Allocation of resources to male and female functions in hermaphrodites

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The question of how a self-fertile hermaphrodite will distribute the resources that it allocates to reproduction is studied by means of the ESS approach. Different models of the relations between allocation to male function, the male and female fertilities, and the selfing rate, yield different conclusions about how much resource should be allocated to male function. Values below a half are obtained with one model, while another can give values greater than a half. Even with no selfing, values other than a half are usually obtained; with both models studied, the values decrease with increasing selfing. If the selfing rate is assumed to be independent of the fraction of resources allocated to male function, it can be shown that the ESS allocation to male function always decreases as selfing increases. The types of relations that might be expected in species with different types of breeding biology, and some data on allocation to male function, are reviewed.

The implications for the fitness of male- and female-sterility mutations are discussed. It is argued that the concavity or convexity of the curve relating female fertility to male fertility is not a good guide to when hermaphroditism should exist when there is some selfing. Even with a concave relation, male-sterility mutants can have a higher fitness than hermaphrodites, if there is some selfing and inbreeding depression. Also, when the selfing rate depends on allocation to male function, an hermaphrodite ESS does not always exist when the function is concave (as it does when there is no selfing), and such an ESS may exist when the relation is convex. The fitness of male- or female-sterility mutants may also depend on the existence of 'fixed costs'. It is shown that these do not affect the ESS allocation of resources.

KEY WORDS:— Resource allocation – hermaphrodites – male-sterility – female-sterility – dioecy – androdioecy – gynodioecy.

CONTENTS

INTRODUCTION

The aim of this paper is to examine resource allocation to male and female function in hermaphrodites, using the ESS approach. There are two reasons for studying this problem. First, allocation to sex functions is in itself an interesting problem, which has been studied in its own right, both theoretically (Maynard Smith, 1971, 1978; Charnov, Maynard Smith & Bull, 1976; Charnov, 1979) and observationally (Fischer, 1980; Vernet & Harper, 1980; Lovett Doust & Harper, 1980; Lovett Doust & Cavers, 1980). Second, arguments about the evolution of hermaphroditism or dioecy have been based on ideas about the amount of resources hermaphrodites will be likely to devote to male or female function (Charnov et al., 1976; Charnov, 1979). If we knew how hermaphrodites distribute their reproductive resources between the two sex functions, we could deduce how much resource could be saved by, for example, a male-sterile mutant type; it has been argued that the resources freed by loss of male or female function might be transferable to the sex function that remains (Darwin, 1877; Charnov et al., 1976; Charlesworth & Charlesworth, 1978a). This kind of study should therefore enable one to answer in a rigorous fashion the question: what circumstances are favourable for the establishment of females (with loss of male function) or males, in hermaphrodite populations?

Previous theoretical work on allocation to male and female function in hermaphrodites has assumed that there is no self-fertilization (Maynard Smith, 1971; Charnov et al., 1976; Charnov, 1979). The purpose of the present paper is to extend this to any rate of selfing. This seems important because many hermaphrodite plants and animals are self-compatible, though natural rates of selfing are known for only a few species.

By analogy with the effect of inbreeding on sex-ratio in dioecious species (Hamilton, 1967), it has already been realized that self-fertilizing hermaphrodites are likely to allocate low amounts of resource to male function, compared with outbreeders, but this problem has not previously been explicitly considered. In considering the conditions for the evolution of dioecy in plants, it is also important to take the possibility of selfing into account, because dioecy appears usually to evolve in self-compatible species (Baker, 1959).

We shall not consider questions about how much resource will be allocated to reproduction (i.e. production of offspring), rather than to other functions such as growth of the soma or attraction or reward of pollinators by plants. The problem of total allocation to reproduction has been studied theoretically by means of the reproductive effort model (e.g. Schaffer & Gadgil, 1975). The question of allocation to reproduction in males and females of dioecious species is closely related to that of total allocation to reproduction in hermaphrodites, and will not be mentioned any further here.

MODEL

We assume that there is some constant total quality of resource to be allocated to sex function in an hermaphrodite (or monoecious) organism. Of this total, the proportion devoted to male reproduction is denoted by r. As r increases, realized female fertility decreases, while male fertility will increase. Writing b for male fertility, we can express female fertility as $f(b)$. Both b and $f(b)$ are functions of r;

they are equivalent to α and β, respectively, of Charnov *et al.* (1976). For reasons discussed later, b and $f(b)$ may often be non-linear functions of r, so that in general $f(b)$ is a non-linear function of b. Increased allocation to male function may also increase the selfing rate s (the fraction of female gametes fertilized by male gametes from the same individual). The selfing rate is therefore a function of r and thus of b; we shall write it as $s = h(b)$. We shall ignore the possibility that pollen is appreciably used up by selfing, but will assume that selfing requires very small quantities of pollen (Darwin, 1877; Cruden, 1977) so that the quantity of pollen an individual has available for outcrossing is unaffected by its selfing rate. Finally, we take into account the fact that the products of self-fertilization are likely to be selectively inferior, by writing $1-\delta$ for their fitness relative to the fitness of progeny produced by outcrossing.

Our method is to find the ESS value of b (which determines that of r) for an hermaphrodite, with respect to invasion by mutants that cause small changes in the sex allocation phenotype from the prevailing one. To do this, we use the technique of Lawlor & Maynard Smith (1976) for determining the population value of b which is such that the fitness of a rare genotype that differs slightly from the rest of the population is always less than the fitness of the common type in the population. This reduces to evaluating the first and second derivatives of the fitness of a rare genotype i, with respect to the value of b_i that characterizes it, and determining the population value b^* for which these derivatives satisfy the standard conditions for the fitness to be a local maximum when $b_i = b^*$. In the present case, we shall assume that the outcrossed progeny are produced by random mating. We can then use equations (1) of Charlesworth & Charlesworth (1978a) to write the fitness of a rare genotype i in a population consisting mostly of individuals with a phenotypic value b, as

