

# EFFECTS OF REPRODUCTIVE COMPENSATION, GAMETE DISCOUNTING AND REPRODUCTIVE ASSURANCE ON MATING-SYSTEM DIVERSITY IN HERMAPHRODITES

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Hermaphroditism allows considerable scope for contributing genes to subsequent generations through various mixtures of selfed and outcrossed offspring. The fitness consequences of different family compositions determine the evolutionarily stable mating strategy and depend on the interplay of genetic features, the nature of mating, and factors that govern offspring development. This theoretical article considers the relative contributions of these influences and their interacting effects on mating-system evolution, given a fixed genetic load within a population. Strong inbreeding depression after offspring gain independence selects for exclusive outcrossing, regardless of the intensity of predispersal inbreeding depression, unless insufficient mating limits offspring production. The extent to which selfing evolves under weak postdispersal inbreeding depression depends on predispersal inbreeding depression and the opportunity for resource limitation of offspring production. Mixed selfing and outcrossing is an evolutionarily stable strategy (ESS) if selfed zygotes survive poorly, but selfed offspring survive well, and maternal individuals produce enough “extra” eggs that deaths of unviable outcrossed embryos do not impact offspring production (reproductive compensation). Mixed mating can also be an ESS, despite weak lifetime inbreeding depression, if self-mating reduces the number of male gametes available for outcrossing (male-gamete discounting). Reproductive compensation and male-gamete discounting act largely independently on mating-system evolution. ESS mating systems always involve either complete fertilization or fertilization of enough eggs to induce resource competition among embryos, so although reproductive assurance is adaptive with insufficient mating, it is never an ESS. Our results illustrate the theoretical importance of different constraints on offspring production (availability of male gametes, egg production, and maternal resources) for both the course and outcome of mating-system evolution, whereas unequal competition between selfed and outcrossed embryos has limited effect. These results also underscore the significance of heterogeneity in the nature and intensity of inbreeding depression during the life cycle for the evolution of hermaphrodite mating systems.

**KEY WORDS:** Inbreeding depression, mating system, mixed mating, outcrossing, selfing.

Hermaphroditic organisms exhibit diverse mating systems, ranging from complete selfing to exclusive outcrossing (Goodwillie

et al. 2005; Jarne and Auld 2006). Two opposing genetic features have long been recognized as key influences on this continuum. Each selfed offspring contributes two copies of maternal alleles to the next generation in contrast to one copy for outcrossed offspring, which strongly favors selfing (Fisher 1941). This genetic-transmission advantage is offset in populations with appreciable genetic load by poor performance of selfed offspring, whose high

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homozygosity increases the chance of expression of deleterious recessive traits compared to more heterozygous, outcrossed offspring (Charlesworth and Charlesworth 1999). Consideration of these two factors alone leads to the expectation that complete selfing evolves in diploids when selfed offspring are at least half as fit as outcrossed offspring, on average, otherwise selection favors complete outcrossing (Nagylaki 1976; Lloyd 1979; Lande and Schemske 1985). These contrasting outcomes represent the extremes of the mating-system continuum, but do not explain the common occurrence of mixed mating, the production of combinations of selfed and outcrossed offspring (Goodwillie et al. 2005; Jarne and Auld 2006). Consequently, additional processes that modulate the genetic aspects of mating and contribute to mixed mating have received considerable recent attention (reviewed by Goodwillie et al. 2005).

Mixed mating can be adaptive only if it provides a compromise that capitalizes on the contrasting advantages of selfed and outcrossed offspring. Three mating processes that can promote mixed mating illustrate such compromises. First, reproductive assurance, or increased fecundity caused by autonomous selfing when outcrossing opportunities are limited, can be favored even though the resulting offspring may be genetically inferior to outcrossed progeny (Lloyd 1979; Goodwillie et al. 2005; Jarne and Auld 2006). Second, gamete discounting, which occurs when the use of gametes in self-mating that otherwise could have been involved in outcrossing (Nagylaki 1976; Lloyd 1992), erodes the benefits of selfing, selecting for some outcrossing when selfing is genetically advantageous (Holsinger 1991; Johnston 1998; Porcher and Lande 2005a). The third process, reproductive compensation, occurs when individuals produce more eggs (ovules) than the number of offspring that they can provision. These “extra” eggs reduce the fecundity cost of offspring deaths during development (Minchella and Loverde 1981) resulting from predispersal (early-acting) inbreeding depression, and thereby increase the production of offspring of sufficient genetic quality to reach independence. Such compensation for embryo deaths mitigates the disadvantages of self-mating in populations with high genetic load (Porcher and Lande 2005b; Harder and Routley 2006).

These three processes may be the most common mechanisms responsible for mixed mating by hermaphrodites. Hermaphrodites tend to have limited mobility and often fail to realize their reproductive potential (Ashman et al. 2004; Jarne and Auld 2006). Reproductive assurance alleviates this shortcoming (Eckert et al. 2006), if low fecundity results from insufficient, rather than poor-quality, mating. Indeed, reproductive assurance is the most commonly invoked adaptive explanation for mixed mating (Lloyd 1992; Goodwillie et al. 2005; Jarne and Auld 2006). In contrast, male-gamete discounting is recognized as a common non-adaptive explanation for mixed mating (Lloyd 1992; Goodwillie et al. 2005; Jarne and Auld 2006). In particular, for plants, self-

pollination between flowers on the same individual involves the same interactions with pollen vectors as cross-pollination, so the resulting pollen discounting has been interpreted as an inevitable consequence of outcrossing (Lloyd 1992). The contribution of reproductive compensation to the incidence of mixed mating is less appreciated, because its influence on mating-system evolution has been recognized only recently (Porcher and Lande 2005; Harder and Routley 2006). Nevertheless, this mechanism may be widespread. For example, a survey of seed production following excess cross-pollination for 65 plant species found that only 60% of ovules become seeds (Harder and Routley 2006), suggesting that plants typically produce considerably more ovules than they can mature into seeds.

Despite their significance in the evolution of hermaphroditic mating systems, the relative importance and possible interacting effects of inbreeding depression, reproductive assurance, gamete discounting, and reproductive compensation have not been examined. All mating-system theory considers inbreeding depression explicitly, but the implications of variation in inbreeding depression during the life cycle have received little attention (but see Porcher and Lande 2005 a, b; Harder and Routley 2006). In particular, because recessive lethal traits tend to be expressed earlier than less deleterious traits (Husband and Schemske 1996; Charlesworth and Charlesworth 1999), inbreeding depression may affect selfed offspring more strongly when they depend on parental resources than after they are independent. Mating-system theory also implicitly incorporates female-gamete discounting, or a trade-off between the production of selfed and outcrossed offspring, but this trade-off may have been represented incompletely, because mating-system theory seldom considers consumption of maternal resources by developing offspring (although see Porcher and Lande 2005b; Harder and Routley 2006). Within a framework of nonspecific inbreeding depression and a simple trade-off in the production of selfed versus outcrossed offspring (and perhaps insufficient mating), mating-system theory usually considers the consequences of only one other influence on reproduction (reviewed for plants by Goodwillie et al. 2005). Porcher and Lande (2005 a, b) provided the most complete analyses for plant reproduction; however, they considered pollen discounting and reproductive compensation separately and focused on the consequences of different selfing rates for the evolution of genetic load, so the converse problem focusing on mating-system evolution has not been explored fully.

In this article, we consider the theoretical joint effects of inbreeding depression, reproductive assurance, gamete discounting, and reproductive compensation on the evolution of hermaphroditic mating systems, specifically those of angiosperms. We begin by examining the deterministic influence of reproductive compensation on mating-system evolution when selfing does not alter male outcrossing opportunities, individuals produce many female

gametes, and selfed and outcrossed embryos compete equally for maternal resources. We then consider more realistic situations of limited female reproductive potential, stochastic offspring production, and an advantage of outcrossed embryos over selfed embryos during competition for maternal resources. Finally, we return to the deterministic model and allow male-gamete discounting. Although our analysis incorporates features specific to plant mating, the conclusions should apply generally to hermaphroditic organisms.

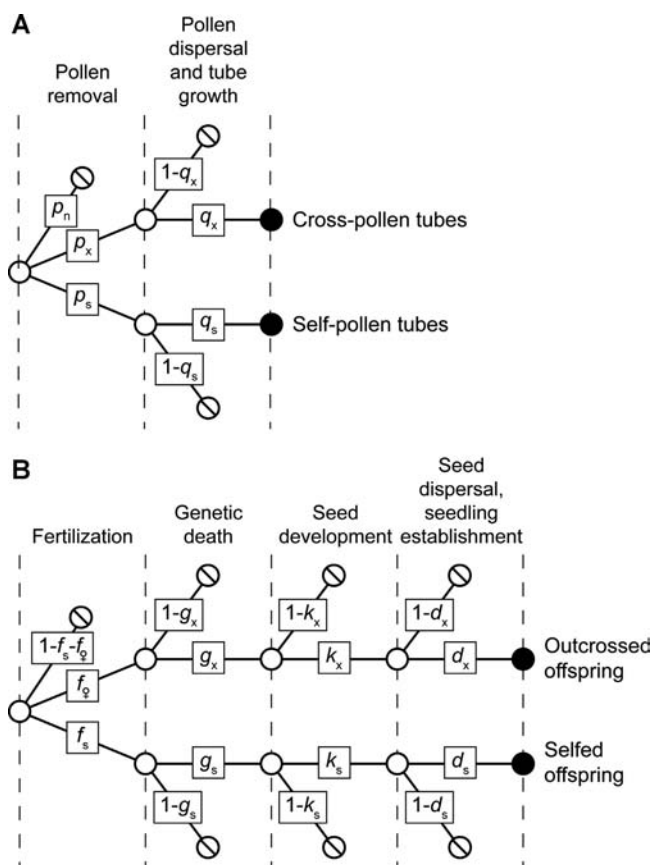
## Mating Models

To explore the consequences of reproductive compensation and male-gamete discounting for mating-system evolution, we model plants that produce  $P$  pollen grains and  $O$  ovules and consider the entire reproductive cycle from pollination to seedling establishment (Fig. 1; see Table 1 for definitions of additional parameters and variables). We assume that ovule and pollen production per

individual remain constant during mating-system evolution, leaving sex-allocation implications for subsequent examination. Mating outcomes within a population depend on the fates of pollen, so we define a plant's phenotype as its contributions of pollen to self-pollination and potential pollen export. Because male-gamete discounting occurs during mating, we focus on selfing that occurs simultaneously with outcrossing. Reproductive assurance can enhance fecundity if insufficient pollen import limits seed production. The plants we model have enough resources to mature only a fraction,  $m$ , of their ovules into seeds, so they produce  $(1 - m)O$  compensatory ovules that can fail after fertilization for various reasons (e.g., genetic death, predation, maternal choice) without affecting maximal seed production. For simplicity, we assume a fixed genetic load in the population, which is not unreasonable given that reproductive compensation allows deleterious alleles to persist in populations, despite the purging effect of inbreeding depression (Charlesworth 1994; Hastings 2001; Porcher and Lande 2005b). This outcome results because compensation allows heterozygous parents to perpetuate recessive lethal alleles by producing more (viable) heterozygous offspring than they would have if compensation had not absorbed genetic deaths of homozygous embryos. Given the preceding assumptions, we seek the evolutionarily stable mating system for which any possible variant phenotype realizes lower or equal fitness to the resident phenotype.

