

## **A General Mathematical Model for Sex Allocation**

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A general matrix equation for evolutionary equilibrium of sex allocation is derived. The equation allows calculation of ESS values of behavioural parameters in sex allocation models, and provides a conceptual framework in which such models can be viewed. A careful discussion is given of a number of examples from the literature. An attempt is made to clarify the assumptions behind different models and relate different results which have been obtained.

### **1. Introduction**

Charnov's (1982) book brings together, and provides a unified treatment of, a wide range of examples of sex allocation problems and discusses the biological evidence available to support the models. The objective in this paper is to provide the framework for a corresponding unification at the mathematical level. A proper mathematical theory can be expected to provide clarity and simplification both conceptually and computationally and the author believes that this is true of the theory provided in this paper. The theory will be illustrated with a few examples from the literature. It will be seen that the theory is capable of revealing the relationship between various models and clarifying the assumptions and the conclusions of each.

It is not intended in this paper to provide a lot of details or to be comprehensive in discussion of the existing models. Such a treatment will come later. The purpose is to outline as clearly and simply as possible the general framework. The main result is a completely general equation for evolutionary equilibrium (the EEE equation (9)) from which a large number of particular equilibrium conditions can be derived.

Some themes will be highlighted briefly, and some notation introduced. One theme is the importance of distinguishing between equilibrium of type frequencies and equilibrium of behavioural parameters. In any sex allocation model there will be a number  $n$  of types of individuals (genotypes or phenotypes), usually genetically determined, and a vector  $\alpha$  of behavioural parameters, also genetically determined, which specifies the reproductive behaviour of the different types. If  $\alpha$  is fixed, the population type frequencies

$q = (q_1, q_2, \dots, q_n)$  will reach an equilibrium which depends on  $\alpha$ . This is an equilibrium of existing genes (at the type-determining loci) and will be reached fairly rapidly, in what is often called ecological time. The behavioural parameters  $\alpha_i$  are assumed to be genetically controlled and are capable of being altered by the introduction of new genetic material (mutations). Over evolutionary time, under the influence of natural selection, we expect these parameters to reach equilibrium values. By my way of thinking, the sex allocation problem should be regarded as one which finds a stable evolutionary equilibrium of  $\alpha$ . Sometimes the literature is confusing on this point; an example is given in the discussion.

Another theme will concern this measurement of fitness. It will be shown that there are four different measurements in the literature which can loosely be described as counting children, grandchildren, great grandchildren and asymptotic number of descendents. The relationship between these will be examined, and it will be shown that they fit into a simple scheme. The relevance to this of a general result of Lloyd (1977) and Heuch (1979) that under some circumstances, at type-frequency equilibrium, each individual has the same gametic fitness, regardless of type, will be discussed.

Also discussed will be the Shaw-Mohler equilibrium equation

$$\frac{dm}{m} + \frac{df}{f} = 0 \quad (1)$$

(so designated by Charnov, 1982) and it will be made clear the special circumstances under which it applies. More general forms of this equation can be derived from the EEE.

One important aspect not discussed is that of stability, both of the type frequency equilibrium  $q$ , for a fixed  $\alpha$  (ecological stability) and of the behavioural equilibrium  $\alpha$  (evolutionary stability). This is an important topic which can be handled nicely in the general framework, but it is left to another time. Thus the equilibrium conditions formulated for  $\alpha$  will be critical point conditions setting differential fitness changes to zero. They are necessary but not sufficient for evolutionary stability. In practice they are strong enough to allow us to find any interior ESS.

## 2. The Model

The reproductive behaviour of a population will be specified by a number of behavioural parameters, for example, number or size of offspring or gametes produced of different types, time spent in various activities, age of maturity, etc. Let  $\alpha = (\alpha_1, \alpha_2, \dots, \alpha_k)$  be the vector of behavioural parameters of interest. There will be trade-offs between various  $\alpha_i$  and the

objective of the model is to find an  $\alpha$  which is evolutionarily stable subject to these trade-offs. The standard method for doing this is to introduce a (mutationally feasible) alternative  $\hat{\alpha}$  and to compare the fitness of  $\alpha$  and  $\hat{\alpha}$  in the  $\alpha$ -population when  $\hat{\alpha}$  is rare. Roughly speaking,  $\alpha$  is evolutionarily stable when the fitness of all feasible alternatives  $\hat{\alpha}$  is less than that of  $\alpha$ .

The fitness of  $\hat{\alpha}$  may not be so easy to write down. As a rule, there will be different *types* of individuals in the population (male, female, hermaphrodite, or different genotypes of each, or different ages of each, etc.) and fitnesses will depend on the type frequencies. These may vary but will usually approximate some stable *type frequency equilibrium* which will generally depend on population behaviour  $\alpha$ . It is customary, when writing down the fitness of  $\hat{\alpha}$  to assume that the population is at this type frequency equilibrium. Assuming this, fitness of  $\hat{\alpha}$  will be measured by counting, in some way, descendents of  $\hat{\alpha}$  individuals. This count may depend on the type of the mutant individual. The overall fitness of  $\hat{\alpha}$  must be some average of its fitness in different types, and to be able to calculate this average, we have to know how  $\hat{\alpha}$  is distributed among different types.

Suppose these complexities can be overcome and the fitness of  $\hat{\alpha}$  can be found. Let  $W(\hat{\alpha}, \alpha)$  be the fitness of a rare behaviour  $\hat{\alpha}$  in an  $\alpha$  population. Then  $W(\hat{\alpha}, \alpha)$  measures the fitness of a rare mutant who happens to act normally (a mutation with no phenotypic effect) and can be taken as the standard of population fitness. A weak condition for evolutionary stability of  $\alpha$  is then

$$W(\hat{\alpha}, \alpha) \leq W(\alpha, \alpha) \quad \text{for all feasible } \hat{\alpha}. \quad (2)$$

If this holds at an interior point  $\alpha$  of the feasible region then we expect the differential condition

$$dW = 0 \quad \text{at } \hat{\alpha} = \alpha \quad (3)$$

to hold. It is this equilibrium condition that will be worked with in this paper. The differential fitness  $dW$  corresponds to a differential shift in behaviour away from  $\alpha$  ( $\hat{\alpha} = \alpha + d\alpha$ ) in the feasible region. There may be many independent directions in which such a shift can occur, each one following an independent trade-off curve. We will get a differential condition (3) for each such trade-off. The solution of all such equations will give us any interior evolutionary equilibrium  $\alpha$ .