$$w_i = \left\{ f(b_i)[1 + h(b_i)(1 - 2\delta)] + \frac{Ub_i}{b} \right\} / 2W, \qquad (1)$$

where

$$U = f(b)[1 - h(b)]$$

and

$$W = f(b)[1 - \delta h(b)].$$

This fitness measure assumes that there are no viability differences between different sex phenotypes, and also that there are no differences in attractiveness to pollinators, or to members of the same species as mates, except for differences due to the differences in male or female allocation themselves (see Discussion). Care of the progeny is, however, included as $f(b)$ is the realized female fertility; in other words the progeny produced by female reproduction are counted only if they survive to maturity. This is necessary in order that the use of the fitness measure will give the correct gene frequency changes from generation to generation (Lloyd, 1977; Charlesworth & Charlesworth, 1978a). The model also assumes that there are no differences in 'fixed costs' of reproduction, so that all hermaphrodite genotypes that are possible can be characterized by their value of r, which determines the values of b and f. The term 'fixed cost' (Heath, 1977) refers to the idea that some structures subserve function of one sex, but not the other. Since all the phenotypes allowed in the ESS treatment are hermaphrodite (or monoecious), they will all require such structures. It follows from this that the ESS values found cannot depend on the fixed costs of male or female reproduction.

ESS ALLOCATION TO MALE FUNCTION

It follows from the previous section that a given value of b in equation (1) is an ESS if $dw_i/db_i = 0$ and $d^2w_i/db^2 = 0$, when $b_i = b$. Since $2W$ is independent of b_i, we need consider only the numerator, i.e. $2Ww_i$.

We have

$$\frac{d2Ww_i}{db_i} = \frac{f(b)[1-h(b)]}{b} + f'(b_i)[1+h(b_i)(1-2\delta)] + f(b_i)h'(b_i)(1-2\delta). \quad (2a)$$

For $b = b^*$ to be an ESS solution, we therefore require

$$\frac{f(b^*)}{b^*} + \frac{f'(b^*)[1+h(b^*)(1-2\delta)]}{1-h(b^*)} = \frac{-f(b^*)h'(b^*)(1-2\delta)}{1-h(b^*)}. \quad (2b)$$

When $h'(b) =$ or $\delta = \frac{1}{2}$, the right hand side of this equation is zero. We shall first study the case of $h'(b) = 0$, in other words the case when the selfing rate is a constant, not affected by the allocation to male function. This is most likely to be true when the species is completely outbreeding or very highly selfing, but even in the case of organisms with intermediate amounts of selfing it may often be the case that the level of selfing is independent of r, for example if the selfing rate is determined by the extent of overlap in time between functionally male and female phases.

Case of constant selfing rate

Since the selfing rate is assumed constant, we can write s for $h(b)$. The ESS equation (2b) becomes

$$F(b^*, s) = \frac{f(b^*)}{b^*} + f'(b^*)g(s) = 0, \quad (3)$$

where

$$g(s) = \frac{1+s(1-2\delta)}{1-s}.$$

It can be seen that $g(s)$ always exceeds 1, and is an increasing function of s and a decreasing function of δ. For b^* to be the ESS, we also require the second derivative of $2Ww_i$ to be negative at b^*. From equation (2a) with $h'(b) = 0$, this is equivalent to $f''(b^*) < 0$†. We shall consider some examples of specific functions below. Assuming that b^* is the ESS, we next ask how b^* is related to the selfing rate s.

Differentiating b^* with respect to s, we have

$$\frac{db^*}{ds} = -\frac{\partial F(b^*, s)/\partial s}{\partial F(b^*, s)/\partial b^*} = \frac{-f'(b^*)g'(s)}{\dfrac{b^*f'(b^*)-f(b^*)}{b^{*2}} + f''(b^*)g(s)}.$$

Since $g(s)$ and $g'(s)$ are positive, and $f'(b^*)$ and $f''(b^*)$ negative, this expression is a negative quantity. The ESS value of b, and thus of r, is therefore a decreasing function of s.

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† Throughout this paper, we shall use the term 'concave' for functions whose second derivative is negative, in accordance with standard usage. The term 'convex' is sometimes used by Charnov *et al.* (1976) and Charnov (1979); it should be applied to functions with positive second derivatives, or to sets bounded by concave curves (as correctly used by Maynard Smith, 1978).

This method assumes that b^* is a continuous function of s, which seems reasonable in biological applications. As pointed out to us by a referee, it is possible to show that b^* decreases with s without making this assumption of continuity, but the details of this method of proof will not be given here.

To obtain further results, it is necessary to assume some specific functional relations between r and the male and female fertilities, b and $f(b)$. The first model we shall study (model I) is:

$$b = r^m \tag{4}$$

$$f(b) = 1 - r. \tag{5}$$

This model is based on one proposed by Charnov (1979). We omit the constants by which he multiplies b and $f(b)$, because, as Charnov points out, they do not enter into the expression for the ESS r value. Since the fertilities in the general fitness measure given above are relative to some standard phenotype, it is clear that this will always be the case, so the constants may be dropped. As explained above, it is necessary that $f''(b)$ is negative, which requires m less than 1. With this model, equation (3) becomes

$$\frac{1 - r^*}{b^*} = \frac{r^*[1 + s(1 - 2\delta)]}{b^* m(1 - s)},$$

giving

$$\frac{1 - r^*}{r^*} = \frac{g(s)}{m}.$$

Since $g(s)$ increases with s and decreased with δ, r^* must decrease with s and increase with increasing m or δ. Its highest value, when $s = 0$ and $m = 1$, is $\frac{1}{2}$. Figure 1 shows some numerical values of the ESS values of r with this model, for various values of m and δ.