### BASIC MODEL OF DETERMINISTIC MATING WITH MANY OVULES AND EQUAL RESOURCE COMPETITION

Our deterministic model considers plants that produce many pollen grains and many ovules per ovary, so the related results are asymptotically true. Suppose that during pollination proportions  $p_s$  and  $p_x$  of a plant's pollen grains leave its anthers and have the potential to fertilize the plant's own ovules and those on other plants, respectively. The remaining proportion of pollen  $p_n = 1 - p_s - p_e$  stays in the anthers (removal failure) and/or is lost without being carried away by a pollen vector (removal loss) and cannot contribute to the plant's fitness (Fig. 1A; see Harder and Routley 2006). We refer to the common resident phenotype as  $\mathbf{p} = (p_s, p_x)$  and the phenotype of a solitary invader as  $\mathbf{p}' = (p'_s, p'_x)$ . Various processes either claim pollen as it moves between anthers and stigmas or cause pollen-tube attrition (see Harder and Routley 2006), so only proportions  $q_s$  and  $q_x$  of the potential self- and cross-pollen contribute to the pollen tubes that enter an ovary and can participate in fertilizing ovules (Fig. 1A). Thus, ovaries of plants that allocate proportion  $p_s$  of their pollen to self-pollination receive  $q_s p_s P$  self-pollen tubes. Correspondingly, all ovaries receive an average of  $q_x p_x P$  cross-pollen tubes, regardless of phenotype, because the invader is so rare that it contributes a trivial fraction of the total cross-pollination in the population.



**Figure 1.** The fates of (A) pollen and (B) ovules considered in the mating-system models. Labeled parameters indicate transition probabilities between consecutive states.  $\odot$  indicates loss of pollen grains or ovules from the reproductive process,  $\circ$  indicates a transitory state, and  $\bullet$  indicates successful entry of pollen tubes into ovaries (A), or seed production (B).

**Table 1.** Parameters and variables included in the mating models that are not illustrated in Figure 1. Note that lower-case symbols denote proportions, whereas upper-case symbols represent numbers. In the text, a variable followed by an asterisk (\*) is an ESS.

Parameter or variable	Definition
$c_s$ and $c_x$	weights that determine the relative success of selfed and outcrossed embryos, respectively, in competition for maternal resources
$D$	$d_s/d_x$
$\delta$ , $\delta_e$ , and $\delta_d$	total, predispersal and postdispersal inbreeding depression, respectively
$f_\sigma$	relative siring success, or the number of ovules fertilized by a plant on other plants, relative to its own ovule production
$G$	$g_s/g_x$
$k$	proportion of the embryos that survived genetic death that subsequently develop into seeds, when selfed and outcrossed embryos compete equally for maternal resources (i.e., $k = k_s = k_x$ )
$K$	$k_s/k_x$
$m$	proportion of ovules that can mature into seeds, given the available maternal resources
$M_s$	$m/g_s$
$M_x$	$m/g_x$
$N_s$ and $N_x$	numbers of self- and cross-fertilized embryos, respectively
$O$	ovule production
$P$	pollen production
$\mathbf{p}$ and $\mathbf{p}'$	two-element vectors that summarize the proportions of pollen involved in self-pollination and export for the resident and invading phenotypes, respectively; $\mathbf{p} = (p_s, p_x)$ and $\mathbf{p}' = (p'_s, p'_x)$
$p_{\min}$	the minimum possible proportion of pollen that is not available for either self-pollination or export
$Q$	$q_x/q_s$
$S$	number of self-fertilized embryos
$t$	proportion of a plant's seeds that is self-fertilized (maternal outcrossing rate)
$W$	absolute fitness per ovule

Note that the latter outcome occurs regardless of the dispersion of cross-pollen among recipient plants. Specifically, if each donor contributes  $q_x p_x P$  pollen tubes to ovaries of  $n$  neighboring plants, each recipient will receive  $q_x p_x P/n$  pollen tubes from each of its  $n$  neighbors for a total of  $n q_x p_x P/n = q_x p_x P$  pollen tubes.

The outcome of fertilization depends on the numbers of pollen tubes and ovules in an ovary. If fewer pollen tubes enter the ovary than the number of ovules, all pollen tubes fertilize ovules and fertilization is *pollen-limited*, so that reproductive assurance could be beneficial. If instead the total number of pollen tubes exceeds the number of ovules, fertilization is *ovule-limited*, in which case we assume that competing self- and cross-pollen tubes fertilize ovules in proportion to their relative frequencies. We denote the proportions of a plant's ovules fertilized by self- and cross-pollen by  $f_s$  and  $f_\sigma$ , respectively (Fig. 1B; subscript  $\sigma$  denotes the female component of outcrossing). Therefore, the proportions of ovules that are self- and cross-fertilized for a plant with phenotype  $\mathbf{p}'$  in a resident population of plants with phenotype  $\mathbf{p}$  are:

$$f_\sigma(\mathbf{p}', \mathbf{p}) = \begin{cases} \frac{q_s p'_s P}{O}, & \text{if } (q_s p'_s + q_x p_x) P \leq O; \\ \frac{q_s p'_s}{q_s p'_s + q_x p_x}, & \text{otherwise;} \end{cases} \quad (1a)$$

and

$$f_\sigma(\mathbf{p}', \mathbf{p}) = \begin{cases} \frac{q_x p_x P}{O}, & \text{if } (q_s p'_s + q_x p_x) P \leq O; \\ \frac{q_x p_x}{q_s p'_s + q_x p_x}, & \text{otherwise,} \end{cases} \quad (1b)$$

respectively. In addition, the expected number of ovules fertilized by the variant on other plants, relative to its own ovule production (i.e., relative siring success) is,

$$f_\sigma(\mathbf{p}', \mathbf{p}) = \begin{cases} \frac{q_x p'_x P}{O}, & \text{if } (q_s p_s + q_x p_x) P \leq O; \\ \frac{q_x p'_x}{q_s p_s + q_x p_x}, & \text{otherwise.} \end{cases} \quad (1c)$$

Whether fertilization is pollen- or ovule-limited depends on a plant's own self-pollination and the export realized by resident individuals.

We represent seed development as a two-phase process. First, zygotes with lethal traits die shortly after fertilization, before consuming appreciable resources. In particular, selfed and outcrossed zygotes survive genetic death with probabilities  $g_s$  and  $g_x$ , respectively (Fig. 1B), with  $g_s < g_x$ , because the higher homozygosity of selfed zygotes should result in more frequent expression of recessive lethal alleles (Charlesworth and Charlesworth 1999). During the second phase of seed development the surviving selfed and outcrossed embryos draw maternal resources, with proportions  $k_s$  and  $k_x$  surviving to become seeds, respectively (Fig. 1B). These



survival probabilities could be affected by both competition for maternal resources, if the number of surviving embryos exceeds the number that can mature into seeds ( $mO$ ), and predispersal seed predation; however, we consider only competition explicitly. For convenience in this section we assume that selfed and outcrossed embryos compete equally for maternal resources, so  $k_s = k_x = k$ , whereas the finite-ovule model presented in the following section incorporates asymmetric resource competition. Thus, the survival probability for an embryo in an ovary of a plant with phenotype  $\mathbf{p}'$  in a resident population of phenotype  $\mathbf{p}$  is,

$$k(\mathbf{p}', \mathbf{p}) = \begin{cases} 1, & \text{if } (g_s f_s[\mathbf{p}', \mathbf{p}] + g_x f_x[\mathbf{p}', \mathbf{p}]) \leq m; \\ \frac{m}{g_s f_s(\mathbf{p}', \mathbf{p}) + g_x f_x(\mathbf{p}', \mathbf{p})}, & \text{otherwise.} \end{cases} \quad (2)$$

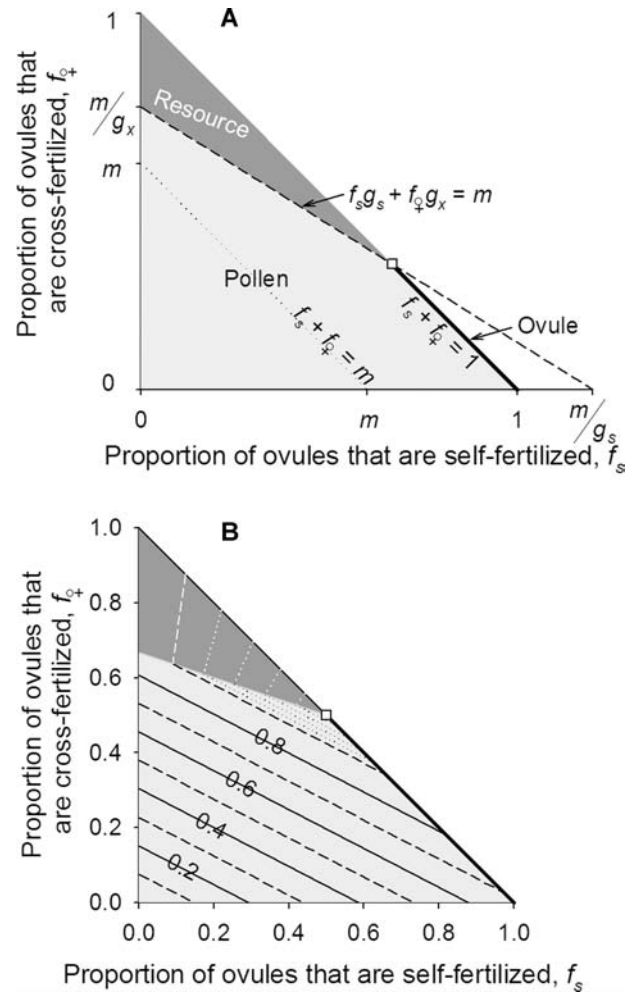
As we model simultaneous self- and cross-pollination, the probabilities of embryo survival do not depend on the relative timing of pollination (for examples of prior and delayed self-pollination see Harder and Routley 2006, M. B. Routley and L. D. Harder, unpubl. ms.).

