EVOLUTIONARILY STABLE REPRODUCTIVE ALLOCATIONS
IN HETEROSTYLOUS PLANTS

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A model is presented for allocation of reproductive energy among ovules and pollen of different types in a heterostylous population of plants with three or more incompatibility types. I assume each flower produces one seed whose fitness depends on the amount of energy allocated to the ovule (which may be type-dependent). I assume pollen is type specific and each flower produces pollen for all types other than its own. I assume the effectiveness of a flower as a pollinator of ovules of a certain type is a function of the amount of pollen of that type it produces. I apply the model to data obtained by Price and Barrett (1982) on *Pontederia cordata.*

In recent years a considerable amount of theoretical work has been devoted to the problem of allocation of reproductive energy between the sexes. Rather than attempt to list references I refer the reader to the book of Charnov (1982). Much of this work has been done with animal populations in mind, the general problem being that of allocation of resources between male and female offspring. Less work has been done on plants, though in many ways plant populations offer a richer and more diverse source of evolutionary tradeoffs in the allocation of reproductive resources.

Dioecious plants provide the strict analogue of (most) animal populations and the problem remains that of allocation between male and female offspring. For monoecious plants in which all individuals are of the same type, the problem is essentially the same, but must be formulated in terms of allocation of resources between male and female gametes (pollen and seeds). But for populations showing any of the numer-

ous intermediate behaviors, the allocation problem becomes more complex and perhaps more interesting. Consider, for example, gynodioecy, in which there are two types of individuals: female, producing only ovules, and hermaphroditic, producing ovules and pollen. There are now two allocation parameters to be studied: (1) the proportion p of females and (2) the proportion r of reproductive energy devoted by the hermaphrodite to pollen. An evolutionary model for resources allocation will require both these parameters to be at equilibrium. For fixed r, the type frequency p will equilibrate in ecological time to a value which depends on r, but r itself can change in evolutionary time under the influence of mutations which shift energy between ovule and pollen production.

More complex still is the allocation problem posed by heterostylous populations. Suppose there are n types of individuals and pollen is type specific, with each flower producing ovules of its own type and pollen for all other types. We now have to find the equilibrium type frequencies, and, for each type, the allocation of resources between ovule and pollen and among pollen of different types.

In this paper I put forward a model for the reproductive allocation problem in a heterostylous population. I assume n types ($n \geq 3$), with each type self-incompatible. A general theorem of Lloyd (1977), discussed in Appendix I, asserts that under rather general assumptions on the genetic determination of types, type frequencies reach equilibrium when individuals of all types have the same (gametic) fitness. Heuch (1979a) has shown that these genetic assumptions apply to

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those heterostylous populations in which the genetics is understood. I first interpret this equilibrium condition (6) for my model. I then derive conditions for the allocation of resources among ovule and pollen production in each type to be evolutionarily stable. Casper and Charnov (1982) have done this analysis for distyly.

Equilibrium Frequencies

Assume each individual has a fixed amount e of reproductive energy to allocate, from which it must produce not only the gametes but also all supporting structures (style and stamen, etc.). Each type must decide what amount x of this energy to spend on ovules. Actually it must also decide, for a fixed expenditure, how large to make its ovules, and therefore how many to make. To simplify matters let's assume each type of individual makes the same number of ovules (in *P. cordata* there is one per flower and number of flowers is independent of type), so that the choice of x is a choice of ovule size. On the other hand, let's suppose that for each j, pollen grains of type j are all of the same size regardless of the plant type which produced them. Thus different expenditures on type j pollen result in different numbers of pollen grains.

