Possible factors influencing vertebrate sex ratios: an introductory overview

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Abstract

Sex ratio theory is one of the more developed areas of evolutionary ecology, yet adaptive explanations for sex ratio variation among vertebrates are still the subject of much debate and uncertainty, partly because it can be difficult to infer process from pattern and adaptive and non-adaptive explanations may be confounding. In this introductory overview, I consider factors which may influence vertebrate sex ratios. I first consider 'theoretical factors', i.e. the adaptive value of the control of offspring sex ratio to parents. I then examine 'empirical factors' which influence parental ability to control offspring sex ratio, focusing on potential constraints imposed by sex determination mechanisms. Finally, I outline some of the evidence for the influence of these factors on sex ratios. © 1997 Elsevier Science B.V.

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1. Introduction

"In most species of animals that can be observed with the naked eye without bending down, about as many males as females are born" (translated from Nagelkerke, 1993). Historically, the study of the sex ratio began with such observations and there followed theories to account for them. Further observations, often stimulated by theory, showed that things were sometimes not quite so simple in large animals. In addition, those biologists prepared to bend down observed many invertebrate species in which there is a distinct majority of females. Research aimed at understanding the evolution of sex ratios has now proliferated hugely, creating a vast literature. It is here my task to provide an overview of factors which may influence the sex ratio, as a general introduction to the
following, more specific, papers in this workshop. I thus do not attempt an exhaustive account. The influential factors I consider are 'theoretical' (what animals 'should' do if they have control over the sex of their offspring, i.e. the adaptive importance of sex ratios) and 'empirical' (whether animals can achieve this control). I thus do not consider all possible types of 'empirical' factors which may influence the sex ratio (e.g. those reported by Clark et al., 1993). Finally, I consider evidence for the sex ratios animals do produce in the context of these theoretical and empirical influences. In the 'can' and 'do' sections, I concentrate on mammals and birds (and thus do not dwell on the sex ratio in fish, amphibia, reptiles or invertebrates). My task has been made both more easy and more difficult by the existence of many previous reviews (e.g. Williams, 1979; Charnov, 1982; Bull, 1983; Clutton-Brock, 1986, 1991; Clutton-Brock and Iason, 1986; Hrdy, 1987; Bull and Charnov, 1988; Cockburn, 1990; Frank, 1990; Gowaty, 1991; Hiraiwa-Hasegawa, 1993; Wrensch and Ebbert, 1993; Godfray, 1994; Krackow, 1995): more easy because these provide excellent summaries of the literature, and more difficult because they have left little unsaid. I hope to paint the broad picture and recommend the above reviews, and the primary literature, to the reader requiring more detail. An eminently readable and recent introductory account of the evolution of sex and sex ratio is provided by Ridley (1993).

2. Sex ratio: the problem, its origin and its solutions

Why did sex evolve and why has it been retained? Given that there is sex, why are there distinct 'sexes' and how many sexes are there? Given that there are two sexes, is one more common than the other and why? Some organisms are asexual, some have 'indistinct' sexes and some have more than two 'sexes': I am not concerned with these here and address only the latter of the above questions. In the remainder of this section I outline some theories which predict optimal progeny sex ratio under a range of circumstances. The following sections consider whether animals have the ability to produce sex ratios in accordance with theoretical predictions and whether they do.

3. The starting point: Fisher's theory of equal investment

It is well known that Darwin (1871) considered the evolution of sex ratios, but left the solution for the future. In 1930, R.A. Fisher proposed an explanation for the sex ratio equality observed in many animal species. Fisher (1930) predicted that population sex ratio biases are returned to equality because of a frequency dependent reproductive advantage of the rarer sex. Briefly, Fisher's argument is that in a population with a biased sex ratio, offspring belonging to the rarer sex have better mating prospects than those belonging to the more common sex. Parents with a genetic tendency to produce more of the rarer sex than the more common sex thus attain a higher than average number of grandchildren. The tendency to produce the rare sex becomes more widespread in the population, and thus the sex ratio bias decreases. The advantage associated with the production of the rare sex decreases with reduction in the extent of sex ratio bias.
Hence, frequency dependent selection returns sex ratio biases to equality. These arguments apply equally to biases in favour of either sex.

Strictly, Fisher's model applies to the ratio of investment required to produce the sexes rather than to the numerical sex ratio. Hence, if one sex were twice as costly to produce as the other, it would be produced half as frequently: the numerical ratio would be biased but the investment ratio would not. Fisher's arguments also apply to the primary sex ratio (at birth, or, in species with post-natal care, at the end of parental investment).

The prediction of equal investment is insensitive to some details of an animal's life history (but not others, see below). For example, it is unaffected by differential mortality between the sexes (after parental investment has terminated): a greater developmental mortality in one sex is exactly compensated for by the increased reproductive success enjoyed by the survivors of that sex (Leigh, 1970). Analogously, the prediction is also unaffected by whether species are monogamous or polygamous: if a few males monopolise mating with females (all of whom mate), the variance in mating success will be low in females but high in males. Despite this difference in variance, the mean reproductive success will be equal between males and females: although mothers producing sons will run the risk that these may never mate, they will be compensated by the enormous rewards of producing sons which do (Bull and Charnov, 1988). I return to this scenario under a slightly different set of assumptions below (see the Trivers-Willard hypothesis).

Fisher's theory predicted the population's mean sex ratio but not the distribution of sex ratios within families or groups (= sex ratio variance). Kolman (1960) showed that, provided the equilibrium population sex ratio is at equality, the sex ratio within groups of offspring is not acted on by natural selection. Kolman's theory leads to expectations of a greater than binomial (overdispersed) variance in family sex ratio in an infinite population. When population sex ratio is perturbed from equilibrium, selection would favour genotypes which (due to genetic drift while at sex ratio equilibrium) over- or under-produced the rare sex (the predicted variance should conform to a Lexian binomial distribution) (Williams, 1979; Harmsen and Cooke, 1983). In small populations (a violation of one of Fisher's and Kolman's assumptions) selection is predicted to reduce the sex ratio variance (Verner, 1965; see also Williams, 1979; Taylor and Sauer, 1980).

4. Subsequent theoretical developments: relaxing Fisher's assumptions

Fisher's model is based on a number of implicit assumptions, which subsequent sex ratio research has elucidated and relaxed (e.g. Williams, 1979; Maynard Smith, 1980; Bull and Charnov, 1988; Frank, 1990; Godfray, 1994). This has led to many new models, most of which have arisen from empirical observations that animals may not meet Fisher's assumptions or predictions. As Myers (1978) put it: "because [Fisher's] theory predicts equal production of the two sexes, any deviation from equality invites interpretation, and prods the imaginations of theoreticians". A similar process has led to the modification and development of theories subsequent to Fisher's. In the following
sections I outline some of the most important modifications which have emerged as a result of such 'prodding'; I make scant reference to empirical work, which is considered in later sections.

