SEX ALLOCATION THEORY FOR BIRDS AND MAMMALS

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INTRODUCTION

Parents divide their reproductive effort into the production of sons and daughters. Darwin (43) was intrigued by the fact that parents usually split their effort so that approximately equal numbers of sons and daughters are raised. He believed that this male:female ratio had been adjusted by natural selection because he understood that the number of females set a limit on reproductive capacity. He could not, however, clearly specify how natural selection shaped the sex ratio. Fisher (51, 52) provided the explanation by noting that frequency-dependent selection stabilizes the sex ratio near equality.

Since Fisher presented his explanation, many examples of biased sex ratios have been observed in nature. For example, Hamilton (71) observed very female-biased sex ratios in parasitic wasps that mate in small groups. Hamilton explained this bias by showing that in these wasps the mating competition among brothers violates a latent assumption in Fisher's argument.

In other examples of observed biases, the explanations put forth provided new dimensions to Fisher's central theory rather than direct exceptions. The most important of these new dimensions for birds and mammals was observed by Trivers & Willard (109). They noted that, in some mammals, healthy mothers tended to produce a relatively higher proportion of sons than did unhealthy mothers. They explained this pattern of variation among families

by suggesting that a healthy son is reproductively more valuable than a healthy daughter and that a mother's health partly determines her offspring's vigor.

The point of these examples is to show how sex allocation theory has grown by a series of interesting observations, single-cause explanations, exceptions and new explanations. This is a natural way for a theory to grow. One problem, however, is that logical flaws slip easily into such a haphazard structure. For example, the Trivers–Willard (109) model about variation in sex ratio among families is nearly always applied simultaneously with Fisher's model for equal sex ratio at the population level. Actually, the assumptions required for the Trivers–Willard model imply that Fisher's theory cannot apply (57). The fact that these two theories are about different types of sex ratio pattern has led to the mistaken belief that the ideas can be applied independently.

The vast literature on sex allocation theory has been reviewed several times recently (12, 14, 27, 77). Several reviews of observed sex allocation patterns in birds and mammals are also available (34, 40, 75). I believe, however, that the logical structure of sex allocation theory has not been adequately reconciled with the natural history of birds and mammals. The main ideas of the theory were developed for organisms with little or no parental care, with mechanisms of sex ratio adjustment such as haplodiploidy or environmental sex determination, with no trade-offs between the sex ratio of a current brood and future reproduction, and often for simultaneous or sequential hermaphrodites.

By contrast with the types of natural history that sex allocation theory has attempted to explain, birds and mammals are characterized by extensive parental care, a sex determination mechanism that to some extent constrains sex ratio, complex mechanisms for adjusting parental investment in the sexes, variation in these mechanisms at all taxonomic levels, and a trade-off between current sex ratio and future reproduction. A complete theory for birds and mammals must show how various aspects of life history may interact in determining the patterns of selection on sex allocation. The theory viewed in total will expose some flaws in the simple single-cause explanations that typify application of sex allocation theory to birds and mammals.

OVERVIEW

Two different perspectives on the theory must be summarized in order to provide an accurate description of its current state. The first is the series of observations and single-cause explanations that defines the history of the field. The second is the set of logical relationships among these single-cause explanations that defines the structure of the theory and the interactions that

must be considered when applying the theory to real cases. For these reasons I review the theory in a loosely chronological way but use hindsight to explain ideas and provide commentary. This approach highlights the logical structure of the theory from a modern perspective and shows how some logical flaws have slipped into common usage.

In the first section of this review I recount the major single-cause forces that shape sex allocation biases. In the second section I describe how the theory has expanded and become more realistic as the ideas were first applied and then authors critically evaluated the structure of the theory in light of these applications.

Early theoretical and empirical studies of sex allocation focused mainly on adaptive significance, with less attention paid to mechanism, genetics, ontogeny, and phylogeny. To some authors this has been irksome, since in an ideal world, knowledge of phylogenetic history and of the genetic and phenotypic bases of variation must precede analyses of adaptive significance. I have delayed discussion of the bases of variation until the third section because these issues were not central to the early development of the field, which was guided by the patterns most easily observed in nature and by the simplest explanations available. I briefly summarize a few of the many fascinating recent discoveries about mechanism. Here as in other sections of the paper I cite empirical studies only to the extent that they help to understand the theory.

Up to now I have been lax about the distinction between the numbers of sons and daughters that a family produces and the relative amount of resources that is devoted to sons and daughters. From this point I use *sex ratio* for the relative number of sons and daughters and *sex allocation* for the relative amounts of energy and resources devoted to sons and daughters.

MAJOR CONCEPTS

Frequency Dependence and Population-Level Patterns

FISHER'S EQUAL ALLOCATION THEORY   Darwin (43) identified the sex ratio as an interesting trait subject to natural selection, but he could offer no coherent theory as to why the sexes are generally equal in numbers. Fisher (51, 52) took up Darwin's famous challenge: "but I now see the whole problem [of sex ratio] as so intricate that it is safer to leave its solution for the future" (52, p. 158).

Fisher's argument for why the sex ratio is approximately equal is one of the most widely cited theories in evolutionary biology. The argument has been repeated in a variety of verbal and mathematical forms. I present Fisher's model in the context in which he originally described it, since it is important

later to show why the idea often does not apply to birds and mammals in the manner generally accepted.

Fisher described his idea in economic metaphor—parents allocate portions of their limited reproductive energies to sons and daughters, and for each sex they get certain returns measured as genetic contribution to future generations. Because each future offspring in the population receives genes equally from its mother and father, the total genetic contribution of males and females is equal in each generation. After noting this equality in the reproductive values of males and females, Fisher (52, p. 159) concluded:

> From this it follows that the sex ratio will so adjust itself, under the influence of Natural Selection, that the total parental expenditure incurred in respect of children of each sex, shall be equal; for if this were not so and the total expenditure incurred in producing males, for instance, were less than the total expenditure incurred in producing females, then since the total reproductive value of the males is equal to that of the females, it would follow that those parents, the innate tendencies of which caused them to produce males in excess, would, for the same expenditure, produce a greater amount of reproductive value; and in consequence would be the progenitors of a larger fraction of future generations than would parents having a congenital bias towards the production of females. Selection would thus raise the sex-ratio until the expenditure upon males became equal to that upon females.

Fisher's argument is indeed compelling—reproductive profits are greater on allocation to the sex with lower total investment. The population is always pulled by frequency-dependent selection toward an equilibrium in which total allocation to the two sexes is equal. Total allocation depends on both the sex ratio and the patterns of parental investment in each son and daughter.

The implicit assumptions in Fisher's argument are often quite robust and, when met, equal allocation is a realistic prediction. Nevertheless, complications raised in the next section show that the equal allocation principle can sometimes be misleading when applied to birds and mammals. To prepare for the extensions to Fisher's theory made by later authors, let us first consider Fisher's own argument more carefully.

Suppose a parent invests some of its limited resources in a son. That son must then compete with the pool of males in his generation for a portion of the fixed genetic profits available to males, which is one half of the future population. The fraction of these fixed profits that a parent can expect by investing in sons depends on the competitive ability of the parent's sons relative to the total competitive ability of competing males in the local population. In the simplest case, suppose there are M males produced by all other parents, and the parent we are considering produces m sons. If all sons are equal, then our parent can expect as its fraction of the total profits in males $m/(M + m)$, or approximately m/M when M is much bigger than m (100). This

expression describes the number of sons produced by a parent relative to the population total. Note that when the number of sons produced by a parent doubles then genetic profits approximately double.

Fisher's argument is cast entirely in terms of investments and profits and is notably unconcerned with numbers of sons. In the Fisherian spirit we could view m as a parent's allocation and M as the total population's allocation to sons, so that expected genetic returns on investment m are $m/(M + m)$, or approximately m/M when M is large. Likewise for females, if f is a parent's investment and F is everyone else's allocation, then genetic returns on f are $f/(F + f)$, or f/F when F is large (100).

Genetic returns on a unit of investment ϵ are ϵ/M for males and ϵ/F for females. This clearly shows that when the population is currently allocating more to females, $F > M$, then investing in males gives greater returns per unit investment than investing in females. Similarly, when the population is currently allocating more to males, $M > F$, then investing in females gives greater returns per unit investment than does investing in males. Since the sex with less total investment is always more profitable, selection will constantly move the population allocation ratio toward $1:1$ (5, 79).

When the population is at equal allocation, then genetic profits are equal for a single unit of resource invested in either males or females, $\epsilon/M = \epsilon/F$ (25, 49, 50, 87, 89). In economic language this means that the marginal returns on additional investment in males and females are equal when the population is at equilibrium. In Fisher's language, this might be said as: For if the marginal returns were not equal, and males, for instance, yielded a higher genetic return per unit investment, it would follow that those parents, the innate tendencies of which caused them to produce males in excess, would, for the same expenditure, contribute a greater amount to the genetic constitution of future populations; and in consequence would be the progenitors of a larger fraction of future generations than would parents having a congenital bias towards the production of females. Selection would thus raise the sex ratio until the marginal returns on expenditure in males became equal to the marginal returns on expenditure in females.

Fisher's theory shows the frequency dependence that occurs in all arguments about sex allocation—the current ratio of total male to female investment, $M:F$, affects the marginal returns per unit investment in males and females. In addition, with further assumptions implicit in Fisher's argument, frequency dependence will lead to an expected $1:1$ allocation ratio. The theoretical extensions in the next section show that frequency dependence is a ubiquitous feature of sex allocation, but that equal allocation is not necessarily the expected result. The expected departure from equal allocation may be particularly pronounced in some birds and mammals.

CHARNOV'S NONLINEAR MODEL   Charnov et al (31) used MacArthur's (87) formulation for sex ratio to study when simultaneous hermaphroditism will be favored over dioecy. In the process, they developed a model for the allocation of resources to male and female function within hermaphrodites. Nonlinear relationships between investment and returns play a key role in their analysis. Charnov (26) extended this model in a way that can be used to analyze the population sex allocation ratio in dioecious species under nonlinear returns (see also 89).

Consider how nonlinear returns may arise. Fisher's argument assumes that when a parent doubles its investment in females, f, that the parent will also double its genetic returns, which Fisher implicitly assumed to be f/F. This simple relationship between investment and profits often does not hold in birds and mammals. Imagine a red deer mother with its daughter. If the daughter has gotten little milk, then doubling the food supply may more than double the expected life-time reproductive success of that daughter. If, on the other hand, the daughter is very well fed, then doubling the food supply probably will less than double the daughter's expected life-time success. In general, when changes in investment are not directly proportional to changes in returns then the investment-return relationship is referred to as "nonlinear."

