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Stabilization of Mixed-Mating Systems by Differences in the Magnitude of Inbreeding Depression for Male and Female Fitness Components

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Although a majority of plant species exhibit either complete selfing or complete outcrossing, a distinct minority exhibit a mixed-mating system, in which both selfing and outcrossing occur (Schemske and Lande 1985). Moreover, in at least some species with mixed-mating systems, selfing rates are genetically variable (Brown and Clegg 1984; Holtsford and Ellstrand 1992; Carr and Fenster 1994; Chang and Rausher 1998), suggesting that these mixed-mating systems are evolutionarily stable. Theoretical attempts to account for such stability have generally focused on assessing the conditions under which two opposing sets of evolutionary processes can generate polymorphisms for selfing rates. One of these processes, originally described by Fisher (1941), arises because an allele that increases the selfing rate automatically enjoys a transmission advantage due to the extra pathway (via self-pollination) by which it may transmit copies of itself to the next generation. Various authors have demonstrated that, under some circumstances, two other processes—inbreeding depression and pollen discounting—may prevent fixation of such a selfing allele and stabilize a selfing-rate polymorphism (Holsinger 1988, 1991; Charlesworth and Charlesworth 1990; Uyenoyama and Waller 1991*b*). In particular, under some circumstances the identity disequilibrium that is expected to arise between loci affecting selfing rate and loci affecting fitness through inbreeding depression may be strong enough to stabilize polymorphisms at both sets of

loci (Holsinger 1988; Uyenoyama and Waller 1991*b*). Alternatively, mass-action models of pollen discounting may produce a similar stabilization (Holsinger 1991).

In the common morning glory *Ipomoea purpurea* L. (Roth), experimental investigations of associations between characters affecting selfing and the magnitude of inbreeding depression (Chang and Rausher 1999) and of pollen discounting (Rausher et al. 1993; Fry and Rausher 1997; Mojonner and Rausher 1997; Chang and Rausher 1998) indicate that neither of these processes, either individually or acting together, can account for apparently stable polymorphisms in two different traits affecting selfing rates: flower color determined by the *W* locus (Rausher et al. 1993; Fry and Rausher 1997; Mojonner and Rausher 1997) and anther-stigma separation (Chang and Rausher 1998, 1999). These observations have led us to seek other possible explanations for maintenance of these polymorphisms. We report here an additional mechanism by which a polymorphism for selfing rates may be maintained: differences among male and female fitness components in the magnitude of inbreeding depression. More generally, this mechanism can yield an evolutionarily stable system (ESS) for a mixed-mating system.

In virtually all prior models of the evolution of selfing (but see Damgaard et al. 1994), inbreeding depression, when it is included, is assumed to affect viability and, thus, affect the overall male and female components of fitness equally (Maynard Smith 1977; Charlesworth 1980; Feldman and Christiansen 1984; Holsinger et al. 1984; Lande and Schemske 1985; Holsinger 1988; Charlesworth and Charlesworth 1990; Charlesworth et al. 1990; Uyenoyama and Waller 1991*a*, 1991*b*, 1991*c*). This assumption has perhaps been warranted because of the virtual absence of information on the relative effects of inbreeding on male and female components of fitness. However, Husband and Schemske (1996) have recently demonstrated that, in plants, inbreeding depression is often most strongly expressed during the reproductive phase of the life cycle, and there is no a priori reason to believe that it would necessarily affect male and female fitness components equally. In fact, Chang and Rausher (1999) provide evidence sug-

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gesting that in *I. purpurea* female fitness is reduced more by selfing than is male fitness.

To examine the consequences of this type of difference, we numerically analyzed a model in which selfing rate is controlled by a single locus having two alleles, *A* and *a*. The selfing rates of genotypes *AA*, *Aa*, and *aa* were designated s_1 , s_2 , and s_3 , where, without loss of generality, it is assumed that $s_1 \leq s_2 \leq s_3$ (with one inequality strict). The male and female components of fitness of an individual that is not inbred are each assumed to be 1, while for inbred individuals, these components are designated M and F , respectively, with $M, F < 1$. Biologically, F is the expected number of fertilized ovules produced by an inbred individual, relative to outbred individuals, calculated from the time of fertilization. It thus represents the standard relative cumulative (multiplicative) fitness of inbred individuals (Molina-Freaner and Jain 1993; Willis 1993; Johnston and Schoen 1996), calculated as

