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FLORAL SEX ALLOCATION IN SEQUENTIALLY BLOOMING PLANTS

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Abstract.—In plants whose flowers develop in a sequence, different flowers may exhibit temporal variation in pollen donation and receipt such that the fitness contributions through male and female functions can vary among flowers. Dichogamy, or directional pollinator movements within inflorescences, can create situations where flowers in different stages in the sequence may differ in the numbers of flowers in the female stage available as potential mates. We present an evolutionarily stable strategy (ESS) analysis of the resource allocations expected in different flowers in hermaphroditic plants when the mating environments vary among flowers. This introduces a modular element into sex-allocation models. Our analysis shows that such variation in the mating environments of flowers can select for differences in sex allocation between flowers. When male and female fertilities are nonlinear functions of the allocations, variation in resource availability can also select for variation in sex allocation among flowers. The influence of dichogamy and pollinator directionality on floral sex allocation is discussed, and the empirical evidence supporting the predictions derived from the model is briefly reviewed. The implications of our results for the evolution of andromonoecy and monoecy are discussed.

Keywords.—Dichogamy, gain curves, male function, mating environment, pollinator movement, reproductive resources, selfing, sex allocation.

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> [W]ith hermaphrodite plants that are strongly proterandrous, the stamens in the flowers which open first sometimes abort; and this seems to follow from their being useless, as no pistils are then ready to be fertilised.
>
> —Darwin (1877, p. 283)

In hermaphroditic plants, the male and female contributions to fitness are each due to the sum of contributions from each of the plant's flowers. It is thus important to incorporate the modular nature of plant reproduction into sex-allocation theory (Stanton and Galloway 1990). In plants whose flowers develop in a sequence, pollen from flowers in different stages will have different opportunities for siring offspring. Therefore, the fitness contributions through male and female functions can vary among flowers. In particular, the numbers of flowers in the female stage that are available as potential mates to each of the male flowers competing for these ovules may differ for flowers at different stages in the sequence. These kinds of difference, which we term differences in the mating environment of flowers, can be quantified in terms of the numbers of ovules available to pollen of flowers that are potential mates of these ovules, for each of the stages of flowering. It seems probable that variation in the mating environments of flowers during the flowering sequence could select for differences in their sex allocation.

Factors such as dichogamy (temporal separation of sexual functions within flowers) and pollinator directionality (movement of pollinators along inflorescences) may produce such differences in the mating environment of flowers (Darwin 1877; Pellmyr 1987; Brunet 1990). In protandrous plants, where the anthers dehisce before the stigmas become receptive, flowers produced early may have a low ratio of available ovules to pollen competing for these ovules, compared with later flowers (fig. 1). In this case, protandry would be expected to select for female-biased allocation in early- compared to late-opening flowers (and protogyny for the opposite pattern). Here, we present an evolutionarily stable strategy (ESS) analysis of the resource allocations expected in different flowers in hermaphroditic plants when the amounts of reproductive resources available and the mating environments vary among flowers. This analysis confirms that variation in the mating environments of flowers can select for variation in sex allocation among flowers. It suggests that variation in resource availability among flowers can under some circumstances also select for variation in sex allocation. The model makes predictions that can be tested empirically (see below). As such predictions involve comparisons of flowers on inflorescences, they are not confounded by any other possible differences between parental plants.

MODEL

Fitness Expressions for the Model Assuming No Allocation to Attraction

The model assumes that there are several different stages of flowers, which might, for example, correspond to the flowers that open in sequence on an inflorescence. We shall refer to these as flower positions. In order to perform an ESS analysis of the consequences of this situation, we need to have an expression for the fitnesses of phenotypes with different possible allocations. Male and female contributions to fitness are sums of contributions from flowers at each position in the sequence. It is assumed that some total amount of resources is available for reproductive functions and that this does not differ between individuals in the population. The reproductive resources could be either those available at flowering or could include resources available for investment into fruits. Let a fixed fraction T_j of the total reproductive resources be available to the jth flower position. We denote by M_j the proportion of the reproductive resources allocated to