This characterization identifies three possible limits on seed production. In general, seed production is fertilization-limited if too few embryos survive genetic death to compete for maternal resources,  $g_s f_s(\mathbf{p}', \mathbf{p}) + g_x f_x(\mathbf{p}', \mathbf{p}) < m$ . However, fertilization limitation arises from either of two causes, so when it occurs we describe seed production as being *pollen-limited* if, in addition, some ovules remain unfertilized,  $f_s(\mathbf{p}', \mathbf{p}) + f_x(\mathbf{p}', \mathbf{p}) < 1$  (Fig. 2A, light gray area), or *ovule-limited* if fertilization is complete,  $f_s(\mathbf{p}', \mathbf{p}) + f_x(\mathbf{p}', \mathbf{p}) = 1$  (Fig. 2A, heavy line). Alternatively, seed production is *resource-limited* when more embryos survive genetic death than can mature given the available maternal resources,  $g_s f_s(\mathbf{p}', \mathbf{p}) + g_x f_x(\mathbf{p}', \mathbf{p}) \geq m$ , regardless of the limit on fertilization (Fig. 2A, dark gray area). (This condition illustrates that  $m < 1$  is necessary for resource limitation, but it is not a sufficient condition, as implied by Porcher and Lande [2005b:  $c < 1$  in their notation].)

After seed development, proportions  $g_s f_s k_s$  and  $g_x f_x k_x$  of the original ovules have become selfed and outcrossed seeds, respectively (i.e., the seed:ovule ratio equals  $g_s f_s k_s + g_x f_x k_x$ ). The female outcrossing rate, measured among seed progeny, equals

$$t = g_x f_x k_x / (g_s f_s k_s + g_x f_x k_x) = f_x / (GK f_s + f_x),$$

where  $G = g_s/g_x$  and  $K = k_s/k_x$ . Because of the generally poorer performance of selfed embryos during seed development, predispersal (early acting) inbreeding depression equals  $\delta_e = 1 - GK$ . Note that both of these mating parameters may depend on the resident outcrossing strategy, if it causes resource competition among developing seeds.



**Figure 2.** Combinations of self- ( $f_s$ ) and cross-fertilized ovules ( $f_x$ ) under which seed production is limited by pollen receipt (light gray area), ovule production (heavy line), and maternal resource availability (dark gray area) when  $g_s < m < g_x$ . Because of the ovule-production constraint ( $f_s + f_x \leq 1$ ), only combinations of self- and cross-fertilization in the shaded areas are possible. In panel A, the dashed line illustrates the transition between pollen and resource limitation,  $f_s g_s + f_x g_x = m$ , and the dotted line depicts the limit on seed production if no embryos died during development imposed by the availability of maternal resources ( $f_s + f_x = m$ ). In panel B, alternating solid and dashed lines indicate isoclines of relative fitness ( $w = W / W_{\max}$ ) in increments of  $w = 0.1$  and dotted isoclines depict increments of  $w = 0.02$ . The transition between resource and ovule limitation (white square: eq. 4) is the ESS mating system in panel B when self-pollination does not reduce pollen export and  $g_s = 0.3$ ,  $g_x = 0.9$ ,  $d_s = 0.7$ ,  $d_x = 0.9$ , and  $m = 0.6$ .

Proportions  $d_s$  and  $d_x$  of the selfed and outcrossed seeds, respectively, disperse, establish, and become reproductive adults (Fig. 1B;  $d_s \leq d_x$ ). Consequently, postdispersal (late-acting) inbreeding depression equals  $\delta_d = 1 - (d_s/d_x) = 1 - D$ , where  $D = d_s/d_x$ . Furthermore, total inbreeding depression experienced by self-fertilized embryos is  $\delta = 1 - GKD$ . Note that although total zygote survival equals the product of pre- and postdispersal

survival, total inbreeding depression is not the product of its pre- and postdispersal components (i.e.,  $\delta \neq \delta_e \delta_d$ ).

We define an individual's fitness as the expected number of haploid genomes passed on to the next generation per ovule, which must lie between zero and two. Thus, the fitness of a plant with phenotype  $\mathbf{p}'$  in a resident population of plants with phenotype  $\mathbf{p}$  is,

$$W(\mathbf{p}', \mathbf{p}) = 2f_s(\mathbf{p}', \mathbf{p})g_s k(\mathbf{p}', \mathbf{p})d_s + f_\sigma(\mathbf{p}', \mathbf{p})g_\sigma k(\mathbf{p}', \mathbf{p})d_\sigma + f_\sigma(\mathbf{p}', \mathbf{p})g_x k(\mathbf{p}', \mathbf{p})d_x, \quad (3)$$

where the three terms on the right-hand side represent contributions through selfed offspring, a plant's own outcrossed seeds, and outcrossed seeds sired on other plants, respectively.

Phenotype  $\mathbf{p}^*$  is a local evolutionarily stable strategy (ESS) if no alternative phenotype realizes greater fitness when all resident plants exhibit  $\mathbf{p}^*$ , or  $W(\mathbf{p}', \mathbf{p}^*) \leq W(\mathbf{p}^*, \mathbf{p}^*)$  for all possible invader phenotypes  $\mathbf{p}'$  near  $\mathbf{p}^*$  (Lawlor and Maynard Smith 1976). Phenotype  $\mathbf{p}^*$  is also a continuously stable strategy (CSS) if a population with a resident phenotype similar to  $\mathbf{p}^*$  can be invaded by a phenotype that is even more similar to  $\mathbf{p}^*$  (Eshel 1983). We seek phenotypes that are both ESS and CSS, as they will be favored by natural selection. In addition to the analytic derivations of  $\mathbf{p}^*$  presented in the Appendix, we investigated evolutionary dynamics toward  $\mathbf{p}^*$  by numerically evaluating the gradient of  $W$  with respect to  $p_x$  and  $p_s$ , given the constraint that  $p_x + p_s \leq 1 - p_n$ .

We derived all analytic results by considering absolute transition probabilities (e.g.,  $q_s$ ,  $q_x$ ,  $g_s$ ,  $g_x$ ; see Appendix); however, most outcomes depend on the ratios of transition probabilities for selfing and outcrossing (e.g.,  $Q$  and  $G$ ), rather than their absolute values. Therefore, we present the results in terms of relative transition probabilities whenever possible. Note that  $Q = q_x/q_s$  is an outcrossing: selfing ratio, whereas  $D$ ,  $G$ , and  $K$  are selfing: outcrossing ratios; see Table 1.

## EFFECTS OF FINITE OVULE NUMBER AND UNEQUAL RESOURCE COMPETITION

We used a stochastic simulation model to consider the effects of two factors that could modify the results of our analytic model. First, most plant species produce relatively few ovules per ovary, a situation in which stochasticity during fertilization and seed development could influence average reproductive performance by competing phenotypes. This effect could occur because both ovule fertilization (eq. 1) and competition among embryos for maternal resources (eq. 2) are decelerating, nonlinear processes, so variation in input (i.e., numbers of pollen tubes and embryos, respectively) reduces mean seed production compared to that expected for the mean input (Jensen's inequality; see Smallwood 1996). The effect of such nonlinear averaging is greatest with large coefficients of variation, which for binomial processes like fertilization and

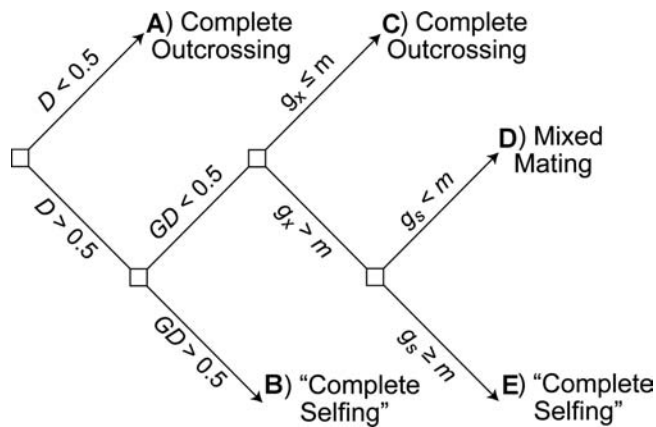
competition occurs when few trials are involved (e.g., for fertilizations  $CV = \sqrt{O\phi(1-\phi)}/O\phi$ , where  $\phi$  is the probability of fertilization per ovule). The second factor that could influence our results involves unequal survival of selfed and outcrossed embryos (i.e.,  $k_s < k_x$ ) owing to inbreeding depression or maternal choice.

Our simulation model determined the optimal mating system in the absence of pollen discounting for specific combinations of  $g_s$  and  $g_x$ , given complete fertilization. Specifically, we considered ovaries with  $O = 40$  ovules, of which only 20 could develop into seeds (i.e.,  $m = 0.5$ ). During a simulation,  $S$  ovules were self-fertilized and the remaining  $40-S$  ovules were cross-fertilized, so fertilization was not pollen-limited ( $f_s + f_\sigma = 1$ ). If fewer than  $mO = 20$  embryos survived genetic death, they all developed into seeds. If more than 20 embryos survived, seed production was resource-limited and 20 embryos were selected to develop into seeds by a weighted lottery, with selfed and outcrossed embryos assigned weights of  $c_s$  and  $c_x$ , respectively, where  $c_s \leq c_x$ . Specifically, if  $N_s$  selfed and  $N_x$  outcrossed embryos remained when the next embryo was to be selected for the development into a seed, a selfed embryo was chosen randomly with probability  $c_s N_s / (c_s N_s + c_x N_x)$ , otherwise an outcrossed embryo was chosen. Finally, selfed and outcrossed seeds became adult offspring with probabilities  $d_s$  and  $d_x$ , respectively. Fitness during a single simulation was calculated as twice the number of surviving selfed offspring plus the number of surviving outcrossed offspring. We calculated the mean (expected) fitness resulting from self-fertilization of  $S$  ovules for 50,000 stochastic simulations for a given combination of  $g_s$  and  $g_x$ . This process was repeated for  $S = 0, 1, \dots, 40$  selfed ovules and the value of  $S$  associated with the maximum fitness was identified as the optimum mating system.