Charnov (26) showed that a nonlinear relationship between parental investment and expected genetic profits typically leads to an expected departure from equal allocation (24, 27, 57, 83, 84, 89). In particular, when the marginal return on additional investment is different for the two sexes, then equal allocation is not expected. In many polygynous birds and mammals, increasing investment in sons appears to give a rate of return different from increasing investment in daughters (33, 35, 38, 109).

Charnov (25) presented a mathematical formulation that closely follows Fisher's verbal argument and the mathematic formulation of Shaw & Mohler (100). For a particular investment in a son, a parent gets a son with a particular level of competitive ability. This competitive ability is then translated into a certain genetic profit depending on the total competitive ability of all other males in the population. The relation between investment and genetic profits may however be nonlinear in Charnov's argument, in contrast with Fisher's assumption of a linear relationship.

Charnov's (25) model is a formal statement of Fisher's insight that marginal returns on male and female investment must be equal at equilibrium (see above). The Charnov model has a very simple mathematical form that can be derived by extension of Fisher's reasoning. I first show how to derive the general result and then examine in detail an example to illustrate when a biased population sex allocation may be expected.

Assume that each of N families in the population invests m in sons and f in daughters. For an investment in males of m, parents get a son with competi-
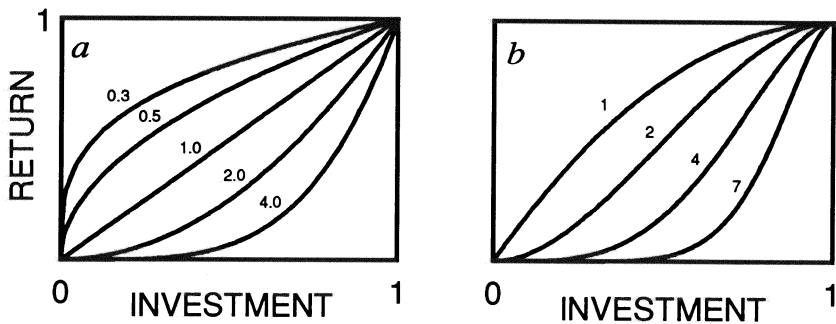
Figure 1 The relationship between parental investment and the expected mating success of sons or fecundity of daughters. The return curves are proportional to $\int_0^k y^{s-1}(1-y)^{t-1}dy$, where k is the amount of parental investment (57). The value of s is given above each curve. In a, $t = 1$ and the returns are proportional to k^s; in b, $t = 2$ and returns are proportional to $(s + 1)k^s - sk^{s+1}$.

tive ability $\mu(m)$ (see Figure 1, which shows a few investment-competitive ability shapes). This son will compete in a population with total male competitive ability $N\mu(m)$, so that expected genetic profits through sons will be $\mu(m)/N\mu(m)$. For an investment in females of f, parents get a daughter with competitive ability $\phi(f)$. This daughter will compete in a population with total female competitive ability $N\phi(f)$, so that expected genetic profits through daughters will be $\phi(f)/N\phi(f)$.

The marginal value criterion states that, at equilibrium, parents will receive the same genetic profits for investing a little bit more in either sons or daughters. As explained above, if greater profits were obtained for extra male investment, for instance, then selection would favor increased male allocation until a balance in marginal values was achieved. With a little extra investment in males, ϵ, the marginal increase in profits would be $[\mu(m + \epsilon) - \mu(m)]/N\mu(m)$. The analogous expression can be written for the marginal increase in profits for females. Thus, the equality of marginal values at equilibrium guarantees that, at equilibrium,

$$\frac{\mu(m + \epsilon) - \mu(m)}{N\mu(m)} = \frac{\phi(f + \epsilon) - \phi(f)}{N\phi(f)}. \qquad 1.$$

Under Fisher's explanation, returns are linear for both sexes, $\mu(m) = am$ and $\phi(f) = bf$, where a and b are constants. Substitution yields the condition $m = f$ at equilibrium, thus proving the equal allocation principle. Whenever μ and ϕ are functions with different shapes, marginal values on male and female investment are not equal when $m = f$, and the principle of equal allocation does not hold (24, 26, 57, 83).

Consider a particular example of how the relationship between investment and profits affects sex allocation. Assume that investment in a son is directly proportional to expected genetic profits from that son, as in Fisher's argument, but that genetic profits from a daughter increase at a diminishing rate as investment in that daughter increases. This might be approximately the case in a polygynous mammal such as red deer (38), where increasing male size may provide a greater rate of return than does increasing female size.

The linear returns on male investment mean that an investment by a parent of m translates into a son with competitive ability of $\mu(m) = am$ (Figure 1a, $a = 1$ and $s = 1$), which in turn translates into a genetic profit of m/Nm. From the left side of Equation 1 the marginal value of further male investment is ϵ/Nm. For daughters, the specific form of the diminishing returns between investment and competitive ability must be specified. Assume that the diminishing returns on female investment mean that an investment of f translates into a competitive ability of $\phi(f) = b\sqrt{f}$ (see Figure 1a, $b = 1$ and $s = 0.5$). Genetic profit on female investment f is therefore $\sqrt{f}/(N\sqrt{f})$. From the right side of Equation (1) the marginal value on further female investment is $(\sqrt{f + \epsilon} - \sqrt{f})/N\sqrt{f}$.

A simple numerical example shows that the principle of equal allocation does not apply in this case. Suppose that the population is currently allocating equal amounts of resource to males and females, $m = f = 1$. Consider how a parent can increase genetic profits with an extra investment of $\epsilon = 0.2$. For males the marginal return will be $0.2/N$, whereas for females the marginal return will be approximately $0.1/N$. When the population is allocating equally to sons and daughters a powerful selection pressure will favor an increase in allocation to sons. Now suppose that the population allocates twice as much resource to the production of sons as to the production of daughters, $m = 2$ and $f = 1$. The marginal return will be $0.1/N$ for both males and females, so a $2:1$ ratio of male to female allocation must be the equilibrium. If the allocation ratio were more male biased than $2:1$, we would find that extra female investment would be favored. Thus, frequency dependence is still a key feature of sex allocation, but equal allocation is not expected (26).

Genetic Control of Sex Ratio

Fisher's model and its extensions discussed above depend on two implicit assumptions about the genetic control of sex allocation. First, sufficient genetic variation must exist so that any phenotypic pattern favored by natural selection can occur. For example, if all genes in the population cause parents to invest twice as much in daughters as in sons, then clearly a two to one allocation ratio will be observed no matter what selective forces occur.

The second assumption is that, from the point of view of the genes controlling sex allocation, a parent must be equally related to sons and

daughters (71, 74, 82, 99; see 106 for a thorough analysis). Suppose, for example, that a matrilineally inherited cytoplasmic gene controls sex ratio (82). The success of this gene depends only on the number of daughters produced; sons do not count at all toward fitness since the gene is not transmitted to sons. Thus, a cytoplasmic gene causing its bearer to produce all daughters will have a higher fitness than will a cytoplasmic gene causing a mixture of sons and daughters. Under cytoplasmic control the population will evolve to an extremely female-biased sex ratio.

Similar complications for sex allocation arise when controlling genes are on the sex chromosomes of birds or mammals (71, 99). Mammals have XX females and XY males. If the controlling genes are on the Y, then selection will favor a very male-biased sex ratio because daughters do not contribute to a Y's fitness, that is, with respect to the Y, fathers and daughters are unrelated. The situation is more complex if the controlling genes are on the X. If the X gene has its effect on sex allocation by acting in the mother, then sex allocation evolves as if controlled by haplodiploid genes (73). Under outbreeding, mother-son and mother-daughter relatedness are equal with respect to the X, and sex allocation evolves as if controlled by autosomal loci. If inbreeding occurs, mothers are more closely related to daughters than to sons, which favors a relatively more female-biased sex allocation than under outbreeding. If the X has its effects by acting in fathers, then selection favors the production of all daughters, since fathers never contribute an X to a son. The reverse patterns apply to birds, which have ZZ males and WZ females.

The theories reviewed below all assume unlimited genetic variety and autosomal control unless otherwise stated. The complications caused by limited genetic variety and nonautosomal control are discussed below in the section on Genetic and Phenotypic Bases of Variation.

Competition among Kin and Biased Sex Allocation

LOCAL MATE COMPETITION   Hamilton (71) noted that several species of small parasitic wasps have extremely female-biased sex ratios. These particular species tend to mate near where they were born. Hamilton explained the sex ratio bias by showing that when brothers compete among themselves for the limited number of mates available in a local group, then parents are favored to invest more resources in daughters than sons. In effect, since the total number of matings available in the local group is fixed by the number of females, the genetic returns to a parent for increasing allocation in males rise at a diminishing rate. If each parent is currently investing m in males and there are N families in the local group, then the fraction of local matings achieved by the sons in each family is m/Nm, and the marginal increase in the number of matings for an increase ϵ in male allocation is $(m + \epsilon)/(Nm + \epsilon) - m/Nm$
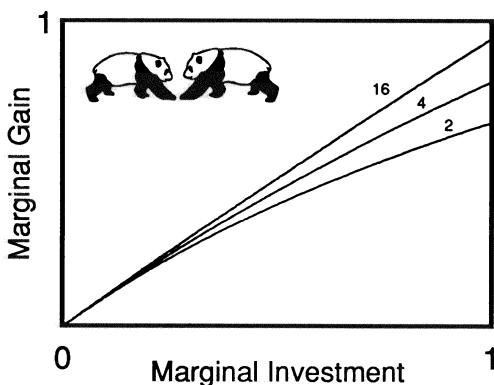
Figure 2 These curves describe the additional mating success of sons for additional parental investment. The numbers labelling each curve are the number of families N contributing sons to the local mating group. The marginal investment is described in the text as $\delta = \epsilon/m$.

or, defining $\delta = \epsilon/m$ as the marginal increase in investment, the marginal gain can be written as $\delta/(1 + \delta/N)$.

Figure 2 shows how the rate of marginal gain increases at a diminishing rate with marginal investment δ and how this effect depends on group size N. The decreasing rate of return on male marginal investment coupled with Charnov's general model for the role of nonlinear returns provides a simple explanation for female-biased allocation under local mate competition. In Hamilton's particular model, however, additional forces come into play (19, 105) as I describe below.

Local mate competition, as with other areas of sex allocation, has been studied with a large number of mathematical approaches (27, 53, 55, 96). I continue to formulate the theory in terms of marginal values, since that approach provides a simple way to link diverse assumptions about natural history while using the simplest mathematics.