$$F = A \times V \times R_f, \quad (1a)$$

where A is relative survivorship from fertilization of a selfed ovule to seed maturation, V is relative survivorship (including germination probability) from seed maturation to commencement of reproduction, and R_f is the relative number of fertilized ovules produced by a surviving inbred individual. Similarly, M is the relative male outcross success of inbred individuals; that is, it is the expected number of ovules on other plants sired by an inbred individual, relative to the number sired by outbred individuals, calculated from the time of fertilization, which is given by

$$M = A \times V \times R_m, \quad (1b)$$

where R_m is the relative male outcross success (number of ovules sired on other plants) of an inbred individual, which includes effects of inbreeding not only on pollen number and viability but also on success at transporting pollen to stigmas on other plants. In this formulation, selfing pollen is included in the female fitness component. The magnitude of inbreeding depression for the two components of fitness are, thus, $1 - M$ and $1 - F$.

In formulating the recursion equations for this system, it is helpful to keep track of inbred and outbred individuals of each genotype separately. We therefore designate by p_i and q_i the frequencies of individuals of genotype i that are inbred (produced by a single parental plant that selfed) and outbred (produced by a cross between different plants), respectively ($i = 1, 2, 3$ corresponds to *AA*, *Aa*, and *aa*). We ignore here the possibility of biparental inbreeding.

The recursion equations for this system are

$$\beta p'_1 = p_1 s_1 F + q_1 s_1 + \frac{1}{4} p_2 s_2 F + \frac{1}{4} q_2 s_2, \quad (2a)$$

$$\beta p'_2 = \frac{1}{2} p_2 s_2 F + \frac{1}{2} q_2 s_2, \quad (2b)$$

$$\beta p'_3 = p_3 s_3 F + q_3 s_3 + \frac{1}{4} p_2 s_2 F + \frac{1}{4} q_2 s_2, \quad (2c)$$

$$\begin{aligned} \beta q'_1 &= p_1(1 - s_1)p_A F + q_1(1 - s_1)p_A \\ &+ \frac{1}{2} p_2(1 - s_2)p_A F + \frac{1}{2} q_2(1 - s_2)p_A, \end{aligned} \quad (2d)$$

$$\begin{aligned} \beta q'_2 &= p_1(1 - s_1)(1 - p_A)F \\ &+ q_1(1 - s_1)(1 - p_A) + \frac{1}{2} p_2(1 - s_2)F \\ &+ \frac{1}{2} q_2(1 - s_2) + p_3(1 - s_3)p_A F \\ &+ q_3(1 - s_3)p_A, \end{aligned} \quad (2e)$$

$$\begin{aligned} \beta q'_3 &= \frac{1}{2} p_2(1 - s_2)(1 - p_A)F + p_3(1 - s_3)(1 - p_A)F \\ &+ \frac{1}{2} q_2(1 - s_2)(1 - p_A) + q_3(1 - s_3)(1 - p_A), \end{aligned} \quad (2f)$$

where

$$\beta = F(p_1 + p_2 + p_3) + (q_1 + q_2 + q_3)$$

is the sum of the terms on the right-hand sides of the equations and

$$p_A = \frac{M(p_1 + \frac{1}{2}p_2) + q_1 + \frac{1}{2}q_2}{M(p_1 + p_2 + p_3) + q_1 + q_2 + q_3}$$

is the frequency of allele *A* in the outcross pollen pool. We deliberately incorporate no pollen discounting in the model because we are interested in whether the differential effects of inbreeding on male and female fitness can, by themselves, lead to evolutionarily stable mixed-mating systems.

In this article, we restrict our analysis to the case in which there is no overdominance for selfing rate; that is,

s_2 is intermediate between s_1 and s_3 . We do so because overdominance is intuitively expected to lead to stabilization of a selfing-rate polymorphism under many circumstances, but determination of whether such polymorphisms are evolutionarily stable to invasion by alleles conferring complete selfing or complete outcrossing is beyond the scope of our current analyses. This assumption of no overdominance also seems biologically reasonable because, in most cases in which the genetic basis of a selfing-rate polymorphism is known, there is no overdominance (Ennos 1981; Marshall and Abbott 1982; Epperson and Clegg 1988; Carr and Fenster 1994; Fry and Rausher 1997; Chang and Rausher 1998).