## Results

### ESS MATING SYSTEM WITH NO POLLEN DISCOUNTING AND MANY OVULES

The effects of reproductive compensation on mating-system evolution are appreciated most easily by considering situations in which self-pollination does not discount the pollen available for export (i.e.,  $p_x = p_x' =$  a fixed positive constant) and all fertilized ovules compete equally for maternal resources (i.e.,  $k_s = k_x$ , so  $K = 1$ ). The absence of pollen discounting has several implications. First, as all plants are assumed to export an equal proportion of pollen, all plants must receive an equal amount of imported pollen. As a result, any fitness difference between the resident and invading phenotypes depends only on the self- and cross-fertilization of a plant's own seeds. In particular, increased self-pollination alters the mating system only by diluting the proportion of ovules fertilized by imported pollen. Consequently, mating outcomes are not frequency dependent and the ESS can

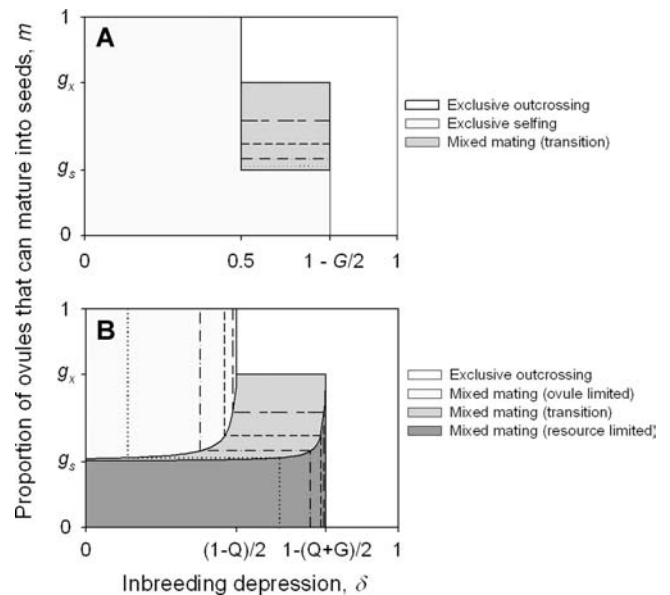


**Figure 3.** Summary of conditions favoring alternative mating systems when self-pollination does not reduce the fixed incidence of pollen export.

be found simply by maximizing the sum of the selfing and female components of fitness given in equation (3) (see Appendix). Second, in the absence of a trade-off with pollen export, increased self-pollination must reduce pollen that otherwise would not be removed from flowers or would be lost during pollen removal (i.e.,  $p_n = 1 - p_s - p_x$ ). As the incidence of cross-pollination,  $p_x$ , is assumed to be a positive constant, exclusive selfing (i.e.,  $p_s = 1$ ) is impossible and instead “complete selfing” is said to occur when  $p_n = 0$  and  $p_s = 1 - p_x$ . However, results presented in the Appendix indicate that when “complete selfing” is favored selection also favors a reduction in the fixed value of  $p_x$ . Thus for such cases, we assume subsequent evolution of  $p_x$  and eventual evolution of exclusive selfing ( $f_s^* = 1$ ).

As a pollen-limited mating system never maximizes fitness (see Appendix), we focus on situations that result in complete ovule fertilization (i.e.,  $f_s + f_g = 1$ ). With no pollen discounting, the optimal mating system depends on a hierarchy of dichotomous criteria, which progressively incorporate more influences on female fertility (Fig. 3). First, exclusive outcrossing ( $f_s^* = 0$ ) is favored if postdispersal inbreeding depression is so strong that selfed seeds are less than half as likely to become reproductive adults than outcrossed seeds ( $D < 0.5$ ; i.e.,  $\delta > 1 - G/2$  in Fig. 4A). This outcome occurs regardless of the relative success of selfed and outcrossed embryos during seed development. Previous models of mating-system evolution have not identified this condition, because it is subsumed by a more rigorous outcrossing threshold ( $\delta > 0.5$ ) in the absence of reproductive compensation (Porcher and Lande 2005b considered only  $D = 0.75$  in their compensation model).

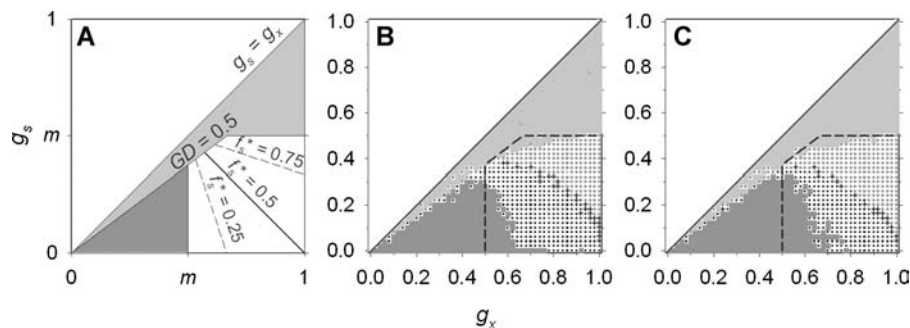
Unlike the previous case, a diversity of mating systems is possible when selfed seeds have relatively high postdispersal survival ( $D > 0.5$ ; Fig. 4A for  $\delta < 1 - G/2$ , and Figs. 3, 5A). Exclusive self-fertilization ( $f_s^* = 1$ ) is favored if self-fertilized



**Figure 4.** Relations of alternate ESS mating systems to inbreeding depression from ovule fertilization to offspring establishment ( $\delta$ ) and the proportion of ovules that could mature into seeds, given available maternal resources ( $m$ ) when (A) self-pollination does not reduce pollen export, or (B) self-pollination causes pollen discounting. These results incorporate the assumption that selfed and outcrossed embryos compete equally for maternal resources (i.e.,  $k_s = k_x$ ) when seed production is resource-limited. Broken lines indicate ESS female selfing rates of  $t = 0.1$  (dotted lines), 0.25 (dash-dotted lines), 0.5 (short-dashed lines), and 0.75 (long dash, short dash line). Note that  $\delta = 1 - (G/2)$  is equivalent to  $d_x = 2d_s$ .

zygotes are at least half as likely to join the next generation as outcrossed zygotes ( $GD > 0.5$ ; i.e.,  $\delta < 0.5$ ). Because selection of exclusive selfing in this situation occurs regardless of the details of ovule production ( $m$ ), it is also predicted by mating-system models that ignore resource competition (Lloyd 1979; Lande and Schemske 1985; Charlesworth et al. 1990; Jarne and Charlesworth 1993).

In contrast, when selfed seeds have relatively high postdispersal survival ( $D > 0.5$ ), but self-fertilized zygotes have relatively poor prospects of success ( $GD < 0.5$ ), the best mating system depends on the extent to which “excess” ovules compensate for genetic deaths of selfed and outcrossed embryos (Figs. 3, 4A, 5A). Exclusive outcrossing evolves if plants do not produce enough ovules to compensate for all predispersal deaths among outcrossed zygotes ( $m/g_x = M_x \geq 1$ ; Figs. 3, 4A, 5A). In this situation maternal resources exceed the demand from the embryos that survive genetic death, so developing seeds do not compete for resources ( $K = 1$ ). If instead ovule production compensates for all predispersal losses of outcrossed embryos, but only some deaths of selfed embryos ( $g_x > m > g_s$ ), a mixture of self- and cross-fertilization is favored (Figs. 3, 4A, 5A). Recall that we are considering cases



**Figure 5.** Optimal mating strategies for all possible combinations of the proportions of selfed and outcrossed embryos that survive genetic death ( $g_s$  and  $g_x$ , respectively), when half of an ovary's ovules can be developed into seeds ( $m = 0.5$ ) and  $2d_s > d_x$ . (A) Results from the analytic model for many ovules when all ovules compete equally for maternal resources. (B and C) Optimal number of self-fertilized ovules when ovaries contain 40 ovules and (B) all embryos compete equally for maternal resources, or (C) outcrossed embryos are 10-fold better competitors than selfed embryos ( $c_x = 10$  and  $c_s = 1$ ), as identified by numerical simulation. Note that combinations above the diagonal are not possible, because we assume that  $g_s \leq g_x$ . "Complete" selfing ( $f_s^* = f_{s\max}$ ) is favored in light-gray areas, whereas exclusive outcrossing is optimal in dark-gray areas. In (A), mixed mating is favored in the unshaded area below the diagonal, with the optimal proportion of self-fertilized ovules ( $f_s^*$ ) indicated by contours. In (B and C), ● indicates optimal self-fertilization of 1–19 ovules (i.e.,  $0 \leq f_s^* \leq 0.5$ ), + indicates optimal self-fertilization of 20 ovules (i.e.,  $f_s^* = 0.5$ ), ○ indicates optimal self-fertilization of 21–39 ovules (i.e.,  $0.5 \leq f_s^* \leq 1$ ), and the dashed line delimits the mixed-mating boundary expected with many ovules. In all cases,  $d_s = 0.33$  and  $d_x = 0.5$ .

in which selfed zygotes perform relatively poorly ( $GD < 0.5$ ), but selfed seeds perform well ( $D > 0.5$ ), so if selfed seeds are among the lucky few that survive genetic death they are very valuable to the maternal parent because they possess only maternal alleles. When mixed mating is optimal, the combination of self- and cross-fertilization that maximizes fitness lies at the transition between resource and ovule limitation,

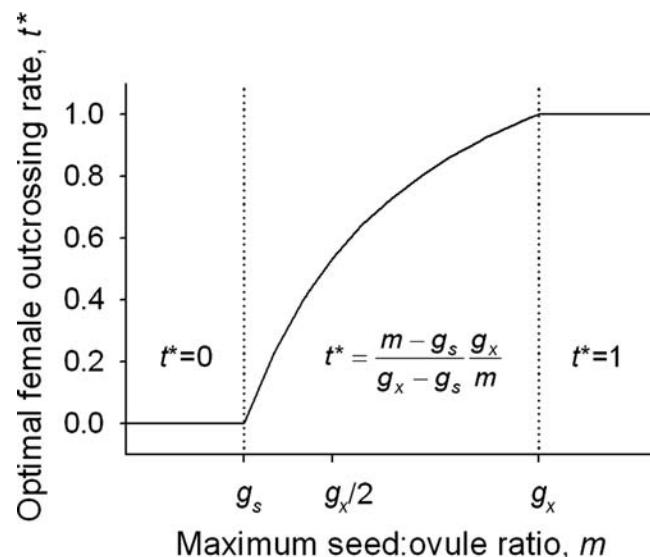
$$f_s^* = f_s^T = \frac{g_x - m}{g_x - g_s} \quad \text{and} \quad f_x^* = f_x^T = \frac{m - g_s}{g_x - g_s}, \quad (4)$$

(Fig. 2, open square) and developing embryos do not compete for maternal resources ( $k_s = k_x = 1$ ). For this situation the optimal proportion of outcrossed seeds, a common measure of the mating system, is

$$t^* = f_x^* \cdot \frac{g_x}{m} = \frac{m - g_s}{g_x - g_s} \cdot \frac{g_x}{m} = \frac{M_s - 1}{M_s(1 - G)} \quad (5)$$

(Fig. 6), where  $g_x/m$  is the relative increase in the proportion of outcrossed embryos during seed development. Equation (5) indicates that the optimal maternal outcrossing rate ( $t^*$ ) increases as the maximum proportion of ovules that can mature into seeds ( $m$ ) approaches the proportion of outcrossed ovules that survive genetic death,  $g_x$  (Fig. 6). Finally, when plants produce enough ovules to compensate for all predispersal deaths ( $g_x > g_s \geq m$ ) exclusive selfing is favored (i.e.,  $f_s^* = 1$ ; Figs. 3, 4A, 5A). Full compensation allows the maternal plant to benefit from contributing two haploid genomes through selfed seeds whose future prospects are at least half as good as those of outcrossed seeds (recall that  $D > 0.5$ ), even though many selfed zygotes succumb to predispersal inbreeding depression.