Discrete, but not necessarily non-overlapping, generations are assumed. (If behaviour is age dependent we can incorporate age and genotype into our notion of type.) Thus the population has a periodic character and we keep track of numbers of individuals by taking a count at the beginning of each cycle.

Assume there are  $n$  different types of mutant individuals and the fitness of  $\hat{\alpha}$  is measured by counting offspring of each type. An important assumption which makes this possible is that there is no sexual interaction between mutant individuals. This assumption allows each mutant individual to be assigned to a unique mutant ancestor one cycle back and permits counting of mutant offspring. The assumption of rarity of the mutation will usually accomplish this in outbred populations. Even with simple forms of inbreeding it is often possible to define "individual" in such a way that sexual interaction between mutants is absent. For example in Hamilton's (1967) model, where there is sib-mating, mated pairs can be designated as individuals (Taylor & Bulmer, 1980; Taylor, 1985), and the count keeps track of different pairs of mutant genotypes.

The key to counting mutant individuals lies in the  $n \times n$  transition matrix  $A = A(\hat{\alpha}, \alpha)$  whose  $(i, j)$  entry  $a_{ij}$  is the number of mutant offspring of type  $i$  contributed to the next stage by one individual of type  $j$ . The  $a_{ij}$  will depend, in general, on both  $\hat{\alpha}$  and  $\alpha$ . If there are  $m_j$  mutant individuals of type  $j$  at one stage, the number  $m'_j$  next stage can be found from the matrix equation

$$m' = Am. \quad (4)$$

Thus the dominant eigenvalue  $\lambda = \lambda(\hat{\alpha}, \alpha)$  of  $A$  measures the asymptotic growth rate of the mutant population, that is, the growth rate observed when the mutant behaviour is in equilibrium proportions among types (given by the dominant right eigenvector of  $A$ ). Thus the measure of mutant fitness should be

$$W(\hat{\alpha}, \alpha) = \lambda(\hat{\alpha}, \alpha). \quad (5)$$

Equation (2) becomes

$$\lambda(\hat{\alpha}, \alpha) \leq \lambda(\alpha, \alpha) \quad \text{for all feasible } \hat{\alpha}, \quad (6)$$

and the equilibrium conditions (3) becomes

$$d\lambda = 0 \quad \text{at } \hat{\alpha} = \alpha. \quad (7)$$

The trouble with this form of the condition is that  $\lambda$  depends in a complicated way on the entries of  $A$  and can rarely be found explicitly. It may be difficult to analyze directly unless  $A$  has a special form (such as the Leslie matrix form in models with age structure; see Charnov, 1979).

A form of equation (7) which is conceptually and computationally simpler is found by working with the dominant eigenvectors of  $A$ . Let  $v = v(\alpha)$  and  $u = u(\alpha)$  be the left and right dominant eigenvectors of  $A(\alpha, \alpha)$ . Then some simple algebra (Taylor & Bulmer, 1981) shows that at  $\hat{\alpha} = \alpha$ ,

$$d\lambda \text{ and } v dA u \text{ have the same sign.} \quad (8)$$

It follows that condition (7) for evolutionary equilibrium of  $\alpha$  can be written

$$v \, dAu = 0 \quad \text{at } \hat{\alpha} = \alpha. \quad (9)$$

Equation (9) will be referred to as the *evolutionary equilibrium equation* (EEE). The differential here corresponds to a differential change of behaviour away from  $\alpha$  in some feasible direction. What makes this equation very useful is that  $v$  and  $u$  are eigenvectors of  $A(\alpha, \alpha)$  and do not depend on  $\hat{\alpha}$ . They are, thereby, often quite easy to obtain and have a simple biological interpretation. Also, different mutants will give different matrices  $A(\hat{\alpha}, \alpha)$  and different  $\lambda$ , but the same  $v$  and  $u$  will always work. Thus different trade-offs can be looked at, or for a given trade-off, different levels of mutant dominance or different sources of control (female, male, worker, etc.) all with the same  $A(\alpha, \alpha)$  and hence the same  $u$  and  $v$ .

Note that equation (9) is a necessary, but not sufficient, condition for evolutionary stability at an interior point (of the feasible domain of  $\alpha$ ). In practice it is strong enough to enable us to find interior ESS's. Stability must be checked separately.

### 3. Heuristic interpretation of the EEE

First the eigenvectors  $u$  and  $v$  are interpreted; of course they are only determined up to a constant multiple. Since they belong to the case  $\hat{\alpha} = \alpha$ , the mutant behaviour in the following discussion is assumed normal. If we allow mutant individual to occur in equilibrium proportions among different types then it turns out that  $u_j$  measures the relative number of individuals of mutant type  $j$ , and  $v_i$  is the asymptotic number of mutant descendents of one individual of mutant type  $i$ . The force of the word "asymptotic" is that this is the contribution to the indefinite future. This may be stated as  $v_i = \lim v_i^{(t)}$  where  $v_i^{(t)}$  is the contribution after  $t$  cycles and the limit (as  $t$  approaches infinity) may have to be normalized. Thus  $u$  measures type frequency and  $v$  measures type "fitness".

These results are not difficult to demonstrate, though a careful mathematical derivation requires the assumption, which we henceforth make, that  $A$  have a unique positive eigenvector. It is a standard result of non-negative matrices that *primitive* matrices (some power has entries  $>0$ ) have this property, and the matrices which arise in our models seem always to be primitive.

These interpretations of  $v$  and  $u$  are reminiscent of and closely related to the interpretation of the dominant eigenvectors of a Leslie matrix, the left as the vector of reproductive values and the right as the vector of relative frequencies of the age classes at stable age distribution.