We have also studied an alternative pair of functions for b and $f(b)$:

$$b = r \tag{6}$$

$$f(b) = (1 - r)^m. \tag{7}$$

This model (II) provides an extreme contrast with the previous case studied. As in the previous case, $m < 1$ is a necessary restriction. Using equation (3), we obtain the result

$$\frac{1 - r^*}{r^*} = mg(s).$$

For this case, r^* is therefore an increasing function of δ and a decreasing function of m and s, and can take any value from 0 to 1. When $m < 1/g(s)$, the ESS allocation to male function exceeds $\frac{1}{2}$. Since $m < 1$, it follows that the value of r^* for this case is always larger than for the previous model. It is also easy to show that the ESS allocation to female function, $1 - r^*$, given by the present model, exceeds the ESS allocation to male function in the previous model provided that $s < 0$, even though the two models are constructed as simple opposites of one another. This illustrates the fact that reproduction as a male has less value when there is some selfing than reproduction as a female (c.f. Charlesworth & Charlesworth, 1978b). Figure 1 shows some numerical examples.
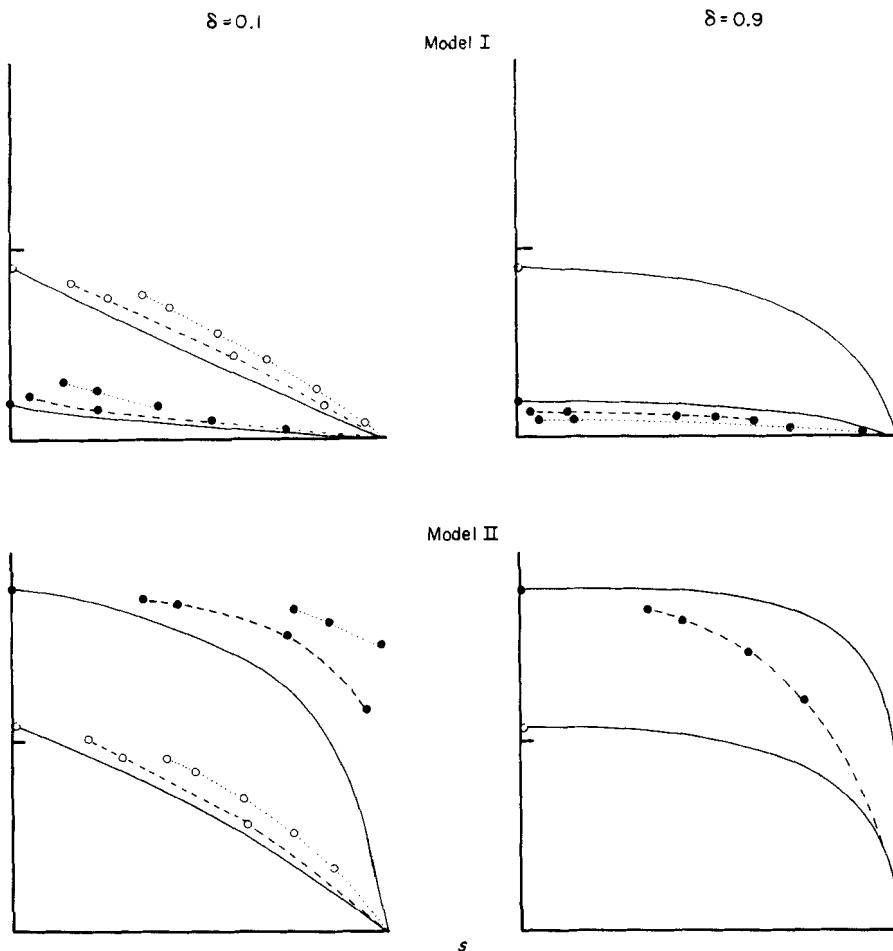
Figure 1. ESS allocation to male function (r^*) plotted against selfing rate (s), for models I & II. ●:m=0.1; ○:m=0.8. The full lines show the results when s is independent of r $(d=0)$. Cases with $d>0$ and various values of c are shown as follows: ----d=0.4; .....d=0.9.

Selfing rate dependent on r

If we assume that allocation to male function affects the amount of self-fertilization, it is necessary to solve the full ESS equation. If $\delta=\frac{1}{2}$, this reduces to (3) and the results are exactly as described in the previous section. For other values of δ, equation (2b) can be solved numerically, assuming some functional relation between s and r. For the solution to be an ESS, the second derivative of $2Ww_i$ must be negative. The expression for this derivative is:

$$f''(b^*)[1+h(b^*)(1-2\delta)]+[2f'(b^*)h'(b^*)+f(b^*)h''(b^*)](1-2\delta). \tag{8}$$

For this to be negative, it is neither necessary nor sufficient that $f''(b^*)$ be negative. We have therefore checked that the values of r obtained by Newton-Raphson iteration of equation (2b) yielded negative values of the expression (8).

To illustrate the effects of assuming s to depend on r, we have used the linear relation

$$s = c + dr.$$

Some ESS results are plotted in Fig. 1. It seems unlikely that d would be very large, but values of 0.4 and 0.9 have been used because smaller values have effects too small to be shown. When $\delta = 0.9$, the assumption that s depends on r often caused the second derivative of the fitness to become positive, especially when m was high, so fewer results are shown for this case than for $\delta = 0.1$. With low δ, the second derivative of the fitness can be negative, even when $f(b)$ is a convex function of b ($m > 1$). With both models I and II, r^* increased with the value of d. With model I, there was an ESS even when m was equal to 1.3, with $\delta = 0.1$ and $d = 0.9$. This yielded higher r^* values than when s was constant. With model II, higher or lower r^* values could result; r^* increased with d but decreased with m.

In all the cases we have studied, the model with selfing rates dependent on r yields an ESS r value that decreases as the ESS s value increases. It does not appear possible to prove that this will always be the case, because the expression for db^*/ds is a complex function of δ and $h'(b)$, even when s is a linear function of r.

