A MODEL OF THE EVOLUTION OF DICHOGAMY INCORPORATING SEX-RATIO SELECTION, ANTHER-STIGMA INTERFERENCE, AND INBREEDING DEPRESSION

RISA D. SARGENT,[1,2] MOHAMMAD A. MANDEGAR,[1,3] AND SARAH P. OTTO[1,4]

[1]*Department of Zoology, 6270 University Boulevard, University of British Columbia, Vancouver, British Columbia V6T 1Z4, Canada*
[3]*E-mail: mohammad@interchange.ubc.ca*
[4]*E-mail: otto@zoology.ubc.ca*

Abstract.—Historically, explanations for the evolution of floral traits that reduce self-fertilization have tended to focus on selection to avoid inbreeding depression. However, there is growing support for the hypothesis that such traits also play a role in promoting efficient pollen dispersal by reducing anther-stigma interference. The relative importance of these two selective pressures is currently a popular topic of investigation. To date, there has been no theoretical exploration of the relative contributions of selection to avoid the genetic costs of self-fertilization and selection to promote efficient pollen dispersal on the evolution of floral traits. We developed a population genetic model to examine the influence of these factors on the evolution of dichogamy: the temporal separation of anther maturation and stigma receptivity. Our analysis indicates that anther-stigma interference can favor dichogamy even in the absence of inbreeding depression. Although anther-stigma interference and inbreeding depression are the key forces driving the initial evolution of dichogamy, selection to match the timing of pollen dispersal to the availability of ovules at the population level becomes a more potent force opposing the further evolution of dichogamy as the extent of temporal separation increases. This result may help to explain otherwise puzzling phenomena such as why dichogamy is rarely complete in nature and why dichogamy tends to be associated with asynchronous flower presentation.

Key words.—Anther-stigma interference, dichogamy, inbreeding depression, pollen discounting, population genetic model, self-fertilization.

Most flowering plant species produce hermaphrodite flowers. It is likely that many floral traits evolved, at least in part, to overcome the peculiarities associated with housing male and female function within the same flower. Two common examples of such traits are herkogamy, in which anthers and pistils are spatially separated in the same flower, and dichogamy, in which anther maturation and stigma receptivity are separated in time rather than space (Lloyd and Webb 1986; Fig. 1). Historically, herkogamy and dichogamy were thought to have evolved to reduce the costs associated with self-fertilization in hermaphrodite flowers (Darwin 1876).

Although its exact frequency is unknown, dichogamy is reported to be extremely common (Lloyd and Webb 1986; Barrett 2003). In a literature survey of 4277 species, Bertin and Newman (1993) found that 3716 species (~87%) exhibited some form of dichogamy. Across-species comparisons reveal considerable variability in the extent of temporal separation of pollen presentation and stigma receptivity (Lloyd and Webb 1986). Indeed, the timing of pollen presentation and stigma receptivity is rarely simultaneous in hermaphroditic flowers. Despite the widespread occurrence of dichogamy, there have been relatively few empirical and/or theoretical explorations of its causes and consequences (but, see Wells and Lloyd 1991; Medan and Bartoloni 1998; Harder et al. 2000; Routley and Husband 2003). Here we address the lack of theory using a population genetic model to examine the relative roles of self-fertilization, inbreeding depression, anther-stigma interference, and sex-ratio selection in the evolution of dichogamy.

From an evolutionary perspective, dichogamy presents an additional puzzle. Frequency-dependent selection causes the rare sex in a population to have a fitness advantage, and thus population sex ratios are predicted to evolve toward equal investment in males and females (Fisher 1930). Dichogamy generates uneven sex ratios across a flowering season (Brunet and Charlesworth 1995; Sargent and Roitberg 2000). Consequently, dichogamy can decrease the likelihood of pollen transfer to early- or late-blooming flowers (Brunet 1996; Medan and Bartoloni 1998; Huang et al. 2004). This mismatch between the timing of the availability of pollen and ovules at the population level should select against dichogamy.

Dichogamy has been described as a mechanism to avoid self-pollination (Darwin 1876). This explanation is complicated by the fact that self-pollination confers a potential fitness benefit, relative to outcrossing. Because a selfing plant can provide both pollen and ovule for its own offspring, as well as pollen to ovules of other plants, it can pass on more copies of its genes to the subsequent generation (Fisher 1941). If, however, inbred ovules have lower fitness than outcrossed ovules, this transmission advantage can be negated. The phenomenon whereby inbred offspring have lower fitness than outbred offspring is known as inbreeding depression. How inbreeding depression operates to reduce fitness is under investigation, but one common explanation is that deleterious alleles are often partially or fully recessive and their deleterious effects are thus compounded in homozygous inbred offspring (Charlesworth and Charlesworth 1999).