Assume that there are $N - 1$ families in the local group, each of which allocates a fraction of their resources m to sons and f to daughters, where $m + f = 1$. Focus attention on the success of the Nth family when allocating $m + \epsilon$ to sons and $f - \epsilon$ to daughters, or the success of the family through daughters when allocating $m - \epsilon$ to sons and $f + \epsilon$ to daughters. The change in expected fitness at equilibrium should be the same in either case according to the marginal value principle.

When allocating $m + \epsilon$ to sons and $f - \epsilon$ to daughters, the expected fraction of matings attained by the focal family is $(m + \epsilon)/(Nm + \epsilon)$, and the value of the females in the local group available for mating is $Nf - \epsilon$. These quantities determine the separate effects of local mating competition and local mating,

respectively. When $\epsilon = 0$, the product of these quantities, which is proportional to the expected number of grandchildren through sons, is f, so the marginal change in grandchildren through sons when investing $m + \epsilon$ in sons and $f - \epsilon$ in daughters is proportional to:

$$\left(\frac{m + \epsilon}{Nm + \epsilon}\right)(Nf - \epsilon) - f.$$

To get the expected genetic return this quantity must be divided by the expected number of grandchildren through males in the entire population, which is proportional to KNf, where K is the number of local mating groups each with N families.

The marginal change in expected grandchildren through daughters when investing $f + \epsilon$ is proportional to $f + \epsilon - f = \epsilon$. The total number of grandchildren through daughters in the population is proportional to KNf. Equating the marginal values for male and female genetic return and assuming ϵ is relatively small (i.e., $\epsilon^2 \approx 0$) yields Hamilton's (71) classic formula

$$m^* = \frac{N - 1}{2N},$$

which can also be written as the ratio $m^*{:}f^*$ is $1 - 1/N : 1 + 1/N$. This ratio form provides an easy interpretation for the forces affecting sex allocation. The genetic valuation of sons is discounted by $1/N$ for the effects of local mate competition with brothers, since $1/N$ is the probability that a male encounters a brother when competing for mates. Likewise, the genetic valuation of daughters is augmented by $1/N$ for the increase in a brother's reproduction that a sister provides through local mating between siblings, since $1/N$ is the probability of sibmating (105). The separate effects of sibmating and mate competition can be seen most clearly in a model in which females disperse before mating (19, 105). In this case there is no sibmating, but males remain at home and compete for mates with their brothers and other neighboring males. In the style of the above models one can show that the ratio $m^*{:}f^*$ is $1 - 1/N : 1$.

LOCAL RESOURCE COMPETITION   Clark (32) observed a male-biased sex ratio in bush babies. In this species young males tend to disperse whereas young females stay near their birthplace throughout life. Clark suggested, by analogy with local mate competition, that competition among sisters for limited local resources may favor parents to invest more heavily in males than females.

The theory is indeed very much like local mate competition, but there is

one difference. Under the Hamilton model, there is both local mate competition among brothers and local mating between siblings (inbreeding), whereas in Clark's model there is local competition among sisters but no inbreeding since males disperse before mating.

A derivation similar to the one for the case of local mate competition can also be based on the marginal value principle. When parents allocate $m + \epsilon$ to males they obtain a fraction $(m + \epsilon)/(KNm + \epsilon)$ of the matings because competition among the dispersing males is global rather than local. When $\epsilon = 0$, this fraction of the total grandchildren is $1/KN$, so the marginal return on male investment is $(m + \epsilon)(KNm + \epsilon) - 1/KN$. When a parent allocates $f + \epsilon$ to daughters that compete among the local group of N families for resources needed for reproduction, it obtains a fraction $(f + \epsilon)/(Nf + \epsilon)$ of the grandchildren through daughters within its local group. Dividing this fraction by the number of groups K yields the expected proportion of grandchildren in the population by this parent. When $\epsilon = 0$ the expected proportion is $1/KN$, so the marginal gain in female genetic returns is $(f + \epsilon)/[K(Nf + \epsilon)] - 1/KN$. Equating male and female marginal values and assuming that ϵ is relatively small (i.e. $KNm + \epsilon \approx KNm$ and $\epsilon^2 \approx 0$) yields (27) the equilibrium proportion of investment in males $m^* = N/(2N - 1)$, which can also be written as $m^*:f^*$ is $1:1 - 1/N$. The latter ratio form makes it apparent that the genetic valuation of daughters is discounted by $1/N$, which is the frequency at which a female will compete with a sister for a limited resource.

Note two unrealistic assumptions in the local mate competition and local resource competition models when applied to birds and mammals. First, both the mating propensity of males and the fecundity of females are assumed to increase linearly with investment, $\mu(m) = am$ and $\phi(f) = bf$, although genetic profits increase nonlinearly because of competition among relatives. Second, the only competition between relatives and the only matings between relatives are assumed to be between siblings. Nonsiblings are assumed to be completely unrelated. These assumptions are discussed below.

Variation in Sex Allocation among Families

KOLMAN'S MODEL OF SEX ALLOCATION AS A NEUTRAL TRAIT   Kolman (79) and Bodmer & Edwards (5) provided the first formal model confirming Fisher's equal allocation theory. Previous analyses considered only sex ratio and implicitly assumed that expenditures per male and female offspring were equal. Kolman also stressed that any level of variation in sex allocation among families may exist at equilibrium. [This point was also briefly noted by Bodmer & Edwards (5).] For example, each family could be allocating equally to the sexes, or one half of the families could be allocating resources only to sons while the other half allocated only to daughters. Natural selection

is indifferent to the variance in sex allocation among families, or, put another way, sex allocation is a neutral character at equilibrium.

Kolman's conclusion about neutrality can be derived in a straightforward way. Using the notation above, a family's fitness is proportional to $m/M + f/F$. When the population is at the Fisherian equilibrium $M = F$, fitness depends only on the family's total allocation to offspring $m + f$ and not on how the family divides this total between males and females.

The neutrality of sex allocation variance among families depends on two implicit assumptions. First, the population must be sufficiently large that an individual family's division of resources to m and f has a negligible effect on the population allocation ratio $M:F$. Verner (111) was the first to analyze this assumption, which is discussed in the next section. Second, lack of selection on the variance rests entirely on the assumption that returns on investment are linear for both sexes. Linearity means that $\mu(m) = am$ and $\phi(f) = bf$ so that doubling investment in a sex within a family always doubles genetic returns regardless of the initial value of investment (see above). Doubling investment in a particular offspring is unlikely to cause an exact doubling of that offspring's expected reproduction, whereas making two identical offspring does exactly double expected genetic returns.

Several later models have shown how nonlinearities can affect the expected distribution of sex allocations among families. These include the Trivers & Willard (109) model for variation in parental resources (see below) and models that consider nonlinearities induced by local mate competition (54, 58, 115) or any factor in general (57). The example given above illustrates the stabilizing effect of nonlinearities: when all families have the same amount of resource to invest, when $\mu(m) = am$ and $\phi(f) = b\sqrt{f}$, and when the population is at its equilibrium, $m^*:f^* = 2:1$, then any individual family deviating from 2:1 will suffer reduced fitness.

Fiala (49, 50) has been the only author to state explicitly that nonlinearities in "sex-specific costs" greatly reduce the expected sex allocation variation among families when there is no variation in parental resources. Because, in this context, he accepted the mistaken distinction between sex-specific costs and sex-specific returns on investment (see below), he failed to appreciate the generality of his own result as a contradiction to Kolman's model. Further discussion of Kolman's model is taken up below in the analysis of Williams's (113) paper.

VERNER'S SEX RATIO HOMEOSTASIS HYPOTHESIS   Verner (111) showed that in small populations selection will tend to reduce the variance in sex ratio among families. To see how this works, consider a particular family in a small population. Assume that the equilibrium sex ratio is 1:1 and that the other

families together produce a biased sex ratio. If the focal family produces a sex ratio that brings the population ratio to 1:1, then for all families, family fitness is independent of its sex ratio, by Kolman's argument, because $M = F$. Verner showed, however, that if the other families produce a biased sex ratio and that an allocation fraction by the focal family of m in males would bring the population to 1:1, the focal family is in fact favored to produce a sex ratio nearer to 1:1 than m. Thus, given the sex ratios of the other families, each family is favored to produce a sex ratio nearer to 1:1 than the sex ratio that would produce a population ratio of 1:1. This process continually pushes deviants from 1:1 back toward equality, so that variance among families is reduced and "sex ratio homeostasis" is favored. The mechanism favoring homeostasis is subtle and can be understood by studying the calculations underlying Verner's Figure 1. Taylor & Sauer (107) have analyzed the magnitude of the homeostatic effect. Further discussion can also be found in Williams (113).

These models of homeostasis assume linearity in return functions μ and ϕ. Nonlinearity causes selection to favor a stable and often nonzero level of sex allocation variation among families. Methods for deriving the distribution of family sex allocation ratios are described later.

THE TRIVERS-WILLARD HYPOTHESIS AND FAMILY-LEVEL BIASES   Trivers & Willard (109) proposed that if one sex gains more from extra parental investment than the other, then parents with relatively more resources will bias their allocation toward the sex with the greater rate of reproductive returns. This idea has fostered much interesting research (22, 27, 33, 41, 75) and provoked some controversy over the interpretation of data (95, 113). Trivers & Willard focused primarily on the predicted positive correlation between a mother's physical condition and the proportion of sons produced. At the end of their paper they briefly outlined the more general prediction regarding the correlation between parental resources and the proportion of resources devoted to sons. I will consider the Trivers-Willard hypothesis as the more general statement about parental resources and sex allocation.

From a theoretical perspective the idea is self-evident. Incorporating the Trivers-Willard effect into a general theory of sex allocation in birds and mammals does, however, raise some important issues. The three main assumptions of the model can be expressed with the symbols used above. Consider first the assumption that one sex gains more from extra parental investment than the other. If m is parental investment in males and $\mu(m)$ is the expected competitive ability and mating propensity of males with investment m, and if f is parental investment in females and $\phi(f)$ is the expected fecundity of females with investment f, then the functions μ and ϕ must be different to

satisfy the assumption that one sex gains more than the other with extra investment. Second, the assumption that parents vary in their resources available for investing in offspring means that $m + f$ varies among families.

Third, the meaning of m and f must be made more precise. A rough description is that the quantity m means the total allocation to males within a brood and f means the total allocation to females. For example, if a family has only one offspring per brood then either m or f must be zero. If a family has many offspring, then m is the sum of the separate allocations to each male offspring and f is the sum over female offspring. Selection favors an allocation strategy that depends on how parents are able to distribute resources among offspring of the same sex, how resources may be split between the sexes, and what the reproductive consequences are for each decision. Thus, the meaning of m and f, $\mu(m)$ and $\phi(f)$, and the Trivers-Willard effect depend on the number of offspring per brood. More careful definitions of these terms and their important biological implications are considered below.