The results shown in Fig. 1 are qualitatively as expected. When $\delta < \frac{1}{2}$, ESS r values are lower than when s is assumed to be constant. This would be expected from a comparison of equations (2b) and (3). With $\delta < \frac{1}{2}$, the left hand term of (2b) must equal a positive quantity, compared with 0 when $\delta = \frac{1}{2}$. Since $F(b^*, s)$ is a decreasing function of b^*, the ESS value of b (and thus of r) must be less than when $\delta = \frac{1}{2}$. A similar argument applies to the case of $\delta < \frac{1}{2}$. Thus, when $\delta = \frac{1}{2}$ selfing is in a sense neutral; it is disadvantageous when $\delta < \frac{1}{2}$, so that the increased selfing that is caused by increased allocation of resources to male function is selected against, thus depressing the ESS r values.

EFFECTS OF REDUCING MALE OR FEMALE ALLOCATION

We would like to be able to answer the question: if all allocation of resources to male function is abolished, how much will female fecundity be increased? The answer to this question determines whether a male-sterility mutation will spread in a non-selfing species (Charnov et al., 1976), and it is also very important in determining whether these mutations can spread in a population with some selfing and inbreeding depression. The condition for spread in such a population is

$$k > 1 - 2s\delta, \tag{9}$$

where k is the increase in female fertility of a male-sterile mutant form relative to that of the orginal hermaphrodite (Charlesworth & Charlesworth, 1978a). In other words, when $s = 0$ a doubling of the female fertility is required. Similarly, one can treat female-sterility mutations (Charlesworth & Charlesworth, 1978a), and partial effects on male and female fertility (Charlesworth & Charlesworth, 1978b).

To study this problem, we need to consider the relation between b^* and $f(b^*)$ for the hermaphrodite population in question. With $f''(b)$ negative the relation is of the form shown in Fig. 2 (concave). Given some definite functions relating b and $f(b)$ to r, we can easily calculate the increase in female fertility that would result from changing r from its ESS value to 0 (male-sterility) or to any lower level (partial male-sterility). This assumes that resources can be completely switched between male and female functions, which is unlikely to be true. In reality, a male-sterility mutation would probably increase female fertility by less
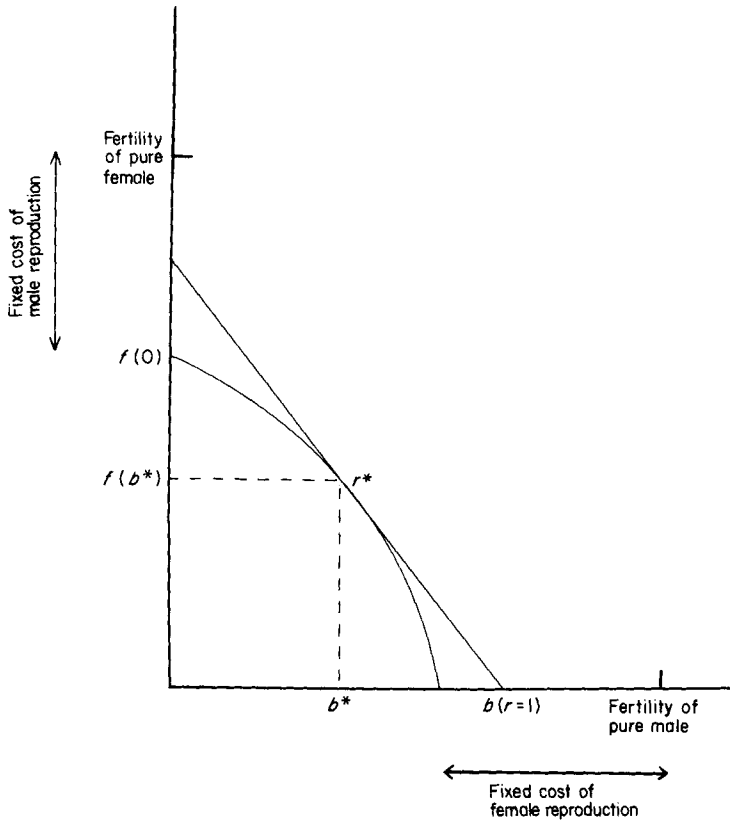
Figure 2. Concave relation between $f(b)$ and b, showing the female fertility of a male-sterile mutant, and the male fertility of a female-sterile mutant. The female fertility of a male-sterile form is $f(0)$; its fertility relative to the ESS hermaphrodite $(f(0)/f(b^*))$ is equal to $1 + k$. Similarly, for a female-sterile form, we have $b(r=o)/b^* = 1 + K$.

than the curve of $f(b)$ against b would predict; this curve should probably be thought of as a boundary limiting the range of possible phenotypes, not as a simple relation between them. On the other hand, if there are 'fixed costs' (Heath, 1977) of male reproduction, a pure female (completely male-sterile) type could have a higher female fertility than $f(0)$ calculated from the $f(b)$ curve (Fig. 2). It should therefore be remembered that the increments in female fertility calculated below for male-sterility mutations represent only the highest values that would be possible in the absence of fixed costs, and not actual values that would be likely to occur. Similar considerations of course apply to female sterility mutations. We will first discuss some results obtained by studying the case when $f(b)$ is linearly related to b. Clearly, the increase in female fertility given by setting b to 0, with a concave relation between $f(b)$ and b, will be smaller than that given by a linear relation. Similarly, the increase in male fertility that would be associated with a mutation to female sterility will be less than if the relation between b and $f(b)$ were linear.