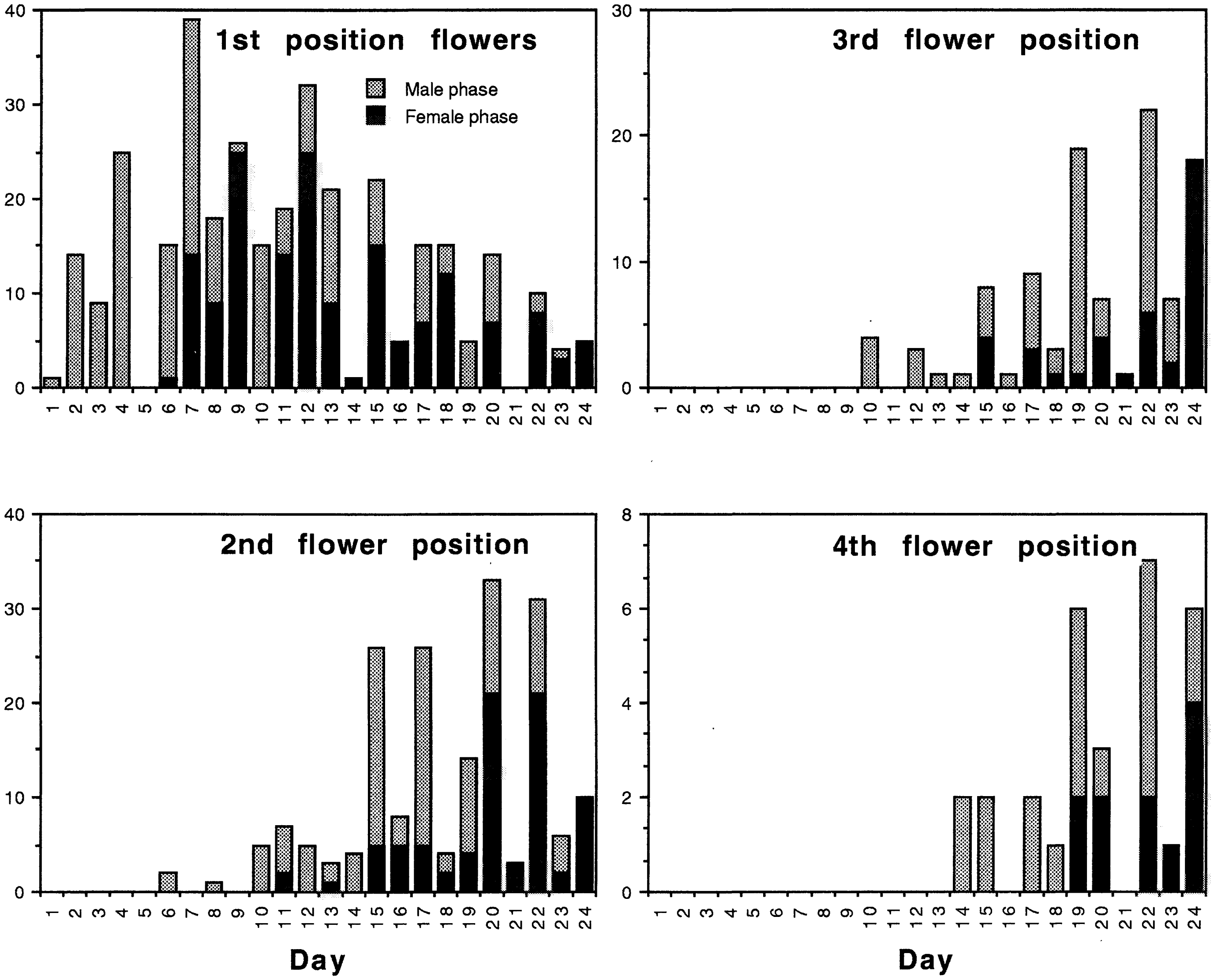

FIG. 1. Sequential blooming in the first four flower positions in inflorescences of *Aquilegia caerulea,* a plant with protandry creating a time delay between the male and female phases of flowers.

male functions by flowers of the jth position, with the remainder being allocated to female functions (i.e., we ignore allocation to attraction, so that allocation to female functions is $F_j = 1 - M_j$).

The ESS value of the male allocation parameters for flowers at the jth position, M_j, was found by the method of Charlesworth (1990), given in the Appendix for the general case in which reproductive resources can be allocated to male or female functions or to pollinator attraction. Here, we give the fitness expressions, ignoring allocation to attraction.

Assuming complete outcrossing and a constant cost per ovule, the number of fertilized ovules from all stages of flowers is proportional to

$$w_f = \sum_j T_j(1 - M_j). \tag{1}$$

Assuming that all fertilized ovules mature into seeds (i.e., resources do not limit seed output), the female contribution to fitness from all stages of flowers is given by this expression. With resource limitation of seed output, the quantity under the summation would become a function of the number of fertilized ovules. We have used a power function, with exponent $k1$, to represent the possibility of resource limitation, as in previous models (Charnov 1982; Lloyd 1984; Charlesworth and Charlesworth 1987). The exponents of the gain curves are not allowed to evolve in the allocation models.

The model assumes a pool of pollen that will in part be deposited on stigmas, and that representation in this pool determines male fertility. Thus, the male contribution to fitness comes from the contributions of pollen from each flower position, to the outcrossing pollen pools of flowers of different positions that are open during pollen production of the flowers under consideration. Let K_{ij} be a matrix of relative probabilities that pollen produced in flowers of the jth position will become part of the pollen pool of flowers at the

ith position. This matrix allows us to separate the pollen-transfer portion of the reproductive process from the effects of the allocation differences on pollen and ovule production. Pollen transfer presumably depends chiefly on the degree of temporal overlap between the male and female flower stages of flowers at different positions, or on pollinator behaviors that influence transfer between flower positions (as well as on the attractiveness to pollinators, which is not discussed further here). The estimation of the K_{ij} values from field data will be described below.

The male contribution to fitness through outcrossing for a particular phenotype is

$$w_m = \sum_j w_{mj} = \sum_j \sum_i w_{mji},$$

where w_{mji} is the number of ovules in flowers of the ith position, multiplied by the ratio of the contribution to their pollen pool from flowers at the jth position to the total pollen pool that is competing for the ovules in question (i.e., the fractional contribution of pollen from the jth flower position to the total pollen pool for flowers of the ith position). The number of ovules available for outcrossing in flowers of the ith position is given by $T_i(1 - M_i)$. In the simplest possible model, the contributions of flowers of each position to the pollen pool for outcrossing are proportional to the allocation parameters, M_j; that is, pollen output from flowers at the jth position is given by $T_j \times M_j$. With no pollen limitation of fertilization nor resource limitation of seed production, this ratio for a given allocation phenotype designated by the subscript 1, in a population with some set of phenotypes at frequencies P_r, is then

$$\frac{T_j M_{1j} K_{ij}}{\sum_r \sum_j P_r T_j M_{rj} K_{ij}}. \tag{2}$$

With the more realistic assumption that pollen output is proportional to the M_j values, but that contributions to the pollen pool show a diminishing-returns relationship with pollen output, we can replace the product $T_j \times M_j$ by a power function, say, $(T_j \times M_j)^k 2$. Note that the relative, rather than absolute, allocation to male function is of interest here, as reproductive resources differ between positions.

To perform an ESS analysis, we need the fitness contribution via male reproduction for a new phenotype (type 2) introduced into a population consisting almost entirely of type 1. For the simplest case discussed above, we have

$$w_{mj} = \sum_i \frac{T_i(1 - M_{1i}) T_j M_{2j} K_{ij}}{\sum_l T_l M_{1l} K_{il}}. \tag{3}$$

The generalizations to the case when either or both of the male or female fertilities show diminishing returns with increasing allocations, can be made simply by replacing the terms in this equation, and that for the female contribution to fitness, by the power functions mentioned above.