CONSEQUENCES OF THE TRIVERS-WILLARD EFFECT AT THE POPULATION LEVEL   The Trivers-Willard effect depends on the assumption that a difference exists between the functions that relate investment to male and female reproductive returns. As discussed above in the section on nonlinear returns, when these functions differ then equal allocation is not expected at the population level. Thus, the Trivers-Willard effect, which is about biases within and among families, has as a corollary an expected bias in the population allocation ratio. Frank (57) presented methods for predicting the magnitude of the population-level bias.

The ways in which various authors have treated the population-level consequences of the Trivers-Willard effect form a complex historical problem. The most common approach has been to apply simultaneously both the Trivers-Willard effect and Fisher's equal allocation theory, a treatment that is logically inconsistent. Authors have often incorrectly raised Kolman's idea for the neutrality of the Fisherian equilibrium as evidence that the Trivers-Willard effect at the family level can coexist with the Fisherian effect at the population level.

DEVELOPMENT OF THE THEORY

By the late 1970s the major ideas in sex allocation theory had been raised. Although each idea was originally formulated within the context of limiting assumptions, with hindsight the main ideas can be listed broadly as: Fisher's model for frequency dependence, which is a consequence of the joint genetic

contributions of the two sexes; Charnov's marginal value model, which extends Fisher's model by allowing for nonlinearity between investment and return; Hamilton's model for competition and mating between relatives; Lewis's model for the genetic control of sex ratio; and the Trivers-Willard model for variation in sex allocation among families.

The late 1970s was also a time of rapidly growing interest in the adaptive analysis of social behavior. Sex allocation was a central platform for testing and debating this approach in evolutionary studies, beginning with Hamilton's (71, 73) papers on how interactions among relatives affect sex allocation and the evolution of fighting, Trivers & Willard's (109) paper on adaptive sex ratio in vertebrates, and Trivers & Hare's (108) effort to test theories of inclusive fitness and parent-offspring conflict through predictions about variation in sex allocation patterns in social insects.

Efforts to test sex allocation theory exposed a number of unrealistic assumptions and new problems. In response, explanations of sex allocation expanded to encompass broader assumptions and new phenomena. I here describe the development of sex allocation theory according to both its chronological development and its logical structure as seen from the present.

Factors Affecting Variation Among Families

MYERS'S MODEL OF FAMILY SIZE AND SEX RATIO COMPOSITION   Myers (95) extended the Trivers-Willard idea of adaptive sex ratio variation by proposing a different mechanism for generating variation. Trivers & Willard had emphasized, for stressed mothers, greater postconception mortality of sons, compared with daughters, although they mentioned that other mechanisms of variation may occur. Myers claimed that postconception mortality is an unlikely mechanism to have evolved by natural selection because it entails a loss in reproductive potential through reduction in lifetime reproductive success.

Myers proposed as an alternative mechanism that parents may be able to adjust the primary sex ratio. For example, if resource limitation causes higher offspring mortality among males than females, then stressed families that produce more daughters will have a greater number of successful offspring. Thus, Myers's idea emphasizes that sex ratio composition of families may be adjusted to maximize the number of successful offspring rather than the average reproductive potential of each offspring. Myers's critique raises the important role of the physiological, behavioral and genetic mechanisms that cause variation in sex allocation among families (see below).

WILLIAMS'S ANALYSIS OF THE DISTRIBUTION OF SEX RATIOS IN A POPULATION   Williams (113) reviewed four models to explain variation in sex

ratio among families. In the first part of his paper he reviewed the logic of these models and deduced contrasting expectations in terms of the variance in sex ratio among families. I summarize the main arguments here.

The mendelian model   According to this model, the sex of each offspring in the population is determined by the random processes of meiosis and fertilization and is independent of variation in parental condition and resources. The expected variance in sex ratio among families is consistent with a binomial distribution. This prediction is difficult to test in mammals since conception sex ratios are rarely available. Birds are more promising in this regard if mortality is low before sexing.

The adaptive model   Williams suggested that mothers in good condition in one breeding season are also likely to be in relatively good condition in the next breeding season. Likewise, those in poor condition are likely to remain in poor condition. If litter size is one, then according to the Trivers-Willard model, mothers in good condition will tend to have a series of sons and those in poor condition will tend to have a series of daughters. Thus, serial autocorrelation in maternal condition and a correlation between maternal condition and offspring sex causes a greater than binomial variance in the sex ratio among the lifetime outputs of mothers.

If litter size ranges from one to three, a purely adaptive (unconstrained) model predicts a sequence of combined litter size and sex ratio strategies according to the level of parental resources (113; Figure 3). Models concerning control of both investment per offspring and litter size trace back to Ricklefs (98) and Smith & Fretwell (101).

In the purely adaptive model shown in Figure 3, parents control number and sex of conceptions directly. The expected transitions between each litter composition depend on the return curves for sons and daughters and the distribution of parental resources in the population (57). No general qualitative trend has been demonstrated for the expected sex ratio variance among litters. Note also the weak correlation between parental resources and litter sex ratio (Figure 3).

If the conception sex ratio is not subject to modification (constrained), then some adjustment may be made by sex-biased abortion, or by sex-biased infanticide if most parental investment occurs after birth (1). In the case of constrained adjustment, the strategies favored by natural selection will depend on the particular mechanism of adjustment and cannot be predicted without further assumptions or data. Under either constrained or unconstrained adjustment, it is not obvious whether the expected variance would be greater or less than binomial. Williams (113, p. 571) suggests in his verbal model that
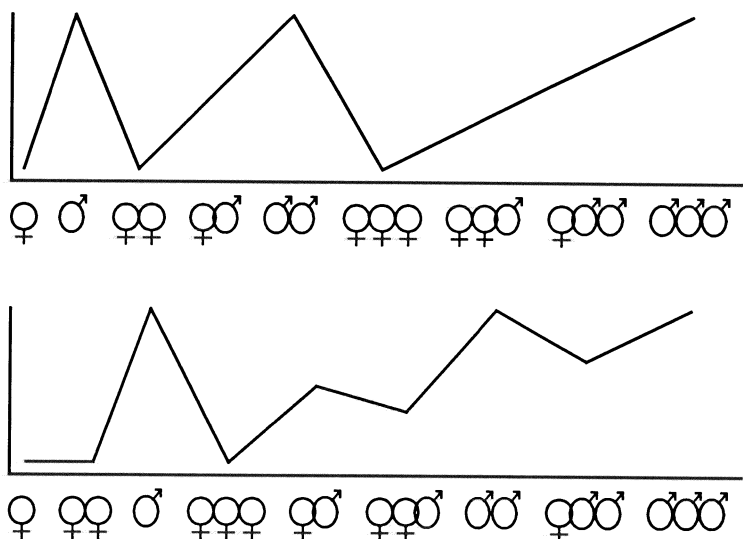
Figure 3   The optimal number and sex of offspring in litters produced by parents with increasing amounts of resource to invest. In both panels males gain more than females from relatively high levels of investment. In the lower panel a single son can be more valuable reproductively than two daughters when given a high level of investment. The graphs in each panel show the litter sex ratio (male frequency) as a function of parental investment.

variance is expected to be greater than binomial since a preponderance of single sex broods is expected. A model to test the logic of this conjecture is feasible but would require many detailed assumptions (57). It is unclear whether a robust prediction would emerge from such an analysis.

In conclusion, the prediction from a strict interpretation of the TriversWillard model in litters with a single offspring may be a variance among lifetime broods that is greater than binomial. The predictions from a range of plausible adaptive models and larger brood sizes are, however, difficult to ascertain without numerous assumptions. In addition, the correlation between parental resources and litter sex ratio is difficult to predict in species with litter sizes greater than two (Figure 3) or in species such as humans that have a significant sharing of resources among the offspring of a series of small litters (see below).

The neutral model   As described above, Kolman (79) had shown that the variance in sex ratio among families is a neutral character. Williams developed this notion to show that under Kolman's model the sex ratio variance among families is expected to be greater than binomial but that, in contrast

with the adaptive model, the neutral model predicts no association between parental resources and sex ratio.

Kolman's model depends critically on the assumption for both sexes of linear returns between investment and reproductive returns. Since at least slight nonlinearities in the returns on male and female investment seem very likely for birds and mammals, Kolman's model and Williams's corollary are inappropriate for these organisms.

The homeostatic model   Selection in a small population favors families that invest as closely as possible to the population optimum under certain conditions (107, 111). Williams concluded that sex ratio variation would be less than binomial if this force were operating.

Models of homeostasis in a small population depend on the assumption that Kolman's neutral equilibrium exists. When there are nonlinearities and all members of the population have the same level of resources to invest, the equilibrium is attracting rather than neutral, which induces a powerful homeostasis (small variance) of an entirely different type from Verner's. When there are nonlinearities and a variance in parental resources—the implicit assumptions whenever one analyzes the potential for adaptive sex ratio variation—the predicted sex ratio variance among families depends on many detailed assumptions (57, 67) and has yet to be worked out for any case.

In conclusion, little can be learned about adaptation and its constraints by analyzing 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. Discrepancies between theory and observation may point to important factors that were previously overlooked (75a).

TRADE-OFFS AMONG SIZE, SEX, AND NUMBER OF OFFSPRING   Myers (95) and Williams (113) pointed out that considering both numbers and sex of offspring complicates predictions about the relationship between parental resources and sex ratio under an adaptive model (Figure 3). McGinley (92) and Gosling (67) extended these ideas and supplied some interesting data.

All of these arguments are verbal and serve to raise possible outcomes, but leave open the question of what is actually expected given particular assumptions. Frank (57) presented a series of formal models that clarifies the types of detail that must be specified and the possible outcomes. In particular, one must first specify the relationships between parental investment and reproductive potential for both male and female offspring. From these functions one can then apply a Smith & Fretwell (101) type of analysis to determine the optimal division of resources among a group of sons when given a fixed total amount for all sons, and the division among a group of daughters when given

a fixed total amount for all daughters (85). This yields a pair of functions that describe the optimal relationships between investment and returns for total male and total female investment.

Given a technique for determining the optimal division of resources among males and among females, one can then calculate the optimal division of resources between the group of males and the group of females in the litter. In each family this division depends on both the family's resources and the distribution of resources among all families (57). For example, simply knowing that for a particular family 50% of the population has more resources is not sufficient to predict behavior. Predictions are of course also sensitive to the genetic variation available for selection and the physiological and behavioral mechanisms available to adjust allocation strategies (57, see below). Thus, generalizations based on verbal arguments should be treated with caution.