Let us measure fitness as expected genetic contribution to the next generation. Suppose a plant which spends x units of energy on ovules has fitness $W(x)$ through these ovules, and a plant which spends y units on type j pollen contributes a mass $V_j(y)$ of pollen to the type j pollen pool (from which all type j ovules receive pollen at random). Suppose a type i flower spends x_i on ovules and for each $j \neq i$, y_{ij} on type j pollen. Then for each i,

$$x_i + \sum_{j \neq i} y_{ij} = e, \qquad (1)$$

and a type i plant has fitness $W(x_i)$ through its seeds and contributes mass $V_j(y_{ij})$ to the type j pollen pool. Let f_i be the frequency of type i in the population. Then the average fitness through ovules is

$$\bar{W} = \sum f_i W(x_i) \qquad (2)$$

and the average contribution to the type j pollen pool is

$$\bar{V}_j = \sum_{i \neq j} f_i V_j(y_{ij}). \qquad (3)$$

Thus the fitness of a type i plant through pollen of type j is

$$f_j W(x_j) V_j(y_{ij})/\bar{V}_j \qquad (4)$$

and the total expected fitness of a type i plant is then

$$F_i = W(x_i) + \sum_{j \neq i} f_j W(x_j) V_j(y_{ij})/\bar{V}_j. \qquad (5)$$

A theorem of Lloyd and Charlesworth (Lloyd, 1977) and Heuch (1979a), which is discussed in Appendix I, says that at equilibrium of type frequencies, all individuals have the same fitness. This means the fitnesses F_i in (5) are all equal, and equal to $2\bar{W}$ (since each seed is the union of two gametes). Thus for all i,

$$W(x_i) + \sum_{j \neq i} f_j W(x_j) V_j(y_{ij})/\bar{V}_j = 2\bar{W}. \qquad (6)$$

These are the conditions for equilibrium of type frequencies. Given the x_i, y_{ij} and functions W and V_j, (6) is a system of $n - 1$ independent equations for the equilibrium type frequencies f_i.

Let me remark that if all types allocate the same energy to ovule production, then $W(x_i) = \bar{W}$ for all i, and for each type its total fitness through pollen,

$$\sum_{j \neq i} f_j W(x_j) V_j(y_{ij})/\bar{V}_j,$$

must also equal $\bar{W}$. Thus each type has the same fitness through ovules and pollen.

Evolutionary Stability

Now I derive conditions for the allocations x_i and y_{ij} to be evolutionarily stable. I assume they are under genetic control and various mutant alleles can arise which shift the allocation in particular types i subject always to (1). Under evolutionary stability the fitness of any such

mutant can be no greater than its "wild type" (normal) allele. Fix attention on a particular i and consider a mutant allele whose allocation in type i flowers is $\hat{x}_i$ and $\hat{y}_{ij}$ where

$$\hat{x}_i + \sum_{j \neq i} \hat{y}_{ij} = e. \tag{7}$$

If the mutant allele is sufficiently rare that it does not alter the population pollen pool, its fitness is

$$\hat{F}_i = W(\hat{x}_i) + \sum_{j \neq i} f_j W(x_j) V_j(\hat{y}_{ij}) / \bar{V}_j. \tag{8}$$

This is the analogue of (2) and (3) in Casper and Charnov (1982) for distyly. A necessary condition for evolutionary stability is that for each i this must not exceed F_i in (5) for all $(\hat{x}_i, \hat{y}_{ij})$ satisfying (7). The standard Lagrange multiplier condition says that at an interior maximum of F_i subject to (7) there is some λ_i for which

$$\partial \hat{F}_i / \partial \hat{x}_i = \partial \hat{F}_i / \partial \hat{y}_{ij} = \lambda_i \tag{9}$$

for all $j \neq i$, at the point (x_i, y_{ij}). Thus, if $j \neq i$,

$$W'(x_i) = f_j W(x_j) V_j'(y_{ij}) / \bar{V}_j = \lambda_i. \tag{10}$$

Equation (10) says that for each i the marginal fitness of a type i plant through its seeds is equal to its marginal fitness through type j pollen for all $j \neq i$. This marginal fitness λ_i has the units of fitness per unit energy.