Inbreeding depression has been invoked to explain the evolution of many aspects of plant reproductive biology, including mating system evolution (Lloyd 1992; Husband and Schemske 1996; Goodwillie et al. 2005). The role of inbreeding depression in the evolution of dichogamy is cur-

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[2] Present address: Department of Integrative Biology, 3060 Valley Life Sciences Building, University of California, Berkeley, California 94720-3140; E-mail: risas@berkeley.edu.
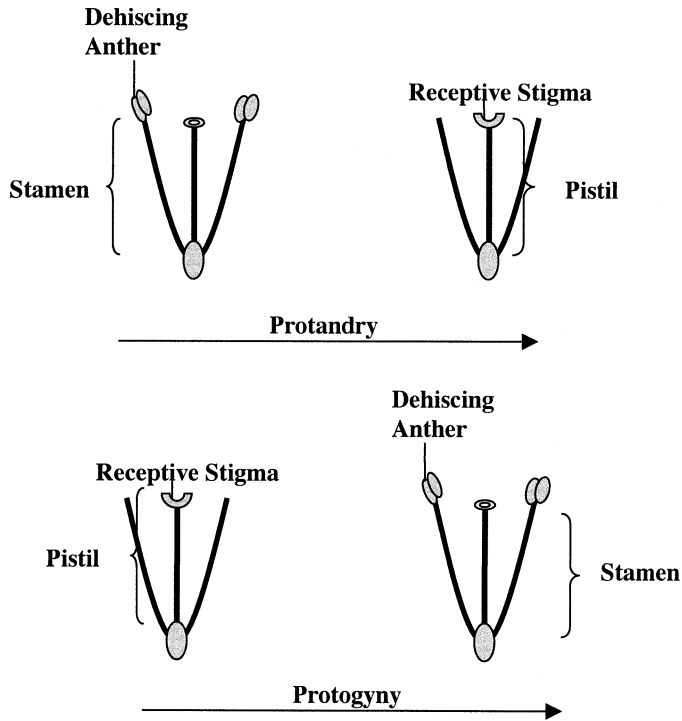
FIG. 1. The order of anther dehiscence and stigma receptivity for a protandrous (top) and protogynous (bottom) species.

rently unclear. While some studies have found support for high inbreeding depression and reduced selfing in dichogamous species (e.g., Dudash and Fenster 2001), others have found no evidence for such a relationship (e.g., Hossaert-McKey and Bronstein 2001).

It also has been suggested that dichogamy may promote more efficient pollination because it alleviates physical interference between anther and stigma function (Holsinger et al. 1984; Lloyd and Webb 1986; Bertin 1993; Routley and Husband 2003). From the male perspective, anther-stigma interference can reduce the total number of outcrossed offspring sired because pollen from the anthers are deposited on the plant's own stigma (or other plant parts), reducing the plant's contribution to the outcrossing pollen pool (pollen discounting; Nagylaki 1976; Harder and Wilson 1998), and/or because the dispersal of pollen to other flowers is physically obstructed by the stigma (e.g., Kohn and Barrett 1992; Fetscher 2001). The significance of anther-stigma interference in the evolution of dichogamy gained attention after a survey of angiosperm species revealed an intriguing pattern: dichogamy is equally common in self-compatible and self-incompatible species (Bertin 1993). It is puzzling that species possessing one mechanism to prevent self-pollination (self-incompatibility) would exhibit a second such mechanism (dichogamy). This observation lends support to the alternative explanation that dichogamy may have evolved to reduce sexual interference between female and male function rather than to avoid self-fertilization (Lloyd and Webb 1986; Bertin 1993; Routley and Husband 2003; Cesaro et al. 2004).

The extent to which sex-ratio selection, the intrinsic advantage of self-fertilization, inbreeding depression, and anther-stigma interference influence the evolution of dichogamy

is currently unknown. Here we develop a model that allows us to explore the relative importance of each factor in the evolution of dichogamy in a population of flowering plants.

