

Split Sex Ratios and the Evolutionary Origins of Eusociality

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The influence of the genetic system of haplodiploidy on the evolution of eusociality has been a central topic in evolutionary biology since it was first discussed by Hamilton (1964) in the context of his invention of inclusive fitness theory. Since then, work on that influence had outstripped the development of inclusive fitness theory itself. Recently, Taylor (1986) has provided a deeper understanding of inclusive fitness theory that allows us to use it to derive a quite general expression for the selective advantage of sib rearing. Three forces can be identified in this advantage: an average relatedness effect, a parental skewed sex ratio effect, and a sex ratio manipulation effect. A simple guiding principle for each sex can be derived on the assumption of maternal sex ratio equilibrium. "Arbitrary ploidy" models explain three apparent "coincidences of cancelling" between the genetic systems of diploidy and haplodiploidy. The concept of reproductive value is central to the new development of inclusive fitness theory, to sex ratio theory, and to the advantage of sib rearing. Reproductive values of the different categories of individual provide theoretical results about equilibrium sex ratios in generalizations of the sphecid and halictid patterns of Seger (1983). The literature on the advantage of sib rearing is illuminated by the analysis of previous sections, which also suggests the potential importance of "split" sex ratios. Sex ratios are split when groups of parents contribute systematically different sex ratios to the same offspring generation. Variability between parents in cost ratio would lead us to expect strongly split sex ratios, but this expectation is countered to the extent that individual plasticity in the sex ratio produced among offspring can lead to unpredictable population sex ratios.

1. Introduction

In this paper, I present models of sib rearing and models of the sex ratio in partially bivoltine species, which are of interest for three reasons. First and most generally, these models elaborate and clarify the explanation suggested by Hamilton (1964) for the association between the evolution of eusociality and male haploidy. The second reason is that sex ratio data is now available for at least one closely studied partially bivoltine species (Brockmann & Grafen, in preparation), and so the predictions of the sex ratio models can be tested against facts. Third, the models use a combination of the reproductive value technique first employed by Fisher (1958) and generalized to haplodiploids by Hamilton (1972) and Benford (1978), and the inclusive fitness method developed by Hamilton (1964). The attraction of this combination is its conceptual clarity; it has recently been developed rigorously in an important paper by Taylor (1986), and I try to explain it simply here.

The new theoretical idea introduced in this paper is the importance of "split sex ratios". An offspring generation has split sex ratios if there are groups of parents

which produce systematically different sex ratios. An example that will be relevant later is where there are two parental generations contributing to the same offspring generation, and the two parental generations produce different sex ratios.

The main points of the paper are that split sex ratios can have important effects on the selective advantage of sib rearing, and so are relevant to the evolutionary origins of eusociality, and that split sex ratios attain different equilibria from unsplit ones, and so are relevant to predictions of sex ratio theory. In order to explain the effects on the selective advantage of sib rearing, the next section of this paper contains an exposition of a newly developing technique that combines inclusive fitness and Fisher's (1958) notion of reproductive value. In the course of this exposition, three forces will be identified in the selective advantage of sib rearing: the average relatedness effect, the parental skewed sex ratio effect, and the sex ratio manipulation effect. Split sex ratios can involve all three of these forces. The assumption that all sex ratios are in equilibrium under maternal control allows a very simple guiding principle to be derived for each sex that expresses the advantage to sib rearing caused by the genetic system of haplodiploidy.

The third section contains models of sex ratios in partially bivoltine species with Seger's (1983) two patterns of generational overlap. Partially bivoltine means having two overlapping generations per year. In the "sphecid" pattern, pupae of both sexes overwinter, while in the "halictid" pattern, it is mated females which overwinter. The models are generalizations of Seger's, and the importance of split sex ratios will be emphasized. These models of sex ratio work by computing the reproductive value of different categories of individual using techniques developed by Taylor (1986), and so as well as constituting sex ratio results, they also quantify effects which in section 2 were left as depending on unspecified reproductive values.

Section 4 presents the main arguments of the paper. Using the ideas developed in preceding sections, a brief review is given of the literature on the connection between haplodiploidy and eusociality.

Section 5 contains some theoretical considerations about the plausibility of assuming split sex ratios in nature. I hope to persuade the reader at least that the extreme opposite is unlikely.

Before proceeding further, it is important to state the circumstances in which haplodiploidy is thought to have had an effect in the evolution of eusociality. We begin with a solitary species in which no sib rearing of any kind occurs. Genetic variation arises (possibly by mutation) so that some individuals are heritably more likely than others to rear sibs instead of their own offspring. (This can plausibly occur only in species with very special sorts of life histories—Charnov, 1978.) One question is whether such a mutation would have a higher selective advantage in a haplodiploid species than in a diploid one. Another is whether such a mistake that occurred only in females would have a higher selective advantage than one that occurred only in males, and whether this differs between diploidy and haplodiploidy. This is as intended a very primitive stage in the evolution of eusociality. Once started on the path of eusociality, there is no particular evolutionary difficulty (in principle!) in understanding further development and refinement. It is the first step that we examine here.

2. The Selective Advantage to Sib Rearing

In this section, we use the inclusive fitness method of Hamilton (1964), as amended by Taylor (1986), to account for deviations from even sex ratios and other disturbances to the relative reproductive value of the two sexes. It will help us to arrive at a formula for the efficiency ratio of Charnov (1978), which is the relative efficiency in sib production as opposed to own offspring production at which an individual is indifferent between those two options. An attractively simple formulation will allow us to divine three separate forces at work determining the selective advantage to sib rearing. Assuming that sex ratios are in selective equilibrium under maternal control will then provide two guiding principles, one for males and one for females, for the influence of the genetic system on the selective advantage of sib rearing.

Hamilton's method was to add the number of males and females reared, weighted by the decision-maker's relatedness to them. If females are rare in the offspring generation, then this sum gives too little weight to each female. The same applies to males. The reason is Fisher's (1958) point that each individual of the rarer sex has more matings than each individual of the commoner sex. An adjustment to inclusive fitness for sex ratio has been made by Oster *et al.* (1976), and with a more explicit justification by Bulmer & Taylor (1977). The weight given to a female should also be proportional to the contribution made by the mass of females to the genetic constitution of future generations, and we shall see shortly how this contribution can vary. Hamilton (1972) derived these weights in the special case of interest to him, and recently Taylor (1986) has shown how to derive them more generally. In the next section we will work out these weights for a number of partially bivoltine life cycles. For the moment, the reader is asked to take it on trust that the contribution of all females to the genetic constitution of future generations (the reproductive value of all females) is known, and is represented as V_f ; and that the reproductive value of all males is known and represented by V_m . (Taking the total genetic constitution of the population as equal to one, we determine by choice of scale that $V_f + V_m = 1$.)

If the reproductive value of all females is V_f , and there are F females in total in the offspring generation, then the average per capita reproductive value of one female offspring is V_f/F . Writing the total number of individuals in the offspring generation as N , and the sex ratio (fraction of males) as s , this can be rewritten as $V_f/N(1-s)$. Of that share in the "genetic stock" of the population, only a fraction counts towards the inclusive fitness of the individual deciding on the sex ratio, and that fraction is its relatedness to each female created, which we may call r_b . Supposing an individual makes f females, then the contribution to its inclusive fitness from females is proportional to $fr_b V_f/N(1-s)$. Making the analogous definitions for males, and multiplying by N for simplicity, we can say that the individual's inclusive fitness is proportional to Z , given by

$$Z = mr_m V_m / s + fr_f V_f / (1-s). \quad (1)$$

This is the measure we will use to compare the value to the individual of rearing sibs instead of rearing offspring. The reproductive values, and the population sex

ratio, are the same in the two cases. The numbers of males and females the individual produces, and the relatednesses, may be different. Let us use r'_m and r'_f to represent the relatednesses to brother and sister, respectively. This formulation assumes that no sex specific competition occurs among the offspring, so it does not apply to local mate competition (Hamilton, 1967) or to local resource competition (Clark, 1978). A more general theory is developed by Taylor (1986).

The next step is to find an expression for Charnov's (1978) efficiency ratio, which we shall denote α . A ratio of one means that if an individual can make as many sibs as offspring, then it is indifferent between the two options. A ratio of more than one means that such an individual would rather rear sibs; and that only an individual that could produce more offspring than sibs would want to rear offspring. Specifically, an individual that could rear α times as many offspring as sibs would be indifferent between rearing sibs and rearing its own offspring.