Given the fitness function $W(x)$ and pollen effectiveness functions $V_j(y)$, it should be possible to solve equations (1), (6) and (10) for the variables f_i, x_i, y_{ij} and λ_i. Note that the equation $\Sigma f_i = 1$ together with the above equations provides

$$1 + n + (n - 1) + n + n(n - 1)$$
$$= n^2 + 2n,$$

independent equations in the same number of unknowns. The equations in (10) are critical point conditions. They are necessary but certainly not sufficient for global or even local evolutionary stabil-

ity. To examine the stability of any solution we need an ESS type condition (Maynard Smith and Price, 1973). This is discussed in Appendix II.

The Case of Pollen Effectiveness Linearly Related to Expenditure

If pollen effectiveness $V_j(y)$ is linear in y, the analysis of the equilibrium equations is simplified. One way to model this is to assume that the production of type j pollen requires an expenditure of z_j on supporting structures (a fixed cost) and that all remaining energy can be converted to pollen at a fixed rate (mass per unit energy). Finally assume that the contribution of a plant to each pollen pool is proportional to the number of grains of that pollen type produced. Letting k_j be the constant which converts energy spent on the pollen itself to mass m contributed, we have $y = z_j + m/k_j$ and so

$$V_j(y) = m = k_j(y - z_j). \tag{11}$$

Let $m_{ij} = V_j(y_{ij})$ be the mass of type j pollen contributed by a type i plant. Then the average contribution is

$$\bar{V}_j = \sum_{i \neq j} f_i m_{ij} = (fM)_j \tag{12}$$

where we have introduced the matrix $M = (m_{ij})$ and denoted by $(fM)_j$ the jth entry of the product fM. Since $V_j'(y) = k_j$, the equilibrium condition (10) becomes

$$W'(x_i) = f_j W(x_j) k_j / (fM)_j = \lambda_i \tag{13}$$

whenever $i \neq j$. Since $n \geq 3$ (this step does not work for distyly!) it follows that all $f_j W(x_j) k_j / (fM)_j$ are equal and hence all λ_i must be equal, say to λ. Thus for all i and j,

$$W'(x_i) = f_j W(x_j) k_j / (fM)_j = \lambda. \tag{14}$$

Equation (14) says that all marginal fitnesses (per unit energy) are equal. That is, there is one number λ which is the marginal fitness through ovule investment for all types and is also the rate at which energy is converted to effective type

TABLE 1. Pollen production of *P. cordata* morphs calculated from Price and Barrett (1982, Tables 3 and 4). Note our table is the transpose of theirs, so that rows correspond to morphs. Thus the 3 × 3 portion of our table contains the matrix M.

| Morph | Pollen production per anther (volume of grain (mm³) × nb.) | | | Total m_i |
| | Anther level | | | |
	l	m	s	
l	—	.1218	.1505	.2723
m	.2093	—	.1362	.3455
s	.1735	.1917	—	.3652

j pollen for all types which make type j pollen. In particular, if W is curvilinear, there is unlikely to be more than one stable x with a fixed value of $W'(x)$, and we conclude all x_i are equal and

$$W(x_i) = \bar{W} \text{ for all } i. \qquad (15)$$

We have already observed in connection with the type frequency equation (6) that this implies that at equilbrium, each type has the same fitness through ovules and pollen.

If all pollen types have the same marginal effectiveness, i.e., if all k_j are equal to some k, then (14) implies that

$$(\bar{W}k/\lambda)f_j = (fM)_j, \qquad (16)$$

which says f is a left eigenvector of the matrix M.

Note that the assumption of linear pollen effectiveness has introduced some degeneracy into our system of equations. The $n + n(n - 1)$ equations (10) are replaced by the $2n$ equations (14) and the n unknowns λ_i are replaced by the single unknown λ. The complete system now has $4n$ equations in $n^2 + n + 1$ unknowns (still counting the x_i as n unknowns). For tristyly ($n = 3$) this gives 12 equations in 13 unknowns. There is a one parameter family of equilibrium states.