THE MODEL

Our model examines the conditions under which an allele for dichogamy invades a population of diploid hermaphroditic plants with perfect (bisexual) flowers and annual (discrete, nonoverlapping) generations. The proportion of a plant's ovules that are available for fertilization at time t is modeled as a continuous probability distribution, $F[t]$, where $\int F[t]\, dt = 1$ (see Table 1 for a list of all parameters and variables). We assume that the ovule availability schedule is the same for all genotypes in the population, on average, although not all plants need be flowering on a given day. For mathematical convenience, we measure time such that $t = 0$ corresponds to the mean date of ovule availability. Because $F[t]$ is not genotype specific, it can be thought of as the average availability of ovules in the population at time t. In contrast, the amount of pollen dispersed by plants at time t is assumed to depend on a plant's genotype, x, and is given by the probability distribution, $V[r_x, t]$. Thus, the mean date of pollen dispersal depends on the plant genotype, x. Because the timing of ovule availability is considered fixed, the degree of dichogamy for a plant of genotype x is measured by the average difference in timing between when the ovules become available for pollination and when pollen becomes available, r_x. This limits our model to genes that affect the timing of pollen function, although it has recently been proposed that one of the most likely developmental pathways affecting the evolution of protandry alters the timing of anther development (S. Kalisz, R. H. Ree, and R. D. Sargent, unpubl. ms.). When $r_x = 0$, the average date of pollen and ovule presentation is the same (adichogamy). When $r_x > 0$, the average date of ovule availability is earlier than the average date of pollen presentation, and genotype x is protogynous. Conversely, when $r_x < 0$, genotype x is protandrous. Thus, we can track the evolution of dichogamy within a population by following the frequency of genotypes with different values of r_x. We assume that the temporal delay between pollen dispersal and ovule fertilization is negligible.

In many plants, stigma presentation can interfere with the export of pollen, and this interference is worsened when pollen and ovule availability overlap extensively (Lloyd and Webb 1986). We define the interference function, $C[r_x, t]$, as the proportion of pollen lost to export due to overlapping anther and stigma development, where interference is a function of both a plant's genotype, x, and time, t. Similarly, $M[r_x, t] = 1 - C[r_x, t]$ indicates the proportion of pollen contributed to the outcrossing pollen pool by genotype x at time t. We assume that the presence of dichogamy reduces anther-stigma interference, and therefore $C[r_x, t]$ is a decreasing function of $|r_x|$ (i.e., $(\partial C[r_x, t])/(\partial |r_x|) < 0$).

Seed production is the result of either self-fertilization or outcrossing. We make the simplifying assumption that pollen is abundant and that its availability does not limit ovule fertilization. The number of selfed ovules of genotype x produced at time t, $S[r_x, t]$, is also assumed to be a decreasing function of the degree of temporal separation between pollen

TABLE 1. Variables and parameters of the model.

Parameter	Description	Gaussian functions
$C[r_x, t]$	proportion of pollen lost to anther-stigma interference for genotype x, at time t	$\int_{-\infty}^{\infty} \exp\left\{\dfrac{-(t - \mu[r_{aa}])^2}{2\sigma[r_{aa}]^2}\right\} C[0]\, F[t]\, dt$
$C[0]$	amount of pollen lost to anther-stigma interference when $r_x = 0$	
D, H, R	frequency of the genotypes AA, Aa, aa, respectively.	
δ	fraction of selfed ovules that are inviable due to inbreeding depression	
$F[t]$	probability distribution of ovule availability at time t	$\dfrac{e^{-(t^2/2)}}{\sqrt{2\pi}}$
$\mu[r_{aa}]$	date of maximum selfing and anther-stigma interference in the Gaussian model	
$M[r_x, t]$	amount of pollen available for outcrossing for genotype x at time t	$1 - C[r_x]$
$O[r_x, t]$	proportion of seeds produced by genotype x at time t that are not selfed	$1 - \exp\left\{\dfrac{-(t - \mu[r_{aa}])^2}{2\sigma[r_{aa}]^2}\right\} S[0]$
$p_{y,t}$	frequency of pollen containing allele y carried by pollinators at time t	
r_x	average difference in timing of pollen and ovule availability for genotype x (also the degree of dichogamy)	
$\sigma[r_{aa}]^2$	temporal variance of the selfing and anther-stigma interference in the Gaussian model	
$S[r_x, t]$	proportion of selfed ovules of genotype x produced at time t $(O[r_x, t] = 1 - S[r_x, t])$	$\exp\left\{\dfrac{-(t - \mu[r_{aa}])^2}{2\sigma[r_{aa}]^2}\right\} S[0]$
$S[r_x]$	proportion of selfed ovules of genotype x	
$S[0]$	proportion of selfed ovules when $r_x = 0$	
ρ	expected sensitivity of a change in pollen available for export, $M[r_{aa}, t]$, to a change in dichogamy, r_{aa}	$\dfrac{C[r_x]\left\{\dfrac{1 + 2\mu[r_{aa}]^2 + \sigma[r_{aa}]^2 + 3\mu[r_{aa}]^2\sigma[r_{aa}]^2}{2r_x(1 + \sigma[r_{aa}]^2)^2}\right\}}{1 - C[r_x]}$
ϕ	effect of the rare modifier on dichogamy averaged over heterozygous and homozygous carriers of the allele	
$V[r_x, t]$	probability distribution of pollen availability for genotype x at time t	$\dfrac{\exp\left\{-\dfrac{(t - r_x)^2}{2}\right\}}{\sqrt{2\pi}}$
ω	expected sensitivity of the timing of pollen presentation to a change in the amount of dichogamy, r_{aa}	$\dfrac{-r_{aa}\left[1 - \dfrac{\exp\left\{\dfrac{-\mu[r_{aa}]^2}{2(1 + \sigma[r_{aa}]^2)}\right\} S[0]\left\{1 - \dfrac{\mu[r_{aa}]/r_{aa}}{(1 - \sigma[r_{aa}]^2)}\right\}}{\sqrt{1 + \dfrac{1}{\sigma[r_{aa}]^2}}}\right]}{1 - S[r_{aa}]}$