To include selfing, the fitness equations above were modified as follows. The female contribution to fitness resulting from flowers at position j was replaced by:

$$T_j F_j[(1 - S_j) + 2S_j(1 - \delta)], \tag{4}$$

where S_j is the selfing rate for flowers of the jth position, and δ is the inbreeding depression (i.e., the lowering of fitness in progeny of selfing, relative to that of outcrossed progeny). In addition, the number of ovules in flowers of the jth position that are available for outcrossing by the pollen pool for that position was replaced by $T_j F_j(1 - S_j)$. The male contribution to fitness from flowers of the jth position becomes:

$$w_{mj} = T_j M_{2j} \sum_i \frac{T_i F_{1i}(1 - S_i) K_{ij}}{\sum_l T_l M_{1l} K_{il}}. \tag{5}$$

Apart from these changes in the fitness formulae, and the corresponding alterations in the derivatives of the fitness functions, the model was as described previously.

After writing the expressions for the derivatives of the fitness equations, we solved for the ESS allocations using the iterative method described in the *appendix,* arbitrarily using 0.1 for all V_A values. The calculations were made on a Macintosh computer, using Microsoft QuickBasic program, and on a PC using a Fortran program. In both cases, the program included the derivatives of fitness, based on the fitness expressions explained above. Calculation of the second derivatives of the fitness function at the ESS was done to test whether the values found were stable.

Estimation of the Matrix of Pollen-Transfer Probabilities

Our model separates the pollen-transfer portion (K_{ij} values) of the reproductive process from the effects of differences in allocation to total pollen and ovule production. To make the model concrete, it is helpful to show how the matrix of K_{ij} values can be estimated from field data. The raw observations consist of records of the numbers of flowers open at each flower position, for each day of flowering, starting with the day of opening of the first flower of the earliest-flowering individual. Ideally, these data could be collected separately for flowers open as each sex. These data are then condensed into tables containing the numbers of flowers in the population that are open and have dehisced anthers on each day of the flowering period, classified by their positions, and a similar table for all flowers with receptive pistils, tabulated by day and by position. These data are denoted by $N^m{}_{cj}$ and $N^f{}_{ci}$, for male and female flowers, respectively, where j refers, as before, to flower position, and c denotes the day.

In reality, the flowers may not be classified as to their sex functions, when they are scored, but the day that each flower opens may be known. In that case, the raw data for a protandrous plant consist of records of flowers at different positions open on each day of observation. Knowing the time course of the protandry, and assuming a fixed average amount of time in the male stage before pistil maturity, these data could be used to construct a table of the numbers $N^m{}_{cj}$ and $N^f{}_{ci}$ of male and female stage flowers open on each day, and the method outlined here could still be used. The same approach could also be used for a protogynous plant. Figure 1 (above) illustrates an example of this type of data for *Aquilegia caerulea.* These data were collected as the first days on which flowers were open (in the male phase), and the female phase was assumed to begin 5 d later than the male

TABLE 1. Estimates of the relative pollen-transfer probability (K_{ij}) values for *Aquilegia caerulea* in Colorado in 1987, calculated from the raw data shown in figure 1.

Position of female flower	Flower position as male (j)				
	1	2	3	4	5
1	0.506	0.422	0.299	0.414	0.524
2	0.077	0.284	0.296	0.630	0.920
3	0.022	0.087	0.095	0.721	1.541
4	≈0	0.024	0.041	0.172	0.359
5	≈0	≈0	≈0	0.072	0.169
Totals	0.611	0.821	0.734	2.101	3.511

phase, based on observations of the average time delay between the sex stages.

To obtain the K_{ij} values, one first needs to know what fraction of the ovules available on a given day, c, will be fertilized by pollen from position j flowers. Assuming that the transfer probabilities are determined by the extent of temporal overlap between the male and female stages of flowers at different positions, this will depend on the fraction of flowers open in the male phase on day c whose position is j. These fractions are easily found from tables of flowers in the male and female phases. We denote these fractions by $f^m{}_{cj}$ given by

$$f^m{}_{cj} = N^m{}_{cj} \Big/ \sum_j N^m{}_{cj}$$

where

$$\sum_j N^m{}_{cj}$$

is the total number of flowers open on day c. The number of position i flowers that will be pollinated by position j donors is therefore the sum, over all days, of these fractions multiplied by the number of ith position flowers whose pistils are receptive on day c, that is,

$$\sum_c f^m{}_{cj} N^f{}_{ci}.$$

To put this on a per-flower basis, and obtain relative K_{ij} values, these sums are divided by the total numbers of flowers at the relevant donor positions,

$$\sum_c N^m{}_{cj}:$$

$$\frac{\sum_c f^m{}_{cj} N^f{}_{ci}}{\sum_c N^m{}_{cj}}.$$

The results for the *Aquilegia caerulea* data of figure 1 are given in table 1.

RESULTS

As qualitatively similar results were obtained for three-, four-, or five-flowered inflorescences, the results as presented for four-flowered inflorescences. We examine several cases to clarify which factors most strongly cause variation in sex allocation among positions. The parameter varied, and the results of the calculations are summarized in table 2.

Obligate Outcrossing

Case 1. No Effect of Position on Pollen Transfer (All K_{ij} Values Equal).—It is helpful to start by considering the case when the probabilities of pollen transfer are independent of the positions of the flowers producing the pollen (i.e., pollen is transferred randomly, and ovules of all flower positions share the same pollen pool, see table 2, first kind of matrix). The ESS allocations then do not differ among positions, unless the amounts of reproductive resources (T_j) differ between positions, and the gain-curve parameters ($k1$ and $k2$) are unequal. When these conditions are satisfied, differences in sex allocation are expected between positions. Figure 2 shows some numerical examples when the value of T_j decreases for later flower positions (the results for the opposite direction of change in T_j values were exactly the opposite of those shown). When the exponent for the male gain curve is larger than that for the female curve ($k2 > k1$), positions with greater amounts of reproductive resources are more male-biased than positions with fewer resources, and the reverse holds when $k2 < k1$ (fig. 2).