A CRITIQUE OF THE IDEA THAT MALES AND FEMALES EACH HAVE A PARTICULAR "COST"   Many papers on sex allocation discuss the idea that males and females cost different amounts of resources to produce—for example, that male mammals are more costly to produce than female mammals. Further, in the process of developing theories, a fixed numerical value is sometimes assigned for the relative cost of producing a male or female. In reality parents across a population invest a wide range of resources in males and a different but wide range in females.

Rather than thinking that males cost more than females, it seems more appropriate to consider that each family adjusts its investments according to its resources and to the differing rates of return, given constraints such as primary sex ratio, the advantages and disadvantages of brood reduction, and the value of saving energy for future reproduction. For example, suppose parents across the population invest between 1.0 and 1.6 units in a male, and 0.7 and 1.3 in a female, and each family adjusts its allocations according to both number and sex ratio of offspring (see 57, p. 64 for a related model). A family that had 4.5 units would have several options for the number, sex, and investment in offspring and for holding some of its current energy for future reproduction. There would be little value in a model of variation among families that analyzed expected sex allocation patterns by assuming that males cost 1.3 units and females cost 1.0 units. The average relative costs of males and females may, however, be a useful quantity when making very broad phylogenetic comparisons (66a).

UNSOLVED PROBLEMS   Many open questions remain in the theory itself and in the methods needed to relate theoretical predictions to observable quantities.

The problem of currency   Theories invariably assume a unidimensional limiting resource that parents divide among offspring or save for future reproduction. In reality parents invest many types of resources. Whether theories that reduce these many dimensions to a single limiting one are robust is unknown. Further, what to measure in the field or lab in order to test predictions is often a troublesome problem. McGinley & Charnov (93) discussed the multidimensional nature of resources in allocation problems. Boomsma & Isaaks (6) discussed the problem of currency in social insects. Bull & Pease (15) developed a method that can be used to estimate the trade-off between son and daughter production and applied their method to data from a polychaete, an organism with no parental care. For species with parental care, their method requires the unlikely assumption that males and females each have a particular constant cost (see previous section). In summary, both the major theoretical questions about multidimensionality and the problems of relating theory to observation remain unsolved.

The trade-off between current and future reproduction   The amount of parental investment in each breeding season may affect a parent's ability to invest in future offspring. For example, when a red deer mother has a son, she will skip breeding in the next season more often than after having a daughter (36). In spider monkeys, in which sons of high ranking females receive more investment than daughters, the interbirth interval is larger after a son is reared (104). In other species, such as humans, the period of parental care overlaps for sequential litters, so that investment in offspring from one litter detracts from resources available for offspring from different cohorts that are simultaneously under parental care.

The problem of defining fecundity per investment period   Williams's (113) analysis shows that litter size plays a crucial role in determining the options available to parents and therefore in the patterns of variation expected among families (see above). Litter size may be only part of a larger problem (20, 22, 57). The parental decisions that affect genetic contribution concern trade-offs between investing in a particular offspring or using those resources to invest in other offspring from the same litter or other offspring from previous or future litters. The number and sex of offspring from past, present, and future litters among which parents can distribute limiting resources determine the options available and thus the patterns of variation that may occur. This number is the fecundity per investment period (57).

Three cases illustrate some possibilities for fecundity per investment period (57). (*a*) Current investment has no effect on past and future litters. Litter size and fecundity per investment period are identical. (*b*) Current investment affects resources available only for the next litter but, to a reasonable

approximation, not more distant future pairs of litters. Fecundity per investment period is the size of sequential litters. (*c*) The period of parental care is long, and all litters must share limiting parental resources. Fecundity per investment period is the lifetime reproductive output of the parents. Humans seem the best example of this last case, which contrasts with Trivers & Willard's (109) and Williams's (113) analyses that assumed humans have a single offspring per investment period. The consequences of different fecundities per investment period are examined below.

Perhaps the most important unsolved problems concern the genetic, physiological, and behavioral mechanisms that generate sex allocation variation among families. These problems are discussed in a separate section below.

Variation among Families and Population Patterns

Commentary on variation among families is usually made independently of predictions about population level patterns because most authors agree that Fisher's equal allocation theory applies. As discussed above, adaptive theories about variation among families, such as Trivers-Willard's, require a difference in the return functions between males and females. This difference usually implies that equal allocation at the population level is not a correct prediction of the theory. Whether expected departures from equality are trivial or important must be addressed explicitly. In this section I review a few key papers on population level patterns.

MAYNARD SMITH'S MODEL FOR THE CONSTRAINT OF SEX DETERMINATION   Maynard Smith (89) developed three models to explain how a bias in population sex allocation may be favored by natural selection. His work was motivated in part by the observed male bias in the population allocation ratio of red deer (35, 36).

Marginal value model   Maynard Smith began by deriving the marginal value result given in Equation 1 above (Maynard Smith's Equation 8), where for investment m in males, parents receive reproductive returns $\mu(m)$ (Maynard Smith's $\psi(m)$), and for investment f in females, parents receive returns $\phi(f)$. As discussed above and by Maynard Smith just following his Equation (9), the marginal value result implies a bias at the population level whenever μ and ϕ are different functions. Maynard Smith also points out that the direction of bias may be toward either males or females depending on the particular assumptions about μ and ϕ. His conclusion, that at equilibrium more will be invested in males if, for a given investment, females are more likely to survive than males, depends entirely on the particular forms for μ and ϕ that he chose. No evidence is given that the conclusion is typical.

Additional frequency dependence   Since Maynard Smith's goal was to explain the observed population bias in allocation toward males in red deer, he considered whether further assumptions associated with the basic marginal value model yielded a more robust conclusion. In particular, he assumed (*a*) that the return functions μ and ϕ are identical except (*b*) that males have an additional frequency dependent component in competitive ability or viability. One example of this frequency dependence would be that male viability depends on the total level of investment in males, for instance, male viability for a given level of investment decreases as the population-wide allocation to males increases. Using these assumptions, Maynard Smith showed that the population sex allocation ratio is expected to be biased toward males or, more generally, toward the sex with the additional frequency dependent component of viability or competitive ability. Note that this frequency dependence is distinct from the Fisherian frequency dependent competition among males that occurs in all models of sex allocation.

Constraint of sex determination and initial investment   Maynard Smith next pointed out that these two models depend on the assumption that a parent makes the same investment in all offspring of a given sex. He suggested that parents may actually be favored to invest heavily in some offspring and little in others to the extent that they can adjust their investments by behavioral or physiological mechanisms (1, 22, 44). In the extreme case if parents know the sex of offspring before any investment has been made, then they can control their family sex ratio. Maynard Smith suggested that if parents have complete control over their family sex ratio, then Fisher's equal allocation argument applies, and we expect total investment in males and females to be equal. No model or assumptions are given under which the claimed robustness of Fisher's equal allocation actually follows. The only available models show that differences between male and female return functions as discussed in Maynard Smith's first model usually lead to biased population allocation when parents can adjust allocation to each offspring (57, see below).

Maynard Smith next examined the effects of a minimum investment in each offspring before its sex is known to the parent. This assumption was intended to match species in which control over offspring sex ratio is at least partly constrained by genetics or physiology. Under various assumptions Maynard Smith showed that parents may be favored to abandon some offspring of the sex that gains more under high levels of investment (1, 22, 44). If, for example, males gain more at high levels of investment, then under some circumstances parents will be favored to raise fewer sons than are conceived but to invest more in each son than each daughter, so that an overall bias in total investment toward males may occur. Again, a number of restrictive

assumptions such as lack of variation in the amount of resources available to parents leaves the quantitative conclusions of this model open to question. This model does, however, represent a major advance because it focuses attention on the types of sex allocation variation that selection may adjust and the types of variation that are constrained by genetics and physiology.

CLUTTON-BROCK'S REVIEWS   Fisher's equal allocation theory predicts that the sex ratio at the end of parental investment should be biased toward the sex with lower average investment. Clutton-Brock et al (36) and Clutton-Brock & Albon (35) found only two cases in which sufficient data were available to consider this prediction. In both red deer and northern elephant seals, more males than females were born, and males typically received considerably more milk than did the females. At the end of weaning, more males were alive in both species even though male mortality was higher. Clutton-Brock and coworkers concluded that investment was probably biased toward males. They considered and rejected Maynard Smith's (89) explanations for biased sex allocation because Maynard Smith had suggested that if certain of his unlikely assumptions did not hold, then equal allocation is expected. As discussed above and further below, the predicted population allocation ratio is unclear for these organisms under both unconstrained models and under assumptions of genetic, physiological, or behavioral constraints. It is clear, however, that equal allocation is an unlikely prediction of any realistic model for these organisms.

CHARNOV'S MODELS   Charnov (26) presented the first model relating differing nonlinear returns per unit male or female investment to expected population allocation patterns. His model was developed for simultaneous hermaphrodites, but the same formulation applies to dioecious organisms. Charnov assumed in his model that all individuals had the same level of resource to invest and that at equilibrium all invested the same fraction in male and female function. The model therefore does not apply to the relationship between variation among individuals and population level patterns.

Charnov (25) presented the first formal model of sex ratio variation among individuals under differing returns per unit male or female investment. This model extends the ideas first presented verbally by Trivers & Willard (109) and applies these primarily to organisms that choose sex in a patchy environment. For example, a female parasitic wasp that lays one egg on each host may choose the sex of each offspring according to the relative host size. Charnov (25) assumed, based on available data, that males are relatively more successful than females when emerging from small hosts and that the opposite holds in large hosts. By assuming that small and large hosts exist as discrete

size categories with fixed probabilities, Charnov calculated the predicted sex ratio in each size class. As expected, males are produced more frequently on small hosts and females on large hosts; the particular ratios depend on assumptions about relative male and female fitnesses and on the relative frequencies of the two host sizes. Bull (11) and Karlin & Lessard (77) have presented more rigorous population genetic analyses of this model. All of these papers concern sex ratio, and no mention is made of relative investment of resources in the two sexes. In general the predicted sex ratio is not 1:1.

In collaboration with Assem and coworkers, Charnov et al (30) presented a series of elegant experiments on parasitic wasps confirming the main predictions of Charnov's (25) model. In the 1981 paper (30) the authors made the more realistic assumption that a continuous distribution of host sizes exists. In addition, they assumed that the fitness of a female relative to a male increases steadily as host size increases. Under these assumptions a single threshold point for host size exists, below which a mother is favored to produce only sons and above which only daughters. The threshold depends on the distribution of host sizes, which is an obvious prediction of the theory and which Charnov et al (30) demonstrate by experiment. Given specific assumptions about the relative fitness of males and females as a function of host size and about the distribution of host sizes, one could in principle calculate the predicted population sex ratio. Further, if host size is taken as a measure of resources allocated to each sex, then population allocation ratios could be calculated (57, see below).