and ovule presentation (i.e., $(\partial S[r_x, t])/(\partial|r_x|) < 0$). Note that $S[r_x, t]$ is simply a measure of the proportion of ovules that are selfed, regardless of the exact timing and mechanisms by which selfing occurs. Thus, prior selfing might be characterized by an $S[r_x, t]$ function that is high at first and decreases over time, whereas a delayed selfer would have an $S[r_x, t]$ function that is low at first and increases with time. The total number of selfed ovules integrated over the flowering season is $S[r_x] = \int_{-\infty}^{\infty} S[r_x, t]\, F[t]\, dt$. The proportion of outcrossed ovules produced by genotype x at time t, $O[r_x, t]$, is the proportion of ovules that are not selfed (i.e., $O[r_x, t] = 1 - S[r_x, t]$, and $O[r_x] = 1 - S[r_x]$). When inbreeding depression (δ) exists, only a fraction, $(1 - \delta)$, of selfed ovules are viable. This assumes that inbreeding depression remains fixed, which need not be true as dichogamy evolves and alters the amount of selfing (see Discussion).

If desired, the amount of pollen available for export can be set equal to a function of the level of self-fertilization, for example, $C[r_x, t] = cS[r_x, t]$, where c is the factor by which selfing decreases the amount of pollen available for export (pollen discounting; Nagylaki 1976). Thus, our method allows for anther-stigma interference to include either pollen discounting (in self-compatible species) or similar export costs in self-incompatible species.

We consider a population comprised of three genotypes: AA (frequency D), Aa (frequency H), and aa (frequency R), where each genotype exhibits a different degree of dichogamy (r_{AA}, r_{Aa}, r_{aa}, respectively). For the purposes of this description, we assume the species in question is protogynous (i.e., ovules are produced before pollen; $r_x > 0$). However, the results are equally applicable to understanding the evolution of protandry (i.e., $r_x < 0$).

TABLE 2. Number and frequency of *Aa* and *aa* seeds in the next generation.

$$N'_{Aa} = DN\left(\int_{-\infty}^{\infty} p_{a,t}O[r_{AA}, t]F[t]\ dt\right) + HN\left\{\frac{(1-\delta)}{2}\int_{-\infty}^{\infty} S[r_{Aa}, t]F[t]\ dt + \frac{1}{2}\int_{-\infty}^{\infty} (p_{A,t}+p_{a,t})O[r_{Aa}, t]F[t]\ dt\right\} + RN\left(\int_{-\infty}^{\infty} p_{A,t}O[r_{aa}, t]F[t]\ dt\right)$$

$$N'_{aa} = HN\left\{\frac{(1-\delta)}{4}\int_{-\infty}^{\infty} S[r_{Aa}, t]F[t]\ dt + \frac{1}{2}\int_{-\infty}^{\infty} p_{a,t}O[r_{Aa}, t]F[t]\ dt\right\} + RN\left\{(1-\delta)\int_{-\infty}^{\infty} S[r_{aa}, t]F[t]\ dt + \int_{-\infty}^{\infty} p_{a,t}O[r_{aa}, t]F[t]\ dt\right\}$$