Case 2. All Flower Positions Equally Successful As Pollen Donors, But Transfer to Ovules of Different Positions (K_{ij} Values) Varies with Both Donor and Recipient Position.—In case 1, the total probability of pollen transfer is necessarily the same for all flower positions. It is interesting to examine the effect of the situations when different flower positions have different success as donors of pollen. Denoting by K_j the total probability that pollen of flowers at a given position is successful in being incorporated in the pollen pool, it is possible (though not biologically realistic) that the K_j values could be the same for all flower positions, even if there is variation in the K_{ij} values. In this case also, the ESS sex allocations of different positions do not vary unless the amount of reproductive resources at each position (T_j values) also varies, even though now the pattern of pollen transfer differs for ovules in different positions (table 2, second kind of matrix).

If the K_{ij} values differ, however, then unlike case 1, variation in the T_j values is sufficient for differences in sex allocation between flowers to evolve. The extent of the allocation differences depends on the relationship between the pollen-transfer probabilities and the amount of reproductive resources available at each position. When donor flowers at position j have a high probability of pollinating flowers from positions with large amounts of reproductive resources (high T_j values), they will have greater reproductive success as males; thus, even if the male and female gain curves are identical, one expects a greater bias in sex allocation than when these flowers pollinate stigmas at positions receiving lesser resource amounts. Figure 3 shows some examples when the values of the parameters in the second type of K_{ij} matrix of table 2 were a = 0.6, b = 0.2, c = 0.1, d = 0.1. To obtain much variation in sex allocation among positions, strong differences were necessary in the K_{ij} probabilities. For the same T_j, k1, and $k2$ values as in figure 2, the results are similar, but male bias is lower for flowers late in the sequence,

TABLE 2. Examples of the types of pollen-transfer matrices used in the calculations, and trends in the ESS sex-allocation patterns among positions in obligate outcrossers. The examples are for four-flowered inflorescences.

Position of ovules (i)	Position of pollen donor (j)				Resources (T_j)	Gain-curve parameters	Allocation patterns
No. Effect of Position on Pollen Transfer							
	1	2	3	4			
1	a	a	a	a	constant	k1 = k2	all $M_j = 0.5$
2	a	a	a	a		k2 ≠ k2	all $M_j = k2/(k1 + k2)$
3	a	a	a	a	variable	k1 = k2	all $M_j = 0.5$
4	a	a	a	a		k1 ≠ k2	$M_1 \neq M_2 \neq \ldots \neq M_j$
Total	4a	4a	4a	4a			
All Flower Positions Equally Successful as Pollen Donors, but Differential Transfer to Ovules of Different Positions*							
	1	2	3	4			
1	a	b	c	d	constant	k1 = k2	all $M_j = 0.5$
2	b	a	d	c		k1 ≠ k2	all $M_j = k2/(k1 + k2)$
3	c	d	a	b	variable	k1 = k2	$M_1 \neq M_2 \neq \ldots \neq M_j$
4	d	c	b	a		k1 ≠ k2	$M_1 \neq M_2 \neq \ldots \neq M_j$
Transfer Different for Pollen from Flowers of Different Positions†							
	1	2	3	4			
1	a	b	c	d	constant	k1 = k2	$M_1 \neq M_2 \neq \ldots \neq M_j$
2	a	b	c	d		k1 ≠ k2	$M_1 \neq M_2 \neq \ldots \neq M_j$
3	a	b	c	d	variable	k1 = k2	$M_1 \neq M_2 \neq \ldots \neq M_j$
4	a	b	c	d		k1 ≠ k2	$M_1 \neq M_2 \neq \ldots \neq M_j$
Total	4a	4b	4c	4d			
Pollen Best Transferred to Flowers of the Previous Position‡							
	1	2	3	4			
1	c	a	b	d	constant	k1 = k2	$M_1 \neq M_2 \neq \ldots \neq M_j$
2	d	c	a	b		k1 ≠ k2	$M_1 \neq M_2 \neq \ldots \neq M_j$
3	0	d	c	a	variable	k1 = k2	$M_1 \neq M_2 \neq \ldots \neq M_j$
4	0	0	d	c		k1 ≠ k2	$M_1 \neq M_2 \neq \ldots \neq M_j$
Total	c + d	a + c + d	a + b + c + d	a + b + c + d			

* Sums of each row and column equal a + b + c + d.

† Sums of each row, but not of the columns, are equal.

‡ In the protandrous case, a > b > c > d. Protogyny can be modeled by the corresponding matrix inverted around the top right to bottom left diagonal.

which have the lowest T_j values. Differences in the gain curves affect the allocations only when small differences in the K_{ij} exist or when the gain curves are very different.

Case 3. K_j Values Differ between Flower Positions.—In biologically realistic cases, variation in K_{ij} values is unlikely to occur without variation in the total probabilities of pollen transfer from flowers of different positions, K_j, and such variation alone can strongly select for variation in sex allocation among positions, even if the proportions of resources allo-

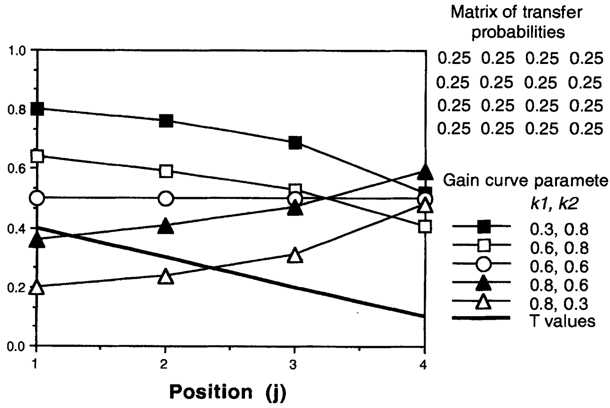

FIG. 2. ESS allocations to male function in flowers of four successive positions when pollen transfer is random (first type of matrix of table 2 with all K_{ij} values equal to 0.25), but total allocation of resources is highest for the earliest flowers and declines for later flowers ($T_1 = 0.4$, $T_2 = 0.3$, $T_3 = 0.2$, $T_4 = 0.1$). Various gain-curve parameter values are shown.