Numerical iteration of the recursion equations indicates that for any pair of alleles A and a , with corresponding genotypic selfing rates s_1 , s_2 , and s_3 , the $M - F$ parameter space is divided into four regions (fig. 1). The boundaries of these regions are formed by two "isoclines," each corresponding to one of the homozygote genotypes. Extensive numerical exploration indicates that each of these isoclines corresponds, to at least six decimal places, to the line given by the equation

$$F = \frac{\alpha}{\phi + M} + \gamma, \quad (3)$$

where $\alpha = (1 - s)/4s^2$, $\phi = (1 - s)/2s$, $\gamma = (2s - 1)/2s$, and s is the selfing rate for the corresponding homozygote genotype. This equation is well defined for all values of $0 < M \leq 1$. For $M = 0$, the isocline is $F = 1 - M$, which is the limit of equation (3) as $s \rightarrow 0$.

Numerical iterations indicate that the equilibrium frequencies of the two alleles are determined by which region of figure 1a the actual value of (M, F) lies in, as follows. In region I, increased outcrossing (fixation of A) is favored. In region II, increased selfing (fixation of a) is favored. In region III, a stable polymorphism is maintained. Although the isoclines defining this and the other regions are not affected by the value of s_2 , as long as $s_1 \leq s_2 \leq s_3$, the equilibrium allele frequencies in this region are determined by s_2 . In region IV, either complete outcrossing or complete selfing is favored, depending on initial gene frequencies.

While this analysis indicates that stabilization of a selfing-rate polymorphism is possible if (M, F) lies in region III, long-term evolutionary stability will be determined by whether a stable polymorphism of this type can be invaded by other alleles with different selfing rates. The stability properties described above imply that the long-term evolutionary equilibrium for outcrossing rate can be described by a very simple model, which we have confirmed by extensive numerical analysis. In particular, the stability properties of the two-allele system imply that the $M - F$

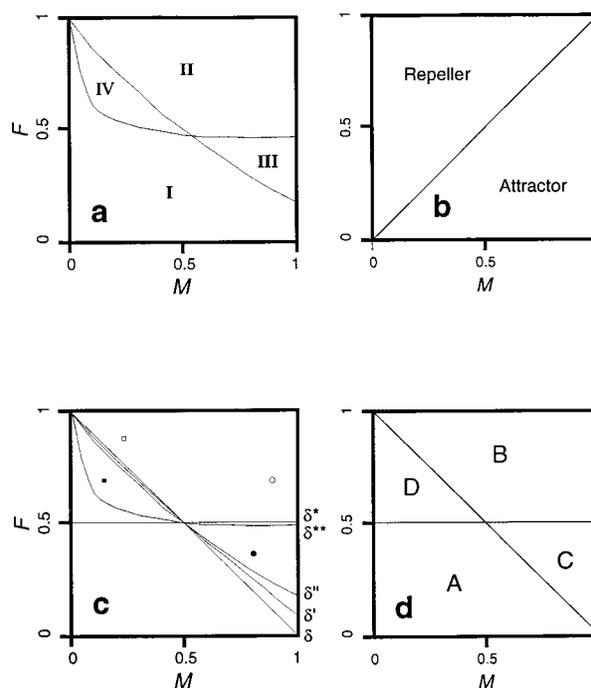


Figure 1: Stability properties of selfing-rate variants for different combinations of male, M , and female, F , fitness components. *a*, For a single locus with two alleles differing in selfing rates of their corresponding homozygotes, the $F - M$ parameter space is divided into four stability regions: region I, allele conferring higher outcrossing favored; region II, allele conferring lower outcrossing favored; region III, stable polymorphism; and region IV, disruptive selection, that is, either allele favored depending on initial frequencies. The isoclines portrayed correspond to $s = 0.2$ and $s = 0.9$. *b*, Parameter space is divided into two regions, within which the point (M, F) acts either as an attractor or a repeller of isoclines. *c*, Illustration of attractor and repeller properties (see text for explanation). *d*, Regions corresponding to different types of evolutionary stability: region A, ESS is complete outcrossing; region B, ESS is complete selfing; region C, ESS is mixed-mating system; and region D, there are two ESSs, corresponding to complete selfing and complete outcrossing.

parameter space is divided into two portions by the line $M = F$ (fig. 1b). In the region below this line, corresponding to combinations of M and F for which $M > F$, the point (M, F) acts as an attractor of the isoclines. Specifically, in a population segregating for two alleles affecting selfing rate, when (M, F) is on the same side of both isoclines corresponding to the two homozygote genotypes, selection will fix the allele corresponding to the genotype with the isocline that passes closer to the point (M, F) .