Three more symbols are needed for our expression for α . We have defined s as the sex ratio in the offspring generation. Now the sex ratio produced by the parent, which will be the sex ratio produced by the deciding individual if it rears sibs and does not manipulate their sex ratio, may be different from the population sex ratio. Let this parental sex ratio be $s + \pi$. $\pi = 0$ means that the parent is producing the population sex ratio, positive π means that the parent produces more males and negative π means it is producing more females. The second symbol is needed to represent sex ratio manipulation by the deciding individual, so let the sex ratio produced when sib rearing be $s + \pi + \delta$. $\delta = 0$ means no manipulation. Finally, it may be that the deciding individual when rearing its own offspring does not produce the population sex ratio. Let it be $s + \phi$. With these definitions, we can show that α is given by

$$\alpha = \frac{r'_m V_m + r'_f V_f + (\pi + \delta)[r'_m V_m / s - r'_f V_f / (1 - s)]}{r_m V_m + r_f V_f + \phi[r_m V_m / s - r_f V_f / (1 - s)]}. \quad (2)$$

Now each of these terms means something very simple biologically, and so I propose to discuss each in turn, identifying three forces that may make α different from one. The two main questions can be phrased in terms of α . "Does haplodiploidy predispose towards sib rearing?" translates into "Is α likely to be significantly greater than one more often under haplodiploidy than under diploidy?" And "Does haplodiploidy predispose females rather than males towards sib rearing?" translates into "Is α likely to be greater for females than males under haplodiploidy, compared with diploidy?"

AVERAGE RELATEDNESS EFFECT

What, then, are the elements of this all-important α ? Consider first the case where all sex ratios produced are the same (that is $\pi = \delta = \phi = 0$). Expression (2) now looks like

$$\alpha = \frac{r'_m V_m + r'_f V_f}{r_m V_m + r_f V_f}. \quad (3)$$

This case is the pure "average relatedness effect". The numerator is the weighted average of relatednesses to sibs, and the denominator is the weighted average of relatednesses to offspring. The weights, which are the same in each case, determine the relative importance of males and females in the averages. When all females together in the next generation have a higher reproductive value (V_f), then relatedness to daughters receives more weight in the average relatedness to offspring, and relatedness to sisters receives more weight in the average relatedness to sibs.

The average relatedness effect does not depend on the sex ratios produced, only on the reproductive value of males and females in the offspring generation. Its simple form allows the following points to be made:

(1) It formalizes the obvious point that it is better to rear closer than distant relatives, e.g. sibs rather than cousins.

(2) Under outbred diploidy, where relatednesses to males and females in both generations are equal, the average relatedness effect will never apply. The average of a half and a half must be a half, no matter how weighted the average may be! (Inbreeding complicates matters, and Bartz (1979) has shown that an inbred diploid would rather rear sibs than mate with an unrelated individual. The technique he used was to calculate average relatednesses to sibs and offspring, but the weights in his average were the fraction of males and females in the brood ignoring the population sex ratio and reproductive value. His results and the results of this analysis will agree where the population sex ratio is a half and the reproductive value of males and females are equal. It is also important to note that where inbreeding occurs, it is likely though not logically necessary that local mate competition or local resource competition also occurs. These would introduce complications beyond the scope of the methods both of Bartz (1979) and the present paper.)

(3) With haplodiploidy, relatednesses are said to be asymmetric, meaning that the ratio of an individual's relatednesses to male and female sibs is not the same as the ratio of its relatednesses to male and female offspring. For example, for a hymenopteran female the relatednesses to sister and brother are 0.75 and 0.5, leading to a sib ratio of 1.5:1; while the relatednesses to daughter and son are 0.5 and 1, leading to a ratio of 0.5:1. This asymmetry means that the weights in the weighted average in (3) do matter. The higher the reproductive value of all females, the more a hymenopteran female should incline towards rearing sibs; and the more a hymenopteran male should incline towards rearing offspring. Notice that the existence, direction and magnitude of this effect do not depend on the sex ratio in any way. They do depend on the asymmetry of relatednesses and the distortion in reproductive values.

(4) With discrete, non-overlapping generations, the average relatedness effect does not operate in either diploids or haplodiploids. The relatednesses and reproductive values in that case combine in a way that ensures indifference between sib and offspring rearing (i.e. $\alpha = 1$) for both males and females.

(5) The average relatedness effect applies equally to males and females under male haploidy, but always acts in opposite directions, so that if one sex prefers to rear sibs, then the other prefers to rear offspring.

SKEWED PARENTAL SEX RATIO EFFECT

The average relatedness effect is the only force that operates when all individuals produce the same sex ratio. We continue to suppose that a sib rearer does not manipulate the sex ratio of its sibs, but allow the possibility that parents may for some reason produce a sex ratio that is not equal to the average sex ratio (the average in the generation in which the reared sibs are destined to emerge as adults). This may be the case if there are sex ratio specializations of any sort, perhaps associated with a habitat, or time of year (Charnov, 1982). Now that π and ϕ may be non-zero, we express (2) as follows

$$\alpha = \frac{r'_m V_m + r'_f V_f + \pi[r'_m V_m/s - r'_f V_f/(1-s)]}{r_m V_m + r_f V_f + \phi[r_m V_m/s - r_f V_f/(1-s)]} \quad (4)$$

The left-hand side of the top and bottom of this fraction are just the average relatednesses, and so it is the expressions in square brackets on the right that are now of interest. They have a very natural interpretation in sex ratio theory. $r_m V_m/s$ is the inclusive fitness gained for producing one male, and $r_f V_f/(1-s)$ is the inclusive fitness gained for producing one female. The term in square brackets is therefore the difference in inclusive fitness gained by producing a male instead of a female, and may be positive or negative.

If the sex ratio is in equilibrium, from the point of view of our individual, then a male and a female bring equal gains in inclusive fitness, and the term in square brackets is zero. The sex ratio equilibrium for one individual depends on whether it is considered as a sib rearer or an offspring rearer. More particularly, if the population sex ratio is in equilibrium for an individual as an offspring rearer, then the existence of asymmetric relatednesses ensures that it cannot be in equilibrium for that individual as a sib rearer. (If $r_m r'_f \neq r'_m r_f$, then both square brackets cannot be zero.) Offspring rearing is assumed to be the background against which our rare sib rearing morph is first judged, so I shall assume for simplicity that the sex ratio produced by our deciding individual as an offspring rearer has been perfected by natural selection in such a way that the marginal male is equal in value to the marginal female. This means that the lower term in square brackets is zero. (4) then becomes

$$\alpha = \frac{r'_m V_m + r'_f V_f + \pi[r'_m V_m/s - r'_f V_f/(1-s)]}{r_m V_m + r_f V_f + 0} \quad (5)$$

The way the skewed parental sex ratio effect works is then as follows. Our deciding individual, having asymmetric relatednesses, would derive more inclusive fitness from a sib of one sex than from a sib of the other. If the parents are producing a bias towards the favourable sex, then sib rearing is favoured; if the parental bias is towards the unfavourable sex, then sib rearing is discouraged. Formally, if π and the square bracket have the same sign, then α is increased; if they are of opposite sign, then α is decreased. With this understanding in mind, the following points can be made:

(1) The effect operates without sex ratio manipulation by the sib rearer. The sib rearer simply takes as fixed the parental sex ratio, but for some reason this is not the same as the average sex ratio in the offspring generation.

(2) The effect operates most consistently with asymmetric relatednesses, because the sex ratio cannot be in equilibrium from the point of view of the individual as a sib rearer and as an offspring rearer simultaneously. With symmetric relatednesses, the square bracketed terms on top and bottom of (4) are equal; to cause α to differ from one, it is then necessary that (a) the sex ratio is not in equilibrium from the point of view of our deciding individual and (b) the individual as an offspring rearer would produce a sex ratio different from his parents' (formally, the square bracketed term is not zero, and $\pi \neq \phi$).

(3) Under haplodiploidy, the effect is not confined to females. The argument that both square brackets in (2) cannot both be zero applies to males as well as females. As males' relatednesses to their sons is zero, the lower term must be negative, and smaller than the upper term. A parental sex ratio skewed towards males will make sib rearing more profitable for males, while one skewed towards females would make sib rearing less profitable. The parental skewed sex ratio effect is equally strong for males and females under haplodiploidy, but works in opposite directions when the population sex ratio is in equilibrium for maternal control.

