INVASION OF UNISEXUALS IN HERMAPHRODITE POPULATIONS OF ANIMAL-POLLINATED PLANTS: EFFECTS OF POLLINATION ECOLOGY AND FLORAL SIZE-NUMBER TRADE-OFFS

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Abstract.—The most common sexual system in animal-pollinated plants is hermaphroditism, while some species are dioecious or gynodioecious and a very few are androdioecious. In this paper, I attempt to explain this pattern by extending previous models for the evolution of sexual systems to incorporate two main features: (1) a portion of investment in pollinator attraction contributes to only female or male function, because one sexual function of a flower is saturated with pollinator visitation earlier than the other sexual function; and (2) there are trade-offs between the size and number of flowers. The analysis was conducted to determine the conditions when females and males can increase in frequency in a hermaphroditic population, assuming either concave or convex pollinator gain curves (relation between investment to attractive structures of a flower and frequency of pollinator visits to the flower). The results suggest that both of the main factors play important roles in the evolution of plant sexual systems: uneven contribution of pollinator-attractive structures and nonlinear trade-offs between flower size and number can destabilize hermaphroditism. When a convex pollinator gain curve was assumed, the effect of nonlinear trade-offs can produce accelerating compensation from the elimination of one sexual function, allowing males to increase for large regions of parameter space, where females could not increase. The last prediction obviously conflicts with the observed rarity of androdioecy in nature, indicating the necessity of exploring pollinator gain curves in more detail.

Key words.—Androdioecy, dioecy, gynodioecy, hermaphroditism, pollinator attraction, sexual systems, size-number trade-offs.

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Most angiosperm species are hermaphroditic, some are dioecious (females and males) or gynodioecious (hermaphrodites and females), and a very few are androdioecious (hermaphrodites and males; Darwin 1877). Previous theoretical studies commonly attribute the higher frequency of hermaphroditism to the fact that pure females or males only contribute to future generations through seed or pollen, respectively. That is, for females or males to invade a large outcrossing hermaphroditic population, they must be at least twice as fit in terms of female or male function, respectively, than hermaphrodites (Llovd 1975; Charlesworth and Charlesworth 1978). The conditions for males to invade become more restricted with increased selfing by hermaphrodites, because selfing reduces the number of ovules available for fertilization by males. It is easier, however, for females to invade hermaphroditic populations when partial selfing occurs with strong inbreeding depression, because females will, on average, produce more high-quality outcrossed seeds than hermaphrodites (Lloyd 1975; Charlesworth and Charlesworth 1978). This is considered to be the main reason for the greater frequency of gynodioecy than androdioecy in nature.

It has been proposed that investment in the structures used by plants to attract biotic pollinators (e.g., perianth) favors hermaphroditism over other sexual systems, because pollinator attraction is a prerequisite for both pollen donation and receipt (Ghiselin 1974; Charnov et al. 1976; Givnish 1980). Morgan (1992) analyzed the role of pollinator-attractive structures in the evolution of plant sexual systems. He constructed a model involving allocation of a limited resource between attractive structures, which benefits both sex functions, and predicted that the spread of females or males in hermaphroditic populations requires at least one of the following conditions, even if hermaphrodites largely depend on self-fertilization for their reproduction: (1) greater allocation to female or male functions results in accelerating gains in female or male fitness; or (2) substantial asymmetry in the benefits accruing to female and male fertility for a given investment in pollinator attraction. However, as Morgan himself pointed out, most empirical studies have suggested that neither of these conditions is satisfied in a wide range of plant species. Thus, for plants with pollinator attractive-structures, it remains uncertain what conditions destabilize hermaphroditism.

In Morgan's model, it was assumed that all investment in pollinator attraction by hermaphrodites is a common cost for both male and female functions, although these functions can have different patterns of diminishing gains. However, a portion of investment in pollinator attraction may contribute to only one of the two sexual functions, because one sexual function of a flower can be saturated with pollinator visitation earlier than the other sexual function of the same flower. The following three simple cases are possible. A portion of the investment in pollinator-attraction benefits: (1) only female function (female priority); (2) only male function (male priority); or (3) all investment in pollinator attraction increases both sexual functions equally (equal priority). Male or female priority would destabilize hermaphroditism, because the relative advantage of hermaphrodites over unisexuals is decreased. However, the effects of priority in pollinator-attractive structures on the evolution of sexual systems have never been examined.

Previous models for the evolution of plant mating systems have typically assumed that trade-offs involving reproductive resource occur only within a flower. Investigators have attempted to quantify those trade-offs by demonstrating neg-

Symbol	Definition			
Parameters subjected to natural selection				
$egin{array}{c} N_x & A_x & A_x & F_x & A_x & M_x & $	number of flowers per individual resources allocated to attractive structure per flower number of ovules produced per flower number of pollen grains produced per flowers			
Constants involved in reproductive resource allocation				
T C	total resource available for reproduction per individual (>0)			
c_o c_p	cost of producing one pollen grain (>0)			
ά	nonlinear constraint against increasing flower size (≥ 1) fixed cost of producing one flower (≥ 0)			
Constants involved in reproductive success				
e	number of ovules cross-fertilized by one pollinator visit			
e_p	number of pollen exported by one pollinator visit $c_{0} = c_{0} + c_$			
s d V(A)	inbreeding depression, defined as $1 - (fitness of selfed progeny/fitness of outcrossed progeny), (0-1) frequency of pollinator visits, a function of A, which satisfied V(0) = 0$			