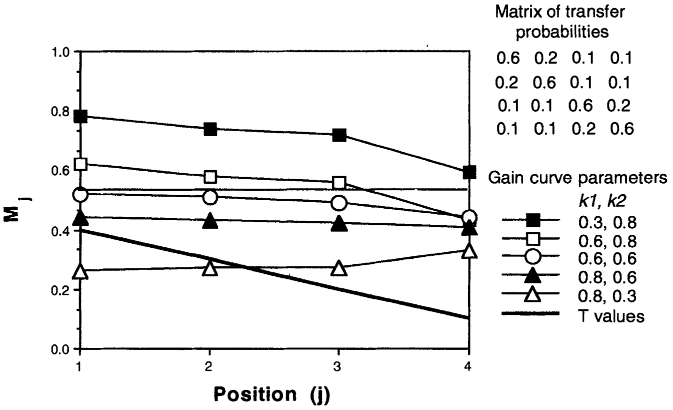

FIG. 3. ESS allocations to male function in flowers of four successive positions when pollen transfer from all flower positions is equally successful (equal K_j values, second type of matrix of table 2). The same set of T_j values, and the same gain-curve parameters, as in figure 2 were used.

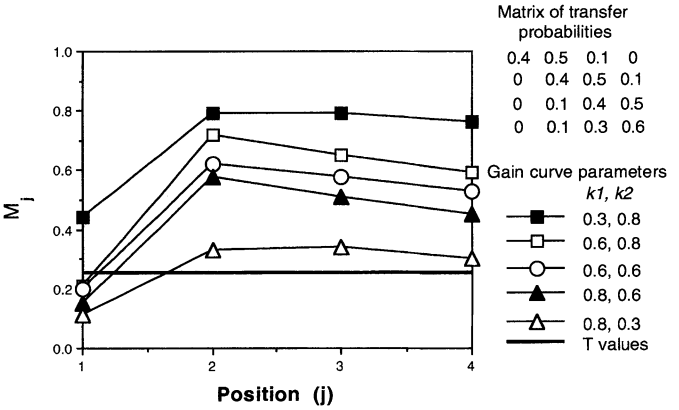

FIG. 4. ESS allocations to male function in flowers of four successive positions under protandry (with a slightly modified form of the last type of pollen-transfer matrix of table 2, adjusted so that the sums of transfers to each ovule position were equal). The T_j values were all 0.25, and the same gain-curve parameters as in figure 2 were used.

cated to reproduction (T_j) are the same for all positions. This remains true even if the exponents of the male and female gain curves are equal, and when donor flower position does not affect transfer of pollen to recipients at different positions (table 2, third kind of matrix).

Flower positions with higher probabilities of pollen-transfer K_j allocate proportionately more reproductive resources to male function relative to positions with lower transfer probabilities (fig. 4). Variation in T_j, and differences between $k1$ and $k2$, do not modify the qualitative pattern of variation in sex allocation among positions. Figure 4 shows an example of the increase in ESS allocation to maleness with successive flower positions, for one hypothetical example of a protandrous situation with K_j values 0.4, 1.1, 1.3, and 1.2. This example is not intended to be particularly realistic. It does demonstrate, however, that under protandry (which implies that the first flowers have low pollen success), the ESS allocations may differ between the earliest and later positions, without large differences between the allocations of flowers of the different later positions. Moreover, the last flower position has a lower total pollen success than the preceding one, and that the allocation to maleness is correspondingly lower than of the previous position (resulting from the lower K_j value for the final flower position). In other words, the allocation pattern need not be monotonic.

When the different factors predict different trends, strong variation in the probability of pollen transfer among positions (the K_j values) determines the pattern of variation in sex allocation among positions. Only when the values of K_j are uniform or differ little from one another will resource distribution among positions and the exponents of the gain curves control the trends in sex allocation among positions (fig. 2).

In some cases, differences between expected allocations of different flower positions were extreme, amounting essentially to unisexuality of flowers at one or more positions. For example, using the transfer probabilities estimated from the *A. caerulea* data given in figure 1 and table 1 (first four positions only), and with the same T_j values as in figures 2 and 3, the ESS allocations to maleness were 0.29 for position 1 and 0.89 for position 4, when both gain-curve exponents were 0.6. Higher values of the exponents made the latest flowers even more male, and less female, in their allocation.

Selfing Populations

Selfing Rate Constant at All Positions.—When the selfing rate is constant among positions, it influences the ESS sex allocation but not the pattern of sex allocation among positions (results not shown). Like previous sex-allocation models without differences between flowers (Charlesworth and Charlesworth 1981; Lloyd 1987), our model found an increase in relative allocation to female function (decrease in sex allocation) with increased selfing and an increase in the relative allocation to male function with increased levels of inbreeding depression. Variation in reproductive resources among positions, differences in the exponents to the female and male gain curves, and variation in the probabilities of pollen transfer for pollen at different positions had the same influence on the pattern of variation in sex allocation among positions as for the case of obligately outcrossed hermaphrodites.

Selfing Rate Variable among Positions.—With selfing, the fitness contribution through female, but not through male, function depends on the level of inbreeding depression (eqs. 4, 5). When inbreeding depression is 0.5, the fitness contribution through female function is independent of the level of selfing, but when it is less than 0.5, flowers with higher selfing rates propagate more genes through female function relative to flowers with lower selfing rates; the reverse is true when inbreeding depression is greater than 0.5 (eq. 4).