With a linear relation, the female fertility of a form with $b = 0$ is

$$f(0) = f(b^*) - b^*f'(b^*).$$

From equation (2b), we have

$$b^*f'(b^*) = -\frac{f(b^*)}{g(s)}\left[1 + \frac{h'(b^*)b^*(1-2\delta)}{1-s}\right],$$

$$\therefore \quad \frac{f(0)}{f(b^*)} = 1 + \frac{1}{g(s)}\left[1 + \frac{h'(b^*)b^*(1-2\delta)}{1-s}\right].$$

If s is assumed to be constant, this becomes

$$\frac{f(0)}{f(b^*)} = 1 + \frac{1}{g(s)}.$$

Thus a male-sterile mutant will have an increase in female fertility, relative to that of the ESS hermaphrodite, of less than $1/g(s)$. For model I, for example, it is easy to show using the expression derived above for the ESS value of r when s is constant, together with equation (5), that

$$\frac{f(0)}{f(b^*)} = 1 + \frac{m}{g(s)}, \tag{10}$$

giving an increase in female fertility of $m/g(s)$, relative to the ESS hermaphrodite. Writing out the expression $1/g(s)$ in full, we have

$$k = \frac{1-s}{1+s(1-2\delta)}, \tag{11}$$

while condition (9), for the spread of a male-sterility mutation, can be rearranged as:

$$k > 1 - s + s(1 - 2\delta).$$

This condition cannot be satisfied by the quantity (11) above when $\delta \leqslant \frac{1}{2}$. Thus, a mutation that re-allocates to female function all resources that the ESS hermaphrodite devotes to male function, cannot have a higher fitness than the hermaphrodite, when $f(b)$ is a linear or concave function of b, unless $\delta > \frac{1}{2}$.

Similar reasoning can be applied to female-sterility mutations. The condition for spread of such a mutation is (Charlesworth & Charlesworth, 1978a)

$$1 + K > 2(1 - s\delta)/(1 - s) = 1 + g(s), \tag{12}$$

where K is the increase in male fertility of the female-sterile form, relative to that of the original hermaphrodite. With a linear relation between $f(b)$ and b, the male fertility when $r = 1$ is $b(r = 1)$, given by

$$b^* - f(b^*)/f'(b^*) = b^* + \frac{b^*g(s)}{1 + b^*h'(b^*)(1-2\delta)}.$$

If s is constant, this gives

$$\frac{b(r = 1)}{b^*} = 1 + g(s).$$

A female-sterility mutation cannot therefore satisfy condition (12), when the relation of $f(b)$ to b is linear or concave. For example, with model I and constant s,

the expression for $b(r=1)/b^*$, from equation (4) together with the ESS value of r, is

$$\left[\frac{g(s)}{m}+1\right]^m, \tag{13}$$

which equals the right hand side of (12) when $m=1$, and is less when $m<1$.

Figure 3 shows some numerical examples, assuming constant s and model I. The lower set of graphs shows that a male-sterile form can have an advantage when $\delta>\frac{1}{2}$, if s is high enough. High m values make this more likely, as equation (10) suggests. The upper set of graphs shows results for female-sterility, showing that the condition for this to have an advantage is never satisfied; as expression (13) shows, low values of m make it particularly unlikely that the condition could be satisfied, even if fixed costs are assumed. Similar results were obtained with model II. The general treatment given above applies to this model also, and the analogous expressions to (10) and (13) are readily derived for this case.

If s is not constant, however, it can be possible to satisfy (9) or (12). Most cases with s dependent on r did not do so, but the ESS state with model I with $\delta=0.4$, $m=1.1$, $c=0$ and $d=0.9$ has an r value of 0.415 and an s of 0.374; a male-sterile mutant that could convert all resources saved into increased female function could satisfy (9). With model II, an example satisfying (12) was found with $\delta=0.4$, $m=1.1$, $c=0.5$, $d=0.4$; the ESS has $r=0.254$ and $s=0.601$.

The above considerations suggest that dioecy is much more likely to evolve from hermaphroditism or monoecy via gynodioecy than via androdioecy, since it is difficult to find conditions that allow a female-sterility mutation to invade an hermaphrodite population. There is good evidence that gynodioecy is usually an intermediate stage in the evolution of dioecy from hermaphroditism in flowering plants (Charlesworth & Charlesworth, 1978a). But for full dioecy to evolve from gynodieoecy, it is necessary for mutations causing reduced female fertility to invade a gynodioecious population. To determine the effect of the form of the resource allocation curve on the evolution of full dioecy, it is therefore necessary to examine the conditions for this second step to be feasible, and this will be done below for Models I and II with constant s.

Consider a mutation causing complete female sterility, introduced into a gynodioecious population at equilibrium for a male-sterility mutation causing an increase k in female fertility. If K is the increase in male fertility to male-fertile carriers of the female-sterility mutation, equation (10) of Charlesworth & Charlesworth (1978a) shows that the female-sterility mutation can only increase if

$$K > \frac{1+s(1-2\delta)}{k-s(1-2\delta)} \tag{14}$$

If we assume that the original, all-hermaphrodite population was at the ESS for resource allocation, both K and k can be obtained for Models I and II in the way described above. For Model I, equation (10) shows that k increases with m, so that the right-hand side of (14) decreases with increasing m. $1+K$ in this case is easily seen to equal r^{*-m}, where r^* increases with m. Hence we have