TABLE 1. List of parameters in the model and their definitions. In the text, subscripts on parameters N, A, F, and M stand for the sexual type of the parameters; h, f, and m stand for hermaphrodite, female, and male, respectively.

ative genetic or phenotypic correlations among traits within flowers. However, it is generally observed that pollen production, ovule production, and petal size correlate positively, not negatively, thus casting doubt on the generality of tradeoffs within flowers (for a review, see Fenster and Carr 1997). Lack of evidence for trade-offs within flowers would be expected, if trade-offs occur mainly between investment per flower (hereafter referred to as "flower size") and number of flowers. In fact, a recent study demonstrated that plants with larger flower size have fewer flowers, whereas the dry masses of organs in a flower were positively correlated with each other (Sato and Yahara 1999; but see Worley and Barrett 2000). This suggests that trade-offs between size and number of flowers may be stronger and more general than trade-offs within flowers.

Here, I construct a phenotypic model to analyze how priority in pollinator attractive structure and size-number tradeoffs affect conditions for female and male invasion of hermaphroditic populations with an evolutionarily stable strategy (ESS) allocation and use this model to discuss the conditions required to explain the general pattern in the evolution of plant sexual systems in nature.

THE MODEL

Resource-limit Equations

The parameters are summarized in Table 1. Basic construction of the resource-limit equation of hermaphrodites (wild type) is identical to the "competing and delayed selfing model with nonlinear constraint on flower number and size" in Sakai (1995). In the model, it was assumed that a quantity, *T*, of some resource (e.g., carbon) is available to each individual for reproduction per individual. For algebraic simplicity, the model also assumed an annual life history and no variation in *T* among individuals. In hermaphrodites, *T* is divided equally among N_h flowers of resource cost $A_h + c_o F_h$ + $c_p M_h + \beta$, and thus, can be expressed as

$$T = N_h (A_h + c_o F_h + c_p M_h + \beta)^{\alpha}.$$
(1a)

In this equation, $c_o F_h$ and $c_p M_h$ are the resources allocated

to female and male structures per flower, respectively. Thus, for female or male sterile mutants, T can be expressed as

$$T = N_f (A_f + c_o F_f + \beta)^{\alpha} \quad \text{and} \tag{1b}$$

$$T = N_m (A_m + c_p M_m + \beta)^{\alpha}, \qquad (1c)$$

respectively. Here, subscripts on parameter *N*, *A*, *F*, and *M* represent the sexual type of the individual; *h*, *f*, and *m* represent hermaphrodites, females, and males, respectively. The constant α (\geq 1) represents nonlinear constraints against flower size, which prevents plants producing very large flowers. I included α because the cost of producing a flower probably increases disproportionately with flower size due to resource translocation (Sakai and Harada 2001; see Discussion) and mechanical support or herbivore defense. The constant β (\geq 0) represents the minimum cost of producing a flower, which prevents plants from producing a very large number of flowers even if *A*, *M*, and *F* are very small. I assumed $\beta = 1$ for the numerical calculations in this study.

Fitness Equations

Basic construction of the fitness equation of hermaphrodites is identical to that of Sakai (1993). The fitness of hermaphrodites (denote ϕ_h) consists of reproductive success through selfed seeds, outcrossed seeds, and pollen involved in outcross fertilization on other plants. Reproductive success of females (ϕ_f) derives only from outcrossed seeds, whereas that of males (ϕ_m) derives only from pollen involved in outcross fertilization on other plants.

In the model, reproductive success through selfed seeds in hermaphrodites is expressed as $s(1 - d)F_hN_h$, where *s* is the selfing rate and *d* is inbreeding depression. Here, *s* is assumed to be a constant for simplicity. The reproductive success through outcrossed seeds is expressed as min[$(1 - s)F_h$, $e_oV(A_h)]N_h/2$ for hermaphrodites and min[F_f , $e_oV(A_f)]N_f/2$ for females; min[*x*,*y*] stands for the smaller value of *x* and *y*. Thus, if the number of nonselfed ovules ($[1 - s]F_h$ for hermaphrodites, and F_f for females) is smaller than that of outcrossed pollen captured by a flower ($e_oV[A]$), all nonselfed ovules form outcrossed seeds, but only $e_oV(A)$ ovules of a flower form outcrossed seeds in other cases. The numerator is divided by two because the relatedness of outcrossed seeds to the maternal parent is 0.5. Reproductive success via pollen is $W \min[M, e_pV(A)]N/2$ for both hermaphrodites and males. This equation assumes that all pollen is successfully exported if the amount of pollen produced per flower, M, is smaller than potential pollen export, $e_pV(A)$, but only $e_pV(A)$ grains are exported in other cases. Again, the numerator is divided by two, because the relatedness of seeds fertilized on other plants to the paternal parent is also 0.5. Here,

$$W = \frac{\min[(1 - s)F_h^*, e_o V(A_h^*)]}{\min[M_h^*, e_p V(A_h^*)]},$$
(2)

which represent the ratio of outcrossed seeds to pollen grains successfully exported by hermaphrodites. An asterisk on parameters indicates that the parameters have evolutionarily stable values. Note that the effect of rare sterile mutants on *W* was neglected, because I only examined whether a mutant can increase in frequency when introduced into a large hermaphroditic population.