After mating, the total number of viable seeds with genotype *AA* is the frequency of those genotypes in a parental population of size *N* multiplied by the sum of the number of selfed seeds (discounted by losses incurred due to inbreeding depression whether early or late acting) and outcrossed seeds produced by genotypes containing the *A* allele (i.e., *AA, Aa*):

$$N'_{AA} = DN\left\{(1-\delta)\int_{-\infty}^{\infty} S[r_{AA}, t]F[t]\ dt\right.$$

$$+ \int_{-\infty}^{\infty} p_{A,t}O[r_{AA}, t]F[t]\ dt\right\}$$

$$+ HN\left\{\frac{(1-\delta)}{4}\int_{-\infty}^{\infty} S[r_{Aa}, t]F[t]\ dt\right.$$

$$\left. + \frac{1}{2}\int_{-\infty}^{\infty} p_{A,t}O[r_{Aa}, t]F[t]\ dt\right\}, \quad (1)$$

where $p_{y,t}$ is the frequency of pollen containing allele *y* carried by pollinators at time *t*. For example, $p_{A,t}$ equals the outcrossed pollen from *AA* individuals at time *t*, $(DV[r_{AA}, t]$ $M[r_{AA}, t])$ plus half the outcrossed pollen from *Aa* individuals at time *t*, $(H/2V[r_{Aa}, t]\ M[r_{Aa}, t])$, divided by the total amount of pollen carried by pollinators at time *t*. $p_{a,t}$ is calculated in a similar fashion:

$$p_{A,t} = \left\{DV[r_{AA}, t]M[r_{AA}, t] + \frac{H}{2}V[r_{Aa}, t]M[r_{Aa}, t]\right\}$$

$$\div \{DV[r_{AA}, t]M[r_{AA}, t] + HV[r_{Aa}, t]M[r_{Aa}, t]$$

$$+ RV[R_{aa}, t]M[r_{aa}, t]\} \quad \text{and} \quad (2a)$$

$$p_{a,t} = \left\{RV[r_{aa}, t]M[r_{aa}, t] + \frac{H}{2}V[r_{Aa}, t]M[r_{Aa}, t]\right\}$$

$$\div \{DV[r_{AA}, t]M[r_{AA}, t] + HV[r_{Aa}, t]M[r_{Aa}, t]$$

$$+ RV[r_{aa}, t]M[r_{aa}, t]\}. \quad (2b)$$

The numbers of seeds of the remaining genotypes, N'_{Aa} and N'_{aa}, are calculated similarly (Table 2). The total number of seeds in the next generation, N', is the sum of the number of seeds from the three genotypes $(N' = N'_{AA} + N'_{Aa} + N'_{aa})$. The frequency of each genotype in the next generation is thus $D' = N'_{AA}/N'$, $H' = N'_{Aa}/N'$, and $R' = N'_{aa}/N'$. In the following sections, we use these recursions to investigate the spread of a newly introduced allele, *A*, that alters the timing of pollen availability relative to the timing of ovule availability.

RESULTS

To assess the evolutionary forces acting on dichogamy, we asked when a resident genotype $(aa, \hat{R} = 1)$ could be invaded by a newly introduced allele (*A*) that causes a shift in the pollen presentation schedule. To do so, we performed a local stability analysis of the equilibrium, $\hat{R} = 1$. The results involved a compound parameter, $\phi = (r_{Aa} - r_{aa})(1 - f) + (r_{AA} - r_{aa})f$, which describes the overall effect of the rare modifier on dichogamy averaged over heterozygous carriers (frequency $1 - f$) and homozygous carriers (frequency f), where f is the equilibrium inbreeding coefficient within a population in the presence of inbreeding depression,

$$f = \frac{S[r_{aa}](1 - \delta)}{2 - S[r_{aa}] - \delta S[r_{aa}]}. \quad (3)$$

Thus, ϕ is positive for a mutant allele that increases the degree of protogyny (i.e., $r_{AA}, r_{Aa} > r_{aa}$). Note that the degree of dominance only affects the magnitude and not the sign of ϕ. To obtain interpretable solutions, we assumed the genotypic differences in dichogamy are small (i.e., $r_{AA} - r_{aa} = O(\varepsilon); r_{Aa} - r_{aa} = O(\varepsilon)$). As the total selfing rate depends on the level of dichogamy, alleles that cause a small change in dichogamy also cause a small change in selfing that is proportional to

$$\left.\frac{dS[r_x]}{dr_x}\right|_{r_x = r_{aa}}, \quad (4)$$

which we write as $S'[r_{aa}]$.

Two additional compound parameters, ω and ρ, are key to the results and are described as follows. ω measures the sensitivity of sex-ratio selection to a change in the amount of dichogamy (r_{aa}), where

$$\omega = \int_{-\infty}^{\infty} \frac{\partial V[r_{aa}, t]/\partial r_{aa}}{V[r_{aa}, t]} \frac{O[r_{aa}, t]F[t]}{O[r_{aa}]}\ dt. \quad (5)$$

For example, a plant species with a short flowering season (e.g., alpine species) should exhibit greater sensitivity to a given mismatch in pollen dispersal and ovule availability than a species with a longer flowering season (e.g., tropical species). This is because the same mismatch for the alpine species represents a larger portion of the flowering season than for the tropical species, and hence a larger number of mating opportunities are lost. The compound parameters ω (and ρ below) are calculated by integrating over the distribution describing the proportion of ovules available for outcrossing at time *t*, $(O[r_{aa}, t])/O[r_{aa}])F[t]$. Thus, ω equals the average value of $(\partial V[r_{aa}, t]/\partial r_{aa})/(V[r_{aa}, t])$ weighted by the likelihood that a pollen grain will successfully fertilize an ovule.