4.1. Differential investment returns due to group structure: sexually differential dispersal and competition among kin

One of the assumptions underlying the prediction by Fisher (1930) of equal investment is that the relationship between fitness returns and resource allocation is identical for both sexes. This assumption is violated by 'group structure' if individuals living in groups interact more with each other than members of the rest of the population and the effects of this interaction are sexually differential. There have been many extensions to Fisher's theory which assume group structured interactions. These models predict that competition among same-sex siblings favours a reduction in the sex that competes more severely, leading to sex ratio bias. When interactions are cooperative rather competitive, the direction of the bias may be reversed.

4.1.1. The theory of local mate competition

The theory put forward by Hamilton (1967) of local mate competition (LMC) was the first to consider the effects of group structure on the sex ratio. LMC theory considers violations of Fisher's assumption of panmictic mating. It assumes that offspring mature in discrete and ephemeral groups, mating among themselves before the daughters disperse. Unmated daughters and all sons are assumed not to disperse from the natal group (this assumption, and models which relax it, is reviewed by Hardy, 1994). Under the LMC assumptions, brothers compete among themselves for mating opportunities with females (these constitute a limiting resource). The fitness returns from adding males to an offspring group are diminishing, but those from adding females are not (if optimal clutch size arguments are conveniently ignored); in other words, the fitness of a son depends on the family sex ratio. LMC theory predicts that the optimal progeny sex ratio for mothers to produce depends strongly on the number of other mothers contributing offspring to the mating group. When few mothers contribute offspring, progeny sex ratios should be highly female biased. When many females contribute progeny and panmixis is approached, sex ratios are predicted to approximate sex ratio equality.

Hamilton's LMC theory has stimulated a vast amount of empirical and theoretical research. The theory has been extended in numerous ways (reviewed by e.g. Hardy, 1992, 1994; Antolin, 1993; Luck et al., 1993; Godfray, 1994), generating a number of predictions, further to mean sex ratio bias, which differ from those under Fisher's assumptions. In contrast to its lack of influence on Fisherian primary sex ratios, under LMC post-investment differential mortality between the sexes may be an important selective factor affecting the primary sex ratio (Nagelkerke and Hardy, 1994). The insensitivity of Fisher's sex ratio prediction to the degree of polygamy also no longer applies under LMC: limited male ability to mate with females can increase the predicted sex ratio (Hartl, 1971; see also Stenseth, 1978). In addition, the prediction (Kolman, 1960) of the selective neutrality of group sex ratio variance (at sex ratio equilibrium) is
no longer valid under LMC: model predictions suggest that low sex ratio variance is favoured (Green et al., 1982; Nagelkerke, 1993; Nagelkerke and Hardy, 1994; Nagelkerke, 1996).

4.1.2. The theory of local resource competition

Local resource competition (LRC) theory is similar to LMC in that it considers the mother’s response to sexually differential competition among her offspring. The contested ‘resources’ extend beyond mating opportunities to food, territory, etc. (in fact, LRC is simply a more general statement of LMC, see Hoogland, 1981). Like LMC, LRC theory predicts that mothers should reduce competition among their offspring by biasing the sex ratio towards the sex that competes least for limiting resources (competition can be between parent and offspring or sibling and sibling). Sexually differential competition can arise if one sex disperses from the natal group while the other remains in or nearer to, or disperses later from, the natal area (Gowaty, 1993). If male dispersal is greater (and if dispersal is directionally random), competitive interactions for resources will be greater between female than male relatives and hence a male biased population sex ratio is predicted (e.g. Clark, 1978; Silk, 1984; Bulmer, 1986; Cockburn, 1990; Gowaty, 1993; Hiraiwa-Hasegawa, 1993; (a critical assessment of Clark’s original model is provided by Masters et al., 1982)).

4.1.3. The theory of local resource enhancement

Local resource enhancement (LRE) is the converse of LRC (although there is no theoretical incompatibility). When the non-dispersing sex helps rather than competes with the mother (e.g. in species with sex-biased cooperative breeding), sex ratios are expected to be biased towards the sex which does not disperse (Gowaty and Lennartz, 1985; Emlen et al., 1986; Lessells and Avery, 1987). If cohesive and cooperative groups disperse (i.e. dispersal is non-random), LRE type effects may also operate to favour the dispersing sex (Packer and Pusey, 1987).

4.2. Differential investment returns due to environmental effects

Fisher’s assumption that the relationship between fitness returns and resource allocation is identical for both sexes is violated if the fitness of the individuals of one sex is more adversely affected by some aspect of the environment (the classic example being a lack of parental investment during development) than the other. A series of models has been developed which predict adaptive sex allocation in response to sexually differential returns from investment in progeny (e.g. Trivers and Willard, 1973; Charnov, 1979; Maynard Smith, 1980; Charnov, 1982; Frank, 1990). The starting point for this line of theoretical developments has been the Trivers-Willard hypothesis, which does not consider group structure (see above). However, Trivers-Willard type effects may also be expected in group living species and several modifications have included this as a predicted influence on the sex ratio.

4.2.1. The Trivers-Willard hypothesis: sex ratio according to maternal condition

Trivers and Willard (1973) proposed that when one sex gains more than the other from extra parental investment, parents with relatively more resources to invest (e.g.
parents in good condition) will bias their allocation toward the sex with the greater rate of reproductive returns (interestingly the theory may be a lot older than is generally believed, and precede even Darwin's thoughts on the sex ratio, see Watson, 1982a). The theory was developed for polygynous species in which a few males dominate harems of females and many males never have (or have fewer) mating opportunities. If a mother is able, via her investment (parental care), to influence the success of her offspring, then mothers in good condition are likely to produce male and female offspring of above average success. Conversely, mothers in poor condition (with little resource to invest) are likely to produce relatively unsuccessful offspring. As noted above, although the average mating success of males and females is equal, success varies more among males than females. Owing to this larger variation among males, sons of mothers in good condition are likely to achieve a much higher mating success than daughters produced by mothers in good condition. Similarly, sons of poor quality mothers are likely to have very low success but daughters will fare much better (almost as well as daughters of good quality mothers). Hence, Trivers and Willard's prediction that good condition mothers should produce sons and poor condition mothers should produce daughters.