As an important example suppose behaviour  $\alpha$  is determined by an autosomal gene, and the population is outbred. Then  $\hat{\alpha}$  is determined by a mutant allele and a mutant individual has one such allele at the locus in question. If  $q_j$  is the equilibrium frequency of type  $j$  in the normal population then

$$u_j \sim \pi_j q_j \quad (10)$$

where  $\pi_j$  is the ploidy of type  $j$ . In particular, in a diploid population,  $u_j \sim q_j$ .

Now the EEE will be interpreted. Consider a mutation which is rare but has reached equilibrium proportions (among types) in the population. Suppose the mutant has normal behaviour  $\alpha$ , so that different mutant types have relative frequency  $u_j$ . Now let the mutation cause altered behaviour  $\hat{\alpha}$  for one cycle and then revert to normal. The expected relative number of individuals of each mutant type at the end of this cycle is given by the appropriate entry of the vector  $A(\hat{\alpha}, \alpha)u$ . Since the mutant is now normal, individuals of mutant type  $i$  contribute  $v_i$  mutant descendents to the future. Thus the expected fitness of the mutant is measured by the product  $vA(\hat{\alpha}, \alpha)u$ .

By this heuristic, the ESS condition (2) would be formulated as

$$vA(\hat{\alpha}, \alpha)u \leq vA(\alpha, \alpha)u \quad \text{for all feasible } \hat{\alpha}. \quad (11)$$

The EEE equation (9) is in fact the differential condition corresponding to this maximization condition.

It must be emphasized that equation (11) is a heuristic only and is based on the assumption that the mutation exhibits deviant behaviour for one generation only. It is not true that  $\lambda = vAu$  or even that the condition (6) is equivalent to (11). What is true is the local condition (8), that  $d\hat{\lambda}$  and  $v dAu$  have the same sign, and the EEE equation (9) follows from that.

The heuristic of this section is important, because it has guided much of the pathbreaking work in the modelling of sex allocation. This will now be related to some of the classical literature. Suppose that, instead of using  $v$  to measure the fitness of different mutant types, another vector  $w$  is used. Then, in the heuristic, expected mutant fitness would be  $wAu$  and the differential condition for evolutionary equilibrium would be

$$w dAu = 0. \quad (12)$$

Most of the classic sex ratio results follow from such an equation. The arguments used were often vague, but can be readily translated into precise genetical arguments at autosomal loci with no inbreeding. The fitness vector  $w$  is arrived at by implicitly making an assumption that at some point in the future each type (as a whole) makes the same contribution to the next

stage. For example, in case there are two types, female and male, it is assumed that at some stage total female and male contributions are equal.

Suppose, following the heuristic, it is the  $F_0$  generation in which the mutation produces deviant behaviour. Then the vector  $Au$  counts the  $F_1$  mutant types. If we assume that each  $F_1$  type makes the same contribution to the  $F_2$  generation, then the fitness of a type  $j$   $F_1$  individual is inversely proportional to type  $j$  frequency. Thus

$$w_j = 1/q_j. \tag{13}$$

This choice of  $w$ , which will be called  $v^{(2)}$  essentially counts grandchildren (contribution to  $F_2$ ) of the original mutant individuals. This is the argument used by Fisher (1930) and Shaw & Mohler (1953) and will be called the *grandchild argument*. It shall be seen in the examples that it gives the right answer for the basic diploid and haplodiploid models.

Trivers & Hare (1976), in modelling a more complex system, with haplodiploid genetics and the possibility of worker control of sex ratio and worker-laid males, used, implicitly, another  $w$ . Suppose we assume that all  $F_2$  mutant types contribute equally to  $F_3$ . Then the expected contribution to  $F_3$  of an  $F_1$  type  $j$  mutant is

$$w_j = \sum_i \frac{1}{q_i} a_{ij} (\hat{\alpha} = \alpha). \tag{14}$$

This vector  $w$  is designated as  $v^{(3)}$  because it essentially counts great grandchildren of the original mutant individuals. The arguments used by Trivers & Hare (1976) were based on relatedness coefficients, but if they are interpreted in our matrix framework it is seen that they are using the fitness vector  $v^{(3)}$ . Certainly the formulae they get (their p. 251) for queen, worker, and laying-worker control, are obtained in each case from the condition  $v^{(3)} dAu = 0$  for the appropriate matrix  $A$ .

Notice that  $v^{(3)} = v^{(2)}A$  for  $\hat{\alpha} = \alpha$ . One could imagine a great  $(t)$  grandchild argument using the fitness vector,

$$v^{(t+2)} = v^{(2)}A^t \quad (t \geq 0). \tag{15}$$

It turns out that

$$v^{(\infty)} = \lim_{t \rightarrow \infty} v^{(t)} \tag{16}$$

(the limit may have to be normalized) is the dominant left eigenvector  $v$  of  $A$ , so that, in general, the larger you take  $t$  the better will be your formulae. (Roughly speaking, since  $v^{(\infty)} \sim v^{(2)}A^\infty$ ,  $v^{(\infty)}A \sim v^{(2)}A^\infty A \sim v^{(\infty)}$ .) The formulae obtained by Trivers & Hare using  $v^{(3)}$  were wrong (which is why one

can be sure they used  $v^{(3)}$  but they were numerically close to the correct formulae obtained from  $v$ . Equation (16) gives one way to calculate  $v$ ; but it is considerably easier to calculate it directly from the matrix  $A$ .

The idea of using the objects  $v^{(i)}$  to measure fitness seems to have been suggested by Oster, Eshel & Cohen (1977) and the role of  $v^{(\infty)}$  as an eigenvector was suggested by Benford (1978) who with Charnov (1978) pointed out the discrepancies in the Trivers–Hare formulae for laying workers.

One other candidate for  $w$  which does not fit into the scheme (15) but which shall be called  $v^{(1)}$  because it is obtained by valuing each  $F_1$  individual equally regardless of mutant type must be mentioned. Under this scheme mutant fitness is simply a count of  $F_1$  mutant individuals, so is  $1Au$  where  $1 = v^{(1)}$  is the constant vector. In a sense this was the measure used by Darwin (1871) and indeed Darwinian fitness usually refers to number of offspring. As can be verified in the examples which follow, the condition obtained using  $v^{(1)}$  in the standard male–female sex-ratio model (with constraint equation (20)) is vacuous. This may account for Darwin's difficulty in perceiving the evolutionary reason for 50–50 sex ratio.