Application to *Pontederia cordata*

Price and Barrett (1982) have studied several populations of *P. cordata*, a perennial aquatic with a tristylous breeding system. There are three quite distinct flo-

ral morphs with *long, medium* and *short* styles. Anthers also come in three sizes, *long, medium* and *short* and produce pollen which is specific for the style of corresponding length. Each morph has three anthers of each of the other two lengths; there is virtually no possibility of self fertilization.

Pollen grains are of different sizes, taller anthers producing larger pollen and usually fewer grains but grains produced by homologous anthers in flowers of different types do not appear to differ significantly in size (Price and Barrett, 1982 Table 3). The two types of *long* anthers (on *short-* and *mid*-styled plants) produce about the same amount of pollen as each other, as do the two types of *short* anthers, but the two types of *mid* anthers produce different amounts, the *short*-styled morph producing almost twice as much as the *long*-styled morph. Price and Barrett (1982) discuss this anomaly and suggest that it may have no direct adaptive value, but may be a consequence of developmental constraints. I summarize their pollen production data (Price and Barrett, 1982 Tables 3 and 4) in Table 1, and tabulate total volume of pollen produced by a single anther, where the volume of a pollen grain is calculated with a cylindrical measure: length × width². Total pollen production is seen to differ substantially among morphs, actually decreasing as style length increases.

Seed data from this population show a slight trend for fruit size to increase with style length. Data from the population at Paugh Lake give mean fruit weights (±SD milligrams) to be *long* (style) = 157.9 ± 39.2, *mid* = 153.5 ± 52.8, and *short* = 143.1 ± 33.1. But this difference did not seem to significantly influence a number of standard fitness measures such as germination probability, inflorescences/individual, or seeds/inflorescence.

The *P. cordata* populations studied would appear to be at some definite evolutionary equilibrium (as evidenced for example by the absence of intermediate forms) and I ask whether my model is capable of describing this equilibrium. I

must point out that it is not easy to check the model unless we have some idea of the form of the fitness functions $W(x)$ and $V_j(y)$. If we have a population at type frequency equilibrium (satisfying (6)), we can always claim it to be at evolutionary equilibrium by choosing appropriate fitness functions $W(x)$ and $V_j(y)$ to satisfy (10). Experimental verification of such a claim is difficult because costs and fitnesses are difficult to measure. What I will do is to assume the pollen effectiveness functions $V_j(y)$ are linear, estimate f_i, m_{ij}, and $W(x_i)$ from data, and ask whether our model describes a population at evolutionary equilibrium.

The seed data of Price and Barrett suggest that while seed size is not quite constant among morphs, varying between *short* and *long* by a factor of 15% (*long* being larger), seed fitness seems to be type independent, so it is reasonable to suppose the morphs are putting the same reproductive energy into ovule production. Their pollen data, summarized in Table 1, allow us to estimate the m_{ij}. To obtain the theoretical type frequencies, we solve (6) which, since $W(x_i) = \bar{W}$, can be written as

$$\sum_{j \neq i} f_j m_{ij}/(fM)_j = 1, \qquad (17)$$

and obtain

$$f(long, mid, short) = (.293, .343, .364). \qquad (18)$$

These are comparable to data obtained by Price and Barrett (1982) by taking means over 74 populations of *P. cordata*. These populations exhibited significant heterogeneity in morph frequency, and many of them may not be at equilibrium for a number of reasons (Barrett et al., 1983), but the mean observed population values were

$$f(long, mid, short) = (.255, .346, .399). \qquad (19)$$

Barrett et al. (1983) did the same calculation with the simpler matrix M which has equal pollen production on both types of *long* anther and on both types of *short* anther but twice as much *mid*-pollen from

the *short* morph as from the *long*. Their results were $f(l, m, s) = (.267, .354, .379)$, and differ from the observed means in the same way but not as markedly as mine.