Accordingly, reproductive success of hermaphrodites, females, and males can be expressed as follows, respectively:

$$\phi_h = \{s(1 - d)F_h + \min[(1 - s)F_h, e_o V(A_h)]/2$$

+
$$W \min[M_h, e_p V(A_h)]/2 N_h,$$
 (3a)

$$\phi_f = \min[F_f, e_o V(A_f)] N_f / 2, \quad \text{and} \tag{3b}$$

$$\phi_m = W \min[M_m, e_p V(A_m)] N_m / 2. \tag{3c}$$

ESS Resource-Allocation of Hermaphrodites

For each hermaphroditic population under the three priorities, ESS resource-allocation of hermaphrodites was calculated. In keeping with Sakai (1993), I assumed: (1) under female priority, a hermaphroditic flower produces maximum number of ovules that can be outcrossed with A_h^* (i.e., [1 $s]F_h^* = e_o V[A_h^*]$; (2) under male priority, a hermaphroditic flower produces the maximum number of pollen that can be exported with A_h^* (i.e., $M_h^* = e_p V[A_h^*]$); and (3) under equal priority, a hermaphroditic flower produces maximum numbers of ovules and pollen that can be outcrossed and exported with A_h^* (i.e., $[1 - s]F_h^* = e_o V[A_h^*]$ and $M_h^* = e_p V[A_h^*]$). The reason for these assumptions is, when a flower produces more gametes than above, a fraction of ovules or pollen is wasted without fertilization or export. Also, when a flower produces fewer gametes than given by A_h^* , a fraction of pollinator attraction is wasted. Therefore, $\min[(1 - s)F_h^*, e_oV(A_h^*)]$ and $\min[M_h^*, e_p V(A_h^*)]$ in equation (2) should be $e_o V(A_h^*)$ and M_h^* for female priority, $(1 - s)F_h^*$ and $e_pV(A_h^*)$ for male priority, and $e_o V(A_h^*)$ and $e_p V(A_h^*)$ for equal priority. From these arguments, equation (2) can be written as follows for each priority:

under female priority:
$$W = \frac{e_o V(A_h^*)}{M_h^*},$$
 (4a)

under male priority:
$$W = \frac{(1 - s)F_h^*}{e_p V(A_h^*)}$$
, and (4b)

under equal priority: $W = \frac{e_o V(A_h^*)}{e_p V(A_h^*)}.$ (4c)

ESS allocations of hermaphrodites for each priority, when all parameters $A_{h\nu}$ $F_{h\nu}$ $M_{h\nu}$ and N_h were subject to selection, were obtained by calculations similar to Sakai (1993), using equations (1), (3), and (4). In the calculations, I applied the method of Lagrange's multiplier, which enables us to treat constraint-maximization problems as unconstrained-stationary problems (Intriligator 1971); a stationary point in the analysis gives maximum fitness under constraint of the resource-limit equation. For the each priority, I obtained only one stationary point in the analysis that satisfies $N_h^* > 0$, $A_h^* > 0$, $F_h^* > 0$, and $M_h^* > 0$. The results are summarized in Table 2.

Range of Each Priority

From the definition of priority, female priority occurs when $e_pV(A_h^*) > M_h^*$, and male priority occurs when $e_oV(A_h^*) > (1 - s)F_h^*$. By substituting M_h^* of female priority and F_h^* of male priority into these inequalities, I calculated the condition of each priority (Table 2). Using the conditions and A_h^* of each priority, areas of the parameter space resulting in equal, female, and male priority were calculated numerically (Fig. 1). To evaluate the effects of V(A) shape on the results, all numerical calculations in this study were conducted under each of the following definitions of V(A):

$$V(A) = \log(A + 1)$$
, and (5a)

$$V(A) = \frac{k}{1 + \frac{k - a}{e^{rA}}} - a \qquad (r = 1, k = 2, a = 1).$$
(5b)

Equation (5a) is a logarithmic function and (5b) is a sigmoidal function. Both of the equations satisfy V(0) = 0.

The reason I chose these functions as V(A) is that both of them are diminishing-gain functions, but each function has different properties: concave and convex (at least for small A values). V(A) must be diminishing-gain functions under assumption of trade-offs between flower number and size. Because, if this is not the case (i.e., V[A] is a linear- or accelerative-gain function), then each plant should produce only one large flower when $\alpha = 1$ and $\beta > 0$. This situation would be unrealistic in most of plant species.

In both V(A) functions, types of priority in hermaphroditic population with ESS allocation were mainly determined by c_oe_o and c_pe_p (Fig. 1a). Most of the parameter space around $c_oe_o > c_pe_p$, $c_oe_o \approx c_pe_p$, and $c_oe_o < c_pe_p$ resulted in male, equal, and female priority, respectively. Here, c_oe_o and c_pe_p are the cost of producing one gamete times the number of gametes exported or received per visit, and hence represent the cost of producing outcross gametes per visit, when unfertilized ovules and unexported pollen remain in the flower. Accordingly, it follows that: (1) male priority chiefly occurred when cost of producing gametes per visit was higher for outcrossing seed than pollen; (2) equal priority chiefly occurred when it was almost same for outcrossing seed and pollen; and (3) female priority chiefly occurred when it was higher for pollen than outcrossing seed.