MODELS OF CONDITIONAL SEX EXPRESSION   Charnov (27, pp. 140–141) showed for sequential hermaphrodites that the sex favored when relatively weak or small is expected to be more abundant in the population. Frank & Swingland (62) extended this idea to any case in which sex is conditionally expressed, including cases in which sex is environmentally determined (12, 28) or in which the sex of offspring can be manipulated by a mother in response to the amount of resources she has available for investment. Frank & Swingland (62) stressed that this theory makes a robust prediction about the greater abundance of the smaller or weaker sex, but that population sex allocation under these conditions may be biased toward either sex and that no robust prediction can be made. Thus, the usual interpretation that the cheaper sex is more abundant because of Fisher's equal allocation theory does not apply. Charnov & Bull (29) have also elaborated Charnov's (27) original model.

The most interesting prediction of this theory can be illustrated by considering red deer. The theory predicts that the sex produced when mothers are relatively weak, in this case females, should be more abundant. In fact, more males are born and more are weaned (35, 36). Two assumptions of the

conditional sex expression model may be violated by red deer. First, the model assumes that a mother can freely choose offspring sex, whereas evidence suggests that although weaker red deer females do produce relatively more daughters, they are partly constrained in this regard. Second, the model assumes that investment can be made in males or females but cannot be split between offspring. If a red deer mother has energy available that she saves for future investment, then she may be dividing her resources between offspring even though she produces only one offspring per breeding season.

FRANK'S MODEL FOR INDIVIDUAL AND POPULATION SEX ALLOCATION PATTERNS   Frank (57) presented quantitative predictions for sex ratio and sex allocation under Trivers-Willard type models. In the first model the assumptions are: (a) the amount of resources each family has is k, and k varies according to the probability distribution $g(k)$; (b) returns on total male investment m are $\mu(m)$ and returns on total female investment f are $\phi(f)$; and (c) litter size is one. As described in the previous section, the predicted sex ratio is biased toward the sex produced by parents with relatively low levels of resource, but the population sex allocation ratio may be biased toward either sex. The predicted ratios depend on the male and female return functions μ and ϕ and are also sensitive to the shape of the resource distribution curve g. A variety of related assumptions were also considered.

The second model assumes that litter size may be greater than one and analyzes how parental resources are divided within a litter among offspring of the same sex and between the offspring of opposite sex. Also, as Maynard Smith (89) suggests, sex ratio at conception may be constrained, and some investment d may occur before parents are able to recognize the sex of a particular offspring. The model predicts that sex-biased abortion or infanticide may occur, but the complex trade-offs discussed above between size, sex, and number of offspring prevent any general qualitative conclusions about the distribution of family strategies or the total sex ratio and sex allocation in the population.

One general conclusion did emerge from this set of models. The greater the number of offspring that must share limited parental resources, the more robust Fisher's theory for equal population sex allocation. Recall that when returns on investment are linear for both sexes, then Fisher's prediction follows. In general, the greater the difference in the shapes of the returns on male and female investment, the greater the expected departure from equal allocation. If there is only one offspring for each parental investment period, then the difference between returns on male and female investment will generally be large, and significant departures from equal allocation are expected.

If there are many offspring in each parental investment period, then returns on both male and female investment will be approximately linear because

returns will scale with numbers of offspring (Figure 4). For example, if a parent has already produced 100 sons, then a 50% increase in male investment will yield 150 sons, a 50% increase in return. By contrast, if a parent has one son, a 50% increase in investment in that son or division of resources between two sons will not translate exactly into a 50% increase in return. Figure 4 illustrates the relationship between fecundity and shapes of return curves. Note that fecundity per investment period is not the same as litter size. This point was discussed in the section on *Unsolved Problems*.

SUMMARY FOR POPULATION LEVEL PATTERNS   Fisherian frequency dependence is at the heart of all models of sex allocation, but equal allocation is not expected in low fecundity organisms. Departures from equal allocation increase (*a*) as fecundity declines, (*b*) as the amount of parental care increases and thus parental ability to manipulate allocation increases, and (*c*) as the intensity of sexual selection increases, and thus differences in the return curves for individual sons and daughters increase.

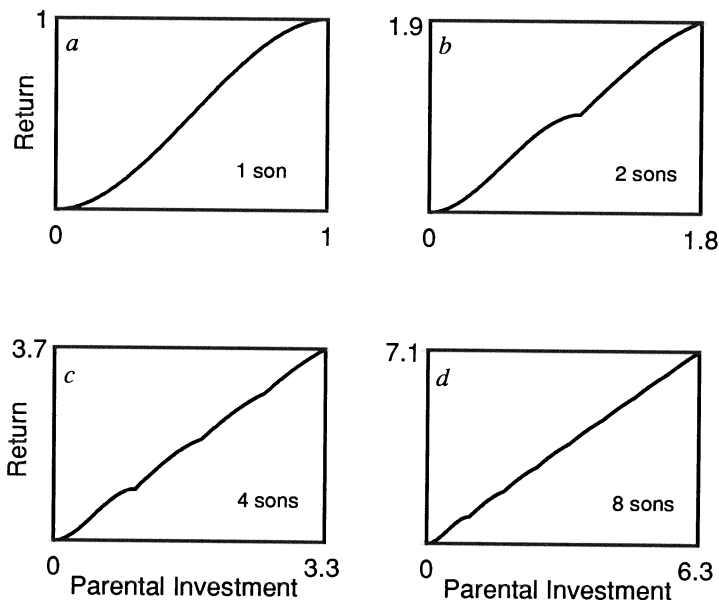Not enough data are available nor has enough theory been done to provide

Figure 4   The relationship between parental investment in sons within an investment period and expected total reproductive return for these sons. The relationship between investment and return for each son is nonlinear as shown in *a*. As number of sons increases the return curve rapidly approaches linearity. These curves show simultaneous optimization of size and number of sons. The return on each son is given by $h(z) = \int_0^z y(1 - y)dy$, which is also shown in Figure 1*b* with $s = 2$. In this case the return on total investment k split among n sons is $nh(k/n)$.

strict limits on expected departures from equal allocation under different assumptions. Based on an earlier paper (57), my own conjecture for ranges of predicted population sex allocations given as units of male investment per hundred units female investment (followed by fraction invested in males) is: between 54 (0.35) and 186 (0.65) for few offspring per period (one to two); smoothing toward a range of 67 (0.40) to 150 (0.60) fairly quickly as offspring numbers go to medium size (three to six); and then slowly approaching a robust equal allocation as the number of offspring per investment period continues to increase. These arguments assume no limits on the genetic, physiological, and behavioral variation available for natural selection to mould parental investment patterns, and the arguments assume outbreeding and no competition among relatives.

Extensions for Observed Genetics, Dispersions, and Demographies

SEX CHROMOSOMES AND POPULATION CYCLES IN LEMMINGS   Sex chromosome polymorphisms and segregation distortion cause strongly female-biased sex ratios in varying lemmings *(Dicrostonyx torquatus)* and wood lemmings *(Myopus schisticolor)*. Bull (12) summarized the main observations and theory; newer data and theory can be found in Gileva (65) and Bulmer (18), respectively.

These species possess X and Y chromosomes that act similarly to other mammals. In addition both species possess X^*, such that X^*X and X^*Y are females. In *Dicrostonyx*, the Y is sometimes absent so that X^*O is female and XO is male.

Myopus X^*Y females produce only X^* ova and all female broods, and YY zygotes are never formed (70). In *Myopus* the predicted equilibrium sex ratio is 25% males under the assumptions of equal fertility for all genotypes and normal segregation in all except X^*Y females (4, 13). The observed sex ratio in laboratory colonies is generally below 25% (summarized in 13). Bull & Bulmer (13) pointed out that segregation distortion in favor of Y sperm actually may cause an increase in the expected proportion of females, but no evidence for Y distortion has been found in *Myopus*. Their model also demonstrated the surprising conclusion that an autosomal modifier enhancing segregation distortion of the Y would be favored even though it causes a further deviation of the sex ratio from 1:1.

Dicrostonyx X^*Y (and X^*O) females apparently segregate sex chromosomes normally, thus producing some inviable YY (OO) zygotes, but there is at least partial reproductive compensation for this loss in fertility (64–66). Depending on a range of likely assumptions about reproductive compensation, the predicted sex ratio varies from 36% to 42% males (13). Data from laboratory colonies tend generally to be below this predicted range. Following

up on the prediction of Bull & Bulmer's (13) model for *Myopus,* Gileva (65) has shown that Y sperm have a segregation advantage of 0.56 ± 0.01 in *Dicrostonyx.* Bulmer (18) has developed a theory incorporating Y distortion and has shown that, as in *Myopus,* Y distortion in males actually causes a decrease in the predicted frequency of males. Bulmer (18) analyzed various assumptions based on the observed genetics that could explain the observed sex ratio and frequencies of genotypes.

Several authors have suggested that the female-biased sex ratios of lemmings are an adaptive response to their unusual population cycles (19, 91, 102); other authors have argued against the cycles as a cause of biased sex ratio (13, 18). If lemming populations are frequently broken up into small isolated demes after a population crash, and subsequently each deme expands at a rate increasing with its frequency of females, and if a deme's contribution to the population after a crash depends on its size before the crash, then female-biased sex ratios are expected. On the basis of the observed Y segregation distortion in *Dicrostonyx,* Bulmer (18) concluded that population cycles are unlikely to maintain the X^* system because simpler mechanisms are available for sex ratio modification and because his analyses are consistent with an outbred population structure. He concluded that the X^* karyotype exists because an appropriate suppressor, which would be favored by selection, has not yet arisen. Current data are not sufficient to separate these competing explanations or to suggest any compelling alternatives. All of the theories presented assume Fisherian equal allocation as a point of departure and ignore male-female differences in return curves and the low to medium fecundity per investment period.

COMPETITION AND COOPERATION AMONG KIN   Competition among siblings of the same sex favors a reduction in investment in that sex (see above, 19, 32, 71, 105). Observed biases in population sex ratio have led several authors to consider kin interactions as an explanation, including the effects of cooperative rather than competitive interactions.

In red deer, population sex ratio and sex allocation both appear to be male biased (35, 36). Females tend to remain near the area in which they were born, raising the possibility that females compete for resources with sisters or their mother. Such local resource competition could explain the observed male bias. This argument is considerably weakened by the fact that elephant seals share many life history characteristics with red deer such as one offspring per litter, large sex dimorphism with bigger males, and intense male-male competition for mates. Elephant seals also have a male-biased sex ratio and allocation ratio, but they do not appear likely to experience local resource competition. Invoking local resource competition for red deer leaves unexplained the similar sex allocation pattern of elephant seals (36). Cockburn

(41, 42) summarized several other cases of male-biased sex ratios and analyzed these in the context of local resource competition. Direct evidence for female-female competition is generally lacking, but across several species male-biased dispersal tends to correlate positively with male-biased sex ratios.