SEX RATIO MANIPULATION EFFECT

The sex ratio manipulation effect is the only force involving discrimination by the sib rearer between brothers and sisters. If the sex ratio is not in equilibrium for an individual as a sib rearer, then by altering the sex ratio of the sibs towards the more favourable sex, the individual can make sib rearing more profitable in terms of inclusive fitness. This increases the chance that sib rearing is more advantageous than offspring rearing. Formally, this can be seen in (2): if the square bracketed term in the numerator is not zero, then α is increased by making δ of the same sign as that term.

There is likely to be a sex difference in the importance of this force in haplodiploids, and it arises because a male is related to his brothers and sisters in the same ratio (0.5:0.25) as a female is related to her sons and daughters (1:0.5). Therefore, if the sex ratio is in equilibrium for females as offspring rearers, then it will also be in equilibrium for sons as sib rearers. Males can therefore gain no advantage by manipulating the sex ratio of their sibs. A female as sib rearer, on the other hand, has a different ratio of relatednesses to males and females, from a female as an offspring rearer; and therefore can gain by manipulating the sex ratio of sibs.

GUIDING PRINCIPLES ON THE ASSUMPTION OF MATERNAL SEX RATIO EQUILIBRIUM

The three forces above explain in principle how sex ratios and reproductive values combine to influence the selective advantage to sib rearing. Valuable simplifications can be achieved of these general formulae by assuming that the population sex ratio

is in equilibrium for one parent. It is most useful for application to the haplodiploids to suppose it to be the mother. An argument given in section 3 shows that then

$$s = \frac{r_m V_m}{r_m V_m + r_f V_f}.$$

Letting B represent the sex ratio among sibs, and F the sex ratio among offspring, we can write α_f and α_m , the critical efficiency ratios for females and males, as

$$\alpha_f = \frac{B + 3(1 - B)}{2}, \quad \alpha_m = \frac{1}{2(1 - F)}. \quad (6)$$

These results assume that the population at large is at equilibrium, but that individuals may vary in the sex ratios they produce. It is noteworthy that any pattern of reproductive values, however produced, leads to these very simple forms when population equilibrium is assumed.

(6) gives the guiding principle for females. For males, we take a rather strong hint dropped by Trivers & Hare (1976). They argued that as sib rearing by females becomes common, and a female biased sex ratio starts to be established in the population, males become more valuable as parents in a Fisherian way because they become rarer. They will therefore be selected not to rear sibs. This is an important point in its own right, but it also suggests that the relative efficiency as a sib rearer and offspring rearer may depend on rather different things for males and females. If females are limited by resources, then relative efficiency will depend on the chance of surviving to establish a nest, the relative quality of nest sites, and whether two foragers can rear more or less than twice as many offspring as one. These extrinsic considerations are conveniently represented by Charnov's α . For males, the situation is different. It is usual to assume that eusociality arose in species where the reproductive success of males is limited by matings. The relative efficiency of sib and offspring production for a male, therefore, depends on the sex ratio of breeding adults; and this quantity is intrinsic to the theory, and will vary systematically with certain components of it. While the analysis above is correct for males so far as it goes, it is more useful to have a formulation in which these systematic dependencies are made clear.

Great simplifications are achieved by making twice the assumption of maternal sex ratio equilibrium. First, for mothers producing the generation in which our decider is an adult; and second for our decider's generation as parents. We also suppose that the decider's generation contributes to only one offspring generation. Let β represent the reproductive value of a male as a sib rearer divided by the reproductive value of a male as an offspring rearer, so that $\beta > 1$ means that sib rearing would be favoured. Algebraic manipulations, relegated to the appendix, then show that

$$\beta = \frac{1 - \bar{F}}{1 - F} e^{\frac{c_f \sigma_m}{c_m \sigma_f}}. \quad (7)$$

The first quotient is the fraction of females in the deciding male's offspring relative to $1 - \bar{F}$, the average fraction of females among the offspring of mated females. e

represents the efficiency of a male as a sib rearer *compared to a female of his own generation as an offspring rearer*. c_m and c_f are the costs (in the decider's parents' generation) of producing a male and a female; and σ_m and σ_f represent the probability of survival (up to the time of the decision) of males and females. The ratio of c 's and σ 's represents the deviation of the breeding sex ratio from the ratio of reproductive values. This expression for β is true no matter what the reproductive values are, and no matter how they came about.

(6) and (7) are then our guiding principles for females and males. The main conclusions from them are drawn in section 4. Here, I note how these results would look under diploidy, and discuss why the male principle contains unfamiliar terms. Under diploidy, α_f would be one, so that maternal sex ratio equilibrium removes all genetic tendency towards or against sib rearing for females. For males, β would lack the first of its three factors, and so lose all dependence on the genetic system. The remaining terms exist because when males are limited by matings, the success of a male as a sib rearer and as a producer of offspring is best compared with the success of females in the same role. The maternal equilibrium in the previous generation guarantees equal reproductive value per unit of investment in males and females in the decider's generation. If males and females are equally costly, and survive equally, then this guarantees equal reproductive value for a male and a female as offspring producers. If males are more common because they are cheaper to produce, or if males suffer less juvenile mortality, then the males that survive to take the decision will be comparatively more numerous and therefore less valuable per individual than the females that survive to make the decision. This is the reason for the quotient of c 's and σ 's. Under diploidy, therefore, these forces would remain.

This completes my survey of the forces towards sib rearing. In the remainder of this section I will explain which precise notion of relatedness I have used, and then I introduce and explore briefly "arbitrary ploidy" models.

RELATEDNESSES

In giving relatednesses I have used the regression definition of Hamilton (1970), and this differs from the "life-for-life" values of Hamilton (1972) which are used, for example, by Trivers & Hare (1976). The two schemes are shown in Table 1. The difference between them is that the "life-for-life" values contain a correction appropriate to the reproductive values that hold in haplodiploidy with discrete, non-overlapping generations. When that simple case is being analysed, use of the life-for-life coefficients allows us to drop the reproductive value weights from (2) and all subsequent formulae. As Taylor (1986) has argued, this convenience becomes a hindrance when more complicated models are considered in which the reproductive values are needed anyway. There is no difference of substance between the two schemes.

The regression relatednesses can be thought of as the expected fraction of the recipient's genotype that is identical by descent with a random allele in the donor's genotype. This is natural, as it gives the donor's valuation, as an offspring producer, of the recipient (who donates a random allele to each offspring), compared to the

TABLE 1

The relatednesses between some categories of relatives under two definitions of relatedness: Hamilton's (1972) life-for-life definition as employed by Trivers & Hare (1976), and Hamilton's (1970, 1972) regression definition, as employed by Taylor (1986) and in the text of this paper. Only outbred relationships are considered. The life-for-life values contain an implicit correction for the fact that in a haplodiploid species with discrete generations, twice as much of the reproductive value is contained in females as in males. Quick methods of calculating these values are (1) life-for-life: what fraction of the donor's genes are identical by descent with any of the recipients, (2) regression: what fraction of the recipient's genes are identical by descent with any of the donor's. These methods do not work for inbreeding. Notice that within-sex values are the same, and between-sex values must be multiplied by the ratio of ploidies of donor to recipient

<i>Sex of donor</i>	<i>Relationship of recipient</i>	<i>Life-for-life</i>	<i>Regression</i>
Female	Mother	0.5	0.5
	Father	0.5	1.0
	Sister	0.75	0.75
	Brother	0.25	0.5
	Daughter	0.5	0.5
	Son	0.5	1.0
Male	Mother	1.0	0.5
	Father	0.0	0.0
	Sister	0.5	0.25
	Brother	0.5	0.5
	Daughter	1.0	0.5
	Son	0.0	0.0

donor's valuation, as an offspring producer, of himself (who donates a random allele to each offspring).

ARBITRARY PLOIDY MODELS

The reader will not have been surprised that diploids are indifferent between sib and offspring production in the simplest case. All relatednesses are a half, and the reproductive values of the sexes are equal. It should be more surprising that both male and female haplodiploids are also indifferent in the simplest case between sib and offspring rearing. The purpose of the arbitrary ploidy models I now introduce is to explore whether this, and other similar results, are merely "coincidences of cancelling" or whether they can be seen more directly as expected properties of the genetic system.