Actually Darwin came close to, but did not actually get, the grandchild argument. In the standard male–female situation considered by Darwin, the grandchild argument is essentially a count not of offspring but of number of matings of offspring. Darwin did realize that an offspring that didn't mate was worth nothing and this allowed him to find Fisher's argument for monogamous species. In such species, he argued (1871, Part II, Chapter VIII), an excess of one sex would mean some members of the other sex couldn't mate, and would give increased fitness to those who produced more of the rarer sex. But he failed to come to grips with the fitness advantage associated with multiple matings. For example, in the polygamous species, he felt that an excess of females would be corrected by natural selection only if the excess were “inordinately great” (Part II, p. 317).

#### 4. Basic Examples

The technique will be illustrated with a number of examples. In each case, having found the matrix  $A$ , the right and left eigenvectors  $u$  and  $v$  of  $A$  at  $\hat{a} = \alpha$  must be calculated. This could be done directly with the appropriate system of linear equations, but there are often shortcuts. Assume an autosomal mutant with outbreeding so that  $u$  can be obtained by equation (10). In case  $A$  is  $2 \times 2$ , one eigenvector can be obtained directly from the other. For example, it is always true that

$$v = (a_{21}u_1, a_{12}u_2). \quad (17)$$



There is an interesting interpretation of this. Use the names female and male to designate type 1 and type 2 respectively. In the following examples  $Q = q_1/q_2$  is used to denote the population female/male ratio. Then, using equation (10)

$$v = (a_{21}\pi_1q_1, a_{12}\pi_2q_2) \sim (a_{21}\pi_1, a_{12}\pi_2/Q). \quad (18)$$

Since  $\pi_1$  is female ploidy,  $v_1 = a_{21}\pi_1$  is total gametic contribution per female to next generation males. Similarly  $a_{12}\pi_2$  is the same per male to females. In the case of random mating and all offspring "produced" by the female, each male expects  $Q$  mates and  $v_2 = a_{12}\pi_2/Q$  is the total gametic contribution of a male to female offspring *per mate*.

#### EXAMPLE 1. STANDARD MALE-FEMALE, DIPLOID

Assume two types, female and male, with female autosomal control of the sex of her offspring, non-overlapping generations, and outbreeding. Each female must choose the number of female and male offspring to have, so let  $f$  and  $m$  denote the numbers of each kind she contributes to the next generation. Thus the behavioural parameters are  $\alpha = (f, m)$  and the trade-off between  $f$  and  $m$  is mediated by some underlying allocation of resources, and can usually be written in the form

$$C(f, m) = R \quad (19)$$

and interpreted as requiring the total cost of  $f$  females and  $m$  males to equal some given resource level  $R$ . The trade-off curve (19) is often concave down reflecting the possibility of some penalty, in numbers of offspring, attached to heavily biased sex ratios. The classic sex ratio arguments used linear trade-off curves of the form

$$f + m = K, \quad (20)$$

the total number  $K$  of offspring being given. Feasible mutants  $\hat{\alpha} = (\hat{f}, \hat{m})$  can occupy any point on the curve. In an  $\alpha$  population the equilibrium type frequency is

$$q = q(\alpha) \sim (f, m)$$

and  $Q = f/m$  is the population female/male ratio. The mutant types are female and male, and the transition matrix is

$$A = \frac{1}{2} \begin{bmatrix} \hat{f} & Q\hat{f} \\ \hat{m} & Q\hat{m} \end{bmatrix}$$

since every male expects  $Q$  mates. By equation (18), since both  $\pi_j = 2$ ,

$$v \sim (m, f) \sim \left( \frac{1}{f}, \frac{1}{m} \right). \quad (21)$$

Since "hats" only appear in the first column of  $A$ , the EEE (equation (9)) becomes

$$\frac{df}{f} + \frac{dm}{m} = 0, \quad (22)$$

the classical Shaw-Mohler (1953) equation. Written in the form

$$\frac{df}{dm} = -\frac{f}{m} \quad (23)$$

it can be interpreted as saying that at any evolutionary equilibrium of  $\alpha = (f, m)$ , the slope of the trade-off curve (19) must equal  $-f/m$ . In the classic case, equation (20),  $df/dm = -1$  and equation (23) gives  $f = m$ . Equation (21) suggests that the coefficients  $1/f$  and  $1/m$  in the Shaw-Mohler equation should be regarded as measuring relative value (in terms of asymptotic fitness) of placing a gene in a female or male offspring.

#### EXAMPLE 2. STANDARD MALE-FEMALE, HAPLODIPLOIDY

Make all the assumptions of Example 1, but with a haplodiploid genetic system. The matrix is

$$A = \frac{1}{2} \begin{bmatrix} \hat{f} & 2Q\hat{f} \\ \hat{m} & 0 \end{bmatrix}$$

and since  $\pi_1 = 2$ ,  $\pi_2 = 1$ , equation (18) gives  $v \sim (2m, 2f) \sim (1/f, 1/m)$ . Again we get the classical Shaw-Mohler equation (20).

#### EXAMPLE 3. HAPLODIPLOID-WORKER CONTROL

Assume each female makes sterile daughters who function as workers to raise the reproductive offspring. If it is assumed that they have control over the sex ratio (genes at the mutant locus affect worker behaviour) the matrix becomes

$$A = \frac{1}{2} \begin{bmatrix} \frac{f + \hat{f}}{2} & 2Q\hat{f} \\ \frac{m + \hat{m}}{2} & 0 \end{bmatrix}.$$

Implicit in this is the assumption that if only half the workers in a family are mutant, then only half the reproductive resources will be allocated in the mutant way. The matrix  $A$  is of course the same as for Example 2 and  $v = (m, f)$  and  $u = \begin{bmatrix} 2f \\ m \end{bmatrix}$  (which we now need) are the same. The EEE (equation (9)) gives

$$\frac{df}{dm} = \frac{-3f}{m} \tag{24}$$

In case of a linear trade-off with  $\hat{f} = 1 - \hat{r}$ ,  $\hat{m} = \hat{r}$ ,  $r = 1/4$  is obtained. This result was first obtained by Trivers & Hare (1976).