To investigate evolutionary stability, I take the theoretical type frequencies in (18) and the m_{ij} from Table 1 and assume all $W(x_i)$ are equal. From the evolutionary equilibrium condition (14) we obtain

$$k_j \simeq \frac{(fM)_j}{f_j} = (.461, .290, .249). \qquad (20)$$

These are relative estimates of the mass of pollen of each type inserted into the pollen pool per unit energy allocated (after fixed costs have been met). It is difficult to imagine any reason why these should not be nearly the same, in particular, why *long*-specific pollen should be so much cheaper to produce and get into the pollen pool than *mid*- or *short*-.

Another way to look at (20) is to suppose for a moment that the k_j are all equal and that the population is not at evolutionary equilibrium. If we still suppose all $W(x_i)$ equal then (20) (which estimates the $(fM)_j/f_j$) tells us that the marginal fitness $f_j W(x_j) k_j/(fM)_j$ of the production of type j pollen (per unit energy) is significantly smaller for $j = 1$ (*long* specific pollen) than for the other two types. Thus there should be evolutionary pressure on *mid*- and *short*-styled plants to shift allocation of energy away from *long*-specific pollen.

DISCUSSION

There are a number of points that need further exploration.

1) Heuch (1979*b*) and Barrett et al. (1983) have discussed the phenomenon of self-fertilization. There may well be some small but type-dependent probability of illegitimate mating through self-fertilization. The consequences of this on the population equilibrium are slight. It should not be difficult to incorporate this into our model for evolutionary stability.

2) The assumption of linear pollen effectiveness which I made in the application of the model to *P. cordata* may

not be very good. If anything we might expect that a flower which increased its production of pollen of a certain type by, say, 10% would increase its paternity of seeds of that type by somewhat less than 10%, especially if the flowers were insect-pollinated. An experiment of Barrett et al. (1983 Table 7) suggests that this might be the case. We can incorporate this factor into the *P. cordata* data by altering the matrix M so that the larger (non-zero) entry in each column is reduced in favor of the smaller. This will have a noticeable effect only on column 2. This may reduce somewhat the number $(fM)_2$, but will not do anything to resolve the problem posed by (20), that there seems to be too much *long*-type pollen produced.

3) Barrett et al. (1983) have determined that seeds from different morphs of *P. cordata* have the same fitness. This result must be looked at carefully. Have they accounted for all the important determinants of fitness in the field (such as effects of competition and maturation date)?

4) The size of pollen grains increases with anther level from *short* to *long* by a factor of 7. Can we find an evolutionary explanation for this? Ganders (1979) has suggested that this is an adaptation to increase the number of pollen grains available to reach *short* styles which are less accessible than *long* styles. To incorporate this phenomenon we would need a model in which seed fitness depended not only on seed size but on amount of pollen available at the corresponding anther level.

5) Price and Barrett (1982) state that in most tristylous species similar amounts of pollen are in fact produced, among morphs, at the same anther level. In terms of M this means the (off-diagonal entries of the) columns are constant $m_{ij} = b_j$ for $i \neq j$, $m_{jj} = 0$. This is not the case for *P. cordata*, and they are interested in the reason. My model gives no evolutionary reason for expecting the columns of M to be constant. If I assume for example that seed fitnesses $W(x_i)$ are all equal and marginal pollen costs k_j are all equal, then

(16) and (17) together imply the row sums m_i of M are all equal. If the columns were constant, $m_{ij} = b_j$ for $i \neq j$, then $m_i = \sum_{j \neq i} b_j$, and constant m_i implies constant b_j, so all off-diagonal entries would have to be the same. Also (16) would imply all f_i equal (isoplethy).

6) Price and Barrett (1982) suggest that pollen production differences may sometimes have no direct adaptive value but be a consequence of different developmental constraints in different morphs. Certainly in order to have much confidence in the standard type of ESS modelling done in this paper, we must have a reasonable idea of how such development constraints might function. This is an important but difficult problem.