The cancelling out that occurs is between reproductive values and relatednesses. These are themselves calculated from the genetic system, which I shall summarize in four whole numbers: the ploidy of the gametes passed from father to son (g_{mm} , say), from father to daughter (g_{mf}), from mother to son (g_{fm}) and from mother to daughter (g_{ff}). Also let $p_m (=g_{mm} + g_{fm})$ and $p_f (=g_{mf} + g_{ff})$ be the ploidies of males

and females, respectively. For ordinary diploidy, each g equals one. For haplodiploidy, the first of these numbers (g_{mm}) is zero because no gamete is passed from father to son, but the rest of the gametic ploidies are equal to one. We can ask for any apparent coincidence between diploidy and haplodiploidy, what property of these arbitrary ploidies ensures it, and then we will understand why diploidy and haplodiploidy should share this or that feature.

The method of analysis consists in computing reproductive values and relatednesses from the arbitrary gametic ploidies. Then the following results are easy to obtain. First, what is the equilibrium sex ratio when it is under the control of parents of one sex? For male and female control, respectively, it is

$$\frac{g_{mm}}{g_{mm} + g_{fm}} \quad \text{and} \quad \frac{g_{mf}}{g_{mf} + g_{ff}}.$$

In other words, the same fraction of offspring should be males in equilibrium as that fraction of the controlling individual's own genome that came from its father. Applied to diploids, this gives a half immediately as it should. For haplodiploids, it gives a half immediately for females; but for males it gives an equilibrium with all daughters, reflecting the fact that a male would prefer all his mate's offspring to be female. The crucial feature that a haplodiploid female shares with diploids of both sexes has now been identified.

The second question is: when are individuals indifferent between sib and offspring rearing? As the relatednesses and reproductive values are known in terms of the gametic ploidies, we can work out the inclusive fitness of sib and offspring rearing using (1). In the absence of sex ratio manipulation, and at sex ratio equilibrium, it can be shown that the advantage to offspring rearing is proportional to, for males and females respectively,

$$\frac{g_{fm}}{p_m p_f} (g_{mf} - g_{fm}) \quad \text{and} \quad \frac{g_{mf}}{p_m p_f} (g_{mf} - g_{fm}).$$

Hence, both sexes are indifferent provided the gamete passed from father to daughter and the gamete passed from mother to son (i.e. the two cross-sex gametes) have the same ploidy. Any genetic system with this property must therefore have indifference for both males and females between rearing offspring and sibs, when there are discrete non-overlapping generations.

The third question is: must the balance of advantage between rearing sibs and offspring be tipped in opposite directions for males and females by changes in the reproductive values of the two sexes? If it must, then the average relatedness effect cannot promote sib rearing in males and females at the same time. The direction of tipping of the balance depends on which is the higher, the ratio of relatednesses between brother and son, or between sister and daughter. A single quantity whose sign reveals this is $r_m r'_f - r'_m r_f$. In terms of the gametic ploidies, $r_m r'_f - r'_m r_f$ turns out to be, for males and females, respectively,

$$\frac{g_{fm}}{p_m p_f p_f} (g_{mm} g_{ff} - g_{mf} g_{fm}) \quad \text{and} \quad \frac{g_{mf}}{p_m p_m p_f} (g_{mf} g_{fm} - g_{mm} g_{ff}).$$

From this we see that they can never be both positive or both negative. Further, if the cross-sex gametes are both not null, then these quantities must always be of opposite sign: either both are zero, or one is positive while the other is negative. The conclusion we may draw from this is that it is quite a general property of genetic systems that the balance of advantage between rearing sibs and offspring will be tipped in opposite directions for males and females by changes in reproductive value. It is impossible that they should be tipped in the same direction. (Impossible is a strong word, and I hasten to remind the reader of the restriction of the assumption of outbreeding. Note, however, that this final result does not depend on discrete, non-overlapping generations.)

We have now explored three common features of diploidy and haplodiploidy, and found what properties of those genetic systems are responsible for them. Note that as an unexpected bonus, we also know things about a genetic system in which 7-ploid males pass 2-ploid gametes to sons and 4-ploid gametes to daughters, while 5-ploid females pass 5-ploid gametes to sons and 1-ploid gametes to daughters! (It seems likely there are evolutionary objections to a system like this, as well as mechanical problems with the production of gametes.)

3. Reproductive Values Under Partial Bivoltinism

This section has a number of purposes. The reader was asked in the last section to take it on trust that the reproductive value of all males and that of all females could be taken as given. In this section, I will explain why this should be so, and also demonstrate how these reproductive values can be calculated in reasonably complicated cases. Once calculated, these reproductive values are immediately useable as predictions about sex ratios in species with the corresponding pattern of generational overlap. Brockmann & Grafen (in preparation) present data on the pipe-organ mud-dauber wasp of North America, *Trypargilum politum*, a partially bivoltine species in part of its range, and compare it with the predictions given here.

The plan for this section is to discuss the idea of reproductive value and show its importance. Then a brief discussion of how it can be calculated in general will be followed by the examples of generalized versions of Seger's sphecid and halictid patterns of generational overlap in partially bivoltine haplodiploids.

The concept of reproductive value is due to Fisher (1958), and is quite a general concept that extends beyond problems of sex ratios. Reproductive value is also useful in models with overlapping generations (Charlesworth, 1980). The idea is to associate with subsets of the population numbers that represent their importance as progenitors of future generations. Subsets such as males and females, or different ages in an age-structured model.

The reproductive value of a subset is a measure of its importance as a progenitor of future generations. The definition of the measure is that it is the fraction of the gene pool in many generations time which is descended from individuals in that subset, in the absence of selection, mutation and drift. For example, Hamilton (1972) showed that with discrete, non-overlapping generations, two-thirds of the

reproductive value of a haplodiploid species is vested in females at any one time, and only one-third in males.

These reproductive values can be thought of in another way. With only one reproductive category, a gene frequency cannot change in the absence of selection, mutation and drift. With more than one reproductive category, there is a separate gene frequency for each category; and it is possible that they do change. For example, if all females in a haplodiploid species have genotype *AA*, while all males have genotype *B*, then the gene frequencies of *A* are 1 in females and 0 in males. After one generation, the females all have genotype *AB*, and the males have genotype *A*, so the frequencies are 0.5 and 1. Subsequent values are (0.75, 0.5), (0.625, 0.75) and so on. We would like a way of taking an average gene frequency that does not change in the absence of selection, mutation and drift. The only average of this kind is to weight the gene frequency of each reproductive category by its reproductive value. In our example, it is easy to check that, weighting the female frequencies by 2/3 and the male ones by 1/3, the average gene frequency is equal to 2/3 in each of the generations. The concept of reproductive value is discussed more formally by Taylor (1986).

The vital thing about reproductive value is that it is not only useful but also quite easy to calculate in many cases. As an illustration of this, I will quickly run through the relevant part of Fisher's (1958) sex ratio argument. Take the normal diploid case, with discrete, non-overlapping generations. Then the reproductive value of all males in the parental generation is seen to be equal to the reproductive value of all females. The reason is that every offspring has exactly half its genes from its father and half from its mother. Therefore half of all the genes in the offspring generation (and so all subsequent generations as well) come from males in the parental generation and half come from females. This argument works by reference to relationships between classes of individual, and comes to a conclusion about the reproductive value of the whole class without having to consider how many individuals are in each class. The same kind of argument is used below for more complex cases.