The original Trivers-Willard hypothesis applies to species in which the litter or clutch size is one. Williams (1979) and McGinley (1984) have pointed out that if mothers produce varying numbers of offspring the predictions may be changed. If each mother has a fixed total amount of resource to invest, but good condition mothers have more than poor condition mothers, then good condition mothers may be expected to produce more offspring than poor quality mothers. However, good condition mothers may invest fewer resources per offspring than poor condition mothers: according to Trivers-Willard reasoning, poor condition mothers should produce more sons (but fewer offspring in total) than good condition mothers. A prediction opposite to the original!

A number of studies have examined the notion of 'condition' in more detail. Parental 'condition' may vary in a number of ways, such as 'social rank' (discussed below), which may mean that a particular resource may not be 'fully transferable' between the sexes. This and other modifications and alternatives to the Trivers-Willard hypothesis is further discussed by Burley (1982) and Clutton-Brock (1991). The hypothesis has not been without its critics (Ridley, 1993). Myers (1978), for example, criticised it on mainly empirical grounds, and proposed an alternative hypothesis that poor environmental conditions will lead to a production of the cheaper sex, which allows maximisation of the numbers of offspring produced. For example, poor condition mothers, which have insufficient resources to produce an offspring of the more expensive sex, may have the choice of producing no offspring or one offspring of the cheaper sex. Myers' approach has itself been criticised: Oksanen (1981) pointed out that Myers' assumption that reducing the number of offspring does not enhance the survival of the mother or her female offspring is likely to be artificial.

The Trivers-Willard hypothesis concerns family-level sex ratio adjustment in relation to a mother's ability to invest in progeny. However, the hypothesis has consequences for the sex ratio at the population level even though it remains difficult to make a general prediction (Frank, 1987, 1990; Frank and Swingland, 1988). Frank (1990) further points out that it has often, and incorrectly, been assumed that due to the selective neutrality of sex ratio variation in populations at Fisherian equilibrium (Kolman, 1960), the Trivers-
Willard family level effect and the Fisherian population level effect can co-exist. This cannot be the case since the assumptions of returns for investment made by the two theories are different. Under the assumptions of the Trivers–Willard hypothesis, sex ratio variance is expected to be greater than binomial (overdispersed) (Williams, 1979).

4.2.2. The advantaged daughter hypothesis: sex ratio according to maternal rank

In some primate species, daughters remain in their natal groups and tend to inherit the social ranks of their mothers and may thus achieve higher reproductive success than daughters of lower ranking females. Sons, however, disperse from the natal group and the social rank (and hence reproductive success) they achieve may be independent of their mother's rank. Hence, high ranking mothers should produce daughters, while low ranking mothers should produce sons (see Hiraiwa-Hasegawa, 1993).

Although this prediction may seem the opposite of that of the Trivers–Willard hypothesis (good quality mothers should invest in sons, not daughters), there is actually no theoretical discrepancy. In its wider sense, the Trivers–Willard hypothesis predicts that 'good quality' (e.g. in good physical condition or high ranking) mothers should invest more heavily in the sex which benefits most from resource (rank, maternal milk, etc.) investment. Which sex this is, for example in a primate society, presumably depends on the relative importance of nutritional and social privileges received by good quality mothers' offspring.

4.2.3. Silk's hypothesis: advantaged daughters and local resource competition

Both local resource competition theory (for population level sex ratio phenomena) and the advantaged daughter hypothesis (for family-level sex ratio phenomena) were developed as a result of studying primate societies. It is thus not surprising that elements of the two ideas have been combined to explain birth sex ratios in relation to maternal rank in species with both sexually differential dispersal and within-group social structure (Silk, 1983). If males disperse and females tend to remain in the natal group (groups are assumed to be large, containing more than just close relatives), females will compete more amongst themselves for resources than will males: LRC theory predicts a population-wide male biased sex ratio (see above). If females attempt to reduce recruitment of immature females into the group (in order to reduce competition) and if the success of these attempts depends on their rank relative to that of the mother of the immature, then low ranking females should produce fewer daughters than sons since their daughters may be prevented from securing a place in the group. The entry of daughters of higher ranking mothers into the group will, however, be safeguarded by their mother's social standing (see Hiraiwa-Hasegawa, 1993). Thus, both the advantaged daughter hypothesis and Silk's modification of LRC predict that the sex ratio will be dependent on maternal rank, and a uniform sex ratio bias (as predicted by LRC theory) is not expected.

Note that in this scenario both group structure and differential investment returns play a role in influencing optimal sex ratio, while (historically) each began as a separate set of modifications to Fisher's model. A very similar fusion of theory has been made by researchers considering sex ratio in parasitoid wasps. As outlined above, Hamilton formulated LMC theory by considering group structure. In a separate modification of
Fisher's theory, Charnov et al. (1981) predicted optimal sex allocation when parasitoid host quality (analogous to maternal quality) varies and influences females relatively more strongly than males (this is in essence a version of the Trivers-Willard hypothesis). These two developments were later combined to consider host quality effects under group structured mating (Werren, 1984; further developments are reviewed by Hardy, 1994). A fully integrated sex ratio theory, considering all possible influences, is likely to prove unsatisfactorily intractable, but it is encouraging to observe the merging of initially disparate developments.

4.2.4. The first cohort advantage hypothesis: sex ratio according to reproductive timing

The latest modification of Trivers-Willard type arguments has been made by Wright et al. (1995) and arose from a study of polygynous opossums. When mothers produce two litters of young, offspring of the first litter are larger than those in the second litter. Owing to the size difference, males from the first litter (cohort) have a mating advantage over second cohort males: thus mothers should produce more males in their first than in their second litter.

4.3. Some further considerations: non-Mendelian inheritance and gene-culture coevolution models

I conclude this section by briefly noting two 'unusual' influences on the sex ratio. Fisher's original model assumed that each offspring has two parents and that sex ratio genes are autosomal and segregate in a Mendelian fashion. However, both these assumptions may sometimes be violated. For instance, segregation distortion can alter the production of X- and Y-bearing gametes in the heterogametic sex, and 'cytoplasmic factors' (which exhibit uniparental inheritance and non-Mendelian segregation) can skew the sex ratio markedly. These effects almost certainly occur in invertebrates more frequently than in vertebrates (see reviews by Bull and Charnov, 1988; Cockburn, 1990; Wrensch and Ebbert, 1993; Godfray, 1994 for entries into the theoretical and empirical literature), although there is a tantalising hint that humans may also be occasionally affected (see Ridley, 1993, p. 104).