Similarly, ρ indicates the sensitivity of anther-stigma interference (measured as a decline in the proportion of pollen available for export), $M[r_{aa,t}]$, to a change in dichogamy (r_{aa}), where

$$\rho = \int_{-\infty}^{\infty} \frac{\partial M[r_{aa}, t]/\partial r_{aa}}{M[r_{aa}, t]} \frac{O[r_{aa}, t]}{O[r_{aa}]} F[t] \ dt. \qquad (6)$$

For example, species that exhibit herkogamy (spatial separation of anther and stigma within a flower) may be less prone to anther-stigma interference (Fetscher 2001). Consequently, the amount of anther-stigma interference should be less sensitive to dichogamy in such species (i.e., ρ closer to zero). Conversely, plants with larger inflorescences may suffer greater between flower anther-stigma interference (ρ larger in magnitude; e.g., because geitonogamy causes more substantial pollen discounting) and therefore may be under stronger selection to evolve dichogamy (e.g., Harder et al. 2000). Although ρ and ω are difficult to measure empirically, one could design selection experiments (e.g., Routley and Husband 2005) to quantify how a change in dichogamy alters the extent of anther-stigma interference (measuring ρ) and/or the mismatch between pollen presentation and ovule availability (ω) over a flowering season.

General Conditions for Invasion

As described in Appendix 1, we found the leading eigenvalue governing the spread of the rare A allele to be:

$$\lambda = 1 - \frac{\phi\{(1 - 2\delta)S'[r_{aa}] + (\omega + \rho)O[r_{aa}]\}}{2(1 - \delta S[r_{aa}])} + O(\varepsilon^2). \qquad (7)$$

The difference between the leading eigenvalue and one, $\lambda - 1$, measures the rate of spread of the A allele and can be thought of as a measure of the strength of selection acting on the A allele while rare. When $\lambda - 1 > 0$, the A allele increases in the population because of its effects on dichogamy. Here we determine what conditions allow the spread of the A allele, that is, lead to $\lambda - 1 < 0$.

Assuming that the A allele increases the degree of protogyny ($\phi > 0$, it will spread if the term in braces in equation (7) is positive. This term consists of three parts. The first part, $(1 - 2\delta)S'[r_{aa}]$, describes the effects of the intrinsic advantage of selfing and the fitness cost of inbreeding depression (δ) on the fate of the allele, where $S'[r_{aa}]$ describes the change in the total number of selfed ovules with an increased degree of protogyny, r_x. We assume that $S'[r_{aa}]$ is negative for a protogynous species, implying that dichogamy reduces the level of selfing. Consequently, $(1 - 2\delta)S'[r_{aa}]$ is positive when $\delta > \frac{1}{2}$ and negative when $\delta < \frac{1}{2}$. When inbreeding depression is strong ($\delta > \frac{1}{2}$), selfing drives selection for an allele that increases dichogamy. This term is equivalent to the classical condition under which outcrossing is favored (Fisher 1941).

The second part of the numerator, $\omega O[r_{aa}]$, describes the effects on outcrossing success of a change in the timing of pollen presentation (ignoring anther-stigma interference). ω describes the degree to which increasing dichogamy alters the match in timing between the presentation of pollen and the presentation of ovules at the population level. ω is expected to be negative for a protogynous species because larger values of r_{aa} result in a greater mismatch. The effect of ω on the evolution of dichogamy is proportional to $O[r_{aa}]$, the proportion of outcrossed seeds. Because ω is typically negative, this second part will be negative, indicating that a mismatch between pollen and ovules drives selection for adichogamy, rather than dichogamy. This term measures the evolutionary advantage of producing an equal sex ratio (Fisher 1930) at every point in time, an evolutionary force selecting against dichogamy.