The general method, as described by Taylor (1986), is to list the categories of interest, and write down what fraction of the genes in each category at a later time come from each category at an earlier time. We can illustrate this with Seger's (1983) sphecid pattern of generational overlap in partial bivoltinism (Fig. 1). Here, males and females overwinter as pupae. Emerging as the spring generation, they produce offspring for the summer generation of the same year, and also for the spring generation of the following year. The summer generation leave offspring only to the following spring generation. All the reproductive value of the species is contained in the overwintering pupae, and so two categories are male pupae and female pupae overwinter. Four other categories appear when we consider how the reproductive value of the species is held at the time when the summer generation is alive. Male and female summer adults are two of them. The other two are those male and female pupae laid by the spring generation and destined to skip the summer generation, emerging the following spring. By working out how genes flow between these six categories, the reproductive value of each can be worked out. The flow will be

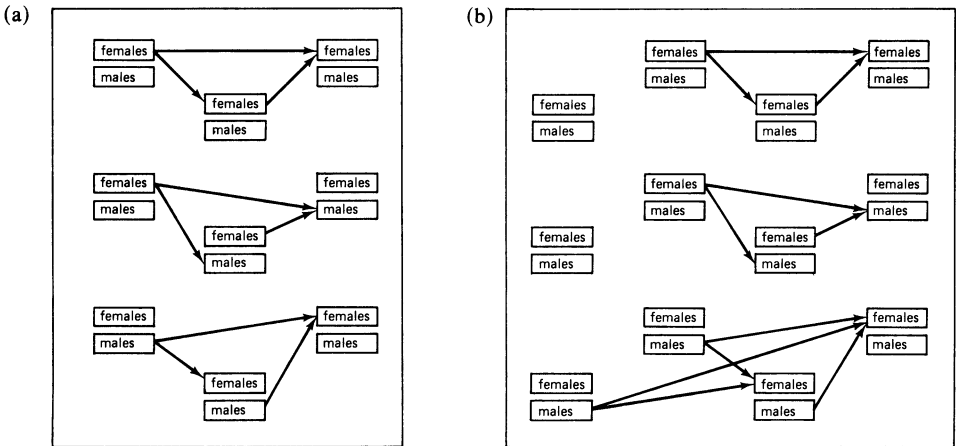


FIG. 1. (a) The pattern of gene flow in Seger's (1983) sphecid pattern of generational overlap. The top, centre and bottom parts show the gene flows from females to females, females to males and males to females respectively. Within each part, the upper pairs of boxes represent the early generations and the lower boxes represent the late generation. The early generation overwinter as pupae, and time flows from left to right. Whenever one box receives more than one arrow in a diagram, it is necessary to specify the fraction of genes coming from each of the sources, and these fractions are the parameters in Table 2. α_1 , α_2 and β refer to the "double-arrived" boxes in the top, centre and bottom parts of the figure, respectively. (b) The pattern of gene flow in Seger's (1983) halictid pattern of generational overlap. The top, centre and bottom parts show the gene flows from females to females, females to males and males to females respectively. Within each part, the upper pairs of boxes represent the early generations and the lower boxes represent the late generation. Mated females of the early generation overwinter as adults, and time flows from left to right. Whenever one box receives more than one arrow in a diagram, it is necessary to specify the fraction of genes coming from each of the sources, and these fractions are the parameters in Table 3. The parameters describing the "multiply arrowed" boxes are α for the top part; β for the centre part; θ for the left-hand box in the bottom part, and γ_1 and γ_2 for the right-hand box in the bottom part.

described in terms of parameters such as "the fraction of spring females whose father was in the summer generation of the preceding year". The reproductive values are shown in Table 2 alongside the matrices.

A biological appreciation of how partial bivoltinism influences reproductive values can be gained by considering a simple case of Seger's sphecid pattern of generational overlap. Suppose the spring females leave offspring only to the summer generation, and the only overlap of generations occurs when males from the spring generation survive to mate with females of the summer generation. If none of the spring males survived, then the reproductive value of males and females in each generation would be one-third and two-thirds respectively, in each generation. As more and more of the summer females are mated by spring males, however, the reproductive value of spring males increases because they are gaining genetic representation in future generations at the expense of summer males. This means that the spring males become more valuable relative to the spring females, and that the summer males become less valuable relative to the summer females. These distortions to the reproductive values of the two sexes bring the average relatedness

TABLE 2

The matrix showing the flow of reproductive value through generations in a generalization of Seger's (1983) sphecid pattern of generational overlap, for haplodiploids. In the sphecid pattern, pupae overwinter. Alongside the matrix is given the reproductive value of each category of individual, which in mathematical terms is the right eigenvector with unit eigenvalue of the matrix. EGM means early generation males, LGM = late generation males, EGF = early generation females, LGF = late generation females. The early generation is the one which reproduces first in the year. The definitions of most symbols are implicit in the matrix, as α , β etc. are defined as the fraction of genes coming from and going to certain sources. $K = 3 - \alpha_1 + 2\alpha_2 + 2\beta$

From	To				Reproductive value
	EGM	EGF	LGM	LGF	
EGM		$\alpha_2/2$		$1/2$	$(1 - \alpha_1 + 2\alpha_2)/K$
EGF	β	$\alpha_1/2$	1	$1/2$	$2(1 + \beta)/K$
LGM		$(1 - \alpha_2)/2$			$(1 - \alpha_2)(1 + \beta)/K$
LGF	$1 - \beta$	$(1 - \alpha_1)/2$			$2(1 - \alpha_1 + \alpha_2(1 - \beta))/K$
	1	1	1	1	

effect of section 2 into play. If natural selection acted freely on the sex ratios, the spring generation would be male biased and the summer generation would be female biased. Note that the reproductive values are not automatically restored to their old values by this adjustment of the sex ratio.

These effects on reproductive value are relatively straightforward. There is another, subtler, effect that does not occur in diploids. Because of male haploidy, males are specialists in daughter production; while females specialize (at least relative to males) in son production. The increase in value of males in the first generation will therefore tend to increase the value of females (the specialist male producers) in the parental generations; while the increase in value of the females in the second generation will tend to increase the value of males (the specialist female producers) in the parents to the second generation. We can apply this to the simple version of Seger's model discussed in the previous paragraph. As summer females are more important than summer males, this makes the female specialists (i.e. the males) in the spring generation more valuable. This reinforces the already existing bias in reproductive value, and explains why the sex ratio biases predicted by Seger (1983) are more extreme in haplodiploidy than in diploidy.

I now explain how the reproductive values given in Tables 2 and 3 can be used as results of a sex ratio model. We saw in the previous section that the inclusive fitness gains from producing a male and a female were

$$r_m V_m/s \quad \text{and} \quad r_f V_f/(1-s).$$

TABLE 3

The matrix showing the flow of reproductive value through generations in a generalization of Seger's (1983) halictid pattern of generational overlap, for haplodiploids. In the halictid pattern, mated females overwinter. Alongside the matrix is given the reproductive value of each category of individual, which in mathematical terms is the right eigenvector with unit eigenvalue of the matrix. The symbol for the categories are as in Table 2, with the addition of OLG = "old" late generation males, which represents the reproductive value gained by old generation males through surviving to mate with early generation females (who then overwinter before reproducing). The early generation is the generation which reproduces first in the year. The definitions of most symbols are implicit in the matrix, as α , β etc. are defined as the fraction of genes coming from and going to certain sources. $2K = \gamma_2(1 + (1 - \theta)(1 - \beta)/2) + (1 + \gamma_1/2) \times (2 - (1 - \beta)\theta) + (1 - \alpha)/2$

From	To					Reproductive value
	OLGM	EGM	EGF	LGM	LGF	
OLGM			$\gamma_1/2$		$(1 - \theta)/2$	$((1 - \theta)(1 - \beta)(\gamma_2 + (1 - \alpha)\theta/2) + (1 - (1 - \beta)\theta/2)(\gamma_1 + (1 - \alpha)(1 - \theta)/2))/(2K)$
EGM			$\gamma_2/2$		$\theta/2$	$(\gamma_2 + (1 - \alpha)\theta/2)/2K$
EGF		β	$\alpha/2$	1	1/2	$(1 - (1 - \beta)\theta/2)/K$
LGM	1		$(1 - \gamma_1 - \gamma_2)/2$			$((2 - \alpha - \beta)(1 - \theta) + (1 + \beta) \times (1 - \gamma_2))/4K$
LGF		$1 - \beta$	$(1 - \alpha)/2$			$(\gamma_2(1 - \beta) + (1 - \alpha))/(2K)$
	1	1	1	1	1	

Now the sex ratio is in equilibrium for an agent when these are equal, and so the equilibrium sex ratio expressed as fraction of males, s^* is given by

$$s^* = \frac{r_m V_m}{r_m V_m + r_f V_f}$$

The prediction for s^* can therefore be found by taking the reproductive values for males and females in the desired generation, and substituting them for V_m and V_f . The reader is reminded of the assumptions of no local mate competition and no local resource competition.

The sense in which s^* is the equilibrium sex ratio needs some elaboration. It is only with a sex ratio of s^* in the offspring generation that parents can be indifferent between producing sons and daughters. Now, the question arises whether this sex ratio is an investment ratio or a ratio of numbers. It is, strictly, neither, but is a ratio of reproductive values. The problem arises when two parental generations contribute to the same offspring generations, and when the relative cost of making a son and a daughter differs for the two parental generations. When can the sex

ratio in the offspring generation be said to be in equilibrium? Normally, this would occur when the investment in the two sexes was in the same ratio as the ratio of reproductive values defined by s^* . But when some of the offspring have been contributed by the other parental generation, the question arises how they should be counted towards the ratio of investment. The answer is that each parental generation must be considered to have its own equilibrium, and that investment in all offspring should be evaluated as if they had been produced by the parental generation with whose equilibrium we are concerned, and not with the investment actually made in them. So the investment ratio in the offspring generation will be different from the point of view of the different parental generations if the relative cost of males and females differs between them.