Finally, in societies in which there is a cultural preference for offspring of one sex, primary sex ratios may be influenced. Recent models (Kumm et al., 1994; see also Judson, 1994) have included cultural practices as a trait which is passed on from parent to offspring. Kumm et al. (1994) were specifically interested in the practice of sex biased infanticide (or abortion, neglect or abandonment) which is widespread in many (particularly Asian) human societies (e.g. Hrdy, 1987; Tuljapurkar et al., 1995). Usually it is females which are the least preferred sex. The effect of sex biased infanticide on the primary sex ratio is predicted to depend on whether or not there is an associated fitness cost to the parents. If infanticide reduces the total number of offspring produced (i.e. the offspring killed cannot be fully replaced) then parents with a genetic tendency to produce the preferred sex (males) will be selectively favoured and the primary sex ratio will become male biased. However, if there are no fitness costs in terms of future reproductive output associated with infanticide (for example in China where the 'one child policy' means that parents are limited to a maximum of only one offspring and are
thus able to replace fully an aborted or killed daughter with a son) then the primary sex ratio becomes female biased, due to Fisherian frequency dependent selection for the rarer sex. Thus, infanticide will become increasingly more common and birth sex ratio increasingly more biased. There is no concrete evidence as to whether these model predictions have any relevance to real phenomena, but some ‘straws in the wind’ suggest that they may (e.g. Judson, 1994).

5. Sex determination mechanisms and constraints to sex allocation control

Theory highlights the adaptive value of control of offspring sex (note that sex ratio models usually assume that mothers control the sex ratio, although some assume some degree of constraint, e.g. Maynard Smith, 1980; Frank, 1987). Here I consider whether animals possess mechanisms which allow them this control, focusing on the mechanism of sex determination. A bewildering variety of sex determination mechanisms is found among animals (e.g. Bull, 1983; Janzen and Paukstis, 1991; Cook, 1993; Mittwoch, 1996). Sex determination mechanisms can be genetic or environmental. Both types are found among vertebrates. In this section I outline several sex determination mechanisms and consider some consequences for sex ratio control. It should be noted that there may be both adaptive and non-adaptive explanations for an observed sex ratio; the non-adaptive explanations arising as incidental side effects of sex determination processes or animal physiology. This area remains controversial and unresolved, particularly for heterogametic vertebrates (e.g. Williams, 1979; Huck et al., 1990; Krackow, 1995).

5.1. Environmental sex determination

Some fish and reptiles have environmental sex determination. In some fish species, gender is controlled by the ‘social environment’ and an individual may switch sexes once or even many times during its lifetime (Crews, 1994). In these species the ‘sex ratio decision’ is made by the individual and not by its parent. In some fish, amphibians and reptiles (all crocodilians, many turtles and some lizards) the incubation temperature of the embryo controls the individual’s sex, which then remains fixed (Bull and Charnov, 1989; Janzen and Paukstis, 1991; Crews, 1994; Mittwoch, 1996). When groups of embryos are incubated at the extremes of the normal temperature range, all hatchlings are the same sex (sex ratio bias does not result solely from differential mortality), while at intermediate temperatures both sexes may be produced within a brood (Harrey et al., 1995). There is variation between species in whether males or females are produced at extreme temperatures, in some species males are produced at cooler temperatures and females at warmer temperatures, and in other species the reverse is the case. A further variant is the production of females at both extremes and males at intermediate temperatures (Bull and Charnov, 1989). By their egg-laying behaviour, mothers can exert some control over the sex, and thus sex ratio of their progeny. Temperature dependent sex determination does not per se lead to the expectation that any particular sex ratio will be, on average, produced (however, it does perhaps generate the expectation of a overdispersed clutch sex ratio variance).
5.2. Genetic sex determination

Most genetic sex determination mechanisms can be classified as diplo-diploid or haplo-diploid (there are exceptions, e.g. aphids, see Foster and Benton, 1992).

5.2.1. Haplo-diploidy: arrhenotoky and pseudo-arrhenotoky

To my knowledge, all haplo-diploid species are invertebrates, and are either arrhenotokous (e.g. many Hymenoptera, spider mites and Thysanoptera; Wrensch and Ebbert, 1993) or pseudo-arrhenotokous (e.g. phytoseiid mites, Sabelis and Nagelkerke, 1993). It is useful to consider these briefly as a contrast to the diplo-diploid, heterogametic vertebrates discussed below.

Under arrhenotoky, fertilised (diploid) eggs generally develop into female offspring and unfertilised (haploid) eggs into males. Once mated, females store sperm in the spermatheca (a sperm storage organ), and potentially control the sex of offspring by regulating the fertilisation of eggs (e.g. Gerber and Klostermeyer, 1970). The association between sex and ploidy can be explained by genetic balance and allelic diversity models (Cook, 1993; Luck et al., 1993). Allelic diversity models assume that female offspring are heterozygous at sex-determining loci and male offspring are either homozygous diploids (which are often inviable) or hemizygous (haploids). When allelic diversity is low (e.g. owing to inbreeding) the sex of diploid progeny is not completely under maternal control (Cook and Crozier, 1995). A further consequence of arrhenotoky is that virgin females are able to reproduce but are constrained to produce male offspring only. Whether this constitutes a disadvantage for virgin females depends on both the mating structure of the population and the sex ratios produced by other females (Godfray, 1990).

Under pseudo-arrhenotoky, males arise from fertilised eggs but become haploid after inactivation and/or elimination of the paternal chromosome set. This is also under maternal control (Sabelis and Nagelkerke, 1987; Nagelkerke and Sabelis, 1991). Because sperm are required for son production, virgin females in pseudo-arrhenotokous species cannot reproduce.

Haplo-diploid sex determination generally provides females with a large degree of control over the sex of their offspring. Furthermore, there is generally no a priori reason to expect that the mechanism may automatically generate any particular sex ratio. In this sense, and somewhat like animals with temperature dependent sex determination, sex ratio decisions in haplo-diploids are generally 'unconstrained'.