Examination of fitness isoclines close to the maximum reveals that the three limits on seed production differ in their fitness consequences. For example, consider the situation that favors mixed mating, for which the optimal mating system lies at the intersection between pollen, ovule, and resource limitation (Fig. 2B). The dashed line in Figure 2B closest to the optimal mating system illustrates combinations of self- and cross-fertilization



**Figure 6.** The relation of the optimal maternal outcrossing rate ( $t^*$ ) to the maximum proportion of ovules that can develop into seeds ( $m$ ) with no pollen discounting, ovule fertilization is not pollen-limited, and the ESS mating system occurs at the transition between resource and ovule limitation. Based on equation (5).



for which fitness is 90% of the maximum possible. This line is closest to the optimum in the area of the figure that represents pollen limitation, next closest in the direction of ovule limitation and farthest in the direction of resource limitation. Consequently, pollen limitation results in the steepest fitness gradient, whereas resource limitation results in a shallow gradient, so selection should act more strongly to alleviate pollen limitation and least strongly to counteract resource limitation, with intermediate selection against ovule limitation. These results expose two conclusions. First, the intense selection under pollen limitation places a premium on reproductive assurance; however, increased selfing to provide this assurance rarely produces the ESS mating system. Second, in the absence of pollen limitation (i.e.,  $f_s + f_\sigma = 1$ ) deviations from the optimal mating system toward more cross-fertilization, which aggravates resource limitation, should be more common than elevated self-fertilization, which intensifies ovule limitation.

#### ESS MATING SYSTEM WITH NO POLLEN DISCOUNTING AND FEW OVULES

Stochasticity in embryo survival resulting from the production of a finite number of ovules slightly increases the range of conditions that favor exclusive outcrossing, rather than mixed mating (compare Fig. 5A, B). Given both stochasticity in the incidence of genetic deaths and the greater survival of outcrossed embryos than selfed embryos ( $g_x > g_s$ ), a slight increase in cross-fertilization reduces the chance that too few ovules will survive genetic death to consume the available maternal resources. This bet-hedging against ovule limitation also reduces the range of conditions under which self-fertilization of 50–100% of ovules is optimal (compare isocline for  $f_s^* = 0.5$  in Fig. 5A, B). In general, the transition between pure outcrossing and mixed mating was difficult to assess accurately (Fig. 5B), because a range of selfing fractions,  $f_s$ , near the optimum often resulted in nearly equivalent fitness. This result is consistent with the shallow gradient in fitness associated with an increase in cross-fertilization from the optimum observed with the analytic model (Fig. 2B).

Whether self- and cross-fertilized embryos compete equally or unequally for maternal resources also has little effect on the optimal mating system, even for ovaries with few ovules (compare Fig. 5B, C). Indeed, a tenfold competitive advantage for outcrossed ovules ( $c_x/c_s = 10$ ) expanded the conditions favoring outcrossing only slightly, even in the presence of stochasticity.

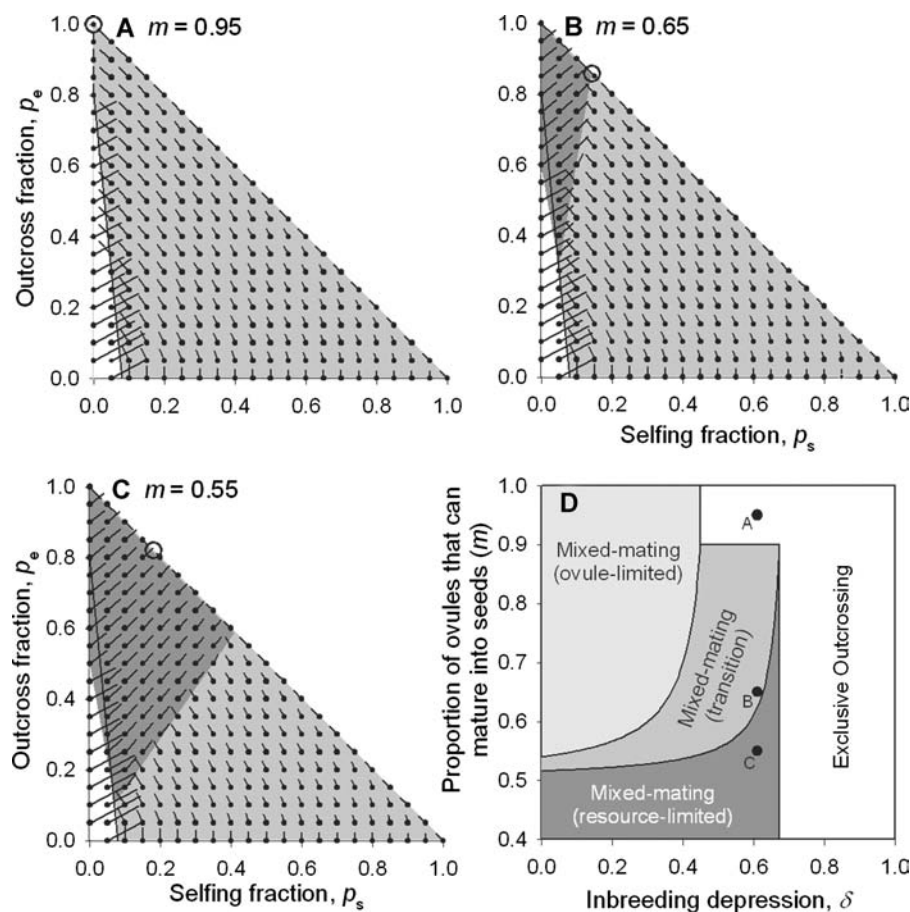
#### ESS MATING SYSTEM WITH COMPLETE POLLEN DISCOUNTING AND MANY OVULES

We now consider the consequences of complete pollen discounting, for which each pollen grain involved in self-pollination reduces the pollen available for export. This model assumes that a

fixed minimum proportion of pollen is not removed from anthers or lost during removal,  $p_{\min}$ , so  $p_x = 1 - p_s - p_{\min}$  when pollen vectors remove all the pollen available for export. Because plants of different phenotypes now contribute unequal numbers of cross-pollen tubes to ovaries, a plant's paternal success now depends on the pollination strategies of other plants in the population. The resulting frequency dependence complicates identification of the ESS (see Appendix).

Pollen discounting allows a broader range of ESSs and mating-system evolution need not follow a direct trajectory to the ESS. The vectors in Figure 7A–C depict the direction and strength of selection (log transformed) for different pollen allocations ( $p_s$ ,  $p_x$ ) given the three combinations of reproductive compensation and inbreeding depression indicated in Figure 7D. The long vectors for conditions that cause pollen limitation (white areas) illustrate that in such situations selection strongly favors some self-pollination for reproductive assurance. Note in particular that the selection vectors associated with reproductive assurance rarely point toward the ESS, so that alleviating pollen limitation of fertilization takes (short-term) precedence over offspring quality. In contrast, when seed production is not pollen-limited the direction of selection on pollen allocation depends on whether the current allocation and the ESS invoke the same constraint on seed production. If so, selection acts first to commit all possible pollen to pollination (e.g., Fig. 7C, dark gray area) and then to “tune” the mating system along the  $p_x + p_s \leq 1 - p_{\min}$  constraint. If instead the ESS involves a different limitation than currently prevails, selection usually first shifts pollen allocation to the transition between resource and ovule limitation (e.g., Fig. 7C, light gray area), then increases the pollen involved in pollination along this transition, and finally moves allocation along the  $1 - p_{\min}$  constraint. Thus, the trajectory followed during mating-system evolution is guided by the various constraints on pollination, fertilization, and seed production. We now focus on the ESSs under different conditions (see Appendix), which always involve complete fertilization (i.e.,  $f_s + f_\sigma = 1$ ; Fig. 7A–C).

Complete pollen discounting greatly expands the range of conditions that favor some outcrossing (compare Fig. 4A, B). Indeed, exclusive selfing is never an ESS mating system with complete pollen discounting (Fig. 4B) if fertilization is not pollen-limited (also see Holsinger 1991). This outcome arises because once stigmas receive enough pollen to fertilize all ovules, increased allocation of pollen to self-pollination both intensifies competition between a plant's own pollen grains for access to its own ovules and reduces potential siring opportunities on other plants. The synergistic impacts of local mate competition and pollen discounting on siring success are sufficient to counteract the twofold genetic benefit of self-fertilization, even in the absence of inbreeding depression.



**Figure 7.** Selection gradients for mating-system evolution in the presence of complete pollen discounting for the conditions identified in panel D. Each vector indicates the direction and relative strength of selection on a ln-scale when all plants with the resident phenotype allocate proportion  $p_s$  of their pollen to self-pollination and proportion  $p_x$  to export, and  $p_{n\min} = 0$ . Resident strategies are indicated by the circle at each vector's origin. The selection gradient is given by the vector  $(\partial W/\partial p_s, \partial W/\partial p_x)/W$ , where  $W$  is defined in equation (3). In panels A–C seed production is limited by ovules (light gray area), resources (dark gray area), and pollen (white area).