This has important implications, for example that if two parental generations with different cost ratios contribute to the same offspring generation, then in equilibrium at least one of the parental generations will produce offspring of one sex only. Equilibrium with both sexes being produced occurs when the value of a marginal male ($r_m V_m / s$) and the value of a marginal female ($r_f V_f / (1 - s)$) are equal. But if they are equal for one parental generation, with its evaluation of the investment ratio(s), then they cannot also be equal for the other parental generation if its evaluation of the investment ratio is different. So in equilibrium we must have one of the three following situations. (1) One generation makes all males, and from its point of view the marginal male is worth more than the marginal female; the other generation produces both sexes, and the investment sex ratio in the offspring generation is given by s^* from this generation's point of view. (2) The same but with the sexes reversed. (3) One generation makes all males, and from its point of view the marginal male is worth more than the marginal female; the other generation produces all females, and from its point of view the marginal female is worth more than the marginal male. In this third case, s^* is greater than the investment sex ratio from the point of view of the male producing generation, and less than the investment sex ratio from the point of view of the female producing generation. If the cost ratios are not very different, then this will give a fairly precise prediction for the observed sex ratio.

Finally, I remark that the power of reproductive value is convincingly demonstrated by another use to which Tables 2 and 3 can be put. Suppose a female has a choice over which generation her offspring will emerge in. The reproductive values of males in the early and late generations can be used to obtain an equilibrated "generational ratio" in exactly the same way as an equilibrated sex ratio was derived above. The reproductive values are a natural feature of population structures in time.

In this section, I have discussed sex ratio in the simple case, without local mate competition, local resource competition, inbreeding or varying relative costs of son and daughter production. That is the case of main importance for this paper. Inbreeding is not connected in logic with sex specific competition between sibs, but the two are likely to be found together in nature. While inbreeding by itself can be handled within the framework of this paper (simply by calculating relatednesses appropriately), the complications for sex ratio of local mate competition and local resource competition require the more general approach of Taylor (1986).

4. A Brief History, with the Case for Split Sex Ratios

The main problem in explaining the role of split sex ratios is the confusion about which factors are really important in favouring sib rearing. I hope that the preceding sections have provided a conceptual framework in which the reader can see how things work for sib rearing and for partial bivoltinism, thereby preparing the reader to understand the following fairly simple account of the history of the subject of the selective advantage of sib rearing, along with the case for the potential importance of split sex ratios. The history is conceptual and in a way unhistorical—I am interested in how we now understand what was done, and not in how those who did the work understood it at the time.

I begin by stating the conclusions of section 2. They were that, on the assumption of maternal sex ratio equilibrium in the population at large, females are predisposed towards rearing sibs by a factor of

$$\frac{B+3(1-B)}{2}$$

where B is the sex ratio the particular female would produce among her sibs, while males would be predisposed on account of genetic influences towards rearing sibs by a factor of

$$\frac{1-\bar{F}}{1-F}$$

where F is the sex ratio produced by the particular male's mates, and \bar{F} is the average sex ratio produced by mated females. These two simple conclusions hold with any perturbations of reproductive values and concomitant changes in sex ratio, provided each sex ratio is in equilibrium under maternal control. The advantage to a female varies from a 50% loss in reproductive value when rearing all sons ($B=1$), to a 50% gain when producing all sisters ($B=0$). The advantage to a male varies from an infinite gain when his mate would produce all sons ($F=1$), to a proportional loss equal to the sex ratio when his mate would produce all daughters ($F=0$).

The subject was begun by Hamilton (1964), who proposed that the asymmetric relatednesses found in haplodiploidy could account for the high incidence of eusociality among the Hymenoptera compared to other insects. He also suggested that they could explain why females but not males help in the Hymenoptera, compared to the situation in termites where both sexes help. His analysis of the female's advantage came to exactly the correct conclusion, as the extra complications arising from variations in reproductive value cancel out on the assumption of maternal sex ratio equilibrium. For males, Hamilton did not consider that although nothing could be gained from sibs, variations in the sex ratio of offspring might create predispositions towards rearing sibs.

Hamilton (1972) continued his exploration of the subject. Pursuing a justification for applying his inclusive fitness method to haplodiploidy, he showed that the reproductive value of all males equalled one half that of all females in the case of discrete non-overlapping generations. He also used the regression coefficient of

relatedness (Hamilton, 1970), and weighted it by the relative reproductive value and sex ratio to get "life for life" coefficients of relatedness. These elements, fused together by Hamilton into these life-for-life coefficients, are what we must keep separate in order to disentangle the consequences of life cycles more complicated than those with which he was concerned.

The next major step was taken by Trivers & Hare (1976), who applied considerable subtlety of argument to provide a powerful case for the importance of haplodiploidy in the evolutionary origins of sib rearing. The ingredients used to derive α in (2) are all used by Trivers & Hare when they consider the equilibrial sex ratio; but when discussing the advantage to sib rearing, they concentrate exclusively on the sex ratio manipulation effect, neglecting the average relatedness effect and the parental skewed sex ratio effect. Their other main force was worker laying, which I have neglected here. The first main argument of theirs I wish to review is the case that the ability to discriminate between male and female eggs or larvae need not have been present in the beginning of sib rearing. They argue that sib rearing may occur purely for reasons of efficiency, i.e. with $\alpha = 1$, and would do so with equal facility in diploids and haplodiploids. Once it had begun, however, selection *in haplodiploids only* and *in females only* would then favour two tricks (preferential treatment of sisters, and the laying of own sons) which would make sib rearing more advantageous. Then, when fluctuating conditions restored the relative efficiency of sib and offspring rearing, diploids and haplodiploid males would revert to offspring rearing, while it was still advantageous for haplodiploid females to rear sibs. Thus haplodiploidy can be important even though the very first helpers could not distinguish male from female sibs.

Trivers & Hare's second main argument was that the relative efficiency of sib and offspring production depended in the male on quantities intrinsic to the theory, namely the sex ratio and reproductive values. It was for that reason that in section 2 (7) and not (6) was taken as the comparative advantage towards sib rearing for males.

Charnov (1978) denied the importance of haplodiploidy, on the grounds that the simultaneous mutant required, one that biased the sex ratio and reared sibs, was implausible. This ignores the first main argument of Trivers & Hare (1976), which Charnov describes as "difficult to follow" (p. 453). Charnov's main point was that the interests of the potential sib rearer's mother should be considered. The choice between sibs and offspring for the potential sib rearer is a choice between offspring and grandoffspring for the potential sib rearer's mother. The mother is therefore strongly selected to manipulate her offspring (if possible) to rear the offspring's own sibs, under all the circumstances we have discussed in this paper. Charnov argued that this constant feature was more likely to be important than more ephemeral biases in the offspring's interests that arose only in special circumstances. This constant feature applies equally to haplodiploidy and diploidy, and to males and females.

Craig (1980) pointed to an error in the reasoning of Hamilton (1972) and Trivers & Hare (1976), but one which turns out on closer analysis to be benign. They had believed that a population-wide female biased sex ratio would encourage sib rearing

by hymenopteran females. Craig argued that the sib rearer must produce a sex ratio more female biased than the population average to gain an advantage. This is seen in (2) above—without variation in sex ratios, only the average relatedness effect operates, as π , $\pi + \delta$ and ϕ all represent deviations from the population average. Craig's point is therefore correct when the average relatedness effect does not operate, that is, when the reproductive value of males is a half that of females. When the reproductive values are not in this ratio, then the average relatedness effect either favours or inhibits sib rearing in all females, and the imbalance in reproductive values also alters the maternal equilibrium sex ratio. Further, it does so in such a way that a female bias corresponds to favouring sib rearing, while a male bias occurs when sib rearing is inhibited. Craig's point is correct as a description of the operation of the parental skewed sex ratio effect, but it turns out that when maternal sex ratio equilibrium holds, there is a correlation between that force and the average relatedness effect, and this effect does not depend on sex ratios that are biased relative to the population sex ratio.