In all these examples  $v^{(2)} \sim v$  and the grandchild argument gives the right answer. This property of standard diploid and haplodiploid genetic systems was first pointed out by Hamilton (1967, p. 477). The following result generalizes this. Suppose there are two types with autosomal control of sex ratio, outbreeding and non-overlapping generations. Let type  $j$  ploidy be  $\pi_j$  and let a typical type  $i$  offspring obtain  $\pi_{ij}$  chromosomes from type  $j$  parents. (It follows that  $\pi_i = \pi_{i1} + \pi_{i2}$ .) Then the grandchild argument will work provided  $\pi_{12} = \pi_{21}$ . To prove this let  $z_i$  denote the number of type  $i$  offspring (after one cycle) per type 1 parent and let  $Q = q_1/q_2 = z_1/z_2$  be the type 1/type 2 ratio at breeding. The transition matrix is

$$A = \begin{bmatrix} z_1 \pi_{11} / \pi_1 & Q z_1 \pi_{12} / \pi_2 \\ z_2 \pi_{21} / \pi_1 & Q z_2 \pi_{22} / \pi_2 \end{bmatrix} \quad (\hat{\alpha} = \alpha).$$

and from equation (18),

$$v \sim (z_2 \pi_{21}, z_1 \pi_{12}) \sim (\pi_{21}/q_1, \pi_{12}/q_2)$$

which is  $\sim v^{(2)}$  if  $\pi_{21} = \pi_{12}$ .

In standard male-female diploidy and haplodiploidy,  $\pi_{12} = \pi_{21} = 1$  and the grandchild argument works, as has been seen. This result continues to hold with worker control, but not if there is some laying of males by workers. If workers lay a proportion  $1 - p$  of males, then (under haplodiploidy) the expected female to male chromosome contribution is

$$\pi_{21} = p \cdot 1 + (1 - p)(1/2)$$

which is different from the male to female contribution  $\pi_{12} = 1$ , when  $p < 1$ , and the grandchild argument fails. As another example Charnov (1982, p. 94) presents an overlapping generation model in which there is some adult survival to the next cycle. This can be treated in the present framework by regarding surviving adults as special kind of offspring for which  $\pi_{ii} = \pi_i$ . This causes  $\pi_{12} \neq \pi_{21}$  and the grandchild argument fails. Finally, an example

in which the above result does hold is found in distyly with no within-type crosses.

EXAMPLE 4. POLLEN-OVULE TRADE-OFF IN GYNODIOECY

Assume the female produces  $x_1$  seeds and the "male" produces  $x_2$  seeds and  $y_2$  pollen grains. Assume outbreeding and diploidy with autosomal control of behaviour. Suppose proportions  $r_1$  of the female's seeds and  $r_2$  of the male's seeds are male. Then the behaviour is parameterized by  $\alpha = (r_1, r_2, x_2, y_2)$  and there are three ESS problems to consider: what is  $r_1$ , what is  $r_2$ , and what is  $x_2$  and  $y_2$ . Each will be given by an equilibrium equation which will involve all variables. For each problem the same matrix  $A$  is used:

$$A = \frac{1}{2} \begin{bmatrix} (1-r_1)x_1 & 2(1-r_2)x_2 + Q(1-r_1)x_1 \\ r_1x_1 & 2r_2x_2 + Qr_1x_1 \end{bmatrix} \quad (\hat{\alpha} = \alpha) \quad (25)$$

where  $Q = Q(\alpha)$  is, as usual, the female/male ratio at type frequency equilibrium. From the fact that  $\begin{bmatrix} Q \\ 1 \end{bmatrix}$  is a right eigenvector of  $A$  an implicit formula for  $Q$  is obtained

$$Q = \frac{(1-r_1)Q + (1-r_2)x}{r_1Q + r_2x}, \quad (26)$$

where  $x = x_2/x_1$  is the male/female fecundity ratio through seed. From equation (18) is obtained

$$v \sim (r_1Q, 2(1-r_2)x + (1-r_1)Q). \quad (27)$$

Examine the pollen-ovule trade-off for the male. Then

$$A = \frac{1}{2} \begin{bmatrix} (1-r_1)x_1 & (1-r_2)\hat{x}_2 + (\hat{y}_2/y_2)((1-r_2)x_2 + Q(1-r_1)x_1) \\ r_1x_1 & r_2\hat{x}_2 + (\hat{y}_2/y_2)(r_2x_2 + Qr_1x_1) \end{bmatrix}$$

and the EEE equation (a) gives

$$\frac{dx_2}{dy_2} = -\frac{x_2}{y_2} \left[ 1 + \frac{Q(1-r_1)v_1 + r_1v_2}{x(1-r_2)v_1 + r_2v_2} \right] \quad (28)$$

where  $v_i$  are given in equation (27). This is a rather general formula for pollen-ovule trade-off in gynodioecy.

A few special cases are obtained by making assumptions about the  $r_i$ . With female heterogametic genetics and Mendelian production and acceptance of gametes,  $r_1 = 1/2$  and  $r_2 = 1$  are expected. Then equation (26) solves to give the equilibrium ratio of types

$$Q = 1 - 2x \quad (29)$$

(Lewis, 1941) and equation (27) gives  $v \sim (1, 1)$ . Then equation (28) gives

$$\frac{dx_2}{dy_2} = -\frac{x_1 - x_2}{y_2} \tag{30}$$

This has a nice geometric interpretation illustrated in Fig. 1.

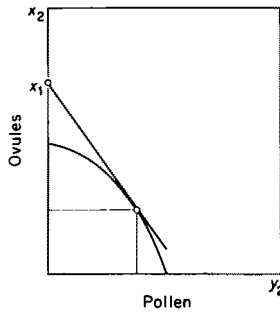


FIG. 1. The trade-off curve gives the feasible ovule-pollen choices  $(x_2, y_2)$  for the hermaphrodite in a gynodioecious population. The point  $x_1$  is the ovule production of the female; it is above the curve because she does not have to pay the fixed costs of pollen production. The evolutionary equilibrium point  $(x_2, y_2)$  given by equation (30) is the point at which the tangent from  $x_1$  meets the trade-off curve.