Compared to the nondiscounting case, the inbreeding-depression threshold that favors exclusive outcrossing now depends on the relative success of self- and cross-pollen, decreasing by  $q_x/2q_s$  ( $= Q/2$ ; compare Fig. 4A, B). This change is probably relatively small for self-compatible species, as a pollen grain with export potential has a much smaller chance of entering an ovary than a potential self-pollen grain (i.e.,  $q_x \ll q_s$ ). Thus, although the details of pollination and pollen-tube growth influence the evolution of exclusive outcrossing, their effects are limited compared to those caused by postfertilization differences between selfing and outcrossing. Note that even when conditions favor exclusive outcrossing, some self-pollination is advantageous if it alleviates pollen limitation (Fig. 7A).

Pollen discounting greatly expands both the conditions that promote mixed mating and the diversity of ESS mixed-mating patterns. As with the nondiscounting case, the transition between ovule- and resource limitation can be an ESS mixed-mating system, which occurs if

$$g_s + \frac{(g_x - g_s)Q}{1 - 2\delta} > m > \frac{2(1 - \delta) - G}{2(1 - \delta) - G - Q(1 - G)} g_s$$

$$\text{for } \delta \leq \frac{1 - Q}{2} \quad (6a)$$

or

$$g_x > m > \frac{2(1 - \delta) - G}{2(1 - \delta) - G - Q(1 - G)} g_s$$

$$\text{for } \frac{1 - Q}{2} < \delta \leq 1 - \frac{Q + G}{2} \quad (6b)$$

(see Appendix). If  $q_x$  is very small, as is likely for most species with granular pollen, then  $Q \cong 0$  and equation (6b) describes essentially the same conditions for mixed mating as observed in the nondiscounting case (compare Fig. 4A, B). Thus, the effect of reproductive compensation on the evolution of an ESS at the transition between resource- and ovule limitation is largely unaffected by pollen discounting. In contrast, pollen discounting creates conditions that additionally allow mixed-mating ESSs with ovule or resource limitation.

An ESS mixed-mating system that involves chronic ovule limitation of seed production evolves when

$$m > g_s + \frac{(g_x - g_s)Q}{1 - 2\delta}, \quad \text{given } \delta < \frac{1 - Q}{2}. \quad (7)$$

These conditions include two situations. First, if ovule production does not compensate for all genetic deaths of outcrossed zygotes (i.e.,  $m \geq g_x$ ) resource limitation is impossible and a mixed-mating ESS must involve ovule limitation (see Fig. 2A). Indeed, mixed mating with ovule limitation can be an ESS even when ovule production does not compensate for any embryo deaths (i.e.,  $m = 1$ : along the top of Fig. 4B; also see Holsinger 1991). Second, pollen discounting promotes ovule-limited mixed mating for most values of  $g_s < m < g_x$  if inbreeding depression is less than  $(1 - Q)/2$  (Fig. 4B). In particular, if  $g_x$  is very small, so  $Q \cong 0$ , the right-hand side of the first condition of equation (7) exceeds  $g_s$  only slightly. With ovule-limited mixed mating, the ESS depends on all aspects of reproduction, except the proportion of ovules that can mature into seeds ( $m$ : Table 2). Over most of the range of inbreeding depression that allows ovule-limited mixed mating the ESS involves predominant selfing (see dotted and dashed lines in Fig. 4B), with a minimum proportion of outcrossed seeds of  $t = Q / (G + Q[1 - G])$  when  $\delta = 0$ .

A resource-limited mixed-mating system evolves when

$$m < \frac{2(1 - \delta) - G}{2(1 - \delta) - G - Q(1 - G)} g_s, \quad \text{given } \delta < 1 - \frac{Q + G}{2} \quad (8)$$

(Fig. 4B). As with equation (7), the right-hand side of the first condition of equation (8) approximates  $g_s$  if  $Q$  is very small. When  $m < g_s$  complete ovule fertilization always leads to resource limitation (see Fig. 2A), so any mating system must be resource-limited, whereas very restrictive conditions allow a resource-limited ESS when  $m > g_s$  (Fig. 4B). Again, the ESS depends on all aspects of reproduction, except the proportion of ovules that can mature into seeds (Table 2). Resource-limited mixed-mating ESSs typically involve predominant selfing (see dotted and dashed lines in Fig. 4B), with a minimum  $t = Q / (2 - G)$  when  $\delta = 0$ .

## Discussion

The models described above provide a general framework for investigating the evolution of hermaphroditic mating systems and synthesize the results of many previous analyses. Our models provide additional support for claims since Darwin (1876) that selfing often persists in populations when it provides reproductive assurance (reviewed by Eckert et al. 2006), as the strongest selection identified by our models occurred when too few ovules (eggs) were fertilized to maximize offspring production (Figs. 2B, 7A–C). We also found the well-known dichotomy between selfing and outcrossing (e.g., Lloyd 1979; Lande and Schemske 1985) when selfing does not affect male outcrossing and ovule (egg) production does not exceed an individual's resource capacity to produce offspring (along top axis of Fig. 4A). Male-gamete discounting and production of compensatory ovules (eggs) modify this outcome differently and largely independently. On one hand, male-gamete discounting promotes some outcrossing to convert local mate competition for self-fertilization into outcrossing opportunities when weak inbreeding depression otherwise favors selfing (Fig. 4B; Holsinger 1991; Johnston 1998; Porcher and Lande 2005a). On the other hand, production of “extra” eggs ( $m < 1$ ) can allow individuals to benefit from the genetic-transmission advantage of selfing when strong predispersal inbreeding depression would otherwise favor outcrossing (Fig. 4; Porcher and Lande 2005b).

Our models also expose new insights on mating-system evolution and identify specific conditions favoring particular ESS outcomes. Significantly, these models illustrate that the prevailing constraint on offspring production governs the course of mating-system evolution (Fig. 7) and the ultimate ESS (Table 2, Fig. 2B). The overall ESS mating system never involves pollen limitation (Figs. 2B, 7), so mixed mating associated with reproductive assurance always represents a suboptimal solution to insufficient outcrossing. Furthermore, the widespread observations of pollen limitation among angiosperms (reviewed by Ashman et al. 2004) seem enigmatic from an evolutionary perspective, unless they

**Table 2.** Characteristics of the mixed ESS mating systems when self-mating discounts opportunities for outcross siring and the ESS involves limitation of seed production by resources or ovule production, or the transition between these constraints. Equations 6 and 7 detail the conditions that favor these different outcomes (also see Fig. 4B). See Table 1 and Figure 1 for parameter definitions.

Limitation on seed production under ESS	Proportion of pollen allocated to self-pollination ( $p_s^*$ )	Proportion of ovules that are self-fertilized ( $f_s^*$ )	Proportion of outcrossed seeds ( $t^*$ )
Resources	$(1 - p_{\min}) \left[ 1 - \frac{G}{2(1 - \delta) - Q} \right]$	$\frac{2(1 - \delta) - G - Q}{2(1 - \delta) - G - Q(1 - G)}$	$\frac{Q}{2(1 - \delta) - G}$
Transition	$\frac{(1 - p_{\min})Q(1 - M_x)}{Q(1 - M_x) + M_x - G}$	$\frac{1 - M_x}{1 - G}$	$\frac{M_s - 1}{M_s(1 - G)}$
Ovules	$(1 - p_{\min}) \left[ 1 - \frac{1}{2(1 - \delta) - Q} \right]$	$\frac{1 - 2\delta - Q}{1 - 2\delta}$	$\frac{Q}{G(1 - 2\delta) + Q(1 - G)}$

represent common misinterpretation of the effects of poor-quality pollen, rather than insufficient pollen (see Harder and Routley 2006; Aizen and Harder 2007).

Given that selection strongly promotes sufficient mating to fertilize all female gametes, or at least more than can mature into independent offspring given available maternal resources (Figs. 2B, 6), mating-system evolution should typically occur in a context of ovule- and/or resource limitation. Most previous mating-system models assumed complete fertilization and ignored resource limitation, so they implicitly involved ovule limitation. As we have defined it, ovule limitation of seed production occurs when all ovules are fertilized, but too few embryos survive genetic death to compete for maternal resources. If most embryos survive, then mating-system evolution can do little to improve seed production, although it may increase the proportion of selfed offspring that contribute two gene copies to the next generation. In this case, ovule limitation should also favor reallocation of resources from potential seed production to increased ovule production. In contrast, poor embryo survival implies extensive fertilization by poor-quality pollen, which should select for floral mechanisms that promote high-quality pollination. In most mating-system models, including those presented here (e.g., Figs. 2B, 7A–C), this response involves selection for increased outcrossing. In contrast, resource limitation occurs only when a parent produces more female gametes than can mature into offspring (i.e.,  $m < 1$ ; Fig. 2A), which intrinsically allows compensation for deaths caused by predispersal inbreeding depression. Consequently, resource limitation favors selfing when postdispersal inbreeding depression is weak (Fig. 3), because competition among developing embryos can exclude valuable selfed embryos that contain only maternal genes and have survived predispersal inbreeding depression. These contrasting effects of ovule and resource limitation create opportunities for mixed mating to be an ESS, if the occurrence of one limitation or the other depends on the proportions of outcrossed and selfed embryos.

Our models indicate universal and distinct roles for the relative, intrinsic performance of selfed and outcrossed embryos ( $G$ ) and seeds ( $D$ ) in mating-system evolution (Table 2, Figs. 3, 4). The genetic consequences of self-fertilization for reduced offspring performance have been recognized as significant influences on mating-system evolution since Darwin's assertion that "nature abhors perpetual self-fertilisation" (1876, p. 8); however, the contrasting natures of predispersal inbreeding depression ( $1 - G$ ) and postdispersal inbreeding depression ( $1 - D$ ) have been appreciated only recently (Husband and Schemske 1996; Charlesworth and Charlesworth 1999) and the implications of this contrast remain to be explored fully. Our analyses reveal that intense postdispersal inbreeding depression ( $D < 0.5$ ) by itself is sufficient to select for exclusive outcrossing (Fig. 3: Fig. 4A,  $\delta > 1 - G/2$ ; Fig. 4B,  $\delta > 1 - [Q + G]/2$ ). Consequently, self-incompatibility

should be especially prevalent in species subject to strong postdispersal inbreeding depression. More diverse mating systems are possible with weak postdispersal inbreeding depression ( $D > 0.5$ ). Thus, mating-system evolution depends fundamentally on the dynamics of inbreeding during the life cycle.

Temporal variation in the severity of inbreeding depression is an essential feature of the adaptive role of reproductive compensation, which influences mating-system evolution primarily when selfed *zygotes* survive poorly compared to outcrossed *zygotes* ( $GD < 0.5$ ), but selfed *seeds* realize high relative survival ( $D > 0.5$ ; Figs. 3, 4). In this situation, production of extra female gametes allows a heterozygous maternal hermaphrodite to produce families comprised of both outcrossed offspring with relatively good predispersal survival and the small proportion of selfed offspring that are heterozygous for early acting lethal alleles and also have relatively good postdispersal survival. As angiosperms commonly produce more ovules than they can mature (Harder and Routley 2006) and predispersal inbreeding depression is often much stronger than postdispersal inbreeding depression (Husband and Schemske 1996), reproductive compensation may frequently contribute to adaptive mixed mating.