The problem in the literature was how to get a female biased sex ratio plausibly. In a very important paper, Seger (1983) introduced models that produced biased equilibrium sex ratios. Seger's main arguments are two, and important enough to repeat here. First, in considering the evolutionary origins of sib rearing we must consider species in which parents and offspring are around at the same time (which in a species that is adult for less than a year means bivoltinism or multivoltinism), and in which generations overlap so that they are contributing to the same offspring generation (partial bivoltinism). Otherwise there is no question of one individual rearing sibs instead of its own offspring. Second, Fisher's theory of the sex ratio does not apply straightforwardly to partially bivoltine species, because the assumptions are not met. According to Seger, we therefore have, *in exactly the case we must consider for the origins of sib rearing*, the potential for sex ratio biases which can "act as preadaptations for the evolution of eusociality".

In terms of our analysis of forces in section 2, Seger's model invokes only the average relatedness effect, because all sex ratios produced for a given offspring generation are equal. The average relatedness effect operates because the patterns of generational overlap alter the reproductive values of males and females in the way discussed in section 3.

The main consequence of Seger's discovery was to add to that of Trivers & Hare (1976) another defence of Hamilton's idea that haplodiploidy may favour eusociality against Charnov's objection that an unlikely coincidence was required—that the same mutant must combine biasing the sex ratio towards females and sib rearing.

More recently, Stubblefield & Charnov (1986) as well as Taylor (1986) have made the point that the Seger effect works whether or not the sex ratio biases actually occur; all that matters is that they would occur if the necessary variation arose. While this is true, the extent of the equilibrium sex ratio bias is a perfect summary of the force towards sib rearing. Although one formulation (2) makes sex ratios irrelevant to the advantage to sib rearing, another (6) makes sex ratio central on the hypothesis of maternal sex ratio equilibrium. Stubblefield & Charnov pursue

the Charnovian line that haplodiploidy is likely to be unimportant. They show that the Seger effect does exist, but argue that it is likely to be small.

It is at this stage in the argument that split sex ratios become important. Split sex ratios occur when sets of females contribute systematically different sex ratios to the same offspring generation. Perhaps large females leave sons and small females leave daughters; or early females leave sons and late females leave daughters; or females in woods leave daughters while females in fields leave sons. Seger's (1983) model did *not* involve split sex ratios: although different offspring generations had different sex ratios, all the contributors to the same offspring generation produced the same sex ratio for it. Where necessary, this meant that the same individual would leave one sex ratio in one set of offspring, destined for one generation, and a different sex ratio in offspring destined for another. Split sex ratios lead to π and/or ϕ being non-zero. This in turn invokes the parental skewed sex ratio effect, which can have an important effect on the advantages of sib rearing.

Seger (1983) and Stubblefield & Charnov (1986) assume that sex ratios are not split—so that whenever two parental generations contribute to the same offspring generation they do so with the same sex ratio. In the next section, I explain why this should at least not be taken for granted. In the rest of this section, I explain the consequences of allowing split sex ratios. I will argue that they can have important effects, despite Stubblefield & Charnov's reassurance (not in these words) that their assumption of unsplit sex ratios does not affect the substance of their conclusions.

The advantage to sib rearing for females was shown in section 2 to be

$$\frac{B + 3(1 - B)}{2}$$

Now Seger's models work by providing reasons why the equilibrium sex ratio should be female biased, so that a female producing the equilibrium sex ratio will gain by rearing sibs. If sex ratios can be split, then we must suppose that there are females with high and low values of B in a population. If the daughter can detect and behave according to the cue which her mother is using to decide whether to produce males or females, such as mother's size, time in the season or shade, in our examples above, then females will be predisposed to rear sibs in those conditions under which their mothers are producing a female biased sex ratio.

If sex ratios are split, then, it becomes unnecessary to produce a bias in the equilibrium sex ratio, because some females are already producing a sufficient female biased sex ratio. Further, the extent of the bias depends only on the sex ratio produced by the mothers of the sib rearers, and not on the sex ratio biases in the population as a whole. Seger's emphasis on partial bivoltinism and his distinction between sphecid and halictid patterns of generational overlap are thus seen to be crucially important when sex ratios are not split, and all females produce the population sex ratio, but unimportant when sex ratios are split, and the possibility exists for sib rearing to arise conditional on parental sex ratios.

This potential importance of split sex ratios is a fairly obvious thing, but I would stress the new points here. First, that the sex ratio produced while sib rearing is the only important thing for a female, and particularly that overlap of generations does

not affect the relationship between that sex ratio and the advantage to sib rearing. This implies that the whole range of comparative advantages for a female can be obtained in any pattern of generational overlap. Second, that if split sex ratios occur, then cues must exist for the parent to detect; and these may be detectable by the offspring.

The tendency of males towards rearing sibs has been mainly neglected by authors subsequent to Trivers & Hare (1976). If sex ratios are unsplit, then the genetic system cannot predispose them to rear sibs or to rear offspring. However, split sex ratios do allow this. To the extent that their mates are likely to produce sons, males will be predisposed to rear sibs, and to the extent that they are likely to produce daughters, males will be predisposed to prefer to mate. Thus suppose that early mating females leave females to the next generation, while late mating females leave sons. Then daughters of the early mating females will be predisposed to rear sibs because they will rear sisters; and sons of the early mating females will be predisposed to rear sibs because their mates would produce mainly sons.

The conclusions about the influence of haplodiploidy on the selective advantage of rearing sibs therefore depend strongly on sex and whether sex ratios are split. Without split sex ratios, females are predisposed for or against rearing sibs depending on whether the equilibrium sex ratio is female biased or male biased; and males are altogether unaffected. The strength of the effect on females may be limited because extreme conditions are needed to make the equilibrium sex ratio strongly biased. With split sex ratios, females are predisposed for or against sib rearing depending on whether the sex ratio produced by their mother is female biased or male biased; and males are predisposed for or against sib rearing depending on whether their mates would produce a sex ratio that is more male biased or more female biased than the average mated female's. As shown in the next section, extreme conditions are not required for individuals' sex ratios to be highly male or female biased. In both cases, a female's reproductive value may suffer a 50% loss, or make a 50% gain, through rearing sibs rather than offspring, purely as a consequence of the genetic system of haplodiploidy. Haplodiploidy would increase a male's reproductive value infinitely through rearing sibs, if his mate would produce no daughters; while the proportional loss in reproductive value, should his mate produce all daughters, equals the average sex ratio produced by mated females.

5. Reasons to Expect Split Sex Ratios

In the previous sections, the possible importance of split sex ratios has been explained. Split sex ratios occur where, among those contributing to a single offspring generation, some parents produce systematically more females than average and some produce systematically more males. In the extreme case, the parents would be divided into male and female producers. For our purposes, a sex ratio bias is "systematic" if offspring can detect it by attending to external cues, possibly the same cues that determine the bias of the parents. In this section I consider whether we should expect to find split sex ratios in nature. First, arguments will be given that split sex ratios should be expected; and second, one important argument against

will be developed. I cannot pretend to settle the empirical matter of whether they actually occur.

We begin by considering the selective forces at work in an ordinary, diploid, Fisherian population. It has long been recognized that when the population average sex ratio is 1:1 there is no selective advantage to individuals producing exactly the 1:1 ratio over those producing highly biased ratios. Individuals are indifferent between producing sons and daughters at the population equilibrium. While all individuals are identical in their abilities to produce sons and daughters, this indifference is curious but of no great importance. Trivers & Willard (1973) considered the possibility that parents vary: in their case, females in good condition were supposed to be able to produce high quality males or average females; while females in bad condition were supposed to be able to produce poor quality males or average females. Selection will favour the first group of females to produce sons, and the second group to produce daughters. The indifference in the case with identical parents shows that there is no force tending to maintain equality of sex ratio in the case with varying parents. The first group of females should produce all sons; and the second group all daughters.

We may safely generalize this result. If there are groups of females that have different cost ratios for producing males and females, then selection will favour extreme sex ratios, with males produced by females with a comparative advantage in son production, and females by those with a comparative advantage in daughter production. The difference in cost ratio may arise in two ways. A typical example of the first case would be where some females work twice as hard to make a son as a daughter, and others work twice as hard to make a daughter as a son, but the offspring once produced are the same. This could arise if sons and daughters required different resources, and if habitats varied in the availability of those resources. The second case is that of Trivers & Willard, where the difference lies in the quality of the offspring produced. Here we may measure the cost ratio in terms not of numbers of males or females per unit effort, but rather in terms of some measure of quality per unit investment. Expected number of grandoffspring through an individual would be a reasonable measure of this quality.