With constant probabilities of pollen transfer for pollen at different positions (equal K_j), the average number of ovules available for fertilization is the same for pollen at all positions. Under these circumstances, one expects a value of inbreeding depression of 0.5 to lead to allocation of the same proportion of reproductive resources to male function in all flowers, irrespective of their selfing rates. With inbreeding depression greater than 0.5, plants should allocate proportionately more reproductive resources to male function in flowers with larger selfing rate; and, with inbreeding depression less than 0.5, plants should allocate proportionately more resources to female function in flowers with greater selfing rates. These patterns were observed with T_j constant or $k1 = k2$.

When the reproductive resources allocated to each position also vary and the exponents to the female and male gain curves differ from one another, these factors affect the pattern of variation in sex allocation among positions (case 1, above), and that was found in the case of selfing populations also. Similarly, when the probability of pollen transfer (K_j) and the selfing rate vary for different flowers, the matrix of pollen-transfer probabilities determines the trends in sex allocation expected among positions. As for obligate outcrossers, variation in the probability of pollen transfer among positions is the strongest determinant of the pattern of variation in sex allocation, and only when differences among the values of K_j are small or absent do variation in reproductive resources and different gain curves influence the pattern.

DISCUSSION

Pollen-Transfer Probabilities

We have shown that sex allocation among positions is strongly influenced by the matrix of pollen-transfer probabilities such that positions with more successful pollen transfer allocate proportionately more reproductive resources to male function than do flowers of other positions. The probabilities of pollen transfer in our model depend on the ratios of available ovules (flowers in the female stage on potential mates) to the numbers of potential competitors (flowers in the male stage competing for the ovules in question).

Why might these ratios differ between flower positions? Dichogamy (time delay between expression of male and female functions within flowers) and pollinator movements on inflorescences can create different transfer probabilities for pollen at different positions and thus influence sex allocation. We discuss the influence of these two factors on pollen transfer and sex allocation.

Dichogamy

Dichogamy shifts the flowering phenology of flowers in the female stage relative to flowers in the male stage (see fig. 1 for protandry). It therefore modifies the number of potential mates (flowers in the female stage) at different positions available to pollen from a given position without changing the number of male flowers competing for access to these ovules. With protandry, the ratio of potential mates to pollen competitors (flowers in the male stage competing for access to female flowers) is lowest in first-position flowers and increases in later-position flowers. As a result, fewer stigmas are available when first-position flowers shed pollen, but plenty of pollen is around when these flowers have receptive stigmas. Protandry thus tends to reduce the probability of pollen transfer from first-position flowers but tends to increase it for last-position flowers (compared to an adichogamous species). Therefore, the reproductive success of first-position flowers is expected to be greater through female (relative to male) function, whereas the reverse pattern is expected in later-opening flowers. Our analysis confirms that this selects for lower (relative) allocation to male function in early-opening flowers and to lower female function in later-opening flowers. Protogyny creates the opposite pattern.

The female bias expected with protandry, for example, could manifest itself by hermaphroditic flowers opening earlier than male flowers in andromonoecious plants, female flowers opening earlier than hermaphroditic flowers in gynomonoecious plants (Pellmyr 1987), or early-opening hermaphroditic flowers allocating most of their resources to female functions, and later-opening flowers allocating more resources to male functions (Brunet 1990). The empirical evidence accumulated so far suggests that in andro- and gynomonoecious plants, early flowers are more female-biased than late flowers in protandrous species, whereas the reverse is true with protogyny (reviewed in Pellmyr 1987), although some exceptions exist (see Anderson and Symon 1989). It appears that species with hermaphroditic flowers do not necessarily allocate their reproductive resources equally among male and female functions (Lord 1980; Bawa and Webb 1983; Thomson 1989; Brunet 1990; Spalik and Woodell in prep.), and the pattern of variation is in some cases associated with dichogamy (Brunet 1990).

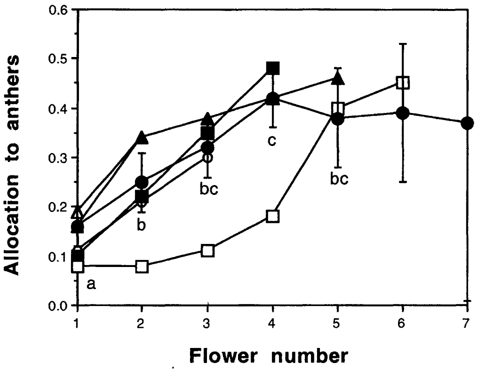

FIG. 5. Estimates of allocations to male function in flowers of successive positions in *Aquilegia caerulea,* in inflorescences with different numbers of flowers (filled circles show data for all flowers combined; inflorescences with different numbers of flowers are denoted as follows: open triangles, two-flowered inflorescences; open circles, three flowers; filled squares, four flowers; filled triangles, five flowers; open squares, six flowers). Allocation is expressed as the proportion of total dry weights of flowers and fruits that were due to anthers. For the combined data, error bars equal to 2 SE are shown, and letters indicate significant differences by Tukey's test.