Conditions for the Spread of Females and Males

I investigated conditions for the spread of females and males, when they are introduced into a large hermaphroditic

TABLE 2. Conditions under which the investment in pollinator attraction contributes only to female function (female priority), only to male function (male priority), and equally to both sexual functions (equal priority). For each priority, ESS allocation of hermaphrodites was also presented.

Priority	Condition	ESS allocation of hermaphrodites
Female priority	$[(1 + s - 2sd)c_p e_p - c_o e_o]V'(A_h^*) > 1 - s$	$A_{h}^{*} = V(A_{h}^{*}) \left\{ \frac{1}{V'(A_{h}^{*})} + (\alpha - 1) \frac{2(1 - sd)}{1 + s - 2sd} \left[\frac{c_{o}e_{o}}{1 - s} + \frac{1}{V'(A_{h}^{*})} \right] \right\} - \beta$
		$N_{h}^{*} = T \left/ \left\{ \frac{2(1-sd)}{1+s-2sd} \alpha V(A_{h}^{*}) \left[\frac{c_{o}e_{o}}{1-s} + \frac{1}{V'(A_{h}^{*})} \right] \right\}^{\alpha}$
		$F_h^* = e_o V(A_h^*)/(1 - s)$
		$M_{h}^{*} = \frac{1-s}{c_{p}(1+s-2sd)}V(A_{h}^{*})\left[\frac{c_{o}e_{o}}{1-s} + \frac{1}{V'(A_{h}^{*})}\right]$
Male priority	$[(1 + s - 2sd)c_p e_p - c_o e_o]V'(A_h^*) < -(1 + s - 2sd)$	$A_{h}^{*} = V(A_{h}^{*}) \left\{ \frac{1}{V'(A_{h}^{*})} + (\alpha - 1) \frac{2(1 - sd)}{1 + s} \left[c_{p} e_{p} + \frac{1}{V'(A_{h}^{*})} \right] \right\} - \beta$
		$N_{h}^{*} = T \left/ \left\{ \frac{2(1 - sd)}{1 - s} \alpha V(A_{h}^{*}) \left[c_{p} e_{p} + \frac{1}{V'(A_{h}^{*})} \right] \right\}^{\alpha}$
		$F_{h}^{*} = \frac{1 + s - 2sd}{c_{o}(1 - s)} V(A_{h}^{*}) \left[c_{p} e_{p} + \frac{1}{V'(A_{h}^{*})} \right]$
		$M_h^* = e_p V(A_h^*)$
Equal priority	Cases other than those above	$A_{h}^{*} = V(A_{h}^{*}) \left\{ \frac{1}{V'(A_{h}^{*})} + (\alpha - 1) \left[c_{p} e_{p} + \frac{c_{o} e_{o}}{1 - s} + \frac{1}{V'(A_{h}^{*})} \right] \right\} - \beta$
		$N_{h}^{*} = T \left/ \left\{ \alpha V(A_{h}^{*}) \left[c_{p} e_{p} + \frac{c_{o} e_{o}}{1 - s} + \frac{1}{V'(A_{h}^{*})} \right] \right\}^{\alpha}$
		$F_h^* = e_o V(A_h^*)/(1 - s)$
		$M_h^* = e_p V(A_h^*)$

population at the ESS allocation. This procedure implicitly assumes two types of mutations can occur that affect the sexual allocation: (1) mutations of small effect, which allow hermaphrodites to reach ESS allocation; and (2) sterility mutations of large effect, which allow unisexuals to exist in the hermaphroditic ESS population.

A sterile mutant can increase in frequency if its fitness is greater than the mean fitness of hermaphrodites. I identified the reallocation strategy giving the sterile mutants maximal fitness when introduced into the ESS hermaphroditic population. This is the approach adopted by Morgan (1992). Hermaphroditic populations in which these reallocation mutants do not increase in frequency are stable against all sterile resource reallocation mutants. Using this criterion, I calculated the optimal resource allocation of females and males (Appendix) and summarize the results in Table 3. I calculated conditions for the spread of sterile mutants (Table 4) by substituting the ESS allocation of hermaphrodites (shown in Table 2), optimal allocation of females and males (shown in Table 3), and W for each priority (equations 4a–c) into the fitness equations (equations 3a–c).

From these conditions, areas of the parameter space where unisexuals can increase in frequency were calculated numerically (Fig. 2). In contrast to the previous model, my model predicts that unisexuals can increase in frequency over a wide range of parameters, while it includes costs of pollinator attraction. Under combination of high self-fertilization and strong inbreeding depression, females can increase in frequency regardless of the shapes of pollinator gain function. When no self-fertilization occurs (i.e., s = 0.0), invasion by unisexuals requires a nonlinear constraint against increasing flower size (i.e., $\alpha > 1.0$) and a sigmoidal pollinator gain curve. In this case, females can invade for most female-priority ranges of $c_o e_o$ and $c_p e_p$, males invade for most male-priority ranges, but neither unisexual invades for equal-priority ranges.