$$\frac{\partial K}{\partial m} = -(\ln r^*)r^{*-m}\frac{\partial r^*}{\partial m} > 0.$$
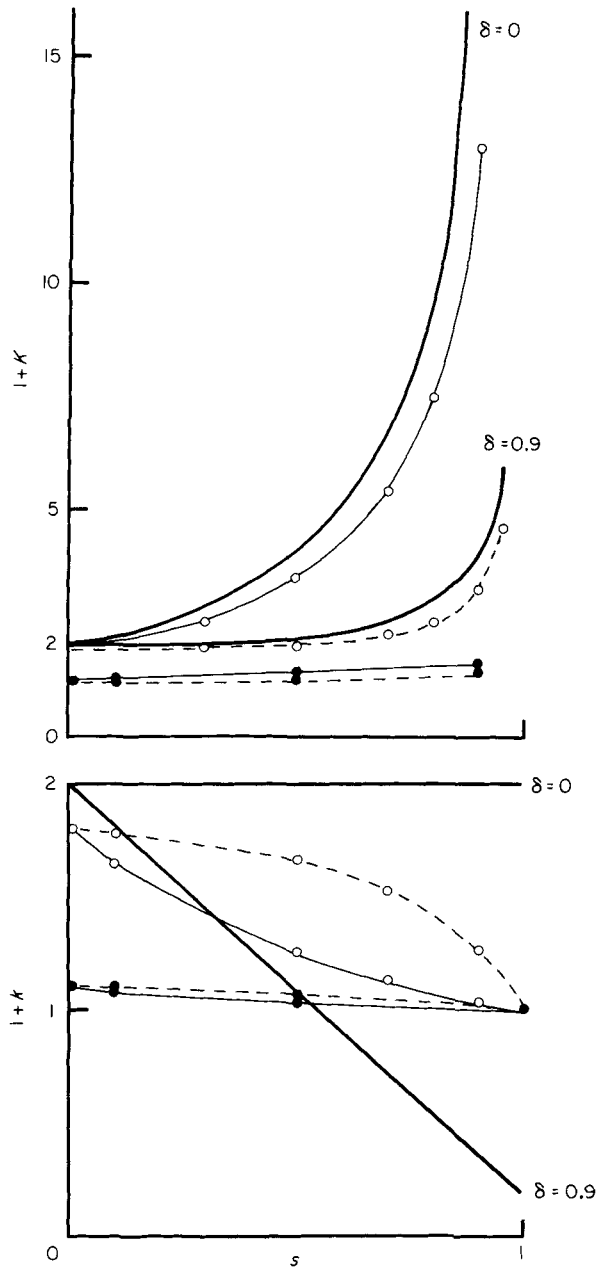
Figure 3. Comparison of the conditions (thick lines) for spread of mutations abolishing male allocation (lower graph) or female allocation (upper graph), with the values (calculated from the ESS r values) for female fertility of male-sterile types, and male fertility of female-steriles. Model I is assumed, and no fixed costs are included. $-$:●:$m=0.1$; ○:$m=0.8$; ⸺ $\delta=0$; $- - - -$ $\delta=0.9$.

K therefore increases with m, despite the fact that the ESS resource allocation to male function also increases with m.

It follows that it becomes increasingly difficult to satisfy (14) as m decreases, since the left-hand side decreases while the right-hand side increases. This parallels the behaviour of the condition for the invasion of the hermaphrodite

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population by a male-sterility mutation (equations 9 and 10). A similar argument holds for Model II. In this case, we find $1+k=(1-r^*)^{-m}$ and $1+K=r^{*-1}$, with r^* decreasing with increasing m. It is easily seen that both K and k again increase with m.

These considerations therefore suggest that the form of the resource allocation curve has a similar effect on the conditions both for initial invasion of an hermaphrodite or monoecious population by a male-sterility mutation, and for subsequent invasion of the resulting gynodioecious population by a female-sterility mutation. The more concave the curve, the more unlikely are both of these events, for both Model I and Model II.

DISCUSSION

Resource allocation in hermaphrodites

The results described above show that the treatment of resource allocation to male and female functions by the ESS method can readily be extended to the case of self-fertilizing populations, and can even be used when the allocation to male function affects the selfing rate. Unfortunately, we cannot use this method to make predictions about resource allocation in real species, because we do not know the relations between r and male fertility, female fertility, or selfing rate, for any species. It is, however, possible to make plausible speculations about the form that these relations would be likely to take. For example, Charlesworth & Charlesworth (1978b) suggest that it is unlikely that the selfing rate will vary greatly with the output of male gametes (which may be taken as a measure of r) unless r is very small. It is therefore probably reasonable to assume that s is a concave function of r and that, as assumed here, in the neighbourhood of the ESS, s is a linear function of r with a small slope.

When we consider likely relations between r and b or $f(b)$, a number of possibilities exist, depending on the details of the reproductive biology of the species in question (for further discussion, see also Lloyd, 1979). This question has mostly been discussed in terms of the relation between $f(b)$ and b, which is important in the context of the stability of hermaphroditism when there is no selfing (Charnov et al., 1976); when $f(b)$ is a convex function of b, there is no internal ESS, in other words hermaphroditism is unstable to the introduction of males or females. This is also true with selfing, provided that s is independent of r, but is not true when s depends on r. It is therefore preferable to discuss separately the relations of r with b and $f(b)$, and then to derive the relation of $f(b)$ to b. It is important to remember that b and $f(b)$ are realized male and female fertilities and may be difficult to measure in nature. In both animals and plants, male fertility is likely to be hard to measure. In plants, seed production may not be a good estimate of $f(b)$ in situations where there is much competition between the progeny of individual plants (see below). In animals, competition between sibs after the end of parental care (which is when we can measure realized fertility) is likely to be less, because animals are mobile. It should also be noted that r cannot easily be measured. Apart from problems of finding the correct units (see Harper, 1977), the resources devoted to parental care will generally be harder to measure than those for gamete production. In plants, for example, r will always be overestimated by measurements made at the time of gamete production. Pollen/ovule ratios (Cruden, 1977) thus do not measure r,

though differences in P/O ratios between species with the same size of seed should indicate differences in r.

Before discussing in detail the results of the ESS calculations, we will first consider the kinds of relations that might exist between r and b and $f(b)$. Charnov (1979) proposed the relations used in model I above, and suggested that m would often be less than 1 (concave relation). He pointed out that, with this model, the ESS r value will be $m/(1+m)$ when there is no selfing. This is a special case of equation 3 above, and shows that even when $s=0$, the allocation to male and female function will not in general be equal. This conclusion differs from that of Maynard Smith (1971).

It certainly seems reasonable to assume that male fertility will not increase indefinitely with allocation to male function, if only because the number of ovules available for fertilization is finite. Thus Charnov et al. (1976, factor (1)) suggest that "low mobility limits male reproductive success." Scarcity of pollinators (factor (3) of Charnov et al., 1976) may also tend to limit the maximum value of b that plants can achieve. (It might also result in a decreased outcrossing rate.) Another factor affecting insect-pollinated plants is saturation of the insect vectors (Charnov, 1979). Wind-pollinated plants would therefore be expected to have a more nearly linear relation between r and b, than insect pollinated plants, though there might be a curve when r is very high. A convex relation, in which b increases slowly when r is low, and faster as r increases, could also arise in some circumstances; for example in insect-pollinated plants in which pollen is the main floral reward (pollen flowers, see Vogel, 1978). Schaffer & Schaffer (1977, 1979) have evidence that some pollinators of Agave species select for large inflorescence size, and that this generates a convex relation between allocation to flowers and seed set. Similar results were obtained, at least for stems with small numbers of flowers, by Willson, Miller & Rathke (1979). It seems possible that attraction of pollinators by means of pollen might result in a similar effect.