Few allocation data exist for species with hermaphroditic flowers, but *Aquilegia caerulea,* a protandrous species, shows the predicted pattern (Brunet 1990). In inflorescences with 2–6 flowers, fruit dry weights showed a highly significant decrease from first to last flowers. Stamen weights tended to decrease very slightly with position, but the difference was significant only in two-flowered inflorescences. Figure 5 shows the allocation values calculated from these data. Similar patterns were found when sex allocation was measured before pollination. Ovule number and fruit and seed set decreased from early to late flowers (Brunet 1990, in prep.). In another population, first-position flowers produced seeds in 42.2% of carpels, compared with only 0.003% of flowers in the last position on the inflorescence (usually fourth to sixth position), a highly significant difference (44 [SE ± 1.0] and 41 [SE ± 0.001] flowers, respectively). The mean numbers of seeds in follicles with seeds were also much lower for last than for first flowers (first flowers: 26.3 ± 6.9; last flowers 0.098 ± 0.001). The differences were not caused by depletion of resources by seed maturation in early flowers. An experiment done in 1987 provides the evidence for this. Pollination in all but the last flowers of several inflorescences was prevented by covering the stigmas with straws. Fruit and seed set were zero in the 34 last-position flowers. When pollination was prevented for all but first-position flowers, fruit and seed set were increased, compared with control flowers at that position (fruit set, 80.8 ± 6.8; seed set, 119.4 ± 17.7; control values given above). Thus, although the results for first-position flowers strongly suggest that maturation of seeds in other flowers of the same inflorescence diminishes resources for first-position fruits and seeds and lowers their numbers, it is nevertheless not possible for flowers late in the sequences to use these resources to mature seeds. In other words, late flowers do not participate much in female reproduction.

To determine whether differences in the probabilities of pollen transfer are responsible for the observed variation in sex allocation among positions, one needs to quantify the influence of dichogamy on pollen-transfer probabilities. Data on flowering phenology similar to those of figure 1 can provide information on pollen-transfer probabilities for flowers at different positions. Species with the strongest degree of dichogamy should have the greatest differences in sex allocation among positions. For any level of dichogamy, the influence on pollen-transfer probabilities should also be greater in species where the number of days between expression of male and female function represents a significant fraction of the length of the flowering period for any position. Although the model requires differences in the flowering phenology of flowers at different positions, it does not require synchrony of flowering of different individuals. The magnitude of the differences in contributions to the pollen pools for stigmas of different flower positions will, however, depend on the degree of synchrony, which will therefore influence the quantitative patterns of allocation to be expected.

If all flowers on a plant open at the same time (simultaneous blooming) and if individual plants differ in their times of flowering, the probabilities of pollen transfer between individuals in a population will be affected like those between flowers at different positions discussed above. With protandry, pollen of early-flowering individuals has few stigmas to fertilize, but when these individuals are in the female stage, pollen will be plentiful. The reverse is true for individuals blooming late in the flowering season. If plants can adjust their sex allocation in response to the mating environment, one might expect early-flowering individuals to allocate relatively more reproductive resources to female function and later-opening individuals to allocate more to male function, as suggested by Pellmyr (1987). However, Pellmyr's discussion does not strictly apply to different allocations of flowers in the same inflorescences. Protogyny would create opposite patterns.

Pollinator Movement

If pollinators show directionality in their movements on inflorescences, this may influence the probability that pollen from given positions reaches stigmas at different positions. Pollinators that tend to move from bottom- to top-position flowers within inflorescences will go from top- to bottom-position flowers when moving between inflorescences. If pollinators pick up some fresh pollen from each flower visited while displacing some of the pollen previously collected, such that most pollen carried comes from the last flower visited, directionality of movements will influence the probability of pollen transfer among flowers. These assumptions seem biologically justified (Robertson 1992). This effect may be greatest in self-incompatible species, where pollen deposited on a plant's own stigmas will not lead to fertilization of ovules.

Bumblebees tend to move up inflorescences (Pyke 1979; Waddington and Heinrich 1979; Corbet et al. 1981; Best and Bierzychudek 1982; Haynes and Mesler 1984). Most of the plants in these studies were sequential bloomers with flowers at the bottom of inflorescences opening first. Waddington and Heinrich (1979) demonstrated that bees can learn to modify their pattern of movement depending on nectar rewards. This suggests that pollinator directionality may be quite common in hermaphroditic species. Although the influence of pollinator directionality on probability of pollen transfer and sex allocation among positions remains speculative at this point, it represents a plausible factor that deserves some empirical attention. To test whether directionality in pollinator behavior does indeed influence pollen-transfer probabilities, one could use color dyes to label pollen from flowers of different positions. At present we are aware of no such data, nor are data on allocations available.

Resource Variation

Besides differences in pollen-transfer probabilities, flowers at different positions also may vary in the total amounts of resources allocated to reproduction. Such variation could result if flowers at the base of the inflorescence appropriate more of the reproductive resources than do more distant flowers (Lee 1988), or from temporal processes if flowers opening earlier on the inflorescence start producing ovules and developing seeds earlier and acquire more of the reproductive resources via source-sink relationships (Lee 1988). In the models presented here, reproductive resources were assumed to vary among positions, but the relative amount of reproductive resources allocated to each position was fixed (was not allowed to evolve). We thus examined only the effect of resource variation on sex allocation among positions, not the evolution of this variation. Determining which factors influence the pattern of reproductive resource allocation is an interesting related question that has not been previously addressed, but it can be examined separately and is beyond the scope of the present work. This factor deserves further study, as it is likely to be of real biological importance. To date, other theoretical models that examined the factors influencing flower or inflorescence number on a plant (Cohen and Dukas 1990; Schoen and Dubuc 1990) have assumed constant costs per flower.

For variation in reproductive resources (without differences in pollen transfer) to influence floral sex allocation in sequentially blooming plants, the exponents of the female and male gain curves must differ from one another. The evolution of variation among flowers in sex allocation is then similar in principle to the evolution of variation among individuals when the distribution of resources vary. Different exponents of the male and female gain curves imply that the shape of the return function—that is, the relationship between investment in a sexual function and the reproductive return from that sexual function—differs for male and female investments. Following Frank (1987), positions with more reproductive resources should be biased toward the sexual function with the largest exponent to its gain curve (given exponents smaller than or equal to one). This is indeed what we found. According to these principles, when transfer probabilities for flowers at different positions are equal and when the exponents to the male and female gain curves are equal, no variation is expected in sex allocation among positions, even when resources vary among positions.