The last part of the numerator, $\rho O[r_{aa}]$, describes the effects of a change in dichogamy on anther-stigma interference. We expect ρ to be positive for a protogynous species, reflecting the assumption that dichogamy causes a decline in anther-stigma interference and an increase in pollen available for export. This final term therefore indicates that anther-stigma interference is a selective force favoring dichogamy. If anther-stigma interference is entirely due to pollen discounting ($C[r_x, t] = cS[r_x, t]$), then ρ can be rewritten as

$$\rho = \int_{-\infty}^{\infty} \frac{-c(\partial S[r_{aa}, t]/\partial r_{aa})}{1 - cS[r_{aa}, t]} \frac{O[r_{aa}, t]}{O[r_{aa}]} F[t] \ dt. \qquad (8)$$

When $(O[r_{aa}, t])/(1 - cS[r_{aa}, t])$ is near one (because selfing is rare or pollen discounting is severe, $c \approx 1$), ρ becomes $-c\{(S'[r_{aa}])/(O[r_{aa}])\}$. Under these circumstances, equation (7) indicates that pollen discounting reduces the intrinsic advantage of selfing by an amount c, allowing dichogamy to evolve more readily. Note that for a protandrous species, ϕ, $S'[r_{aa}]$, ρ and ω all switch signs so that the same conclusions can be drawn about the evolution of protandry as protogyny.

Our general analysis describes how different evolutionary forces balance to affect the evolution of dichogamy. Because of our focus on alleles that have a small effect on dichogamy, there are no significant interactions between the terms in the model, and the various forces acting on dichogamy combine in an additive fashion. Equation (7) reflects two well-known advantages of dichogamy (avoiding inbreeding through $(-2\delta)S'[r_{aa}]$ and reducing anther-stigma interference through $\rho O[r_{aa}]$) as well as two disadvantages of dichogamy (reducing the intrinsic advantage of selfing through $S'[r_{aa}]$ and shifting pollen presentation to times when ovule availability is lower through $\omega O[r_{aa}]$). To determine the net effect of these conflicting selective forces requires empirical data on the factors that we have identified (especially δ, ω, and ρ).

Critical Inbreeding Depression

From equation (7) we calculated the critical amount of inbreeding depression, δ^*, above which dichogamy evolves from the current degree of separation (r_{aa}) to a greater degree of separation,

$$\delta^* = \frac{1}{2} + \frac{\rho O[r_{aa}]}{2S'[r_{aa}]} + \frac{\omega O[r_{aa}]}{2S'[r_{aa}]}. \qquad (9)$$

As discussed earlier, $S'[r_{aa}]$ is typically negative and therefore $(\rho O[r_{aa}])/(2S'[r_{aa}])$ will be negative, indicating that anther-stigma interference decreases the level of inbreeding depression necessary to drive the evolution of dichogamy. Conversely, the mismatch in the timing of pollen presentation to the availability of ovules, $(\omega O[r_{aa}])/(2S'[r_{aa}])$, is expected to be positive, making it more difficult to evolve greater dichogamy. It is the interaction between these processes that determines whether a greater degree of dichogamy can evolve. For example, if anther-stigma interference is sufficiently strong, $(\rho O[r_{aa}])/(2S'[r_{aa}]) \ll 0$, the right side of equation (9) becomes negative, indicating that dichogamy is favored regardless of
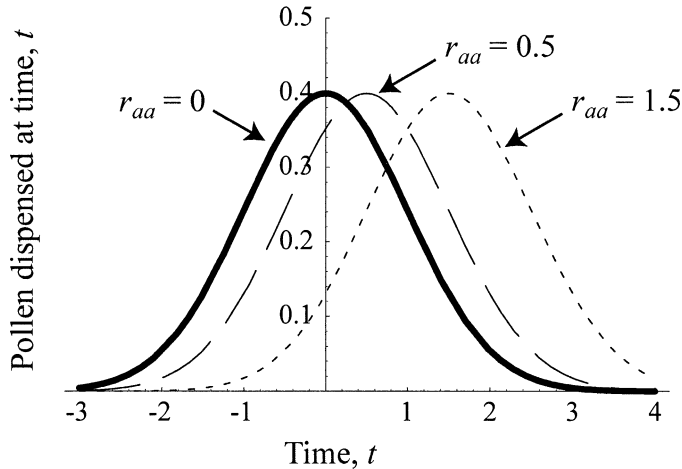
FIG. 2. Pollen and ovule availability as a function of time according to a Gaussian distribution with a standard deviation of one. The case where $r_{aa} = 0$ (thick curve) also represents the temporal availability of ovules in the model. For comparison, in Figures 4–6 the ESS degree of dichogamy is always less than one standard deviation.

the level of inbreeding depression, providing a possible explanation for the evolution of dichogamy in species that possess obligate outcrossing mechanisms (e.g., self-incompatibility).