DISCUSSION

Evolutionary Stability of Hermaphroditism

Hermaphroditism can be destabilized over a wide range of parameters (Fig. 2), even if the cost of pollinator attraction is taken into consideration. Morgan (1992) showed that hermaphroditism of animal-pollinated plants can be destabilized when there is substantial asymmetry in benefits accruing to fertility for a given investment in pollinator attraction (i.e., gain-curves) between ovule fertilization and pollen donation. However, he also pointed out that empirical studies suggest that shape of gain-curves do not differ substantially between sexual functions, leaving open the question of evolution of sexual systems that include unisexuals in animal-pollinated

 $-C_{p} \times e_{p}$ -(Cost of pollen per visit) Areas of parameter space resulting in equal, female, and FIG. 1. male priority, when V(A) was (a) a logarithmic function and (b) a sigmoidal function of investment in attractive structures. Each type of line corresponds to a particular value of α , as indicated on the figure. For each type of line, the area between the two lines results in equal priority, and the lower right and upper left areas of the equal-priority area result in female priority and male priority, respectively. This evaluation was conducted for each combination of three values of s (selfing rate) and two values of d (inbreeding

depression), each presented in a separate panel. $\beta = 1$ was assumed

10 0

10 0

0

for the all calculations.

plants. Although my model assumed both of the sexual functions share identical shapes of pollinator gain-curves, it also assumed that one sexual function of a flower could be saturated with pollinator visitation earlier than another sexual function of a flower. This assumption of priority is one reason for destabilizing hermaphroditism in my model, because the advantage of hermaphrodites relative to unisexuals should be reduced under female or male priority, where a fraction of pollinator-attractive cost contributes only to female or male function. In fact, the model predicts that hermaphroditism is

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10

TABLE 3. Optimal resource allocation of females and males when introduced into a large hermaphroditic population with ESS allocation.

likely to be an ESS for most of the equal-priority areas, where the whole cost of pollinator attraction is shared by both female and male function (Fig. 2). Therefore, these results suggest that sexual systems including unisexuality are likely to evolve in taxa for which a larger portion of pollinator-attractive organs contribute to only one sexual function. However, to test this prediction using comparative analysis might be difficult, because hermaphroditic species with such a large, disproportionate, attractive organ would be evolutionary unstable, and thus unlikely to exist in nature.

Another factor that destabilizes hermaphroditism in the model is nonlinear trade-offs between flower size and number; areas of parameter space where unisex can increase in frequency were generally larger if the trade-offs are nonlinear (Fig. 2). This effect of nonlinear trade-offs was commonly magnified by a sigmoidal V(A) function. For example, when s = 0.0, hermaphroditism can be destabilized only when V(A)is sigmoidal (Fig. 2). The reason for this would be: (1) nonlinear trade-offs occur between flower size and number limit flower size, and (2) this limitation decreases the number of ovules or pollen within a flower, while it does not significantly reduce the cost of pollinator attraction in a flower, because V(A) is sigmoidal. Consider an extreme situation, where flower size and the cost of pollinator attraction are nearly constant. Under male priority, for example, hermaphroditic flowers allocate more of resource to ovules than to pollen (e.g., in the case of s = 0.0, allocation to ovules is $c_o F^* = c_p e_p V[A_h^*] + V[A_h^*]/V'[A_h^*]$, while allocation to pollen is $c_p M^* = c_p e_p V[A_h^*]$, because a portion of pollinator-attractive cost is allocated to male function and it consumes resource to produce pollen. In this case, males can produce more than twice as much pollen as hermaphrodites, because, as I assumed, males and hermaphrodites have almost identical flower size and the cost of pollinator attraction, allowing reallocation to occur only between pollen and ovule production within a flower. Even if males produce excess pollen, pollinator visitation hardly limits its dispersal, because the number of gametes within a flower is restricted by the nonlinear trade-off, not by efficiency of pollinator-attraction.

Priority	Mutant	Range of parameter space where sterility mutant can increase in frequency
Female priority	females (male sterility)	$\left[\frac{1+s-2sd}{2(1-sd)}\frac{V(A_{f}^{*})}{V(A_{h}^{*})}\frac{c_{o}e_{o}+\frac{1}{V'(A_{f}^{*})}}{\frac{c_{o}e_{o}}{1-s}+\frac{1}{V'(A_{h}^{*})}}\right]^{\alpha} < \frac{1-s}{2(1-sd)}\frac{V(A_{f}^{*})}{V(A_{h}^{*})}$
	males (female sterility)	$\left[\frac{1+s-2sd}{2(1-sd)}\frac{V(A_m^*)}{V(A_h^*)}\frac{c_p e_p + \frac{1}{V'(A_m^*)}}{\frac{c_o e_o}{1-s} + \frac{1}{V'(A_h^*)}}\right]^{\alpha} < \frac{1+s-2sd}{2(1-sd)}\frac{V(A_m^*)}{V(A_h^*)}\frac{c_p e_p}{\frac{c_o e_o}{1-s} + \frac{1}{V'(A_h^*)}}$
Male priority	females (male sterility)	$\left[\frac{1-s}{2(1-sd)}\frac{V(A_{f}^{*})}{V(A_{h}^{*})}\frac{c_{o}e_{o}+\frac{1}{V'(A_{f}^{*})}}{c_{p}e_{p}+\frac{1}{V'(A_{h}^{*})}}\right]^{\alpha} < \frac{(1-s)}{2(1-sd)(1+s-2sd)}\frac{V(A_{f}^{*})}{V(A_{h}^{*})}\left[\frac{c_{o}e_{o}}{c_{p}e_{p}+\frac{1}{V'(A_{h}^{*})}}\right]$
	males (female sterility)	$\left[\frac{1-s}{2(1-sd)}\frac{V(A_m^*)}{V(A_h^*)}\frac{c_p e_p + \frac{1}{V'(A_m^*)}}{c_p e_p + \frac{1}{V'(A_m^*)}}\right]^{\alpha} < \frac{1-s}{2(1-sd)}\frac{V(A_m^*)}{V(A_h^*)}$
Equal priority	females (male sterility)	$\left[\frac{V(A_f^*)}{V(A_h^*)} \frac{c_o e_o + \frac{1}{V'(A_f^*)}}{c_p e_p + \frac{c_o e_o}{1 - s} + \frac{1}{V'(A_h^*)}}\right]^{\alpha} < \frac{1 - s}{2(1 - sd)} \frac{V(A_f^*)}{V(A_h^*)}$
	males (female sterility)	$\left[\frac{V(A_m^*)}{V(A_h^*)} \frac{c_p e_p + \frac{1}{V'(A_m^*)}}{c_p e_p + \frac{c_o e_o}{1 - s} + \frac{1}{V'(A_h^*)}}\right]^{\alpha} < \frac{1 - s}{2(1 - sd)} \frac{V(A_m^*)}{V(A_h^*)}$