It is not known whether variation in reproductive resources influences variation in sex allocation among individuals and among flowers in natural populations of hermaphroditic plants. Empirical data are needed to determine this. As differences in pollen-transfer probabilities from different positions have a strong influence on sex allocation among positions, it is important to eliminate this factor from consideration. A first step would be to determine whether variation in sex allocation among flowers occurs in species where this factor does not apply, that is, in adichogamous hermaphrodites without pollinator directionality in which reproductive resources differ among positions. If variation in sex allocation among flowers is common in such populations, one can then ask whether the mechanism proposed here can explain it. This would require measuring the shapes of the male and female gain curves in natural populations—a very difficult task.

Selfing-Rate Differences

With synchronous flowering and dichogamy (Lloyd and Webb 1986) or temporal dioecism (Cruden and Hermann-Parker 1977), there is no overlap of pollen presentation and stigma receptivity among flowers within a plant, and hence no geitonogamous selfing. Strong within-flower dichogamy reduces within-flower selfing. In sequential bloomers, certain combinations of flowering phenology and dichogamy can cause variation in selfing rate among flowers. With protandry, if first-position flowers on a plant open synchronously a few days before later-position flowers, first-position flowers will generally reach the female stage when later-position flowers are in the male stage. Selfing rates may then be greater in early flowers than in later ones.

Whether variation in selfing rate among hermaphroditic flowers exists in natural populations of dichogamous sequential bloomers awaits investigation. However, variation in selfing rates expected in the situations just described is unlikely to have a major influence on sex allocation among flowers. Our results indicate that selfing-rate differences among flowers can influence sex allocation to a major extent only when the pollen-transfer probabilities do not differ. Dichogamy in sequential bloomers would most likely create variation in pollen-transfer probabilities among positions, which would generally be the dominant factor controlling allocation patterns of flowers.

The Evolution of Andromonoecy and Monoecy

The role of dichogamy and pollinator directionality in the evolution of plant breeding systems has received some attention (Webb 1981; Lloyd and Webb 1986), but these effects have not previously been incorporated into allocation models. Our results suggest that temporal variation in pollen donation and receipt may play a role in the evolution of these breeding systems. Large differences in the transfer probabilities for pollen from different flower positions can lead to the evolution of andromonoecy and monoecy in sequential bloomers. These models support the view that the evolution of andromonoecy is based on allocation of resources, in particular where male flowers enhance male fitness through pollen donation (Bertin 1982). They also show that avoidance of inbreeding need not be a condition for the evolution of monoecy, as was already clear empirically because some monoecious species are self incompatible (Lloyd and Webb 1986).

Modular Approach to Sex Allocation

Stanton and Galloway (1990) have previously examined how floral sex allocation can influence an individual's reproductive success. In their model, floral sex allocations are randomly assigned to individuals, and each flower on a plant is identical. Owing to this assumption, their work does not examine the evolution of floral sex allocation, although they stress the importance of considering the modular structure of plant reproduction when dealing with sex allocation. The model presented here explicitly introduces the modular nature of inflorescences into sex-allocation theory.

Although discussed mostly in terms of flowers within inflorescences, the model analyzed here can of course be applied to units other than flowers, such as umbels, inflorescences, or tillers. As long as they open sequentially on a plant, and flowering is fairly synchronous within these units, one can assign positions to units, according to the order in which their flowers open, and then examine sex-allocation patterns among them. Similarly, on plants with many flowers, sex allocation can be examined among groups of flowers on the inflorescence, where flowers within sufficiently synchronous groups can be identified as different "positions" in terms of the model presented here.

Conclusion

The chief conclusion of these calculations is that the evolution of allocations to male and female functions can be affected by pollen-transfer probabilities between different flowers and by differences in the total resources plants devote to different positions when the gain curves relating reproductive success to allocation differ for the two sex functions. Both kinds of differences between flowers are biologically plausible, and there is some empirical evidence for their occurrence. We have also reviewed the small amount of evidence suggesting that differences in maleness actually occur between flowers of plants that seem to satisfy the conditions of our model (principally, that blooming is sequential). This correspondence in a situation where different flowers on individual plants are considered, and there are no confounding factors such as environmental or genetic differences between individuals, validates the allocation approach.

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Appendix

Method of Analysis

The method is based on a quantitative-genetic approach that assumes that the evolution of a character is determined by the vector of partial derivatives of fitness with respect to the parameters of interest, together with a matrix of additive variances and covariances (Charlesworth 1990). We describe the analysis for the most general case studied, in which the reproductive resources may be allocated to the three functions, male and female primary reproductive structures, and structures for pollinator attraction. The ESS values of the male, female, and attraction-allocation parameters for flowers at the jth position are denoted by M_j, F_j, and A_j, where $F_j = 1 - M_j - A_j$. For this example, the vector of derivatives of fitness with respect to the allocation parameters under selection can be written as

$$\nabla \bar{w} = \left(\frac{\partial \bar{w}}{\partial \bar{M}}, \frac{\partial \bar{w}}{\partial \bar{A}}, \frac{\partial \bar{w}}{\partial \bar{F}}\right) \tag{A1a}$$

$$\approx \left(\left[\frac{\partial w}{\partial M}\right]_M + \left[\frac{\partial w}{\partial A}\right]_A + \left[\frac{\partial w}{\partial F}\right]_F\right), \tag{A1b}$$

where w is the fitness expression. To obtain the matrix of variances and covariances, we use the relation: $\delta F = -(\delta M = \delta A)$, which gives:

$$V_A(F) \approx V_A(M) + V_A(A), \tag{A2a}$$

$$C_A(F, M) \approx -V_A(M), \tag{A2b}$$

$$C_A(F, A) \approx -V_A(A). \tag{A2c}$$

The matrix of additive genetic variances and covariances is therefore:

$$G = \begin{bmatrix} V_A(M) & 0 & -V_A(M) \\ 0 & V_A(A) & -V_A(A) \\ -V_A(M) & -V_A(A) & -V_A(F) \end{bmatrix}. \tag{A3}$$

These expressions were used to compute the vector of allocation values in the next generation, and the calculations were iterated until the vector of allocations converged.