SUMMARY

A number of papers, for example Heuch (1979a, 1979b), have studied type frequencies of heterostylous plant populations at equilibrium. Barrett et al. (1983) have adapted Heuch's (1979a) analysis to a system, such as that in *P. cordata*, in which pollen is type-specific and each flower produces pollen for all types other than its own. I adopt this assumption, and suppose the proportion of reproductive energy the flower allocates to the production of its ovule and to each type of pollen is under evolutionary control. Casper and Charnov (1982) have studied this question for distyly with a somewhat simpler model. The assumption that the allocation is at evolutionary equilibrium leads to the conditions (10). These conditions together with the constant energy equation (1) and our version of Heuch's population equilibrium equation (6) determine the allocations and the type frequencies. It is not easy to analyze these equations without making some simplifying assumptions on the form of the cost functions. To give an example of what such an analysis can produce, I assume pollen effectiveness is proportional to the variable component of energy invested in pollen and deduce the ESS conditions (14).

I apply my model with this assumption of linear pollen effectiveness to the data of Price and Barrett (1982) on *P. cordata*, and find that the fit is not particularly good. A population with equal seed fitnesses, with their observed values m_{ij} of pollen production, and with marginal pollen effectiveness k_j all equal, could not be at evolutionary equilibrium. There should be evolutionary pressure to reduce the production of *long*-specific pollen.

There are a number of extensions of the model which may be worth exploring. More general models of pollen effectiveness should be examined as well as more general cost functions. The model could be extended to allow selfing and inbreeding depression. My feeling is that before it is worthwhile analyzing too many variations, we must have some better idea of the form of fitness functions (for ovule and pollen) and cost functions (for reproductive resources) in plant populations.

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APPENDIX I. Equal type fitnesses at equilibrium.

I formulate and prove a slight generalization of a theorem of Lloyd (1977) on equal phenotypic fitness at equilibrium, and indicate that a general equilibrium theorem of Heuch (1979) for heterostylous populations is a special case of this theorem.

Let there be m phenotypes $P_1, \ldots, P_m$ in a population at non-zero frequencies $p_1, \ldots, p_m$, and n alleles $a_1, \ldots, a_n$ at a number of loci controlling these phenotypes. Assume discrete, non-overlapping generations and measure fitness of a genotype by counting the expected number of gametes that a zygote of that genotype will contribute to next generation zygotes. Different genotypes may correspond to the same phenotype and in that case assume that for each j all genotypes having phenotype P_j have the same fitness w_j. Let $\bar{w} = \Sigma\, p_j w_j$ be mean population fitness.

Let G_j be the vector of length n whose ith component g_{ij} is the probability that an allele drawn randomly from a random (controlling) locus of a type-j individual is a_i. Let $G = (g_{ij})$ be the $n \times m$ matrix whose jth column is G_j. Assume G has a rank m, that is, the "allelic composition" vectors G_j are linearly independent. (This certainly requires $n \geq m$.) With these assumptions the result is that at equilibrium (of the type frequencies p_j under natural selection) all phenotypes have the same fitness: $w_j = \bar{w}$ for each j.

The proof I give is a slight modification of that of Brian Charlesworth (Lloyd, 1977). Let $q_i = \Sigma\, g_{ij} p_j$ be the probability that a random allele at a random (controlling) locus is a_i. Next generation, $q_i' = \Sigma\, g_{ij} p_j w_j / \bar{w}$. At equilibrium, $q_i' = q_i$, and so, $\Sigma\, g_{ij} p_j (w_j - \bar{w}) / \bar{w} = 0$ for all i. Letting $x_j = p_j (w_j - \bar{w}) / \bar{w}$, this can be written as the vector equation $\Sigma\, x_j G_j = 0$. Since the G_j are assumed linearly independent we deduce $x_j = 0$ for all j. Since $p_j \neq 0$, it follows that $w_j = \bar{w}$.