5.2.2. Diplo-diploidy: heterogamety

Many diplo-diploid species have an XY-like chromosomal, or heterogametic, sex determination mechanism. In these the sex chromosomes inherited at the time of fertilisation dictate whether an individual develops as a male or as a female; one sex is heterogametic (e.g. XY is male) and the other homogametic (e.g. XX is female). Many insects have chromosomal sex determination, and among vertebrates it is found in mammals and birds, as well as some reptiles (Bull and Charnov, 1988; Harrey et al., 1995).
I have argued above that environmental sex determination mechanisms and haplo-diploidy are, in general, unlikely to constrain the achievement of a particular sex ratio. At least, sex ratios are not expected a priori from consideration of the sex determination mechanism alone (however, asymmetric relatedness between kin which arises as a result of haplo-diploidy can influence sex ratios under specific sets of conditions). In contrast, heterogamety is thought to put severe constraints on the production of biased sex ratios (Hamilton, 1979; Bull and Charnov, 1988) and on the control of sex ratio variance (Williams, 1979; Huck et al., 1990). The classic evidence for this is that most attempts to select artificially for female biased sex ratios in diplo-diploid agricultural animals have met with spectacular failure (Bull and Charnov, 1988; but see Watson, 1982b). Furthermore, owing to Mendelian segregation (and to the lack of gene expression in the gametes in most animals), heterogamety leads to the a priori expectation of sex ratio equality. Thus, Fisher's (adaptive) theory and potential constraints arising from the sex determination mechanism each provide candidate explanations for the unbiased sex ratios commonly observed in heterogametic animals (these explanations are not necessarily mutually exclusive), but Fisher's theory does not predict binomial sex ratio variance while Mendelian inheritance does. Nonetheless, both biased and non-binomial sex ratios have been reported among heterogametic species (see Section 6). Even when sex ratios are non-Fisherian, this does not necessarily imply adaptive control of sex ratio by parents; often there are non-adaptive explanations for the same phenomena and usually there is insufficient evidence to distinguish the alternatives (Clutton-Brock, 1991). Nevertheless, it is worth considering how heterogametic species could potentially overcome sex determination constraints to produce adaptively biased sex ratios (reviewed in more detail by e.g. Cockburn, 1990; Krackow, 1995).

Consider first mammals, in which females are the homogametic sex (XX) and males heterogametic (XY). All eggs produced by females are X-bearing while, in terms of sex chromosomes, males produce two types of sperm, X and Y in equal numbers as a consequence of meiotic cell division. Offspring sex is determined by whether an X- or a Y-bearing sperm fertilises the egg. To control the sex of their offspring, female mammals must either actively prevent or facilitate the passage of one type of sperm through the reproductive tract, select sperm at the site of fertilisation (pre-fertilisation control) and/or selectively abort embryos of the undesired sex (post-fertilisation control). Evidence is accumulating that the timing of copulation with respect to ovulation may influence the sex ratio produced by mammals (e.g. Huck et al., 1990; Hornig and McClintock, 1994; Clark and Galef, 1995).

Now consider birds, in which females are the heterogametic sex (WZ) and males homogametic (ZZ). Thus, sex chromosomes carried by all sperm are the same (Z) while those in eggs may be Z or W. To control the sex of their offspring, female birds must either control the production or release of W and Z gametes (in contrast to mammals) or (like mammals) exercise post-fertilisation selective abortion.

It is still moot which of these two systems of heterogamety is likely to provide the best opportunity for pre-fertilisation control. Female mammals potentially control the chemistry of the reproductive tract but for this to be successful, X- and Y-bearing sperm must also express selectable differences: this is a rather controversial area (see Cockburn, 1990; Huck et al., 1990; Krackow, 1995). Female birds need 'only' control the
gametes they themselves produce, but this may not be possible: again uncertainty often remains (see e.g. Cockburn, 1990; Dijkstra et al., 1990; Zijlstra et al., 1992). Frank (1990) provides further discussion of the potential consequences of heterogamety for sex ratios in bird and mammals.

Post-fertilisation control has been suggested as a mechanism for achieving adaptive control of progeny sex ratio under heterogamety (Trivers and Willard, 1973; and see Maynard Smith, 1980) but since this entails a reduction in lifetime reproductive success compared with controlling the sex ratio at conception, pre-conception control may be favoured (Myers, 1978; Cockburn, 1990). Post-conception control is discussed more fully by Gosling (1986), Cockburn (1990, 1994), Huck et al. (1990), Krackow (1990, 1992, 1995), Krackow and Gruber (1990), Wiebe and Borlotti (1992) and Hornig and McClintock (1994).

In a detailed review of potential physiological mechanisms of sex ratio adjustment in mammals and birds, Krackow (1995) concluded that, although a number of mechanisms probably exist, there is presently no evidence that these are actually used to achieve adaptive sex ratio control (see also James, 1993 and references therein). Krackow (1995) speculates that these mechanisms may not be sufficiently precise to guarantee the desired sex ratio, and that disadvantages may arise if other sex ratios are consequently produced.

6. Evidence

It is not my intention to tender an exhaustive review of the results of empirical sex ratio research in this section: this introductory overview would rapidly grow into a number of very thick books (see e.g. Wrensch and Ebbert, 1993). Instead, I concentrate mainly on mammals and birds and provide a summary of what I perceive to be the major trends and most important case studies. The following reviews, which appeared in the last decade, can be consulted for more detailed accounts of vertebrate sex ratios: Clutton-Brock (1986) (birds), Clutton-Brock and Iason (1986) (mammals), Bull and Charnov (1989) (reptiles), Cockburn (1990) (marsupials), Hiraiwa-Hasegawa (1993) (primates), Gowaty (1991) (birds), and a ‘classic’ is that of Williams (1979). Recent reviews of invertebrate sex ratios have been provided by, e.g. Hardy (1992, 1994), Craig and Mopper (1993), Wrensch and Ebbert (1993) and Godfray (1994).

6.1. Getting and interpreting the evidence: some general problems

Before proceeding to a discussion of evidence for individual theories outlined in previous sections, it is worth noting some generalities emerging from empirical studies of the sex ratio (mainly on birds and mammals but with some mention of the Hymenoptera).

6.1.1. Biased or not biased?

It is well known that sex ratio biases in the Hymenoptera can be extraordinary (Hamilton, 1967; Wrensch and Ebbert, 1993; Godfray, 1994). In contrast, sex ratio
biases in birds and mammals are usually small, if found at all (although a fairly large degree of sex ratio bias has recently been found in the Seychelles warbler; Komdeur, 1996). A consequence of this small degree of sex ratio bias among heterogametic vertebrates is that the literature abounds with claims and counter-claims that sex ratios are, or are not, biased or non-random (e.g. Clark, 1978; Williams, 1979; Clutton-Brock et al., 1981; Ankney, 1982; Masters et al., 1982; Cooke and Harmsen, 1983; Olsen and Cockburn, 1991; Hiraiwa-Hasegawa, 1993; Krackow, 1993a, 1995; Wright et al., 1995). As Hiraiwa-Hasegawa (1993) states: “researchers who did not find skewed sex ratio [in primates] generally feel that the few observed sex ratio variations are stochastic errors”. As pointed out in several reviews (e.g. Cockburn, 1990; Festa-Bianchet, 1996), a further potential problem is that a posteriori analysis of sex ratio data may have led to over-amplified support for the theory if only ‘interesting’ results have been reported.