In view of the knife-edge nature of the 1:1 equilibrium from the individual's point of view, it is surprising that split sex ratios are not commonly found. Even very slight differences in cost ratio should produce strong biases among an individual's offspring. The partial bivoltinism which, following Seger (1983), we may assume to have been present during the first stages of the evolution of sib rearing supplies extra opportunities for split sex ratios to arise. There may be differences between the adults of the early and late generations in time in the season and size, affecting the relative ability to accrue resources of different sorts, and in synchrony of emergence, affecting the difficulty of finding a mate. If the generation to which an individual belongs can be a cue affecting sex ratio, then when two parental generations contribute to the same offspring generation there is no force to prevent their contributed sex ratios from drifting apart.

Finally, split sex ratios are more plausible in haplodiploids, where control of fertilization is a mechanism of parental sex determination that is known to be used

(see Charnov (1982) for a review and examples). These are the reasons why split sex ratios are to be expected.

According to these arguments, split sex ratios should be expected. I now consider two arguments against. The first I shall only mention, and it is that the animals may be too unsophisticated, or natural selection too coarse an instrument in this case, for these "finely tuned" adjustments to be made. Split sex ratios are not specially at risk from this argument compared to theories of sex ratios in general. The importance of the analysis in section 2 is that one force, the average relatedness effect, does not depend in any way on adjustments in the sex ratio.

The second force likely to reduce the extent of split sex ratios is uncertainty. In the standard Fisherian model, there is a very small force towards variance reduction, of the order of the inverse of the population size. It was pointed out by Verner (1965), and depends on stochastic fluctuations in the population sex ratio. An analogous but potentially much stronger force exists in the present case. Suppose that females in rainy areas should produce sons, while those in drier areas should produce daughters. Suppose further that over an immense length of time, during which weather conditions remained unnaturally constant, the threshold amount of rainfall has been adjusted by natural selection so that the population sex ratio was in equilibrium. Now if the constant spell is broken by a particularly rainy year, most females will be in rainy areas and so produce sons. Those few daughter producing females in dry areas will, through the scarcity of females among the offspring, make a very large contribution to the reproductive value of the next generation. It will be seen that selection during a period of variable weather conditions would favour intermediate sex ratios, which are biased in the expected direction according to the cost ratio but are not all sons or all daughters. They are held at intermediate levels as a kind of bet-hedging against extreme years.

Why is it that the small force of Verner (1965) has become so important that even in a very large population, bet-hedging can occur? The cause of selection for bet-hedging is unpredictable variability in the population sex ratio. Verner depended on the variation between stochastically independent individuals, so that the average becomes less and less variable as the population increases in size. Once a population adopts environmental cues as determinants of the sex ratio, individuals cease to be stochastically independent, as the value of the cue will affect all individuals, and so the population sex ratio can suffer large fluctuations. Longer-lived animals would be less affected by this variability than shorter-lived ones, as only a fraction of the reproductive value of a long-lived species will be present in one year's offspring.

The case of sex ratios that are split between different parental generations that contribute to the same offspring generation could be strongly affected by this uncertainty. The early generation might be acting under considerable uncertainty about the productivity of the late generation. If a storm in July could cut short the production of daughters by the late generation, then the early generation should insure itself by producing some daughters along with the sons that in an average year would be more advantageous.

The aim of this section has been to show that there are strong reasons to expect split sex ratios, particularly in haplodiploid species that are partially bivoltine, and

a force against them. Models could help to delineate conditions under which one or other force has the upper hand, but simple measurements of relevant sex ratios among partially bivoltine haplodiploids would be better. Generational splits should be fairly easy to detect; splits according to local conditions would be reflected in spatial variability of sex ratio, or, for individually varying circumstances, in greater than binomial variability of sex ratio at one site. Note that a split sex ratio is not a difference between the adult sex ratios in the two generations of a year, but instead differences between contributions to a single generation.

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APPENDIX

In this appendix, it is required to show how the assumption of maternal sex ratio equilibrium leads from (2) to the simplification (6) for females and males, and how it leads to (7) for males. If the population sex ratio, s , is in equilibrium for an agent with relatednesses R_m , R_f to males and females, then according to section 3, s will be given by

$$\frac{R_m V_m}{R_m V_m + R_f V_f}$$

Let us assume that the numbers of the sexes are weighted by $\gamma:1-\gamma$ with respect

to this value, so that

$$s = \frac{\gamma R_m V_m}{\gamma R_m V_m + (1 - \gamma) R_f V_f}$$

Now $\gamma = 1/2$ means the sex ratio is in equilibrium for the agent, $\gamma < 1/2$ means the sex ratio is female biased, and $\gamma > 1/2$ that it is male biased relative to the agent's equilibrium. Let τ be the sex ratio among offspring, and τ' among sibs. Combined with (2), we then have the following expression for α

$$\frac{\tau(r_m/R_m) + (1 - \tau)(r_f/R_f) + (2\gamma - 1)(-\tau(r_m/R_m) + (1 - \tau)(r_f/R_f))}{\tau'(r'_m/R_m) + (1 - \tau')(r'_f/R_f) + (2\gamma - 1)(-\tau'(r'_m/R_m) + (1 - \tau')(r'_f/R_f))}$$

Assuming maternal equilibrium means taking R_m and R_f as 1 and 0.5, respectively, and letting γ equal a half, so eliminating the third terms in the numerator and denominator. We therefore have

$$\alpha = \frac{\tau(r_m/R_m) + (1 - \tau)(r_f/R_f)}{\tau'(r'_m/R_m) + (1 - \tau')(r'_f/R_f)}$$

The expressions in (6) follow immediately on substituting B for τ in the case of females, and F for τ' in the case of males. (τ' for females and τ for males turn out to be irrelevant.)

The argument for (7) for males is rather different. First we wish to evaluate the relative per capita reproductive value of a male relative to a female, as parents, that is, as non sib-rearers. This quantity is relevant to the mothers of the deciding generation, and assuming them to be indifferent between producing males and females allows us to say that the reproductive value of males *per unit investment* equals half that for females (because mothers are twice as related to their sons as to their daughters). Two factors permit a discrepancy between the reproductive values per capita and per unit investment. First, the investment per individual may differ between the sexes; second, the fraction of individuals surviving from the time of investment to the time of the decision may differ between the sexes. Taking these into account, we may express the ratio of the per capita reproductive value of males to females as

$$\frac{1}{2} \frac{c_m \sigma_f}{c_f \sigma_m}$$

where c represents costs and σ represents survivorship. As this argument applies to the average values of males and females, it assumes that the male as a parent will gain the average sex ratio for that generation.

The next task is to find the reproductive value of a male as a sib rearer in terms of the reproductive value of a female of its sister's generation as a parent. Per unit investment, a male as a sib rearer gains exactly half as much reproductive value as a female as parent, because the relevant relatednesses for the male are half those of its mother. The number of sibs raised by a male divided by the number of offspring raised by a female of its sister's generation as a parent is the relative efficiency of a male as a sib rearer. Let us denote it e . Then the required value is $e/2$.

It will be seen that the two derived quantities are the reproductive value of a male as a parent, and the reproductive value of a male as a sib rearer, in terms of the same standard: namely the reproductive value of a female of the male's generation as a parent. It follows that the ratio of reproductive values for a male as a sib rearer compared to a parent is the ratio of those quantities, that is

$$e \frac{c_f \sigma_m}{c_m \sigma_f}.$$

As noted above, this value assumes that the male as a parent would produce the population average sex ratio. We desire an expression true for a male producing an arbitrary sex ratio. A male parent's reproductive value is proportional to the number of daughters he produces. If the average fraction of daughters produced by a mated female is $1 - \bar{F}$, and if the sex ratio produced by a particular male's mates is $1 - F$, then he will have a reproductive value of $(1 - F)/(1 - \bar{F})$ compared to the average. This factor divided into the previous formula yields (7).

This completes the work of the appendix, except for one comment. Throughout the paper, I have assumed that males and females are equally costly to produce. The reason is that phrasing every argument in terms of investment would have been cumbersome and led to the same conclusion. In the appendix, however, the distinction makes a difference, and this is why cost ratios and survivorships enter in. Only in the appendix are the same animals considered as individuals (i.e. deciders) and reproductive value for others (i.e. evaluated as offspring). This occurs when we use the assumption of maternal sex ratio equilibrium among the parents of the deciding generation.