Let me make two remarks. The equation for q_i' assumes that at each locus zygotes receive alleles from their parents in correct Mendelian proportions. This is a hidden assumption which I now make explicit. Phenomena such as meiotic drive and lethal genotypes may violate this. Secondly, it is zygotic fitness of phenotypes which we conclude is equal. If there is differential mortality of phe-

notypes between zygote and adult stage, adult fitnesses may not be equal.

Heuch (1979a Prop. 1) has provided a simple condition which guarantees the linear independence of the G_j and which often obtains in those heterostylous populations for which we understand the genetics. Suppose the phenotypes $P_1, \ldots, P_m$, and the alleles $a_1, \ldots, a_n$ have been arranged so that for each j, allele a_j occurs only in P_j and possibly $P_1, \ldots, P_{j-1}$. Then the matrix G is lower triangular (in the first m rows) and the columns G_j are linearly independent. Heuch's result is actually formulated in terms of adult frequencies and fitnesses, but he assumes no selective differences among phenotypes between zygote and adult stages. I must also assume this to apply the result. This assumption should not be confused with the possibility that seeds of different size may have different fitness. Seed size is dependent on maternal, not seed, phenotype. My assumption is that there are no fitness differences between seeds that depend on *seed* phenotype. With this assumption, (6) follows from the result of this Appendix.

APPENDIX II. Analysis of stability.

I analyze the stability of the equilibrium determined by our equations using a standard ESS approach (Maynard Smith and Price, 1973; Taylor and Jonker, 1978). A complete analysis is rather complicated, and I feel the model is rather young for this to be worthwhile. The restricted analysis I give here certainly conveys the character of the arguments.

The idea behind an ESS analysis is to take a population at equilibrium and introduce a mutant subpopulation with non-equilibrium parameter values at a low frequency $\epsilon > 0$. The presence of the mutant subpopulation perturbs the population parameters. Calculate the fitness of the normal and the mutant individuals in this perturbed population. The ESS condition for the stability of the equilibrium is that for sufficiently small $\epsilon > 0$, the normal fitness must strictly exceed the mutant fitness.

In any such argument one must specify which types of mutants are to be considered. Thus the result of any ESS analysis is always that the equilibrium is stable under certain types of mutation. The analysis given below is restricted because I have restricted attention to mutants which alter the parameters for one type only. In particular, I assume the mutant allele is in linkage equilibrium with the loci controlling the heterostyly and expresses itself only in type i. Also I consider only mutants which are structurally similar to the corresponding normal type. A mutant which decided to eliminate one another level completely would save both fixed and variable costs. The calculation of the relative fitness of such a mutant involves a comparison of these two types of costs and I do not consider this. To make calculations simpler I also assume the linear pollen effectiveness (11). It follows, in particular, that $W(x_i) = \bar{W}$ for all i.

So let us take a fixed i and suppose a proportion ϵ of type i plants are mutant and invest $\hat{x}_i$ in ovules and $\hat{y}_{ij}$ in type j pollen contributing $\hat{m}_{ij} = V_j(\hat{y}_{ij})$ to the type j pollen pool. We assume that ϵ is small enough that the existence of the mutant does not affect the type frequencies f_j, but it does affect the composition of the pollen pool. Thus in the perturbed population the size of the type j pollen pool (for $j \neq i$) is no longer $(fM)_j$ but equals

$$S_j = \sum_{k \neq j} f_k m_{kj} + \epsilon f_i(\hat{m}_{ij} - m_{ij}). \qquad (A1)$$