This explanation for this behavior is illustrated in figure 1c, in which the solid circle represents a particular combination of M and F within the attractor region. Consider a population that is initially completely outcrossing (isocline δ) and into which a mutation causing a small degree of selfing is introduced (isocline δ'). The phase diagram

then corresponds to figure 1a, in which regions III and IV are defined by the isoclines δ and δ' . Because the (M, F) point lies in region II, the mutant allele, which increases selfing, is favored and will go to fixation. In other words, the original homozygote is replaced with a new homozygote, having an isocline closer to the attractor (M, F) . Subsequently, another mutation may arise that confers a slightly higher selfing rate, corresponding to isocline δ'' . The boundaries of regions III and IV are then the lines δ' and δ'' . The (M, F) point still lies in region II, and hence the new mutant, conferring increased selfing, is again favored. Once again, the isocline of the fixed allele lies closer to (M, F) . This process will continue until selfing rate is sufficiently high that a new mutation causes the boundaries of regions III and IV to encompass the (M, F) point, at which a stable polymorphism is achieved. By similar reasoning, introduction, into a completely selfing population, of a mutation that causes a small degree of outcrossing yields regions III and IV corresponding to lines isoclines δ^* and δ^{**} . The (M, F) point then lies in region I, which leads to fixation of the mutation conferring increased outcrossing. Therefore, from either extreme, selection will cause outcrossing rates to evolve to an intermediate value, thus producing an evolutionarily stable mixed-mating system. Numerical iteration indicates that the allele corresponding to the homozygote with an isocline passing through (M, F) is stable to invasion by any other allele and, thus, represents an ESS.

Because selfing rates are restricted to $0 < s < 1$, isoclines are constrained to lie within the region defined by δ and δ^* in figure 1c. It is possible, however, for (M, F) to lie outside of this region yet still satisfy the criterion $M > F$, as, for example, the open circle in figure 1c. In this situation, the ESS allele's isocline can not pass through (M, F) . However, the ESS still corresponds to the allele with the isocline closest to (M, F) . For the open circle in figure 1c, this line corresponds to δ^* (complete selfing). The point (M, F) , thus, still acts as an attractor of the isoclines.

For combinations of (M, F) lying above the line $M = F$ (fig. 1b), the point (M, F) acts as a repeller of the isoclines. For example, for (M, F) corresponding to the solid square in figure 1c, an allele conferring complete outcrossing (isocline δ) is favored over any allele conferring slightly reduced outcrossing (isoclines δ' or δ'') because (M, F) lies in region I. Similarly, for the same (M, F) , an allele conferring complete selfing (isocline δ^*) is favored over any allele conferring slightly reduced selfing (isocline δ^{**}) because (M, F) lies, in this situation, in region II. This behavior means that fixation of an allele with an isocline passing through (M, F) represents an anti-ESS, while complete selfing and complete outcrossing represent locally stable ESSs.

As previously, although isoclines are constrained to lie between δ and δ^* in figure 1c, a point (M, F) satisfying $M < F$ may lie outside the region defined by these isoclines (e.g., the open square in fig. 1c). In these situations, (M, F) still acts as a repeller (e.g., for the open square, complete selfing, corresponding to isocline δ^* , is favored).

The qualitative evolutionary stability associated with a particular set of male and female inbreeding-depression values, (M, F) , as deduced by the above considerations, is summarized in figure 1d. Regions A and B correspond to complete outcrossing and complete selfing, respectively, being evolutionarily stable. Region C corresponds to a stable mixed-mating system, which may or may not exhibit genetic variation for selfing rate, while in region D, both complete selfing and complete outcrossing are locally evolutionarily stable. Moreover, the conditions for a stable mixed-mating system have a straightforward relationship to total fitness (defined as the average of male and female fitness components: $W = 1/2[M + F]$) and total inbreeding depression ($1 - W$): $W > 0.5$ and $F < 0.5$; that is, total inbreeding depression is less than 0.5, while inbreeding depression is greater than 0.5 for the female component of fitness.