Similar speculations can be made for female fertility. A linear relation between $f(b)$ and b is plausible (Charnov, 1979), but Givnish (1980) has suggested that when a plant has seed dispersal by fruit eaten by animals, its female fertility may increase faster, the more fruit is produced, i.e. the higher the allocation to female function. A similar effect could arise if the proportion of seed lost to seed predators decreases with quantity of seed produced.

In the absence of knowledge of these relations for real species, it does not seem worthwhile to find ESS r values for many different functions. The study of ESS r values (above) illustrates the method for two sets of relations, both of which yield concave relations of $f(b)$ to (b) when their m values are less than 1. Model I assumes $f(b)$ is a linear function of r, and b a concave function, as suggested by Charnov (1979). This model yields ESS r values below $\frac{1}{2}$ unless $s=0$, and even when $s=0$ the ESS value of r is less than $\frac{1}{2}$ unless $m=1$. When s is a function of r, the ESS r values are increased ($\delta<\frac{1}{2}$) or decreased ($\delta>\frac{1}{2}$) compared with the case of s constant, but no case giving a value greater than $\frac{1}{2}$ was found (Fig. 1). Making s depend on r had in general small effects provided that reasonably small values of the constant of proportionality (d) were used. It is, however, interesting that when s depends on r an hermaphrodite ESS can exist when $m>1$ (convex relation between $f(b)$ and b), and does not always exist when $m<1$ ($f(b)$ a concave function of b).

Model II yields ESS r values above $\frac{1}{2}$, particularly when m and s are small; high δ values also tend to give high values of r. The other conclusions of the study of model I apply also to model II. Model I is likely to be appropriate for animals or insect-pollinated plants, while model II with b proportional to r, might be more plausible for wind-pollinated plants. The concave relation of female fertility to r, assumed in model II was proposed by Maynard Smith (1978:133) as a consequence of seed competition such that the fraction of seeds surviving would decrease as the quantity of seeds increases. Another situation that might yield this type of curve is in a plant with pollen as the main attractant for the pollinator.

In monoecious plants, if we assume that the cost of the reproductive and non-reproductive parts of male and female flowers are the same, the fraction of male flowers gives an overestimate of r; a correct estimate would include the resources given to seeds by their female parents. The considerations outlined above would lead to the expectation that insect pollinated species would have a concave relation, and wind-pollinated ones a more convex relation, between $f(b)$ and r. Thus, other things being equal, we might expect low frequencies of male flowers in insect pollinated species, and higher values in wind-pollinated species. Frequencies of male flowers lower than $\frac{1}{2}$ have often been found in monoecious species (Correns, 1928; Bawa, 1977), but we do not know of any comparison between insect- and wind-pollinated species.

Gynomonoecy (hermaphrodite and female flowers on the same individuals) may perhaps be viewed as a mechanism by which plants can achieve low r values. It would, on this view, be expected to be associated with high selfing rates or highly concave relations between male fertility and pollen output. Andromonoecy (male and hermaphrodite flowers) is a case of higher r values. However, the true r value for such species may be much lower than appears from the low frequency of seed-bearing flowers, if the cost of maturing seed is very high for these flowers. We should therefore probably expect to find andromonoecy in situations where the cost of seed maturation is high, e.g. in species with large seeds (Lloyd, 1979). Factors tending to increase r might also be expected to be associated with andromonoecy. These factors include high inbreeding depression, low selfing rates and a nearly linear or only slightly concave relation between female fertility and $1-r$ (see Fig. 1). A study of andromonoecy in Umbellifer species illustrates these points. Lovett Doust (1980) finds that about 20% of the flowers are hermaphrodite, in a number of species. Lovett Doust & Harper (1980) studied one of these, *Smyrnium olusatrum,* in detail. At the time of flowering, stamens represent about 1.5 times as large a fraction of the floral dry matter as the pistils; by comparing the weights of pistils with that of ripe fruits, these authors estimate that the cost of maternal care is 36 times that of female gamete production. From these data, we can estimate r to be about 0.17, compared with 0.88 if only the weights at the time of flowering were taken into account. The selfing rate of this species is not known, but it is self-compatible and some degree of selfing seems likely.

Data on r exist for very few other species. Fischer (1980) found the mass of testicular tissues in the hermaphrodite fish *Hypoplectrus nigricans* to be much lower than that of ovarian tissue. This species has no parental care, so it is reasonable to use gamete production as a measure of r. Fischer argued that the mating behaviour ('egg trading') of this species generates a concave relation between r and male fertility, while female fertility would presumably be a linear function of

the quantity of eggs produced. Vernet & Harper (1980) studied allocation to sex functions in an hermaphrodite self-compatible species of *Fucus*, also with no parental care. Extremely low estimate of r were obtained; indeed these were much lower than any obtained above, unless very low m was assumed together with high s. For this species, a linear relation between r and $f(b)$ seems reasonable, but neither the relation between r and b, nor the selfing rate, which is probably high, is known. Lovett Doust & Cavers (1980) have measured dry weights of floral parts and mature fruits for three perennial and one annual species of herb with hermaphrodite flowers. One can estimate r from these data, assuming that allocation to male function is given by the mean androecium weight, and allocation to female reproduction by the dry weight of the mature fruit. Details of these species' breeding systems are not known, except that the annual is highly selfing; its r value is 0.03, while the other three species, two of which are to some extent outbreeding, have r values of 0.12, 0.13 and 0.16.