Thus mutant fitness is

$$W(\hat{x}_i) + \sum_{j \neq i} \hat{m}_{ij} f_j W(x_j)/S_j, \qquad (A2)$$

and normal fitness is

$$W(x_i) + \sum_{j \neq i} m_{ij} f_j W(x_j)/S_j. \qquad (A3)$$

Note that (A2) differs from (8) because (A2) calculates fitness in the perturbed population whereas (8) uses the unperturbed population. The fitness difference is

$$\Delta(\epsilon) = W(\hat{x}_i) - W(x_i) + \sum_{j \neq i} (\hat{m}_{ij} - m_{ij})$$
$$\cdot f_j W(x_j)/S_j. \qquad (A4)$$

We must show the following ESS condition:

> For any feasible set of
> values $(\hat{x}_i, \hat{y}_{ij})$
> different from (x_i, y_{ij}), $\qquad (A5)$
> $\Delta(\epsilon) < 0$ for
> sufficiently small $\epsilon > 0$.

We first remark that if for some mutant we have $\Delta(0) < 0$, then (A5) will certainly hold (by continuity). Let us calculate $\Delta(0)$.

$$\Delta(0) = W(\hat{x}_i) - W(x_i)$$
$$\qquad + \sum_{j \neq i} (\hat{m}_{ij} - m_{ij})$$
$$\qquad \cdot f_j W(x_j)/(fM)_j$$
$$\quad = W(\hat{x}_i) - W(x_i)$$
$$\qquad + \lambda \Sigma(\hat{m}_{ij} - m_{ij})/k_j \qquad \text{by (16)}$$
$$\quad = W(\hat{x}_i) - W(x_i)$$
$$\qquad + \lambda \Sigma(\hat{y}_{ij} - y_{ij}) \qquad \text{by (11)}$$
$$\quad W(\hat{x}_i) - W(x_i)$$
$$\qquad - W'(x_i)(\hat{x}_i - x_i) \qquad \text{by (1), (7) and (14).}$$

This will be <0 if for all feasible $\hat{x}_i$

$$W'(x_i) \gtrless \frac{W(\hat{x}_i) - W(x_i)}{\hat{x}_i - x_i} \qquad (A7)$$

depending on whether $\hat{x}_i \gtrless x_i$. Condition (A7) compares the slope of the graph of $\bar{W}$ at x_i with the slope of the secant from x_i to $\hat{x}_i$. It will be true for *all* $\hat{x}_i$ if W is concave-down ($W'' < 0$). If W is S-shaped and x_i lies well into the concave-down part of the curve, it will be true for all $\hat{x}_i$ which lie in, or reasonably near, the set where $W'' < 0$. Assuming this to be the case, we have shown that any

mutant which alters the allocation to type i ovules, is selected against.

It remains to consider mutants for which $\Delta(0) = 0$. For these mutants $\dot{x}_i = x_i$, from what I have just shown, and

$$\Delta(\epsilon) = \sum_{j \neq i} (\dot{m}_{ij} - m_{ij}) f_j W(x_j)/S_j. \qquad (A8)$$

Using the fact that $dS_j/d\epsilon = f_i(\dot{m}_{ij} - m_{ij})$, we calculate

$$d\Delta/d\epsilon = -\sum_{j \neq i} (\dot{m}_{ij} - m_{ij})^2$$
$$\cdot f_i f_j W(x_j)/(fM)_j^2 \qquad (A9)$$

at $\epsilon > 0$, and if $\dot{m}_{ij} \neq m_{ij}$ for some j this is < 0. Condition (A5) follows, and we are finished.

The general (and more realistic) analysis, in which a mutant is permitted to alter the parameters of more than one type, is more difficult because the mutant fitness depends on the relative mutant frequencies in each type, and it is not easy to determine these.

Let me observe that for the case of linear pollen effectiveness I do not expect an equilibrium calculated by (1), (6), and (14) to be stable for all mutants, because the equilibria are not isolated. For example for tristyly, $n = 3$, there is a one parameter family (a curve) of equilibrium points in the constraint surface. We do not expect any one of these to be stable to movements along this curve. This phenomenon deserves closer scrutiny. It may be that the best way out is to assume a more general law of pollen effectiveness.