Johnson (76) summarized data supporting the idea that varying levels of local resource competition could explain variation in birth sex ratios across 15 primate genera. Johnson showed that the sex ratio (frequency of males) is positively correlated with both the intensity of competition within kin groups and the level of female philopatry. The conclusion is made more convincing by Johnson's observation that in primates extreme sex ratios arise only when competition between females is intense or when sex differences in dispersal are reversed (104). Johnson also tests and rejects the idea that size dimorphism is correlated with sex ratio trends.

The model of conditional sex expression presented above provides an alternative and unexplored hypothesis for the primate data. Recall that when investment is made entirely to males or females but not both within any period, then the sex ratio is expected to be biased toward the sex that is typically produced with smaller amounts of resources. No prediction about the sex allocation ratio is made by this hypothesis. The prediction appears to be consistent with at least some of the data, since in macaques and baboons, in which daughters tend to receive more resources than do sons, the sex ratio tends to be male biased. In wild spider monkeys, sons typically receive more investment than do daughters, and the sex ratio is female biased (104). The wild spider monkey data also support the kin competition idea (104), since the males in this species are philopatric whereas females disperse. The data from red deer and elephant seals are against the conditional sex expression model, since in these species males receive greater investment and are the more numerous sex.

From a theoretical perspective a number of uncertainties remain about models of kin interactions. No models have analyzed both nonlinear returns on investment per offspring and the nonlinearities independently generated by kin competition. In primates, for example, a realistic theory must take account of: (a) nonlinear returns on investment per offspring and variation among parents in resources available for investment—these together form the basis for the observed Trivers-Willard variation in sex allocation among families with different resource levels; (b) the trade-offs among sex, size, and number of offspring in a parent's lifetime—the sex of a current offspring is known to affect future reproductive potential; and (c) the role of competitive and cooperative interactions among kin. From a complete theory one could analyze alternatives to the comparative explanation offered by Johnson. It would be valuable to know how alternatives might be separated, and whether one could form more precise predictions for comparisons between populations

of the same species or between groups of closely related species that differ in only one or a few key ways. Finally, as discussed above, it is not valid to rely on equal allocation as an alternative and in some sense null hypothesis.

Packer & Pusey (97) observed that large cohorts of lions tend to have a more male-biased sex ratio than do small cohorts. Cohorts are groups of offspring born within one year of each other in prides of 1–18 adult females. Females in prides tend to be related, since females are philopatric and males disperse. Packer & Pusey explain the male bias in large cohorts by noting that male success depends on being a member of a successful coalition, where coalitions are typically formed from male relatives born in the same cohort. For example, in a small all male cohort (one to two) the males are less likely to form successful coalitions, whereas in large male cohorts the possibility of a successful coalition is considerably higher. Cohort size had only a slight effect on the success of an all female cohort.

Packer & Pusey (97) tested the hypothesis that males are favored in large cohorts by comparing sex ratio in prides when births are relatively more synchronous versus less synchronous. Synchrony is induced by a male takeover of the pride, so the comparison is between recently conquered and stable prides. Recently conquered prides produced a significantly higher fraction of sons (0.57) than did stable prides (0.48). Further, litter compositions of individual females after a takeover support the idea that selection favors groups of males born together. Among litters of size three or four there were a preponderance of litters with three males. Packer & Pusey discuss the trade-offs among size, sex, and number of offspring in a litter.

In all the cases discussed here, the competition and cooperation among kin includes siblings, cousins, and more distant relatives. Hamilton's (71) original model and subsequent work through the early 1980s analyzed only situations in which kin interactions were among siblings. Extensions of the mathematical theory to cover more general types of kin interactions have not uncovered any surprising qualitative conclusions—the key factors are the level of relatedness and the intensity of competition or the value of cooperation. Theoretical developments on generalized kin cooperation have been made by Frank (59) and on generalized kin competition by Frank (54, 55, 56, 58), Bulmer (16), and Taylor (106). Taylor's (106) theory is the most comprehensive, incorporating variation in genetic control of sex allocation and in complex life histories and demographies that affect the relative contribution of male and female cohorts to future generations. Frank (56, 58, 59) provided the simplest models for general kin interactions and the simplest verbal interpretations for the formal theory.

HELPERS AT THE NEST   Male-biased sex ratios have been observed in adults of several cooperatively breeding bird species (8, 9, 45, 46). Female-biased mortality after fledging cannot be ruled out as an explanation, particularly

since males are the philopatric sex. Brown (10, pp. 81–82) summarized evidence suggesting female-biased mortality in several cooperatively breeding species. Gowaty & Lennartz (69) have provided the only evidence showing a male-biased sex ratio among fledglings. They reported 59% males among 168 nestlings in red-cockaded woodpeckers, a species in which many nests have helpers that are mostly male. The weights of male and female nestlings were nearly equal, suggesting that sex ratio and sex allocation are approximately equivalent. Nests with older females and one or more helpers produced 54% males, whereas young females with no helpers produced 69% males (the difference is not statistically significant, but the sample size is small).

Several explanations are consistent with the data from red-cockaded woodpeckers: (a) Females without helpers produced more sons to increase their chance of obtaining help (69). (b) Older females were in some way better at producing daughters (69). There was no evidence that sex-biased mortality was affected by maternal age, nor was there evidence suggesting that females of older mothers were larger or reproductively superior to females of younger mothers. (c) Gowaty & Lennartz (69) suggested that, if older mothers are compared to younger mothers when each has helpers, older mothers were more likely to have sons as helpers and younger mothers were more likely to have nondescendant helpers. Sons as helpers may create intersexual competition because mother and son may not breed together but both will compete for mating at that familial nest. Gowaty & Lennartz (69) therefore favored the explanation that mothers that already have a son (older mothers) were less likely to produce more sons that would increase further the level of intersexual competition than were young mothers that were not experiencing intersexual competition. More generally, patterns of sex-biased territory inheritance may influence sex allocation in several species with helpers. (d) Gowaty & Lennartz (69) proposed and Emlen et al (47) quantified the idea that males were overproduced because they reduced their total costs to their parents by paying back some of the reproductive investment through helping (see also 105).

GENETIC AND PHENOTYPIC BASES OF VARIATION

The direction of evolutionary change and the potential for adaptive modification depend on available variation. The causes of phenotypic variation in sex allocation can take several forms. Consider two extreme cases. First, alternative alleles at a single locus may cause the production of different sex ratios. Second, the population may be genetically monomorphic for a behavioral-physiological mechanism that causes parents to adjust the number, size, and sex of their offspring according to the amount of resources they have to invest. Rare genetic variants may have different parameters controlling this

mechanism such that, for the same level of resources, two genetically different parents would invest differently.

Models that make testable predictions must rest on assumptions about both the selective forces acting and the genetic and phenotypic (material) bases of evolution. In this section I summarize the different types of assumption about variation. Below I consider some of the difficulties of testing theories, which necessarily rest on both selective and material assumptions.

Pure and Constrained ESS

Pure evolutionarily stable strategy (ESS) models assume that individuals behave in such a way as to maximize their (single-locus) autosomal genetic contribution to future generations. This requires that all types of variants can occur and that selection has sorted among these variants. For example, in Figures 3 and 4 each parent adjusts the size, sex, and number of its offspring according to its resource level. These adjustments require that the resource level at which each transition from a smaller to a larger litter size occurs has been adjusted by selection acting on genetic variation in a behavioral-physiological mechanism.

Models of constrained ESS assume that individuals maximize their genetic contribution within the limits of certain material constraints. For example, Trivers & Willard (109) assumed that sex ratio at conception was fixed and that mothers in relatively poor condition aborted a higher frequency of male fetuses. This mechanism sets a limit on possible sex ratio variation among families. Myers (95) made the contrasting assumption that parents could manipulate conception sex ratios according to resources, which led her to a different set of predictions about sex ratio variation. Williams (113) tested a set of models with competing predictions and concluded that the sex ratio at birth in mammals is constrained by the genetic system and not subject to evolutionary modification (see above).

ESS theory and optimization theory are closely related; these approaches have been reviewed by Maynard Smith (88, 90) and, in a less genetical way, by Stephens & Krebs (103). These authors also provided discussions supporting the value of optimization models in the face of clearly unrealistic assumptions, such as unlimited genetic variation available for selection. In essence, optimization provides refutable hypotheses that can be used by field and laboratory workers to show which material aspects of variation are most constraining to adaptation and which forces of selection are most likely to have shaped the phenotypes of a particular population. ESS and optimization are theoretical methods and therefore are neither flawed nor correct. Sometimes they can be used to point out interesting lines of empirical research. When incorrectly applied or interpreted, these methods may be associated with misleading conclusions.

Gene Frequency Dynamics

This approach makes explicit assumptions about the genetic and phenotypic bases of variation and then deduces the expected evolutionary outcome. The clear statement of assumptions about variation and the lack of extrinsic criteria such as optimality and adaptation make this approach an attractive alternative to the theoretically less rigorous methods of optimization and ESS. Ultimately, only a rigorous genetical model can provide a clear description for the constraining effects of particular types of material variation and a complete explanation for evolutionary pattern. It is, however, often difficult to relate the numerous assumptions and predicted gene frequency dynamics to measurable quantities.

Karlin & Lessard (77) have provided a summary of the gene frequency approach with many new extensions to the theory. From a theoretical perspective these models form a complex array based on many different assumptions about genetic control of sex allocation. A summary of these models is beyond the scope of the present paper. From the perspective of developing testable models, given the current knowledge of genetics and currently available research methods, the usable conclusions of the genetical theory are similar to the unconstrained and constrained ESS models. In particular, when variation is unconstrained—any phenotype can enter the population by mutation—then individuals allocate resources in a manner that approximately maximizes their genetic contribution. When variation is constrained, then the expected evolutionary outcomes are sensitive to the particular variety available. If the constraints concern genetic details such as dominance, epistasis, or recombination, then genetic details may sometimes be important to expected outcome (77). If the genetic details are themselves subject to extensive genetic modification, then fully genetic approaches may not yield important differences in prediction from ESS analyses (17). At present, few data bear on the types of genetic variety and on whether the dynamic models provide important and unique predictions when viewed from an empirical perspective.