6.1.2. Adaptive or non-adaptive?

As discussed above, the heterogametic sex determination possessed by birds and mammals represents a potentially severe constraint to the achievement of adaptively biased sex ratios (although it is a good mechanism for producing the Fisherian mean sex ratio). The debate still rumbles on as to whether these organisms can or cannot adaptively control the sex ratio. In contrast, it is widely accepted that arrhenotokous species (e.g. parasitoid Hymenoptera) have control of offspring sex ratios. The predominant opinion is that parasitoid sex ratios are fairly well predicted by optimality theory and are thus ‘adaptive’: nevertheless, there have been doubts, dissent and ructions (e.g. Orzack, 1986; Walter and Clarke, 1992; Hardy et al., 1993; Godfray and Hunter, 1992, 1994; King and King, 1994; King and Lee, 1994; Walter and Donaldson, 1994).

6.1.3. Assessing the offspring sex ratio

Sexing young vertebrates is often difficult and this represents a problem for empiricists because it is of theoretical interest to know the sex ratio of immatures and also to observe whether and how this changes during offspring development. Such observations can indicate potential mechanisms of parental control of sex determination and subsequent investment (e.g. Myers, 1978; Cooke and Harmsen, 1983; Dijkstra et al., 1990; Negro and Hiraldo, 1992; Zijlstra et al., 1992). However, it is not possible to infer correctly initial mean sex ratios from the mean sex ratio observed once young can be sexed (Fiala, 1980) and the importance of differential mortality in generating observed sex ratios can be difficult to evaluate (Clutton-Brock et al., 1985; Austad and Sunquist, 1986; Lambin, 1994). Similarly, in parasitoids the sex ratio at egg-laying is of theoretical interest and is difficult to assess in many species (e.g. Green et al., 1982; Hardy, 1992; Nagelkerke and Hardy, 1994; Hardy and Cook, 1995).

6.2. Evidence for Fisherian sex ratios

At a first glance, Fisher’s (adaptive) theory seems to be supported by the fact that it originally sought to explain: many animals have equal sex ratios. However, a second glance reveals that support for the theory is somewhat more problematical (e.g. Williams, 1979; Bull and Charnov, 1988). Bull and Charnov (1988) point out that there
are two ways in which the theory can be tested: ‘static tests’ compare sex ratios to Fisher’s prediction of equality, while ‘dynamic tests’ observe whether sex ratios return to equality after perturbation. Few dynamic tests have been conducted (but see Burley, 1982) so most evidence is static. However, the mere observation of sex ratio equality does not comprise a proper test of theory: it is also necessary to show that Fisher’s set of assumptions are met (Bull and Charnov, 1988). Strictly, Fisher’s prediction concerns only the ratio of investment in the sexes. Thus, an unbiased numerical sex ratio is not per se evidence for Fisherian sex ratios—it must be accompanied by evidence that the sexes are equally costly to produce. The production costs within each sex are probably quite varied and this complicates the issue considerably (Frank, 1990). Equal investment in the sexes has, however, been reported in some species, e.g. bats (Milligan and Brigham, 1992) and seals (Smiseth and Lorentsen, 1995).

As already noted, a further problem with applying Fisher’s sex ratio to heterogametic species (e.g. mammals and birds) is that, due to meiotic cell division during gametogenesis, heterogamy itself leads to an a-priori expectation of (numerical) sex ratio equality, thus confounding an ‘adaptive’ interpretation of equal sex ratios in heterogametic species. One potential escape from this problem would be to observe the population sex ratio in species with marked sexually differential production costs: Fisher’s equal investment hypothesis predicts a numerical bias, while heterogamety predicts numerical equality. Further, the expectation of sex ratio variances are different. In European sparrowhawks there is a twofold size discrepancy between the sexes, yet Newton and Marquiss (1979) found neither numerical bias nor a difference in food investment between hatching and fledging.

Fisher’s prediction can also be tested in panmictic species with other sex determination mechanisms, thus avoiding the problem of a ‘non-adaptive’ explanation arising from heterogamety. Outbreeding arrhenotokous parasitoids usually do not usually have biased sex ratios (Godfray, 1994) (although Fisher’s assumption of biparentalism is violated by haplo-diploidy, the Fisher equilibrium is still predicted; Bull and Charnov, 1988). Reptiles with temperature-dependent sex determination tend to have a distinct preponderance of females, while fish with temperature-dependent sex determination seem to fit Fisher’s prediction more closely (for further discussion see Bull and Charnov, 1988, 1989; Wibbels et al., 1995).

6.3. Evidence for local mate competition

Although its emphasis was on invertebrates, many of which were haplo-diploids, for mathematical convenience LMC theory was originally formulated for diplo-diploids (Hamilton incorporated haplo-diploid genetics in 1979). LMC remains the major explanation for the female biased sex ratios commonly observed in populations of inbreeding invertebrates, to which it has most often been applied (Wrensch and Ebbert, 1993). Does it operate in vertebrates? Stenseth (1978) used LMC arguments to account for the female biased sex ratios observed in wood lemmings which have non-panmictic mating structures (and an unusual sex determination mechanism). The evidence is, however, circumstantial and the adaptive nature of the bias is controversial (Cockburn, 1990; Krackow, 1995).
6.4. Evidence for local resource competition

There have been several studies claiming support for LRC theory. Much of the evidence comes from primate research (Clark, 1978; Johnson, 1988; Perret, 1990; Hiraiwa-Hasegawa, 1993). In many species there is a tendency for females to remain in the natal group and for males to disperse. The original evidence for LRC (Clark, 1978) has been undermined by subsequent criticism (Hoogland, 1981; Masters et al., 1982), but a number of other studies lend support to the hypothesis. In a comparative study, using zoo rearing data on 15 primate genera, Johnson (1988) showed that sex ratios are more male biased in genera in which (1) within-group resource competition is greater and (2) males have a higher tendency to disperse. There is a degree of support for LRC from studies on marsupials, rodents, carnivores and deer (e.g. Clutton-Brock et al., 1982; Cockburn et al., 1985; Caley and Nudds, 1987; Cockburn, 1990, 1994; Frank, 1990; Holekamp and Smale, 1995; but see Armitage, 1987). LRC is probably not operating in Townsend's voles as local conditions did not affect maternal sex ratio response. Instead, sex ratio is related to population-wide competitive conditions (Lambin, 1994). In spider monkeys it is the female which disperses while males remain in the natal group to breed: female biased sex ratios have been observed (McFarland Symington, 1987). Among birds, the potential importance of LRC has recently been explored by Gowaty (1993) who reasoned that the sex ratio should be related to sexually differential dispersal propensities. Among passerines, females tend to disperse, while in aniseriforms males tend to disperse. Thus, LRC theory predicts female biased sex ratio in passerines and male biased sex ratios in aniseriforms: data support the prediction (Gowaty, 1993). LRC theory is also supported by Komdeur (1996) data on the Seychelles warbler, an insectivorous passerine—LRE also appears to operate in this species and the data are discussed below. A frequent problem with testing the LRC hypothesis is that, in general, enhanced competition for resources among the non-dispersing sex has not been directly demonstrated in vertebrates (Cockburn, 1990; Frank, 1990; Gowaty, 1993).