It is important to emphasize the status of equation (29) in this argument. It is not a condition for evolutionary equilibrium of behaviour. It is simply the type frequency equilibrium which results from assumptions we made about behaviour (on the  $r_i$ ). To emphasize this, it is pointed out how the ESS value of  $r_1$  should be found. The matrix  $A$  for this problem is just  $A$  of equation (25) with hats on the  $r_1$  in column 1. The EEE condition then becomes  $v_1 = v_2$  which becomes, using equation (27)

$$2r_1 = 1 + 2(1 - r_2)x/Q. \tag{31}$$

Then  $r_1$  is obtained by solving equations (26) and (31), given  $r_2$  and  $x$ . In the special case of female heterogamy,  $r_2 = 1$ , equation (31) solves to give  $r_1 = 1/2$  and equation (29) does indeed hold. It has been shown that in this case, the female has no reason to bias her ovule genotype ratio.

Another interesting special case of equation (28) obtains by assuming male heterogamy (Mm) with MM lethal. If we assume Mendelian formation of zygotes (with MM zygotes being resorbed) then  $r_1 = 1/2$  and  $r_2 = 2/3$ , and equation (26) gives

$$x = 3Q(1 - Q)/(2Q - 1). \tag{32}$$

This was first obtained by Lloyd (1973, equation 16). Note that Lloyd's  $F$

is relative ovule production counting the MM lethals. So  $x = 3F/4$ . Also his  $p = Q/(1+Q)$ . The ovule-pollen trade-off condition, equation (28) becomes

$$\frac{dx_2}{dy_2} = -\frac{x_2}{y_2} \frac{2Q^2 - Q + 1}{(1-Q)(2Q+1)} \quad (33)$$

If the  $r_1$  equilibrium analysis is carried out, it turns out that with  $r_2 = 2/3$ , the ESS value of  $r_1$  should not be  $1/2$ . The two equilibrium equations which give the ESS values of the  $r_i$  are not easy to solve, and in any case presumably require some assumptions about the costs involved in discriminating gamete genotypes.

### 5. Lloyd's Equal Fitness Result

A result of David Lloyd (1977) will now be placed in the context of the general model. Loosely stated, Lloyd's result gives conditions under which, at type-frequency equilibrium, all individuals, regardless of type, have the same expected gametic fitness. More precisely, assume non-overlapping generations, and let  $w_j$  be the number of gametes which bear a random *autosome*, contributed by an individual of (wild-) type  $j$  to the next generation. Then the total individual gametic contribution is  $\pi_j w_j$  and in case all types have the same ploidy  $\pi$  (the case that Lloyd considered), the  $w_j$  are measures of total gametic contribution. Lloyd's result is that under certain assumptions about the type determining genetics and gamete formation, the  $w_j$  are all equal, at type frequency equilibrium, for all (feasible) behaviours  $\alpha$ .

To tie this in with the EEE, note that in a sex allocation model with outbreeding and autosomal behaviour,  $w_j$  is the  $j$ th column sum of  $A$  (at  $\hat{\alpha} = \alpha$ ): in symbols  $w = 1A$ . If it is known that  $w_j = \text{constant}$ , this means that  $1$  is a left eigenvector of  $A$ , and so  $v = 1$ . Thus under the conditions of Lloyd's result, the simple Darwinian heuristic  $v = v^{(1)}$  mentioned at the end of section 3 will solve sex allocation problems. It is emphasized that Lloyd's result is not about ESS values of  $\alpha$ , but about type frequency equilibrium  $q$ . It is this that makes it useful when it applies; one can use the fact that  $v = 1$  for all  $\alpha$ , to simplify the EEE, and hence find the evolutionary equilibrium of  $\alpha$ .

This point can be illustrated with the example of tristylly. There are three phenotypes, short, mid, and long, but many genotypes, at least under the standard two locus S-M system (Heuch, 1979), and it is no easy matter to calculate frequencies of different offspring types for a given type, whether we take "type" to be phenotype (with a  $3 \times 3$   $A$ ) or genotype (with a large  $A$ ). But this is precisely what is required to write down  $A$ . Suppose the

conditions of Lloyd's result are such that at type frequency equilibrium  $v = 1$ . Let  $\hat{w}$  denote the vector of column sums of  $A(\hat{\alpha}, \alpha)$ . Then  $vA(\hat{\alpha}, \alpha) = 1A(\hat{\alpha}, \alpha) = \hat{w}$  and the EEE equation (9) becomes

$$(dw)u = 0. \quad (34)$$

To solve the ESS problem it is not necessary to know  $A$ ; all that is needed is  $\hat{w}_j$ , the total mutant gamete contribution of type  $j$  mutants. Of course the type frequency equilibrium  $q$  is still needed, but this can usually be obtained from the equations  $w_j = \text{constant}$ . So such a result is potentially of great utility for ESS calculations.

Unfortunately, the result has limited applicability. The central hypothesis required is that gametes are made, distributed and accepted in proper Mendelian proportions. In sex allocation models in which individuals are manipulating the type of their offspring by altering genotype frequencies of gametes, this hypothesis is certain to fail.

Situations where it may hold are those in which individuals are manipulating not genotype, but size, of gametes, for examples situations in which hermaphroditic individuals are shifting allocation between production of macro- and micro-gametes. Thus Lloyd's result tends to be applicable more to plant than animal models.

As an example, recall section 4, example 4 of gynodioecy. For the simplest case, equation (30), of the general result,  $v = 1$  was calculated. This was the case of Mendelian zygote formation and  $v$  could have been obtained from Lloyd's result. But for the more complicated case of male heterogamy, equations (32) and (33), the assumptions for Lloyd's result fail.