When self-mating discounts outcrossing opportunities, the relative success of male gametes involved in self- versus cross-mating ( $Q = q_x/q_s$ ) also influences mating-system evolution (Table 2, Fig. 4). This parameter incorporates both the dispersal of male gametes and their survival in female reproductive tracts. It influences mating-system evolution by determining the relative impacts on paternal success of local mate competition for self-fertilization and pollen discounting. In the absence of male-gamete discounting, increased self-mating augments an individual's genetic contributions to its own offspring without affecting its contributions to offspring produced by other individuals, so the resulting aggravation of local mate competition bears no siring costs. In contrast, when self-mating reduces outcross siring opportunities, a specific male gamete may have a higher probability of fertilizing an egg on another individual than of succeeding in local mate competition to fertilize a sibling egg. We argued above that  $Q$  is probably quite small for angiosperms with granular pollen, because of the vagaries of pollen dispersal; however, this term may be larger for plants with more efficient pollen transfer (e.g., orchids: Harder and Johnson in press) and hermaphroditic animals with internal fertilization. In general, large  $Q$  elevates the ESS proportion of outcrossed offspring (Fig. 4B), because of the greater probability that a male gamete diverted from self-mating actually contributes to cross-fertilization.

In contrast to male-gamete performance and the intrinsic performance of embryos and seeds, the relative competitive ability of selfed embryos during competition for maternal resources ( $K$ ) had little impact on the ESS mating system in our stochastic model (Fig. 5) and is probably a general outcome. This insensitivity



results for several reasons. When exclusive selfing or outcrossing is favored, the presence of only one class of embryos precludes competition among classes. When the ESS mixed-mating system involves either ovule limitation, or the transition between ovule and resource limitation, the optimal number of embryos surviving genetic deaths is less than or equal to the maximum number that can be developed, given the available resources. Consequently, all surviving ovules should develop, regardless of their relative competitive ability. The possible exception to a limited impact of relative competitive ability could occur when the ESS mating system involves resource limitation. However, we expect this situation to occur rarely and to be transient for two reasons. First, resource-limited mixed mating is favored primarily when individuals produce more female gametes than are needed to compensate for all genetic deaths, even with exclusive selfing (i.e.,  $m < g_s$ ). Such profligate production of female gametes should be countered by selection to redistribute maternal resources to offspring development. Second, mixed-mating ESSs that involve resource limitation also involve predominant self-fertilization and Porcher and Lande (2005b) concluded that “high selfing rates purge most embryonic lethals . . . , regardless of the opportunity for compensation” (p. 680). Thus, regardless of the ESS mating system, the relative competitive abilities of selfed and outcrossed embryos seem unlikely to play a major role in the evolution of hermaphrodite mating systems, as long as self- and cross-fertilization occur simultaneously.

Our models demonstrate that the complete spectrum of hermaphrodite mating systems could arise as evolutionary stable strategies in contrasting mating environments. Clearly, many circumstances could cause deviations from the ESS mating system, especially insufficient pollination, which favors reproductive assurance (Fig. 7). Nevertheless, all of the requirements for adaptive mixed mating incorporated in our models are probably common features of reproduction by hermaphrodites, including: male-gamete discounting (e.g., Harder and Barrett 1995); production of compensatory female gametes (Harder and Routley 2006); and heterogeneity in the nature of inbreeding depression during the life cycle, with lethal traits expressed early when homozygous (Husband and Schemske 1996; Charlesworth and Charlesworth 1999). Thus, the diversity of hermaphrodite mating systems (Goodwillie et al. 2005; Jarne and Auld 2006) may often bear the imprint of selection that maximizes genetic contributions to the next generation, rather than simply the sloppiness of mating, or convenient remedies for insufficient fertilization.

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## Appendix

In this appendix, we derive the ESS allocations of pollen to self-pollination and export, first in the absence of pollen discounting and then with complete pollen discounting. The solutions are asymptotically true for large numbers of ovules per ovary. In all cases, selfed and outcrossed embryos are assumed to compete equally for maternal resources. We also assume that if a plant exports pollen it must also import pollen, and that fertilization is not pollen-limited for any potential phenotype (i.e.,  $f_s + f_\varphi = 1$ , where  $f_s$  and  $f_\varphi$  are defined by eqs. 1a and 1b, respectively, or  $[q_s p'_s + q_x p'_x]P > 0$ ), because selection acts most strongly against incomplete fertilization (see Figs. 2B, 7A–C).

### ESS MATING SYSTEM WITH NO POLLEN DISCOUNTING

When self-pollination does not affect pollen export, individuals with either the resident or invading phenotypes realize equal outcross siring success (i.e., the last term in eq. 3). Consequently, for a given fraction of exported pollen,  $p_x$ , the ESS maximizes maternal fitness, which equals the sum of the fitness gains from selfing and female outcrossing. For an invading phenotype  $\mathbf{p}' = (p'_s, p'_x)$  in a resident population of phenotype  $\mathbf{p} = (p_s, p_x)$ , maternal fitness is

$$\hat{W}(\mathbf{p}', \mathbf{p}) = 2f_s(\mathbf{p}', \mathbf{p})g_s k(\mathbf{p}', \mathbf{p})d_s + f_\varphi(\mathbf{p}', \mathbf{p})g_x k(\mathbf{p}', \mathbf{p})d_x.$$

In the absence of pollen limitation of fertilization, an increase in self-fertilization can switch the constraint on seed production from resource to ovule limitation (Fig. 2A), so the three following cases must be considered to determine which selfing phenotype  $p'_s$  maximizes fitness.

#### Case 1: ( $0 < g_s < g_x < m < 1$ )

In this situation fewer embryos survive genetic death than can develop into seeds, so  $k_s = k_x = 1$  regardless of the number of ovules fertilized. Based on this condition and the definitions of  $f_s$  and  $f_\varphi$  given by equation 1a and b, respectively, total maternal fitness equals

$$\hat{W}(\mathbf{p}', \mathbf{p}) = \frac{2q_s p'_s g_s d_s + q_x p_x g_x d_x}{q_s p'_s + q_x p_x}.$$

The derivative of fitness with respect to  $p'_s$ ,

$$\frac{d\hat{W}}{dp'_s} = \frac{q_s q_x p_x (2g_s d_s - g_x d_x)}{(q_s p'_s + q_x p_x)^2},$$

indicates that total maternal fitness is a continuously increasing or decreasing function of  $p'_s$ , depending only on whether  $2g_s d_s$  is greater or less than  $g_x d_x$ , regardless of the fixed value of  $p_x$ . If  $2g_s d_s < g_x d_x$  a plant always benefits from decreased self-pollination. If  $2g_s d_s > g_x d_x$  increased self-pollination is universally favored, within the constraint that plants allocate a fixed proportion of pollen to export. Because this latter result applies, regardless of  $p_x$ , selection should also favor a relaxation of the export constraint, leading to exclusive self-pollination. Consequently, if both  $p_s$  and  $p_x$  are free to evolve the optimal allocation of pollen to self-pollination and the resulting proportion of self-fertilized ovules are straightforward,

$$p_s^* = \begin{cases} 0, \\ 1, \end{cases} \text{ and } f_s^* = \begin{cases} 0, & \text{if } 2g_s d_s < g_x d_x, \\ 1, & \text{if } 2g_s d_s \geq g_x d_x. \end{cases}$$

#### Case 2: ( $0 < m < g_s < g_x < 1$ )

In this case, fertilized ovules compete for maternal resources for all allocations to self-pollination, and total maternal fitness is,

$$\hat{W}(\mathbf{p}', \mathbf{p}) = \frac{m(2q_s p'_s g_s d_s + q_x p_x g_x d_x)}{q_s p'_s g_s + q_x p_x g_x}.$$

Taking the derivative with respect to  $p'_s$  gives

$$\frac{d\hat{W}}{dp'_s} = \frac{mq_s q_x p_x g_x (2d_s - d_x)}{(q_s p'_s g_s + q_x p_x g_x)^2}.$$

Again, total maternal fitness is a monotonic function of  $p'_s$ , irrespective of the pollen allocation strategy adopted by the rest of the population. When  $2d_s < d_x$  decreased allocation to self-pollen and increased outcross pollen always benefits a plant, otherwise increased self-pollination is always better. The optimal selfing phenotype is again straightforward,

$$p_s^* = \begin{cases} 0, \\ 1, \end{cases} \text{ and } f_s^* = \begin{cases} 0, & \text{if } 2d_s < d_x, \\ 1, & \text{if } 2d_s \geq d_x. \end{cases}$$

#### Case 3: ( $0 < g_s < m < g_x < 1$ )

In this situation, developing seeds compete for maternal resources if  $f_s g_s + f_\varphi g_x > m$ , or equivalently when the fraction of ovules that are self-fertilized falls below

$$f_s^T = \frac{g_x - m}{g_x - g_s},$$

which is equivalent to a plant allocating the fraction

$$p_s^T = \frac{p_x q_x (g_x - m)}{q_s (m - g_s)}$$

of its pollen to self-pollination. Therefore, maternal fitness is,

$$\hat{W}(\mathbf{p}', \mathbf{p}) = \begin{cases} \frac{m(2q_s p'_s g_s d_s + q_x p_x g_x d_x)}{q_s p'_s g_s + q_x p_x g_x}, & \text{if } p'_s < p_s^T; \\ \frac{2q_s p'_s g_s d_s + q_x p_x g_x d_x}{q_s p'_s + q_x p_x}, & \text{otherwise.} \end{cases}$$

Fitness remains a continuous function of  $p'_s$ , but the first derivative with respect to  $p'_s$  is discontinuous at the threshold  $p_s^T$ . The previous cases demonstrate that the fitness function is piecewise monotonic. The first piece is an increasing function only when  $2d_s > d_x$  (see Case 2) and the second piece is an increasing function only when  $2g_s d_s > g_x d_x$  (see Case 1). Note that  $2g_s d_s < g_x d_x$  if  $2d_s < d_x$ , because we assume  $g_s < g_x$ . Hence, the fitness function has three possible characteristic shapes, which result in the following alternate optimal allocations of self-pollen and proportion of self-fertilized ovules:

$$p_s^* = \begin{cases} 0, & \text{if } 2d_s < d_x \text{ and } 2g_s d_s < g_x d_x; \\ p_s^T, & \text{if } 2d_s > d_x \text{ and } 2g_s d_s < g_x d_x; \\ 1, & \text{if } 2d_s > d_x \text{ and } 2g_s d_s > g_x d_x. \end{cases}$$

Consideration of the results for cases 1, 2, and 3 leads to the decision tree presented in Figure 3 for conditions that favor exclusive outcrossing ( $f_s^* = 0$ ), mixed mating at the transition between resource and ovule limitation ( $f_s^* = f_s^T$ ), or exclusive selfing ( $f_s^* = 1$ ).

