex ratio evolution has long been attributed to Shaw and Mohler (1953), who derived an elegant formalization of Fisher's argument. However,

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Edwards (1998), in reconstructing Fisher's sources, discovered that a similar mathematical treatment had been published almost 70 years earlier by Karl Düsing. His Ph.D. dissertation (Düsing 1883, expanded to book length in 1884) is mainly a study of factors associated with variation in progeny sex ratios in 'man, animals and plants' (e.g. maternal age and parity). In the early pages of this work, Düsing poses and answers a question that leads him to construct what is undoubtedly the first formal sex ratio model and perhaps the first mathematical model in evolutionary biology.

Given that animals vary their sex ratios in response to particular conditions of life, why do we not see large overall sex ratio imbalances? The reason, Düsing says, is that deviations from a balanced sex ratio will tend to be self-correcting: an excess of one sex provides a reason to produce more of the other. To make the argument concrete, he assumes a population in which there is a lack of females, and points out that *all the males together have the same number of offspring as all the females*. Because the latter are (by assumption) in the minority, each will have on average more offspring. For example, if there are x females and nx males, and if they produce z offspring in all, then each female will produce z/x offspring and each male will produce z/nx (Düsing 1884 p. 10, see Edwards 2000 for a full translation of the argument). He points out that if a female produced more female offspring, these daughters would produce, collectively, a larger than average number of offspring. Suppose a female produces A sons and a daughters, and another produces the converse (A daughters and a sons). The first will have

$$A\frac{z}{nx} + a\frac{z}{x} \tag{1.1}$$

grandchildren and the second will have

$$a\frac{z}{nx} + A\frac{z}{x}. \tag{1.2}$$

If we assume that $A > a$, such that $A = ba$ (with $b > 1$), then the first female will contribute

$$\frac{az}{x}\left[\frac{b}{n} + 1\right] \tag{1.3}$$

individuals to the second generation, while the second female will contribute

$$\frac{az}{x}\left[\frac{1}{n} + b\right] \tag{1.4}$$

which is

$$\frac{1 + bn}{b + n} \tag{1.5}$$

times as many. Düsing notes that if the population sex ratio is balanced ($n = 1$), then this expression evaluates to 1 for any sex ratio. *No matter what progeny sex ratio a female produces, she will have the same number of descendants in the second generation.* But not so if the sex ratio is unbalanced. For example, if there are twice as many males as females, then the ratio of grandchildren will be

$$\frac{1 + 2b}{b + 2} \tag{1.6}$$

as a function of the difference in progeny sex ratios (b). Düsing contrasts the fitnesses of two females for which $b = 3$; the one producing a threefold female excess has 7/5 as many grandchildren as the one producing a threefold male excess.

In less than two pages, Düsing both clarifies Darwin's argument and quantifies it. He identifies the key underlying fact that total male and female fitnesses must be equal; he identifies relative numbers of grandchildren as the appropriate measure of fitness; he writes a general expression for fitness as a function of the parent's progeny sex ratio b given the population sex ratio n; and he discovers that fitness is unaffected by progeny sex ratios if and only if the population sex ratio is balanced (in effect, the ESS argument). Having given a general theoretical reason why progeny sex ratio adjustment might be advantageous to individuals, he then embarks on a massive empirical review of such adjustments and their correlates in many species. Apparently this subject was as interesting and controversial in Düsing's time as it is today; his analyses of the patterns were much discussed, and his evolutionary model was forgotten (Edwards 1998, 2000, SH Orzack, pers. comm.).

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1.7 Fisher's equal-investment principle

Fisher's (1930) explanation of the sex ratio principle is as brief as Düsing's, but purely verbal and very well known, so we will not dwell on it here except to note that it presents a very important generalization of the earlier arguments. Fisher carefully considers the nature of the constraint on male and female offspring production, and discovers that the sex ratio equilibrium concerns the distribution of parental effort or 'expenditure' (later generalized by Trivers 1972 as 'investment'), not numbers *per se*. For example, suppose daughters are twice as costly to produce as sons. Then a parent with the resources to produce 12 sons might instead produce six daughters. What is the evolutionary equilibrium in this case? At a numerical sex ratio of 1:1 a typical parent could have four sons and four daughters. Males and females will have equal average reproductive success, so a rare male-specialist parent (with 12 sons) would have many more grandoffspring than an average parent (with eight offspring in all), and this advantage would increase the proportion of male-specialist parents (and males) in future generations. Only when males became twice as numerous as females (six sons and three daughters in a typical brood) would parents become evolutionarily indifferent to the sexes of their offspring. Sons would be only half as successful as daughters, but also only half as expensive. Thus, over the population as a whole, we expect to find equal expenditure or investment in the two sexes, not necessarily equal numbers.

This generalization leads immediately to testable predictions. In species where one sex is more costly (to parents) than the other, that sex should tend to be produced in correspondingly smaller numbers. This prediction has held up well in many recent studies of sexually dimorphic social and solitary Hymenoptera. Fisher was aware that human males suffer higher mortality rates in childhood than do females, rendering them less costly per infant born. He argues that the slight but conspicuous male excess at birth is plausibly an adjustment to equalize overall investment in the sexes (at least under patterns of mortality that would have existed in early human societies). This example illustrates the logic that has been used many times since then to connect sex allocation with other aspects of biology.