Now Lloyd's result is formulated. Suppose the population contains  $n$  types (which are regarded as phenotypes), genetically determined, with possibly several genotypes corresponding to the same phenotype. Suppose for a fixed mode of reproductive behaviour  $\alpha$ , the population is at type frequency equilibrium  $q$ . Note that the entries  $q_j$  are phenotype frequencies which are determined by an underlying genotype frequency equilibrium. Now let  $\{B_k\}$  be a list of some of the alleles which assort at the type-determining loci. Let  $f_{kj}$  be the probability that an allele selected at random from a random type  $j$  individual at the  $B_k$  locus is in fact  $B_k$ . Thus if, for example, all type  $j$  individuals are identical at the  $B_k$  locus and heterozygote  $B_k b$  with some other allele  $b$ , then  $f_{kj} = 1/2$ . If type  $j$  individuals are genetically variable at the  $B_k$  locus, then  $f_{kj}$  must be an average over all participating genotypes (weighted by equilibrium genotype frequencies).

The main hypothesis of Lloyd's result is:

(1)  $f_{kj}$  equals the probability that a random gamete, contributed to the next generation by a type  $j$  individual, is  $B_k$ .

That is, if a random allele at the  $B_k$  locus is taken, then  $f_{kj}$  must equal the probability that it is  $B_k$ , conditional on its ancestor one generation back being in a type  $j$  individual. (This restatement of (1) is more general and makes sense in an overlapping generation model.) In practice (1) will be guaranteed if both (1') and (1'') hold:

(1') The gametic contribution of each genotype to the next generation contains  $B_k$  in the correct Mendelian proportion.

(1'') All genotypes belonging to the same type have the same gametic contribution to the next generation.

Lloyd's (1977) result on equal fitness of phenotypes at type frequency equilibrium is the following.

*Lloyd's Result.* Suppose it is possible to choose  $n$  alleles  $B_k$  at the type determining loci for which, at type frequency equilibrium, (1) holds and

(2) The matrix  $(f_{kj})$  is non-singular.

Then  $w_j = \text{constant}$ .

Condition (2) is a technical condition concerning the genetics at the type determining loci. It requires the  $n$  alleles to be "linearly independent". In particular it requires at least as many alleles as types at the type determining loci. Heuch (1979) proved a version of Lloyd's theorem in which he essentially assumed (1) and a stronger version of (2):

(2') For all  $k$ ,  $B_k$  appears in type  $k$  with probability  $> 0$ , but appears in no previous type. This condition requires  $(f_{kj})$  to be upper triangular with non-zero diagonal, and therefore nonsingular. Thus (2')  $\Rightarrow$  (2) and Heuch's result is a corollary of Lloyd's. It is often possible to choose and order the alleles  $B_k$  so that (2') holds. In particular this can be done for the S-M system in tristylous. So in practice (2') is the useful condition.

In summary, for sex-allocation problems with autosomal control and outbreeding, Lloyd's result says that  $v \sim 1$  if (1) and (2) hold. Furthermore, (1) can be replaced by both (1') and (1'') and (2) can be replaced by (2'). Lloyd's result was proved by Charlesworth (Lloyd, 1977) and reformulated by Taylor (1984).

As an example, consider section 4, example 4, with male heterogamy and MM lethal. If Lloyd's result is applied it must be decided what to choose for "types". If we choose *phenotype* (female and male, the latter with two genotypes Mm and MM) then (1'') fails. If we choose *genotype* then there are three "types" determined by 2 alleles and (1'') holds but (2) fails. Of course we know in advance something will fail, because in this case, from equation (27)

$$v \sim (Q/2, 2x/3 + Q/2) \neq (1, 1).$$

Lloyd's result is used in Taylor (1984) to obtain the ESS pollen-ovule trade-off in tristylous. Occasionally, in the sex allocation literature a



“Darwinian fitness” analysis is used ( $v = v^{(1)}$ ) without any explicit justification. Often Lloyd’s result is what is needed to provide this justification.

This section is concluded by mentioning that there are results of quite another kind which conclude that  $v \sim 1$ . Such results say that under suitable assumptions, *when  $\alpha$  is at evolutionary equilibrium*,  $v \sim 1$ . Thus Lloyd’s result requires (type-frequency) equilibrium of  $q$ , but admits a range of  $\alpha$  (one of which will be the evolutionary equilibrium we are seeking), whereas this second kind of result requires (and follows from) the EEE.

As an example of such a result, if the mutations under consideration only affect type  $j$  behaviour, then equation (9) becomes  $v dA_j = 0$ . Consider a mutant which differentially shifts resources from type  $i$  to type  $k$  offspring. Then  $v_i da_{ij} + v_k da_{kj} = 0$ . This says that value (asymptotic fitness) gained through type  $k$  must equal value lost through type  $i$ . If offspring types are equally expensive (at margin) and genetically related in the same way to the type  $j$  parent, then  $da_{ij}/da_{kj} = -1$  and one can conclude  $v_i = v_k$ . If this holds for any pair of offspring types we deduce  $v \sim 1$ .

For example, this can happen in example 1 of section 4. If the  $(f, m)$  trade-off curve (19) is symmetric about the diagonal  $f = m$ , then equation (22) has the solution  $f = m$  and at this point it is indeed the case that  $v \sim 1$ . But it would be logically incorrect to *assume*  $v \sim 1$  (without some justification such as symmetry) and *deduce*  $f = m$  at equilibrium. (If  $v \sim 1$  the EEE becomes  $df + dm = 0$  which would solve to give  $f = m$  in this case.) But a result such as Lloyd’s which relies only on type frequency equilibrium, can be invoked at the outset in the formulation of the EEE.

## 6. Discussion

A glance at the literature testifies that mathematics has become an important ingredient in the modelling of sex allocation problems. Indeed it has a lot to offer this field, not only for its capacity to calculate, but more importantly for its capacity to make precise and simplify our thought processes and, through abstraction, to provide some structural unity to a collection of models. For mathematics to play this role effectively it must be used with great care and integrity and even some skill. Otherwise it almost certainly appears to make things more, rather than less, complex. Hand in hand with this, is the need for careful exposition of all results which use mathematics.