TABLE 4. Condition for females and males to increase in frequency when introduced into a large hermaphroditic population with ESS allocation.

Therefore, males can increase in frequency for large areas of the parameter space where male priority occurs, and vice versa for invasion of females in female-priority areas (Fig. 2).

This result is the same as the classical results from Lloyd (1975) and Charlesworth and Charlesworth (1978): If there is accelerating compensation from the elimination of one sexual function, then hermaphroditism is destabilized. Otherwise, another noncompensatory source of unisexual advantage is required: in the case of females, the outcrossing advantage (i.e., in Fig. 2, females can increase in frequency for a large range of parameters under a combination of self-fertilization and high inbreeding depression). The difference and originality of this model is the source of that accelerating fitness gain: (1) a nonlinear trade-off between flower size and number; and (2) a convex function of investment in attractants and pollinator visitation.

Why Invasion of Males in Hermaphrodites Is Rare in Nature

The model only treats invasion of unisexuals (female or male) in populations of hermaphrodites. As unisexual plants become well established, there may be selection for gender segregation with a gradual reduction in the seed or pollen fecundity of hermaphroditic plants, leading to the evolution of dioecy. Even if this possibility was taken into consideration, the prediction that males can exclusively increase in frequency for a large range of parameter space contradicts the fact that androdioecy is extremely rare (Darwin 1877) and there are no authenticated examples of the evolution of dioecy from androdioecy, although the pathway to dioecy from gynodioecy seems very common (e.g., Connor 1972; Arroyo and Raven 1975; Trexler and Travis 1990; Weller and Sakai 1990).

This contradiction between prediction and observation raises the question of whether the assumption of sigmoidal pollinator gain-curve is met in nature. This is because if it is a sigmoidal function (convex function, at least when A is small), the model predicts that males can increase in frequency for a large range of parameter space, where females cannot increase. Although the spread of males also requires both occurrence of male-priority and nonlinear size-number trade-offs, they are likely to be satisfied in many animalpollinated plants, as shown below. Bell (1985) suggest that male priority generally happens in animal-pollinated plants, because artificial reduction of pollinator-attractive organs of several species decreased the amount of pollen exported from flowers but not seed production. His suggestion is consistent with results from other species (Stanton et al. 1986; Campbell 1989), indicating that male priority widely occurs in animalpollinated plants. Female and equal priority may also be common, however, because outcrossed seed production is limited

FIG. 2. Area of parameter space resulting in females and males can increase in frequency when they are introduced into a hermaphroditic population with ESS allocation. V(A) was assumed to be (a) a logarithmic function and (b) a sigmoidal function of investment in attractive structures. For each of the V(A) functions, this evaluation was conducted for each of three values of α , three values of s (selfing rate), and two values of d (inbreeding depression), each presented in a separate panel. $\beta = 1$ was assumed for all the calculations.

by pollinator visitation in many species (reviewed by Burd 1994). There are no empirical studies quantifying the degree of nonlinearly in the size-number trade-offs of flower, as far as I know. However, a theoretical study showed that sizenumber trade-offs should be nonlinear due to metabolic factors; the organism can reduce the time needed to complete organ growth by increasing the number of organs, and faster completion of organ growth reduces the loss of resources due to maintenance respiration, resulting in a larger total size organ (Sakai and Harada 2001). Sakai (2000) provided some support for this prediction, showing that nonlinearity explains general trends in the size of attractive structures of a flower (i.e., the size of attractive structures is smaller in male flowers than in female flowers in dioecious plants, and flower size decreases with an increase in self-fertilization among hermaphroditic plants).

In spite of the importance of pollinator gain curves for the evolution of plant sexual systems, few studies have attempted to quantify them. Data of Bell (1985) would suggest the gain curve is linear in *Fragaria virginiana*, because per-flower visitation increases steeply and linearly with petal mass. Work by Kudoh and Whigham (1998) on *Hibiscus moscheutos*, however, suggests a concave gain curve, because pollinators ignored flowers of 100% petal-removal treatment, but did not significantly discriminate between flowers of the 50% and 0% removal treatments. Clearly, more studies of this sort are needed.