6.5. Evidence for local resource enhancement

Among birds, LRE is supported by evidence from the cooperatively breeding red-cockaded woodpecker in which helpers are almost always males: offspring sex ratios are male biased (Gowaty and Lennartz, 1985). More generally, sex ratios appear to be male biased in many species of cooperatively breeding birds and it is usually the males which are the helpers-at-the-nest (Emlen et al., 1986 and references therein). Komdeur (1996) study of reproduction in Seychelles warblers provides some of the most recent and striking evidence for sex ratios sensitive to the degree of competition for, or enhancement of, local resources. The warblers are territorial and fledged offspring often remain in the natal territory, acting as helpers feeding their parents' subsequent offspring. In high quality territories the presence of a helper is beneficial to parents but, in poor quality territories, a 'helper' depletes more resource than it gathers for its siblings. Although both sexes can act as helpers, these are more often females than males. Komdeur found that sex ratios were male biased in poor quality territories and female biased in high quality territories. Furthermore, sexually differential mortality can be excluded as a cause of these results, which thus support both LRE and LRC theories.
Among mammals, LRE theory may be supported by the male biased birth sex ratio of African wild dogs, in which adult males help with communal rearing of the young (Malcolm and Marten, 1982). In another African carnivore, the spotted hyena, individuals both cooperate and compete with other members of their clan and the balance between these types of interaction can change in relation to the quality of the habitat. Holekamp and Smale (1995) observed the sex ratio in a spotted hyena clan which subsequently split up during a period of resource scarcity. Before fission, the sex ratio of offspring produced by high ranking females was male biased and after fission these sex ratios were female biased. Spotted hyena males tend to disperse while females usually remain in the natal clan. Hence it is likely that the observed shift in sex ratio was due to a change from predominantly competitive (prior to fission) to cooperative (post fission) interactions between clan members. These data are consistent with both LRC and LRE theories, especially as the observed sex ratio shifts do not seem attributable to sexually differential mortality of juvenile offspring (Holekamp and Smale, 1995). The study by Lambin (1994) of vole sex ratios also provides support for LRE: cooperation between female relatives may occur by joint rearing of the young, communal territory defence or an advantageous synchronisation of offspring production and sex ratios are female biased (Lambin, 1994). However, the degree of cooperation-competition between females is likely to vary with overall population density and Lambin (1994) found that sex ratios were only female biased in years of low density.

6.6. Evidence for the Trivers-Willard hypothesis

The Trivers-Willard hypothesis predicts investment in the sexes dependent on maternal condition. There have now been a large number of empirical investigations of vertebrate sex ratio aimed at evaluating this hypothesis. Austad and Sunquist (1986) performed the first field-based test of the hypothesis by increasing the maternal capacity for investment (by diet supplements) in common opossums (Didelphis marsupialis, a polygynous marsupial). (However, as Watson (1982a) points out, an experiment with similar rationale was carried out 160 years before Austad and Sunquist published their paper!). Females with enhanced diets produced a male biased sex ratio while females which received no diet enhancement produced unbiased progeny sex ratios, thus supporting the hypothesis (but see Wright et al., 1995: My own re-analysis supports Austad and Sunquist’s (1986) conclusions). A general problem in testing the Trivers-Willard hypothesis is the lack of data describing the relative effects of a given amount of parental investment on the survival and reproduction of each sex (e.g. Hrdy, 1987). The data produced by Austad and Sunquist (1986), however, indicate that the post-investment survival of male offspring is more affected by investment than that of female offspring. A similar result has been found in gerbils by Clark et al. (1991a): a given amount of investment has a greater effect on sons relative to daughters (see also Krackow, 1993b). Further, Clark et al. (1990) have shown that parents make a greater investment in individual sons than in individual daughters. The Trivers-Willard hypothesis is supported by much (by no means all) data from a number of other vertebrate species; a degree of controversy remains. For more evidence and discussion see Myers (1978), Clutton-Brock et al. (1981, 1985, 1986), McGinley (1984), Gosling (1986),...

6.7. Evidence for the advantaged daughter hypothesis

A female bias among the offspring of high ranking females and a male bias among the progeny of low ranking females in several primate species is consistent with the predictions of this hypothesis (e.g. Simpson and Simpson, 1982); however, a number of studies have found no such patterns (Hiraiwa-Hasegawa, 1993).

6.8. Evidence for Silk’s hypothesis

Perhaps not surprisingly, Silk’s hypothesis was stimulated and is supported by data collected by Silk (1983, 1988). In bonnet macaques, in which males disperse, population sex ratios are male biased (Silk, 1988). Dominant females produce an unbiased offspring sex ratio but subordinate females produce a preponderance of sons (Silk, 1983, 1988). The hypothesis is also supported ‘in mirror image’ by sex ratios in polygynous spider monkeys in which it is the females which disperse. McFarland Symington (1987) found that the population sex ratio is female biased (as would be predicted by LRC) and that high ranking females produce mainly sons and low ranking females produce daughters. McFarland Symington’s results support the advantaged daughter hypothesis (except that because females disperse the hypothesis becomes one of advantaged sons) because only the sons of high ranking females are likely to achieve significant reproductive success (McFarland Symington, 1987). Note that the population sex ratio bias in spider monkeys is as would be predicted by LRC and individual variation is as would be predicted by the Trivers–Willard hypothesis, but the former theory does not consider maternal condition (rank) and the latter does not consider differential dispersal: thus neither strictly applies until combined into Silk’s hypothesis, under which the two effects operate simultaneously (see Van Schaik and Hrdy, 1991, who also discuss further evidence).