Asymmetric Relatedness and Sex Determination

Lewis (82) showed the interesting consequences that can occur when the genes controlling sex allocation are not equally related to sons and daughters (see above, 71, 74, 99). The most extreme case occurs when part of the genome is transmitted uniparentally, such as the strictly paternal inheritance of the Y chromosome in mammals. If the genes controlling sex allocation are on the Y then selection favors allocation only to sons and not at all to daughters. The reason is simple; a Y is never transmitted to daughters, and thus resources spent on daughters are wasted from the point of view of the controlling genes. The general theory of asymmetric relatedness and sex allocation was recently extended by Taylor (106).

Hamilton (71) noted that although a paternally inherited Y would favor producing only sons, selection would favor suppressors of Y control in the rest of the genome. Genomic competition may often be expected to lead to a stalemate between elements that are primarily matrilineal and those that are primarily patrilineal (2). When Williams (113) surveyed available data and concluded that there was no evidence for adaptive variation of sex ratio among families, he suggested that evolutionary stalemates between X and Y in mammals may have prevented variation.

The notion of evolutionary stalemate highlights a difficulty with genetic models that presume limited genetic variety: There is constant and powerful evolutionary pressure for modification of sex allocation by all parts of the genome, sometimes in conflicting directions. The qualitative features of conflicting modification pressures are fairly easy to predict (73), but a rigorous genetic theory of modification does raise a number of important complications centered around aspects of recombination and linkage disequilibrium (78), and the potential for complex evolutionary dynamics (60).

Birds and mammals provide a particularly interesting contrast with respect to sex determination and sex allocation. Most mammals have simple male heterogamety with XY males and XX females, whereas birds have simple female heterogamety with ZZ males and WZ females (12). This distinction has three interesting consequences. First, if uniparental inheritance of sex chromosomes plays an important role in sex allocation, then mammalian species would more often have male-biased sex allocation ratios than birds. There is no evidence for this at present (34, 40). Second, if the heterogametic sex were more susceptible to mortality because of the hemizygous state of its sex chromosome (70a, rejected by Trivers & Willard, 109, but see 95), then mortality under stress would be male biased in mammals and female biased in birds. Mortality under stress appears to be male biased in both birds and mammals (37), suggesting either that sex-biased parental investment (109) or sex-biased response to stress (37) are more likely explanations than heterogamety.

Third, Hamilton (72) pointed out some of the consequences of the haplodiploid type of inheritance of sex chromosomes. From the perspective of sex chromosomes, male birds value the production of brothers more highly and sisters less highly than their own offspring in terms of genetic relatedness and inclusive fitness, whereas females value their offspring at least as much as their sibs. In mammals females value sisters more highly than their own offspring. Hamilton (72) suggested that the preponderance of male helpers in birds may be associated with these asymmetries in genetic relatedness. Further, by analogy with social insects (108), if helpers control sex allocation, then to the extent that sex chromosomes control behavior, the helpers in birds will be favored to bias allocation strongly to males in their familial nests. Note

that there are two distinct issues: how selection affects whether males help, and given that they help, how selection shapes the tendency of parents (61) or helpers (108) to favor males over females. Given that males help, these males will be favored to allocate more heavily to the sex to which they are more closely related independently of whether helpers are more closely related—at the genetic locus controlling the behavior—to helped offspring than to their own offspring. This is another hypothesis for the observed male-biased sex ratios in birds with predominantly male helpers (see above).

Observed Mechanisms of Variation

The most often repeated observation about the genetics of sex ratio is that little variation exists (27, 88; but see 112). When considering sex allocation, however, much investment occurs after birth and sex-biased allocation and juvenile mortality can potentially be controlled by parents. Thus even if sex ratio at conception or birth were fixed, there is still the possibility of tremendous variation in sex allocation based on behavioral and physiological mechanisms which may themselves have been shaped by selection of genetic variety. I present just two mechanisms for adjusting sex allocation and then briefly discuss genetic variation for sex allocation as opposed to sex ratio. Other studies concerning parental mechanisms for controlling sex allocation have been reviewed elsewhere (22, 27, 33, 34, 40, 41, 75; see also 3, 21, 23, 63, 75a, 80, 81, 94, 114).

Bortolotti (7) studied sex-biased brood reduction in bald eagles. In this species females are about 25% larger than males, eggs hatch asynchronously, and sibling competition may result in brood reduction. Bortolotti analyzed broods with two chicks (modal brood size) and measured the hatching order, size, and sex of chicks. Labeling the four types of brood according to the hatching order and sex, and generally sampling before any mortality of eggs, of 27 broods with two chicks, the observed distribution was M-M (ten), M-F (one), F-M (nine), and F-F (seven). There were significantly fewer M-F broods than expected, and the first chick in mixed sex broods was female 90% of the time (further supporting data were reported in the paper).

Brood reduction through sibling competition depended on differences in hatching date and growth rates among the chicks and on food stress. Bortolloti analyzed growth rates and sensitivity to food stress and suggested that the paucity of M-F broods occurred because these broods were most likely to suffer brood reduction (loss of F) through sibling competition. In addition, in F-M broods under food stress, Bortolloti suggested that the female would grow well and the male could get by because of lower food requirements, yielding a robust female and a surviving male. It seems likely in this species that female size is more important for reproductive success than is male size. He also presented further discussion of brood reduction in this and other species and an analysis of some alternative hypotheses.

Gosling (68) studied sex allocation in coypus (*Myocaster coypus*), a large rodent with a polygynous mating system, female philopatry and male dispersal, and male-male competition. Males are 15% heavier than females. The adult sex ratio is 75 males per 100 females. Gestation is 19 weeks, mean litter size is 5.3, and offspring are suckled for about 8 weeks. Females breed throughout the year.

Gosling dissected 5853 adult females and collected data from 1485 that had embryos old enough to sex. He measured the mother's size; the number of embryos implanted; the number of viable embryos and their mean weight; and the number of male, female, and dead embryos. Gestation stage was inferred from previous data relating known conception date and embryo size.

The data suggest that coypu females controlled sex allocation by selectively aborting entire litters. Young females in relatively good physical condition aborted small litters of predominantly female embryos near weeks 13–14 of the 19 week gestation period. Females conceived soon after aborting a litter. The new litter size (5.82 ± 0.21 Standard Error of the mean) was significantly larger than that aborted (4.17 ± 0.32 SE). By contrast, relatively healthy females retained large litters or predominantly male litters. Neonate size was positively correlated with mother's condition and inversely related to litter size. Neonate size of an individual was positively correlated with its adult size.

In general, the likelihood that selective abortion or sex-biased infanticide would be advantageous depends on the relative costs of gestation versus lactation in mammals or egg production versus fledging chicks in birds. The coypu study shows that selective abortion may be favored under certain circumstances, but the range of conditions under which such mechanisms may or may not be favored is difficult to assess at present. Clutton-Brock et al (39) have also presented an interesting study on gestation versus lactation. They showed that the costs of gestation to the mother's subsequent survival and reproductive success are slight compared to those of lactation.

The studies of eagles and coypus show two very different mechanisms that could be used to manipulate sex allocation in a fitness-enhancing way. Discovering and characterizing the details of such mechanisms represent one of the more exciting challenges in future research. Evolutionary models would be most useful for predicting patterns of sex allocation variation, given the details of the mechanisms available to generate variation. For example, two separate populations with different distributions of resources among mothers may be expected to have different conditional responses at the phenotypic level, that is, they may be expected to have different patterns of sex allocation bias for the same resource level. Predictions could be developed by comparing the fitness (gene frequency dynamics) of competing mechanisms with differing conditional responses for litter size and sex ratio as a response to maternal condition.

The genetic influences on maternal size, litter size, sex ratio, and offspring weight are likely to be complex because of maternal effects. Falconer (48) found that selecting for increased female size in mice yielded larger litter size and smaller offspring. Genetic studies combined with analyses like Gosling's may provide interesting insights into adaptive variation in sex allocation. Marsupials and rodents are particularly promising in this regard because they are often amenable to genetic analysis and because they show a range of potentially interesting mechanisms (41, 63, 75a, 80, 81, 114).

Several difficulties may be encountered, however, when trying to make evolutionary inferences from genetic details measured on a single population at one point in time. For example, lack of observable genetic variation for the parameters controlling conditional phenotypic response does not provide strong evidence against the shaping of the phenotypic mechanism primarily by natural selection. Likewise, observed genetic variation for conditional response that is uncorrelated with other fitness traits does not provide strong evidence against genetic and physiological constraints as important factors in shaping the observed phenotypes (110).

CONCLUSIONS

Sex allocation theory is a set of logical consequences that follow from general assumptions. As such it is, ideally, a standing pool of incontestable logic. Testable predictions can be derived for particular organisms when specific natural history assumptions are added about the relationships between investment and reproductive value, kin interactions, the distribution of resources among parents, and the genetic and phenotypic bases of variation. A test of this type of prediction determines whether the set of specific assumptions provides a good description for the forces that have shaped sex allocation. This approach to understanding sex allocation patterns must rest on a sound and complete logical structure.

The purpose of this review has been to summarize the logical structure of sex allocation theory for birds and mammals. I have emphasized some important logical flaws that have slipped into common usage and some aspects of theory that are not well understood at present. In addition, I have briefly summarized the rapidly growing body of information on the variety of proximate mechanisms that cause sex allocation variation.

The most important logical flaw in common usage is the simultaneous application of the Trivers-Willard hypothesis (109) to predict variation among families and Fisher's (51, 52) hypothesis to explain sex allocation over the total population. I reviewed the literature demonstrating that the assumptions required for application of the Trivers-Willard hypothesis imply that key assumptions of Fisher's equal allocation theory are violated. The expected quantitative departures from Fisher's equal allocation theory are not known at

present, but certain qualitative expectations have been derived (57). These qualitative results highlight the importance of patterns by which parents accrue and invest resources, including the number of young per litter and the trade-off between current and future reproduction. Many important aspects of the theory have yet to be worked out for these key aspects of mammalian and avian life history.

Recent empirical work has just begun to reveal the rich set of physiological and behavioral mechanisms that parents use to adjust sex allocation in their family. Theory has, to this point, offered little in the way of predicting the types of variation that have been observed, and why certain species fail to show what would supposedly be adaptive variation. One future challenge for the theory will be to provide predictions about adaptive modification among closely related populations sharing the same genetic and phenotypic mechanisms of variation. Such predictions will help in understanding the evolutionary forces that have shaped particular mechanisms and the extent to which particular mechanisms may be subject to adaptive modification.

Sex allocation research has played a leading role in the 1980s in broadly mapping the extent and limitations of adaptive variation. As more data accumulate on the particular mechanisms of variation, sex allocation will in the 1990s provide an excellent model system for studying the evolution of behavioral plasticity under physiological and genetic constraints.

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