In any field, at the beginning of the modelling process, there will be many special mathematical results, each new one requiring some pioneering ingenuity to find. After some critical mass of such examples has been

obtained, the time is ripe for the real work of mathematics to begin: the provision of a general conceptual and computational framework within which past examples can be understood and future examples formulated. The modelling of sex allocation is ready for such a framework and this paper represents attempts to put one forward. The ideas behind this formulation are not new; they already appear in the literature in a great variety of papers. But they have not yet been assembled at this level of generality.

As an example of the way in which a general model such as this can be used to aid in the understanding of existing models, the interesting and mathematically complex paper of Uyenoyama & Bengtsson (1981) is considered. They treat a wide range of sex ratio control mechanisms, but we restrict attention to haplodiploidy with "sister" control of brood sex ratio. Thus we have the situation of example 3 of section 4. Also assumed is the linear trade-off, equation (20), between  $f$  and  $m$ . But instead of the one wild-type sex ratio gene of example 3, Uyenoyama & Bengtsson suppose a polymorphism at the sex-ratio locus with two alleles  $A$  and  $a$ . Then there are 5 wild types, 3 female,  $AA$ ,  $Aa$  and  $aa$ , and 2 male,  $A$  and  $a$  (given in order). Departing from the past notation let  $(s_1, s_2, s_3)$  be the female type frequencies and  $(t_1, t_2)$  be the male. So  $\sum s_i = \sum t_i = 1$ . Suppose genotypes  $AA$ ,  $Aa$  and  $aa$  (in sisters) make proportions  $r_1, r_2$  and  $r_3$  of sons, respectively.

Uyenoyama & Bengtsson show that there is a "symmetric" type frequency equilibrium at which the frequency of  $A$  in females and males has a common value  $p = s_1 + s_2/2 = t_1$ , provided there is overdominance,  $r_2 > r_1, r_3$  (which is now assumed), or underdominance  $r_2 < r_1, r_3$ . Furthermore, in this case,

$$pr_1 + qr_2 = pr_2 + qr_3 = r$$

where  $r$  is the overall proportion of males in the population, and  $q = 1 - p$ . They also give a condition (p. 67, equation 7) for the stability of this equilibrium.

This is as far as they go with the analysis. They observe in the discussion 4.4 that the equilibrium sex ratio is not in general 1:3 (the case  $r = 1/4$ ) and in fact may vary considerably depending on the values of the  $r_i$ .

Indeed it may, but it must be pointed out that what they have done in the paper is a type-frequency analysis with fixed assumptions about behaviour  $\alpha = (r_1, r_2, r_3)$ . They should now proceed with the ESS analysis of  $\alpha$ .

This is not hard to do, the argument is sketched because the result is interesting. Focus on a rare mutant form  $\hat{A}$  of the allele  $A$  and suppose  $\hat{A}A$  females have  $\hat{r}_1$  sons and  $\hat{A}a$  females have  $\hat{r}_2$  sons. There are three mutant types:  $\hat{A}A$ ,  $\hat{A}a$  and  $\hat{A}$ , in order, the first two female, the third male. The

transition matrix for sister control, works out to be

$$A = \frac{1}{4} \begin{bmatrix} p(2-r_1-\hat{r}_1) & p(2-\hat{r}_1-r_2) & \frac{1-r}{r} [4s_1(1-\hat{r}_1)+s_2(2-\hat{r}_1-\hat{r}_2)] \\ q(2-r_2-\hat{r}_2) & q(2-\hat{r}_2-r_3) & \frac{1-r}{r} [s_2(2-\hat{r}_1-\hat{r}_2)+4s_3(1-\hat{r}_2)] \\ p(r_1+\hat{r}_1)+q(r_2+\hat{r}_2) & p(\hat{r}_1+r_2)+q(\hat{r}_2+r_3) & 0 \end{bmatrix}$$

and the eigenvectors of  $A$  for the eigenvalue  $\lambda = 1 - r$  are

$$v = \left( \frac{1}{1-r}, \frac{1}{1-r}, \frac{1}{r} \right) \quad \text{and} \quad u = \begin{bmatrix} 2s_1(1-r) \\ s_2(1-r) \\ pr \end{bmatrix}.$$

Two equilibrium conditions are obtained, one with  $\partial A/\partial r_1$  and the other with  $\partial A/\partial r_2$  in place of  $dA$  in equation (9). Both conditions reduce to  $r = 1/4$ . One concludes that even when sex ratio is determined by a one locus polyorphism, it will still evolve, under sister control, to the standard 1:3 ratio. Uyenoyama and Bengtsson are misleading on this point. Space has been taken with this rather special example as it illustrates rather well the value of a general conceptual framework which distinguishes type-frequency and evolutionary equilibria.

Much of sex allocation theory is concerned with the special case of two types, female and male. The basic evolutionary equilibrium equation in this case is the Shaw-Mohler equation (1). There are a number of assumptions behind this equation about the mating and genetic structure of the population and the mechanisms of sex ratio control. If these assumptions are relaxed, a number of interesting generalizations of the equation can be formulated. For example, a more general treatment of control leads to forms of this equation involving coefficients of relatedness, from which special results such as "worker control" (section 4, example 3) can be obtained. In another direction in a separate paper (Taylor, 1985) the phenomenon of inbreeding is treated and a form of equation (1) is derived for more general mating systems. The important thing to note is that such general forms are special cases of the EEE equation (9), and, within the framework of the general model, this equation can always be used directly to obtain particular results.

Another branch of sex allocation theory is concerned with two gamete types, macro and micro. This branch, too, has its "Shaw-Mohler" equation

$$\frac{dx}{x} + \frac{dy}{y} = 0$$

which can be obtained, for a population of hermaphrodites, by setting  $Q = 0$  in equation (28) and dropping the subscript 2. Interesting generalizations of this, such as equation (30) are obtained when there is more than one type in the populations. Behaviour can now become complex and organisms must make female-male, as well as macro-micro gamete, decisions. Each trade-off we are interested in can be formulated with an evolutionary equilibrium equation, but each equation may contain many behavioural parameters, and the resulting ESS is the solution to several simultaneous equations. An important general idea which simplifies the situation is the result of Lloyd discussed in section 5 which supposes that a certain natural probabilistic process makes the type frequency ("male-female") allocation decisions, and the formulation of the resulting macro-micro gamete equilibrium condition is simplified.

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