The primary implication of this analysis is that differences in the magnitude of inbreeding depression for male and female fitness components may favor the evolution of a mixed-mating system. In particular, in species in which the value of (M, F) falls within region C of figure 1d, a mixed-mating system is an ESS. Moreover, for such species, complete outcrossing or complete selfing are evolutionarily unstable states, in the sense that any mutation causing selfing rates that deviate from one of these fixed states will increase in frequency. Such a mutation may become fixed or may equilibrate in a polymorphic state, depending on the exact values of (M, F) and of the mutant's selfing rate, but in either case a mixed-mating system results. The average selfing rate for evolutionary stable mixed-mating systems corresponding to different values of M and F is illustrated in figure 2, which indicates that a large fraction of region C corresponds to ESSs in which both outcrossing and selfing occur at appreciable frequency (e.g., >0.1).

Although our numerical analysis indicates that, for combinations of (M, F) in region C, there is always an ESS corresponding to an allele with a isocline passing through (M, F) , one issue that we have not yet resolved is whether such an allele will actively invade a stable polymorphism of two other alleles with different selfing rates. However, by analogy with the evolutionary genetic stability of sex ratio (Eshel and Feldman 1982) and of oviposition preference (Rausher and Englander 1987), the evolution of which is governed by complex frequency-dependent dynamics resembling those examined here, we conjecture

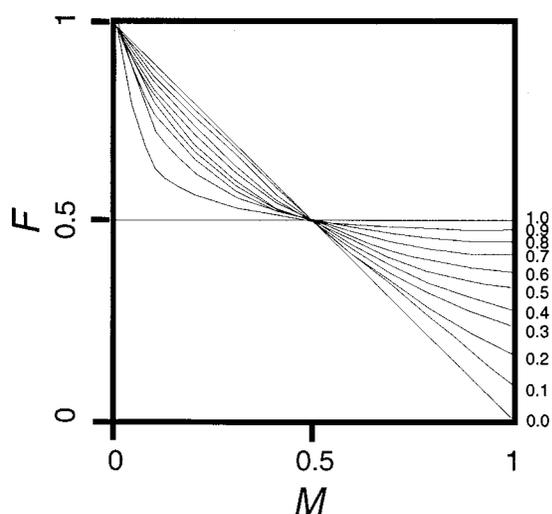


Figure 2: Selfing-rate isoclines. Each line represents the collection of (M, F) points yielding the same ESS selfing rate at evolutionary equilibrium. Equilibrium selfing rates are listed on the right side of the figure next to the corresponding isocline.

that the ESS allele will not actively invade such a polymorphism. Instead, it will coexist with the original alleles in a neutral equilibrium and can only be fixed through the action of random perturbations (“drift”) that move allele frequencies along a line of neutral equilibria. If this conjecture is true, it suggests that stable mixed-mating systems may frequently be expected to exhibit genetic variation for selfing rate.

A second important implication of our analysis is that the estimation of inbreeding effects on only the female component of fitness, including viability subcomponents, may lead to erroneous interpretations of the role of inbreeding depression in the evolution of mixed-mating systems. For example, consider a population with the combination of M and F indicated by the solid square in figure 1c. Application of previous theoretical results to this situation, in which inbreeding depression for the female fitness component is less than $1/2$ (i.e., $F > 1/2$), would suggest that low inbreeding depression by itself would favor the evolution of selfing. However, according to the model presented here, this conclusion would not be valid if the initial state of the population were a low level of selfing (e.g., corresponding to isoclines δ , δ' , and δ''). Because the magnitude of inbreeding depression for the male fitness component is large in this case, (M, F) falls in region D , making complete outcrossing locally evolutionarily stable. By contrast, were the magnitude of inbreeding depression for male fitness small, corresponding to the open circle in figure 1c, complete selfing is the only ESS. This contrast illustrates the necessity of knowing the effect of inbreeding

depression on both the female and male components of fitness for determining the ESS for selfing rate.