### ESS MATING SYSTEM WITH COMPLETE POLLEN DISCOUNTING

We now assume that the  $(1 - p_{nmin})P$  pollen grains that could be involved in pollination contribute interchangeably to either self- or cross-pollination ( $p_x = 1 - p_s - p_{nmin}$ , where  $p_{nmin}$  is constant). In this case, we need to consider only one pollination mode explicitly, and we focus on the proportion of pollen involved in self-pollination. Consequently, equation (3) becomes

$$\begin{aligned} W(p'_s, p_s) &= 2f_s(p'_s, p_s)g_s k(p'_s, p_s)d_s \\ &\quad + f_\sigma(p'_s, p_s)g_x k(p'_s, p_s)d_x \\ &\quad + f_\sigma(p'_s, p_s)g_x k(p_s, p_s)d_x. \end{aligned}$$

Thus, we seek the ESS,  $p_s^*$ , which satisfies  $W(p'_s, p_s^*) \leq W(p_s^*, p_s^*)$  for all  $p'_s$ . As in the previous section, the first derivative of the fitness function is discontinuous at the transition between resource and ovule limitation of seed production, which occurs when plants allocate the proportion,

$$p_s^T = \frac{(1 - p_{nmin})(g_x - m)q_x}{(g_x - m)q_x + (m - g_s)q_s},$$

of their pollen to self-pollination. When  $p_s < p_s^T$  seed production is resource-limited, otherwise seed production is ovule-limited.

To determine whether  $p_s^T$  or some other, possibly intermediate, selfing fraction is the ESS the fitness function must be examined separately for both resource and ovule limitation.

When resource availability limits seed production ( $p_s < p_s^T$ ) the invader's fitness is

$$\begin{aligned} W(p'_s, p_s) &= \frac{m(2q_s g_s d_s p'_s + q_x g_x d_x [1 - p_s - p_{nmin}])}{q_s g_s p'_s + q_x g_x (1 - p_s - p_{nmin})} \\ &\quad + \frac{mq_x g_x d_x (1 - p'_s - p_{nmin})}{q_s g_s p_s + q_x g_x (1 - p_s - p_{nmin})}. \end{aligned}$$

The partial derivative with respect to  $p'_s$  evaluated at  $p'_s = p_s = p$ , gives the selection gradient for  $p'_s$  when all plants adopt strategy  $p$ ,

$$\left. \frac{\partial W}{\partial p'_s} \right|_{(p,p)} = \frac{m([2q_s g_s d_s - q_x g_x d_x][1 - p - p_{nmin}] - q_s g_s d_x [1 - p_{nmin}])}{(q_s g_s p + q_x g_x [1 - p - p_{nmin}])^2}. \quad (A1)$$

When  $2q_s g_s d_s < q_x g_x d_x$  the gradient is negative for all  $p$ , so complete outcrossing maximizes fitness. In contrast, when  $2q_s g_s d_s > q_x g_x d_x$ , a mutant may benefit by elevated selfing if all residents allocate a sufficiently low proportion of their pollen to selfing, whereas reduced selfing is advantageous if all residents self-pollinate extensively, indicating that a mixture of selfing and outcrossing maximizes fitness. This optimal mixed-mating system is found by setting equation (A1) to 0 and solving for  $p_s$  resulting in

$$\begin{aligned} p_s^R &= (1 - p_{nmin}) \left( 1 - \frac{q_s g_s d_x}{2q_s g_s d_s - q_x g_x d_x} \right) \\ &= (1 - p_{nmin}) \left( 1 - \frac{G}{2GD - Q} \right). \end{aligned}$$

Some calculus shows that the second partial derivative of  $W$  with respect to  $p'_s$  is strictly negative when  $p_s = p_s^R$ , implying  $p_s^R$  is a local fitness maximum. Thus,  $p_s^R$  is the ESS if it lies within the range of self-pollination that results in resource limitation, namely  $0 < p_s^R < p_s^T$ .

Alternatively, when seed production is ovule-limited ( $p_s > p_s^T$ ) the invader's fitness is

$$\begin{aligned} W(p'_s, p_s) &= \frac{2q_s g_s d_s p'_s + q_x g_x d_x (1 - p_s - p_{nmin})}{q_s p'_s + q_x (1 - p_s - p_{nmin})} \\ &\quad + \frac{q_x g_x d_x (1 - p'_s - p_{nmin})}{q_s p_s + q_x (1 - p_s - p_{nmin})}. \end{aligned}$$

The partial derivative with respect to  $p'_s$  evaluated at  $p'_s = p_s = p$  is now

$$\left. \frac{\partial W}{\partial p'_s} \right|_{(p,p)} = \frac{q_x[(2q_s g_s d_s - q_x g_x d_x)(1 - p - p_{nmin}) - q_s g_x d_x(1 - p_{nmin})]}{[q_s p + q_x(1 - p - p_{nmin})]^2}. \quad (A2)$$

Again, the selection gradient is negative for all  $p$  when  $2q_s g_s d_s < q_x g_x d_x$ , so complete outcrossing maximizes fitness. In contrast, when  $2q_s g_s d_s > q_x g_x d_x$ , equation (A2) equals zero when all plants allocate the proportion,

$$\begin{aligned} p_s^O &= (1 - p_{nmin}) \left( 1 - \frac{q_s g_x d_x}{2q_s g_s d_s - q_x g_x d_x} \right) \\ &= (1 - p_{nmin}) \left( 1 - \frac{1}{2GD - Q} \right), \end{aligned}$$

of their pollen to self-pollination. Again, some calculus shows that the second partial derivative of  $W$  with respect to  $p'_s$  is strictly negative when  $p_s = p_s^O$ , implying  $p_s^O$  is a local fitness maximum. Thus,  $p_s^O$  is the ESS if it lies within the range of self-pollination that results in ovule limitation, namely  $p_s^T < p_s^O < 1 - p_{nmin}$ .

The preceding analysis reveals that mating systems other than exclusive outcrossing are favored only when  $2q_s g_s d_s > q_x g_x d_x$ , which is equivalent to

$$\delta < 1 - \frac{q_x}{2q_s} = 1 - \frac{Q}{2}. \quad (A3)$$

The ESS in this situation is determined by both the value of  $p_s^T$  with respect to  $p_s^O$  and  $p_s^R$  and whether  $p_s^T$ ,  $p_s^O$ , or  $p_s^R$  are positive or negative. The assumption that  $g_s \leq g_x$  implies that  $p_s^O \leq p_s^R < 1$ , which leads to three possible situations describing the relative relations between  $p_s^T$ ,  $p_s^O$ , and  $p_s^R$ . From above, we know that  $p_s^R$  is the ESS if  $p_s^R < p_s^T$ , or  $p_s^O$  is the ESS if  $p_s^T < p_s^O$ . To determine the evolutionary outcome otherwise note that if  $p_s^O < p_s^T$  and  $p_s > p_s^T$ , then seed production is ovule-limited and selection will favor reduced  $p_s$ . Also note, if  $p_s^T < p_s^R$  and  $p_s < p_s^T$ , then seed production is resource-limited and selection will favor enhanced  $p_s$ . Hence, as the fitness function is piecewise continuous, if  $p_s^O < p_s^T < p_s^R$ ,  $p_s$  will evolve to  $p_s^T$  if it is nonnegative. As the ESS must be positive, to determine the evolutionary outcome, we must consider the following three possible cases regarding the signs of  $p_s^O$  and  $p_s^R$ .

#### Case A: $p_s^O < p_s^R < 0$

In this case, neither  $p_s^O$  nor  $p_s^R$  exceed 0, so they are not feasible mating systems. This situation occurs when  $2q_s g_s d_s - q_x g_x d_x < q_s g_s d_x$ , or

$$\delta > 1 - \frac{q_x}{2q_s} - \frac{g_s}{2g_x} = 1 - \frac{Q + G}{2}. \quad (A4)$$

Given this condition, the partial derivative of fitness with respect to  $p_s$  is negative, regardless of whether seed production is resource or ovule-limited (see eqs. A1 and A2, respectively), so exclusive outcrossing is always favored (i.e.,  $p_s^* = 0$ ). Condition A4 can never be less stringent than the complement of condition A3, because  $g_s \geq 0$ , so A4 provides the more general threshold for complete outcrossing.

#### Case B: $p_s^O \leq 0 \leq p_s^R$

This case occurs when  $q_s g_s d_x \leq 2q_s g_s d_s - q_x g_x d_x \leq q_s g_x d_x$ , or equivalently

$$\frac{1}{2} - \frac{q_x}{2q_s} \leq \delta \leq 1 - \frac{q_x}{2q_s} - \frac{g_s}{2g_x} \quad \text{or} \quad \frac{1 - Q}{2} \leq \delta \leq 1 - \frac{Q + G}{2}.$$

In this case,

$$p_s^* = \begin{cases} 0, & \text{if } p_s^T < 0; \\ p_s^T, & \text{if } 0 < p_s^T \leq p_s^R; \\ p_s^R, & \text{if } p_s^T > p_s^R. \end{cases}$$

#### Case C: $0 < p_s^O < p_s^R$

In this case  $2q_s g_s d_s - q_x g_x d_x > q_s g_x d_x$ , or equivalently

$$\delta < \frac{1}{2} - \frac{q_x}{2q_s} \quad \text{or} \quad \delta < \frac{1 - Q}{2}.$$

The ESS is now

$$p_s^* = \begin{cases} p_s^O, & \text{if } p_s^T \leq p_s^O; \\ p_s^T, & \text{if } p_s^O < p_s^T \leq p_s^R; \\ p_s^R, & \text{if } p_s^T > p_s^R. \end{cases}$$

Note that if the ESS given in cases B or C satisfies  $p_s^* > p_{nmin}$ , then  $p_s^* = p_{nmin}$ . Hence, selection favors lower  $p_{nmin}$  (i.e., selection should favor mechanisms that maximize the potential for pollen to be used for either selfing or outcrossing).