6.9. Evidence for the first cohort advantage hypothesis

Empirical work carried out by Wright et al. (1995) on opossums (Didelphis virginiana) gave rise to and supports the first cohort advantage hypothesis. Mothers produced more males in their first litters and more females in their second litters. There was no
significant correlation between maternal age and condition and the sex ratio of their litters (in contrast to the predictions of the Trivers–Willard hypothesis and results from *Didelphis marsupialis*; Austad and Sunquist, 1986). In kestrels the probability of breeding as a yearling declines for males but not for females as the date of birth gets later in the season. Dijkstra et al. (1990) found that the proportion of males in broods declines with the lateness of the date of birth. The opposite effect was found by Zijlstra et al. (1992) in the marsh harrier: the proportion of males increased with laying date during the season, possibly due to an increased probability of breeding as yearlings among females than among males. Such trends are, however, not found in all raptors (Negro and Hiraldo, 1992).

6.10. Evidence for sex ratio variance

The problem of testing observed sex ratio variances against theoretical prediction can be a thorny one (e.g. Williams, 1979; Frank, 1990). If the sex of heterogametic species were determined by a process of Mendelian segregation during gametogenesis followed by random fertilisation, the distribution of family (= brood, litter) sex ratios would conform to a binomial distribution. However, Kolman's theory predicts overdispersed sex ratios under Fisher's assumptions. Under the assumptions of the Trivers–Willard hypothesis, overdispersed sex ratios may also be expected (Williams, 1979; Frank, 1990). A less than binomial (precise, underdispersed) sex ratio may also be expected under different sets of circumstances (Verner, 1965; Williams, 1979; Green et al., 1982; Frank, 1990). Frank (1990) concludes a discussion of this subject thus: "little can be learned about adaptation and its constraints by analysing only total sex ratio variance among families. To the extent that this approach may be useful, careful derivation of predictions under clearly specified assumptions is needed for each species considered".

Many invertebrate species have now been shown to have low sex ratio variance (see reviews by e.g. Hardy, 1992; Nagelkerke, 1993), these species usually conform well to the assumptions of LMC theory, under which it is clear that sex ratio precision is usually favoured (Green et al., 1982; Nagelkerke, 1993; Nagelkerke and Hardy, 1994). LMC is, however, less readily applicable to vertebrates and, as Frank (1990) points out, the adaptive value of sex ratio variance among vertebrates remains much less easy to specify. However, LRC and LRE are closely related to LMC. Perhaps sex ratio precision would be advantageous under LRC, but under LRE an overdispersed or underdispersed sex ratio may be expected, depending on the details of the model assumptions (note that despite group structure generating increased local interactions, mating structures may approximate panmixis under LRC and LRE). To my knowledge this area has received only passing theoretical attention (Seger and Charnov, 1988).

A number of studies have, however, documented vertebrate sex ratio variances or patterns of progeny production which may indicate the presence of mechanisms for variance control. Williams (1979) found no 'adaptive' difference from binomial variance in the vertebrate data he considered. Harmsen and Cooke (1983) examined the sex ratio in the lesser snow goose, in which the assumptions of the model of Fisher (1930), and thus also of that of Kolman (1960) appear to hold. Sex ratio variance was not overdispersed but fitted well to a simple binomial distribution: Kolman's prediction was
thus not supported. Negro and Hiraldo (1992) also found a binomial variance among brood sex ratios of the lesser kestrel. Evidence for bird sex ratio variances is further discussed by Gowaty (1991). A number of studies have reported sexually non-random laying sequences in birds which may indicate the capacity to control sex allocation and brood sex ratio variance (e.g. Dijkstra et al., 1990; Rednarz and Hayden, 1991; and further references in Clutton-Brock, 1986; Hardy, 1992; Zijlstra et al., 1992).

Among mammals, binomial sex ratio variances were found in pouch young of the marsupial Antichinus stuartii; however, the variance at weaning differed, probably as a result of infanticide (Cockburn, 1994). Lesser mouse lemurs (Perret, 1990) and lions (Packer and Pusey, 1987) have also been found to have non-binomial offspring group variances. In lions, males tend to occur together more often than binomial chance and males disperse in groups formed within the natal pride. The subsequent success of these groups is size dependent, hence an advantage of non-binomial variance (note that the dispersal of individual males is not directionally random and thus does not conform to the LRC hypothesis assumption, but these data do lend support to LRE ideas). Low litter sex ratio variances have been documented in several rodent species: hamsters (Huck et al., 1990), rats (Blumberg et al., 1992), mice (Krackow, 1992) and voles (Lambin, 1994), see also Clark et al. (1991b). It is possible that low variance in hamsters is generated by variation in the binomial probability of sex determination within litters but the adaptive significance of non-binomial sex ratios (in hamsters) remains unclear (Huck et al., 1990). Lambin (1994) found no relationships between maternal condition or local population density and sex ratio variance in voles, but variance did correlate with the season in which litters were born and the overall population density in that year.

The importance of sex ratio variance in vertebrates surely warrants more attention from both empiricists and theoreticians.

7. Conclusions

"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 to the future" (Darwin, 1871).

"Darwin's sentiments have, I suspect, rung a chord in virtually every researcher who has tried to make sense of the exasperating literature concerning the adaptiveness for parents of biasing sex ratios towards either sons or daughters" (Hrdy, 1987).

Sex ratio theory is a well developed area of evolutionary biology with a fascinating complexity of adaptive explanations and predictions. The evidence is equally complex and fascinating, but also frustrating as its interpretation is often difficult, sometimes impossible. It is, however, clear that there are a very large number of factors which could influence sex ratio in vertebrates and invertebrates. It seems that although sex ratio research on vertebrates and invertebrates share a number of problems, some of the basic issues (control of sex ratio, production of biased sex ratios) are much more clearly
resolved among the invertebrates: current research into parasitoid sex ratios is mainly engaged in elucidating the influences (theoretical and empirical) of particular biologies rather than testing the ‘starting points’ of theory (e.g. Godfray, 1990; Nagelkerke and Hardy, 1994; Ode and Strand, 1995; Ode et al., 1995; Hunter and Godfray, 1995). Perhaps the greatest problem facing those studying vertebrate sex ratios is to conclusively resolve whether or not observed sex ratios can be viewed as ‘adaptive’. My guess is that since progeny sex ratio can (at least theoretically) influence parental fitness greatly, adaptive control should have been achieved, but other, different, guesses could be made.

Although not all aspects are currently understood, the study of sex ratio evolution has come a very long way since Darwin made his perplexed remark. This is thanks to the many who have not been content simply to ‘await the future’. In this overview I hope to have highlighted some important, on-going and captivating areas of sex ratio research, and to have made the literature slightly less exasperating for those wishing to gain an initial toe-hold.

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