The possibility that differences in the effects of inbreeding depression on male and female fitness may stabilize a mixed-mating system raises several important empirical issues. First, how frequently is inbreeding depression on prereproductive components of fitness (i.e., A and V) low or nonexistent? This question is important because if $A \times V < 0.5$, M is by definition less than 0.5 , and a mixed-mating system therefore cannot be evolutionarily stable. It is clear that in many species $A \times V < 0.5$ (Husband and Schemske 1996, app.). In these cases, our model indicates that it is unnecessary to determine the relative values of F and M (i.e., to estimate R_f and R_m); complete outcrossing is predicted to be evolutionarily stable because both F and M will be less than 0.5 . However, as the recent survey by Husband and Schemske (1996) indicates, there are also many plant species for which inbreeding is most severe in the reproductive stage and in which there is little or no inbreeding depression associated with A and V . In these cases, the model indicates that whether a mixed-mating system is evolutionarily stable depends on the values of R_f and R_m (the prime determinants of F and M), which must be measured.

A second important empirical issue raised by our analysis is the following: when the magnitude of inbreeding depression affecting A and V is low, how frequently do inbreeding-depression effects differ for male and female fitness? We have found only four investigations, on only two plant species, that have attempted to measure effects of inbreeding on both male and female components of reproductive success. In *Mimulus guttatus* (Robertson et al. 1994; Carr and Dudash 1995, 1997), inbreeding depression for male components of fitness (pollen number and viability) tends to be substantially greater than inbreeding depression for female components of fitness (ovule number and seed number). By contrast, in *Phacelia dubia* (del Castillo 1998), inbreeding depression is strong for seed number but not detectable in male fertility (pollen viability). While both of these studies suggest that the magnitude of inbreeding depression differs for male and female fitness components, and while the *Phacelia* study suggests that inbreeding depression for male fitness may be less than for female fitness, as is required for stability of mixed-mating systems in our model, in neither case is there a statistical assessment of such a difference. Moreover, in all of these studies the effects of inbreeding depression on male fitness are restricted to measurement of the amount and/or viability of pollen produced and are thus incomplete. Specifically, they omit measurement of the effects of inbreeding depression on the success of pollen movement to other plants, effects that could be mediated, for example, through the effects of inbreeding depression on floral mor-

phology and other characters that influence attractiveness to pollinators. There thus appears to be little evidence that can be used to address this issue directly. Nevertheless, limited genetic evidence indicating that traits affecting male and female fitness are influenced by different genes (Coen and Meyerowitz 1991; Meagher 1992; Yanofsky 1995) suggests that a differential impact of inbreeding depression on male and female fitness is at least possible and that future investigations examining this possibility are warranted.

A final empirical issue is, in cases in which male and female fitness components differ substantially, how frequently do the values of male and female inbreeding depression fall within the region of parameter space in which polymorphisms are stable? Although empirical evidence relating to this issue is nonexistent, it seems to us quite conceivable that many of the minority of species exhibiting mixed-mating systems could occupy that region of stability.

One limitation of our model is that it does not allow for the joint evolution of inbreeding depression as selfing rate evolves. In this respect, it is similar to early models of the evolution of selfing rates (Nagylaki 1976; Lloyd 1979; Wells 1979), in which effects of inbreeding depression on male and female fitness were, either explicitly or implicitly, assumed to be equal. In these models, mixed-mating systems are never evolutionarily stable. Our analysis indicates that relaxing the assumption of equal inbreeding-depression effects greatly alters the dynamics of mating system evolution by allowing evolutionary stability of mixed-mating systems.

More recent analyses have incorporated the possibility that inbreeding depression may also evolve (e.g., Holsinger 1988; Charlesworth and Charlesworth 1990; Charlesworth et al. 1990; Uyenoyama and Waller 1991a, 1991b; Latta and Ritland 1993, 1994), although they all assume equal effects of inbreeding depression on male and female fitness. In general, these models indicate that there are circumstances under which mixed-mating systems can be evolutionarily stable, particularly when inbreeding depression is caused by overdominance in fitness (Charlesworth and Charlesworth 1990; Uyenoyama and Waller 1991b) or by partly recessive, very mildly deleterious mutations (Latta and Ritland 1993, 1994). In other words, explicitly allowing inbreeding depression to evolve increases the chances that models will allow the evolution of mixed-mating systems. By analogy, we would expect that incorporation of evolving inbreeding depression into our model would similarly expand the region of the $M - F$ parameter space in which mixed-mating systems are stable. We thus expect the effect of differences in male and female inbreeding depression to be as great in this type of model as in simple models that do not incorporate the possibility of evolving

inbreeding depression. We believe that this possibility warrants analysis.

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