Other possible explanations for the extreme rarity of male invasion in hermaphrodite populations might come from factors that the model did not include. For example, Pannell (1997) emphasized the importance of metapopulation dynamics for favoring the maintenance of females (gynodioecy) over males (androdioecy) with hermaphrodites, when colonies are ephemeral and site recolonization is important. On the other hand, Seger and Eckhart (1996) showed that females are favored over males when male allocation precedes female allocation, when growth and reproduction overlap temporally, and when there is a trade-off between them. In future studies on the evolution of plant sexual systems, the relative importance of these factors will need to be examined theoretically.

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LITERATURE CITED

- Arroyo, M. T. K., and P. H. Raven. 1975. The evolution of subdioecy in morphologically gynodioecious species *Fuchsia* sect. *Encliandra* (Onagraceae). Evolution 29:500–511.
- Bell, G. 1985. On the function of flowers. Proc. R. Soc. Lond. B 224:223–265.
- Burd, M. 1994. Bateman principle and plant reproduction: the role of pollen limitation in fruit and seed set. Bot. Rev. 60:83–139.
- Campbell, D. R. 1989. Measurements of selection in a hermaphroditic plant: variation in male and female pollination success. Evolution 43:318–334.
- Charlesworth, B., and D. Charlesworth. 1978. A model for the evolution of dioecy and gynodioecy. Am. Nat. 112:975–997.
- Charnov, E. L., J. Maynard Smith, and J. J. Bull. 1976. Why be an hermaphrodite? Nature 263:125–126.
- Connor, H. E. 1972. Breeding systems in *Cortaderia* (Gramineae). Evolution 27:663–678.
- Darwin, C. 1877. The different forms of flowers on plants of the same species. Appleton, New York.
- Fenster, C. B., and D. E. Carr. 1997. Genetics of sex allocation in *Mimulus* (Scrophulariaceae). J. Evol. Biol. 10:641–661.
- Ghiselin, M. T. 1974. The economy of nature and the evolution of sex. Univ. of California Press, Berkeley, CA.
- Givnish, T. J. 1980. Ecological constraint on the evolution of breeding systems in seed plants: dioecy and dispersal in gymnosperms. Evolution 34:959–972.
- Intriligator, M. D. 1971. Mathematical optimization and economic theory. Prentice-Hall, Englewood Cliffs, N.J.
- Kudoh, H., and D. F. Whigham. 1998. The effect of petal size manipulation on pollinator/seed-predator mediated female reproductive success of *Hibiscus moscheutos*. Oecologia 117: 70–79.
- Lloyd, D. G. 1975. The maintenance of gynodioecy and androdioecy in angiosperms. Genetica 15:325–339.

- Morgan, M. T. 1992. Attractive structures and the stability of hermaphroditic sex expression in flowering plants. Evolution 46: 1199–1213.
- Pannell, J. 1997. The maintenance of gynodioecy and androdioecy in a metapopulation. Evolution 51:10–20.
- Sakai, S. 1993. Allocation to attractive structures in animal-pollinated flowers. Evolution 47:1711–1720.
- ———. 1995. Evolutionarily stable selfing rates of hermaphroditic plants in competing and delayed selfing modes with allocation to attractive structures. Evolution 49:557–564.
- ——. 1999. Female-biased sexual allocation in cosexual plants: result of sink-limited growth of fruits. Evol. Ecol. Res. 1: 943–957.
- ——. 2000. Size-number trade-off and allocation to flower production in animal-pollinated flowers. Plant Species Biol. 15: 261–268.
- Sakai, S., and Y. Harada. 2001. Sink-limitation and size-number trade-off of organs: production of organs using a fixed amount of reserves. Evolution 55:467–476.
- Sato, H., and T. Yahara. 1999. Trade-offs between flower number and investment to a flower in selfing and outcrossing varieties of *Impatiens hypophylla* (Balsaminaceae). Am. J. Bot. 86: 1699–1707.
- Seger, J., and V. M. Eckhart. 1996. Evolution of sexual systems and sex allocation in plants when growth and reproduction overlap. Proc. R. Soc. Lond. B 263:833–841.
- Stanton, M. L., and R. E. Preston. 1988. Ecological consequences and phenotypic correlates of petal size variation in wild radish, *Raphanus sativus* (Brassicaceae). Am. J. Bot. 75:528–539.
- Stanton, M. L., A. A. Snow, and S. N. Handel. 1986. Floral evolution: attractiveness to pollinators increases male fitness. Science 232:1625–1627.
- Trexler, J. C., and J. Travis. 1990. Phenotypic plasticity in the sailfin molly, *Poecilia latipinna* (Pisces: Poeciliidae). I. Field experiments. Evolution 44:143–156.
- Weller, S. G., and A. K. Sakai. 1990. The evolution of dicliny in *Schiedea* (Caryophyllaceae), an endemic Hawaiian genus. Plant Species Biol. 5:83–95.
- Worley, A. C., and S. C. H. Barrett. 2000. Evolution of floral display in *Eichhornia paniculata* (Pontederiaceae): direct and correlated responses to selection on flower size and number. Evolution. 54: 1533–1545.