1.8 Genetic models I: tracer genes and the Shaw–Mohler equation

Shaw and Mohler (1953) set out to formalize Fisher's argument and connect it more closely to genetics. Their model is extremely simple and transparent, and it forms the basis of most subsequent sex ratio models. The key idea is to calculate the contribution that a parent in one generation (P) makes to the gene pool in the second descending generation (that of its offspring's offspring, G_2), if the parent produces a sex ratio x (proportion males) in the G_1 (offspring) generation where the average sex ratio is X. The focal parent produces n offspring in all, and the population at large produces N. In G_1 there will be NX males and 'all together they will supply half the genes which are transmitted from G_1 to G_2', so each male's share will be $1/2NX$. The focal parent's sons therefore contribute $nx/2NX$ of the genes in G_2, and its daughters contribute $n(1-x)/2N(1-X)$, for a total of

$$\frac{1}{2}\left[\frac{nx}{NX}+\frac{n(1-x)}{N(1-X)}\right]. \tag{1.7}$$

The parent contributes half of the genes carried by each of its nx sons and $n(1-x)$ daughters in G_1, so its net genetic contribution to G_2 is

$$C=\frac{1}{4}\left[\frac{nx}{NX}+\frac{n(1-x)}{N(1-X)}\right], \tag{1.8}$$

or

$$C=\frac{1}{4}\left(\frac{m}{M}+\frac{f}{F}\right), \tag{1.9}$$

'where m and f are the numbers of male and female zygotes in the [focal] progeny while M and F stand for the corresponding numbers in the entire G_1'. C is a measure of genetic fitness because it can be interpreted as the expected frequency in

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future generations of a selectively neutral tracer allele that in generation P was carried only by the focal parent. If the population sex ratio is balanced ($X = 1/2$), then $C = n/2N$ independent of the focal parent's sex ratio (as long as n does not depend on x). But if X is any other value, then some sex ratios x will give rise to larger contributions than others. 'The gene or genes favored are always those whose increase will shift the population sex ratio (X) toward 0.5.'

The paper goes on to show that the equilibrium progeny sex ratio is not affected if male and female offspring, once produced, survive to adulthood with different probabilities; these probabilities cancel out of the expressions for m/M and f/F. Curiously, the paper does *not* extend the analysis to include sexually dimorphic mortality rates *during* the period of parental care, or other sources of differential offspring *costs*, even though Fisher considered this extension verbally and noted the implication that m, M, f and F can be interpreted more generally as net parental expenditures on behalf of male and female offspring. Bodmer and Edwards (1960) modelled Fisher's argument by writing an expression for the reproductive value produced by a unit of parental expenditure, given sex-specific intrinsic costs and probabilities of surviving the period of parental care. This *rate of return* measures 'the selective advantage attached to reproduction with particular sex and parental expenditure ratios'; it is independent of the focal parent's progeny sex ratio when 'the total parental expenditure incurred in respect of children of each sex is equal', confirming 'Fisher's Law'.

Because the *total* (population-wide) male and female investments M and F are directly proportional to the *average* (individual) investments, we are free to normalize the Shaw–Mohler equation to give an average fitness of 1, in keeping with modern conventions in other areas of population genetics

$$W = \frac{1}{2}\left(\frac{f}{F} + \frac{m}{M}\right), \tag{1.10}$$

where F is the average value of f in the population and M is the average value of m. A simple analysis that explicitly incorporates differential costs can then be carried out as follows. The constraint on allowable combinations of female and male offspring can be represented by an equation that specifies the number of daughters that a parent will produce if it also produces m sons. For example, assume the simplest kind of linear trade-off between male and female production, and let each daughter cost c times as much as a son. Then the constraint is $cf + m = r$, or

$$f = \frac{r - m}{c}, \tag{1.11}$$

where r is the total resource available for offspring production (in units of the cost of a son). Substituting the constraint (eq. 1.11) into the fitness function (eq. 1.10) we get

$$W = \frac{1}{2}\left(\frac{\frac{r-m}{c}}{\frac{R-M}{c}} + \frac{m}{M}\right). \tag{1.12}$$

Note that the relative cost of a female (c) cancels out, and that without any loss of generality we are free to set the average resource (R) equal to 1. Thus the constrained fitness function simplifies to

$$W = \frac{1}{2}\left(\frac{r-m}{1-m} + \frac{m}{M}\right). \tag{1.13}$$

What sex ratio (m) will maximize our parent's fitness, given that it has r units of resource? Of course we already know what the answer is supposed to be: parents should expend equal amounts of resource on each sex. If that's what *typical* parents are doing, then $M = {}^1/_2$, and the fitness function further simplifies to

$$W = [(r - m) + (m)] = r. \tag{1.14}$$

Now the parent's sex allocation (m) also cancels out, and its fitness is simply equal to its resource pool. We have explicitly derived the result that each parent is indifferent to the sexes of its own offspring, even where male and female costs differ, as long as there is equal overall *investment* in the population at large ($M = {}^1/_2$).

Of course parents are far from indifferent when overall investment is not equal, and the Shaw–Mohler equation quantifies the fitness differences associated with atypical ('mutant') progeny sex ratios in populations that are away from the evolutionary equilibrium (Figure 1.1). Not only do parents that invest equally in sons and daughters do better than average when most other parents are investing unequally, but parents that over-compensate do even better, and

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