A general conclusion from both models I and II (and indeed any model that yields $f(b)$ as a concave function of b), provided that s is independent of r, is that the ESS value of r is a decreasing function of s (see case of constant selfing rate above). When s increases with r, this result remains true, for the two models studied. It has long been understood intuitively that the genetic value of male gametes decreases as the selfing rate increases, so that when there is a high selfing rate the saving of resources that can be achieved by reducing pollen output outweighs the disadvantage of reduced male fertility; selfing would therefore be expected to be associated with reduced allocation to male function, but we are not aware of any other rigorous treatment of this concept. Charlesworth & Charlesworth (1978b) suggested that this could explain the reduction in pollen output that is frequently seen in highly selfing plants (e.g. Baker, 1965; Cruden, 1977). Here, pollen output is taken as a measure of allocation to male function.

Implications for the evolution of dioecy

Two approaches have been used in attempting to study in detail the question: under what circumstances would species be expected to be dioecious rather than hermaphrodite? Charlesworth & Charlesworth (1978a) studied this question by asking what conditions must be satisfied in order for male- or female- sterility to spread in an hermaphrodite population, leading to gyno- or androdioecy, respectively, and then what conditions are required for the complementary type of mutation to spread, giving dioecy. This approach is based on the idea that two (at least) mutational steps are necessary for the evolution of dioecy from hermaphroditism or monoecy. It is a suitable approach to take if one is interested in the evolution of dioecy in angiosperms, for which it is reasonable to assume an hermaphrodite starting state.

The other approach, due to Charnov *et al.* (1976) asks the question: under what conditions will hermaphroditism be evolutionarily stable? These authors make use of the property that with no selfing, there is no evolutionarily stable hermaphrodite state, if the curve of realized female fertility ($f(b)$ in the terminology of the present paper) against male fertility, b, is convex ($f''(b)$ positive). When there is selfing at a constant rate, this remains true. However, when the selfing rate depends on the allocation to male function, $f''(b)$ negative does not guarantee the existence of an internal ESS, nor is it required (see above).

Charnov *et al.* (1976) suggest that we will find dioecy when there is no hermaphrodite ESS. It certainly seems likely that if we start with a dioecious population in circumstances that generate relations which yield no internal ESS, it will remain dioecious, since an hermaphrodite mutant form would have a lower fitness than either the males or the females. The existence of a concave function (in a species with $s=0$ or independent of r) could thus explain the non-existence of hermaphroditism in an initially dioecious group of organisms (Charnov *et al.*, 1976; Charnov, 1979). Of course, for such a group, we cannot find out the relations between $f(b)$ and b, or s and r, empirically, because only males and females exist. We have to rely on plausible arguments about the form of these relations, based on the reproductive biology of the species in question (see discussion).

The method of finding the ESS allocation to male function can be used whatever the relations between r and the other variables, provided that an internal ESS exists. Having found the ESS, we can use the method of setting r to zero or 1, to determine whether the conditions for spread of male- or female-sterility mutations can be satisfied. This combines the results of resource-allocation studies with the first approach described above. The results (Fig. 3) show that female-sterility mutations are unlikely to spread unless other factors increasing their fitness exist (see below). Male-sterility mutations can spread if s and δ are high enough, even when the relation of $f(b)$ to b is concave. It is also not true that a convex curve of $f(b)$ against b automatically results in the instability of hermaphroditism, when there is some selfing. Many cases were found where this was not true, when s is assumed to depend on r, although in some such cases male- or female-sterility mutations could invade.

So far, we have been assuming that there are no 'fixed costs' attached to male or female reproduction. The importance of such costs was first pointed out by Heath (1977). In biological terms, a fixed cost might arise because a mutant with only one sex function could abolish structures (e.g. ducts, in an animal) required for the other function, and could perhaps divert the resources saved into increasing allocation to the sex function that remains. In other words, fixed costs can be considered as arbitrary increases in fitness accruing to males or females, over and above those calculated by setting r to 1 or 0. In the absence of information about fixed costs, and the possibility of their being converted into allocation to opposite-sex function, we can do no more than suggest situations when they might be important. For example, a male-sterile mutant in an hermaphrodite plant would not receive any such increment in fitness because the flowers must be retained to subserve the remaining female function, as pointed out by Maynard Smith (1978). In this situation there are no (or small) fixed costs of male or female reproduction to be saved by a mutant with only the other sex function. (The mutant might perhaps save some fixed costs by having a shorter duration of flowering than the hermaphrodite. This could, for example, save nectar production.) In such a situation it is very unlikely that female-sterility can be advantageous, and male sterility mutations would be favoured only when there is some inbreeding depression. It would therefore seem that inbreeding depression is likely to play an important role in the evolution of dioecy from hermaphroditism in the angiosperms. This does not, of course, mean that other factors are unimportant. The discussion above, and the results presented in Fig. 3 show that, other things being equal, factors tending to make the curve of $f(b)$ against b highly concave (low m values in models I & II) also tend to make invasion of hermaphro-

dite populations by male or female forms less likely. Discussion of situations that will generate concave or convex relations (as in Charnov *et al.*, 1976; Charnov, 1979) are therefore of value, though as has been emphasized above, one cannot assume that a concave relation implies that hermaphroditism will be found, nor a convex relation dioecy.

Finally, we should make clear that there is a serious difficulty with this approach to the evolution of dioecy: it assumes that the initial, hermaphrodite population will be at its ESS state with respect to resource allocation. In other words, it assumes that sufficient time has passed without change in the environmental conditions that affect the ESS allocation, for the population to reach its ESS state. This is a severe restriction. It appears quite likely that dioecy may often evolve in populations that have recently experienced changes in their environment. Such a population will not necessarily be evolutionarily stable in the new environment; it may, for example, have a selfing rate which differs from that to which it was previously subject, so that the resource allocation would have evolved appropriately for a former selfing rate, and might be quite different from that appropriate for the current one. This situation is likely to arise when a new species of plant colonizes an island. In such a situation, the selfing rate will often be higher than in the native region. It is by no means clear whether this could have anything to do with the fact that dioecy appears to have evolved repeatedly on islands (Baker, 1967; Carlquist, 1966).

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