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Appendix

Optimum Allocation of Females

I analyze the optimal pattern of reproductive resource allocation of females. Here, $F_f = e_o V(A_f)$ holds. This is because, when $F_f > e_o V(A_f)$, a fraction of ovule is wasted without pollination, and when $F_f < e_o V(A_f)$, a fraction of pollinator visitation should be wasted without ovule unfertilized. Thus, equation (3b) in the main text can be written as

$$\phi_f = e_o V(A_f) N_f / 2. \tag{A1}$$

Then by using Lagrange's multiplier λ , the problem is equivalent to the maximization of Φ_f at $A_f = A_f^*$ and $N_f = *N_f$. Here, an asterisk on a parameter indicates that the parameter has an optimal value $\Phi_f = V(A_f) + V(A_f)$

$$\Phi_f = e_o V(A_f) N_f / 2 + \lambda \{ I - N_f [A_f + c_o e_o V(A_f) + \beta]^{\alpha} \}.$$
(A2)
From

$$\frac{\partial \Phi_f}{\partial A_f}\Big|_{\substack{A_f = A_f^* \\ N_f = N_f^*}} = 0, \tag{A3a}$$

$$\frac{\partial \Phi_f}{\partial N_f}\Big|_{A_f = A_f^*} = 0, \text{ and }$$
(A3b)

$$\frac{\partial \Phi_f}{\partial \lambda} \bigg|_{\substack{A_f = A_f^* \\ N_f = N_f^*}} = 0, \tag{A3c}$$

we have

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$$e_o V'(A_f^*) = 2\lambda \alpha [c_o e_o V(A_f^*) + A_f^* + \beta]^{\alpha - 1}$$

$$\times [1 + c_o e_o V'(A_f^*)], \tag{A4a}$$

$$e_o V(A_f^*) = 2\lambda [c_o e_o V(A_f^*) + A_f^* + \beta]^{\alpha},$$
 (A4b)

$$T = N_{f}^{*} [c_{o} e_{o} V(A_{f}^{*}) + A_{f}^{*} + \beta]^{\alpha}, \qquad (A4c)$$

respectively. From equations (A4a) and (A4b), we have

$$A_{f}^{*} = \alpha V(A_{f}^{*}) \left[c_{o} e_{o} + \frac{1}{V'(A_{f}^{*})} \right] - c_{o} e_{o} V(A_{f}^{*}) - \beta.$$
 (A5)

From equations (A4c) and (A5),

$$N_{f}^{*} = T \bigg/ \left\{ \alpha V(A_{f}^{*}) \bigg| c_{o} e_{o} + \frac{1}{V'(A_{f}^{*})} \bigg| \right\}^{\alpha}.$$
 (A6)

Optimum Allocation of Males

I analyze the optimal pattern of reproductive resource allocation of males. Here, $M_m = e_p V(A_m)$ holds. This is because, when $M_m > e_p V(A_m)$, a fraction of pollen is wasted without being exported, and when $M_m < e_p V(A_m)$, a fraction of pollinator visitation should be wasted without pollen available to export. Thus, equation (3c) can be written as

$$\phi_m = W e_p V(A_m) N_m / 2. \tag{A7}$$

Then, by using Lagrange's multiplier λ , the problem is equivalent to the maximization of Φ , which comes from equation (A7) and constraint (1c), at $A_m = A_m^*$ and $N_m = N_m^*$. Here, an asterisk on a parameter indicates that the parameter has an optimal value:

$$\Phi_m = W e_p V(A_m) N_m / 2 + \lambda \{ T - N_m [A_m + c_p e_p V(A_m) + \beta] \}^{\alpha}.$$
 (A8)
From

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$$\frac{\partial \Phi_m}{\partial A_m} \bigg|_{\substack{A_m = A_m^* \\ N_m = N_m^*}} = 0, \tag{A9a}$$

$$\frac{\partial \Phi_m}{\partial N_m} \bigg|_{\substack{A_m = A_m^* \\ N_m = N_m^*}} = 0, \quad \text{and} \tag{A9b}$$

$$\frac{\partial \Phi_m}{\partial \lambda} \bigg|_{\substack{A_m = A_m^* \\ N_m = N_m^*}} = 0, \tag{A9c}$$

we have

$$We_{p}V'(A_{m}^{*}) = 2\lambda\alpha[c_{p}e_{p}V(A_{m}^{*}) + A_{m}^{*} + \beta]^{\alpha-1}$$
$$\times [1 + c_{p}e_{p}V'(A_{m}^{*})], \qquad (A10a)$$

$$We_p V(A_m^*) = 2\lambda [c_p e_p V(A_m^*) + A_m^* + \beta]^{\alpha},$$
 (A10b)

$$T = N_m^* [c_p e_p V(A_m^*) + A_m^* + \beta]^{\alpha}, \qquad (A10c)$$
 respectively. From equations (A10a) and (A10b), we have

$$A_{m}^{*} = \alpha V(A_{m}^{*}) \left[c_{p} e_{p} + \frac{1}{V'(A_{m}^{*})} \right] - c_{p} e_{p} V(A_{m}^{*}) - \beta. \quad (A11)$$

From equations (A10c) and (A11),

$$N_m^* = T \left/ \left\{ \alpha V(A_m^*) \left[c_p e_p + \frac{1}{V'(A_m^*)} \right] \right\}^{\alpha}.$$
 (A12)