Evolution of dichogamy assuming functions are Gaussian

We turn next to an analysis where we specify the forms of the ovule and pollen distributions. Using equation (7), we can then obtain more specific predictions about when dichogamy is expected to evolve and the extent of dichogamy predicted. Specifically, we assume that pollen presentation $V[r_x, t]$, ovule availability $F[t]$, anther-stigma interference $C[r_x]$, and the selfing rate $S[r_x, t]$ are Gaussian functions (see Figs. 2, 3; Table 1; Appendix 2). Unlike the general case, these functions assume equal duration of pollen and ovule presentation. Note that the standard deviation of $F[t]$ and $V[r_x, t]$ were set to one for mathematical convenience (i.e., time, t, is measured such that this is true). The terms needed for equation (7) were then derived using these functions (Table 1).

In the previous section we postulated the sign of the two sensitivity functions, ω and ρ, to draw general conclusions about their effect on the evolution of dichogamy. Using the Gaussian functions, we confirmed that $\omega < 0$ and $\rho > 0$ (Table 1).

Dichogamy is expected to evolve when equation (7) is greater than zero. Evaluating this condition with the Gaussian functions, we expect dichogamy to invade an adichogamous population (i.e., where $r_{aa} = 0$) when the following condition is met:

$$C[0] - S[0]\{1 - 2\delta(1 - C[0])\} > 0. \qquad (10)$$

It is apparent from equation (10) that even in the absence of selfing, some dichogamy is favored provided that there is anther-stigma interference (i.e., $C[0] > 0$).

Interestingly, the effect of mismatched timing between pollen presentation and ovule availability, ω equals zero at $r_{aa} =$

0, using the Gaussian functions. This result reflects the fact that, allowing only small changes in r_x, the loss in ovules available per pollen grain for pollen produced after the mean date of ovule presentation ($t > 0$) very nearly equals the gain in ovules available per pollen grain for pollen produced before $t = 0$ when using the Gaussian functions near $r_{aa} = 0$. Nevertheless, ω becomes an important selective force as the species becomes more dichogamous even with the Gaussian functions.

According to equation (10), the minimum level of inbreeding depression necessary to drive selection for dichogamy from adichogamy is

$$\delta^*_{r_{aa}=0} = \frac{S[0] - C[0]}{2S[0](1 - C[0])}. \qquad (11)$$

The denominator of equation (11) is always positive, and thus the critical inbreeding depression, $\delta^*_{r_{aa}=0}$, is greater than zero when $S[0] > C[0]$. Conversely, if anther-stigma interference is greater than the selfing rate for an adichogamous species, $C[0] > S[0]$, dichogamy is favored, regardless of the extent of inbreeding depression.

Evolutionarily Stable Strategy

We next consider the extent of dichogamy that is predicted over longer evolutionary time frames. An evolutionarily stable strategy (ESS) is one that, once adopted by all members of the resident population, cannot be invaded by another mutant strategy (Maynard Smith 1982). When the frequency of A does not increase, regardless of its effect on ϕ, the resident allele is considered the ESS. This ESS, by definition, cannot be invaded by any genotype with a slightly larger (or slightly smaller) degree of dichogamy. To determine the ultimate level of dichogamy expected using the Gaussian functions, we plotted the ESS for a range of values of the maximum selfing rates (in the absence of dichogamy, $S[0]$) and degree of inbreeding depression (δ) (Figs. 4, 5). Figure 4 illustrates the ESS when anther-stigma interference is absent ($C[0] = 0$). In this case, $r_{aa} = 0$ is the ESS whenever inbreeding depression is less than the critical value, $\delta = \frac{1}{2}$, with some amount of dichogamy evolving when $\delta > \frac{1}{2}$. Because sex-ratio selection (ω) gets stronger as a function of anther-stigma separation, little dichogamy is expected at the ESS unless inbreeding depression and the selfing rate are high (i.e., $S[0] \gg 0$). Even with complete inbreeding depression ($\delta = 1$) in a species that would entirely self if adichogamous ($S[0] = 1$), the ESS level of dichogamy is only $r_{aa} = 0.707$, which measures the number of standard deviations between the mean date of ovule and pollen availability (Fig. 2). A different picture emerges in Figure 5, where 50% of pollen would be lost due to anther-stigma interference in an adichogamous species (i.e., $C[0] = 0.5$). Here adichogamy is the ESS only when inbreeding depression is low enough and selfing common enough to impart a strong intrinsic advantage. However, when selfing rates are low ($S[0] < C[0]$) the cost of anther-stigma interference ensures that some level of dichogamy evolves regardless of δ. Notice also that the ESS level of dichogamy is always higher with anther-stigma interference. Nevertheless, the maximum level of dichogamy is still only $r_{aa} = 0.788$ when $\delta = 1$, $S[0] = 1$, and $C[0] = 0.5$.

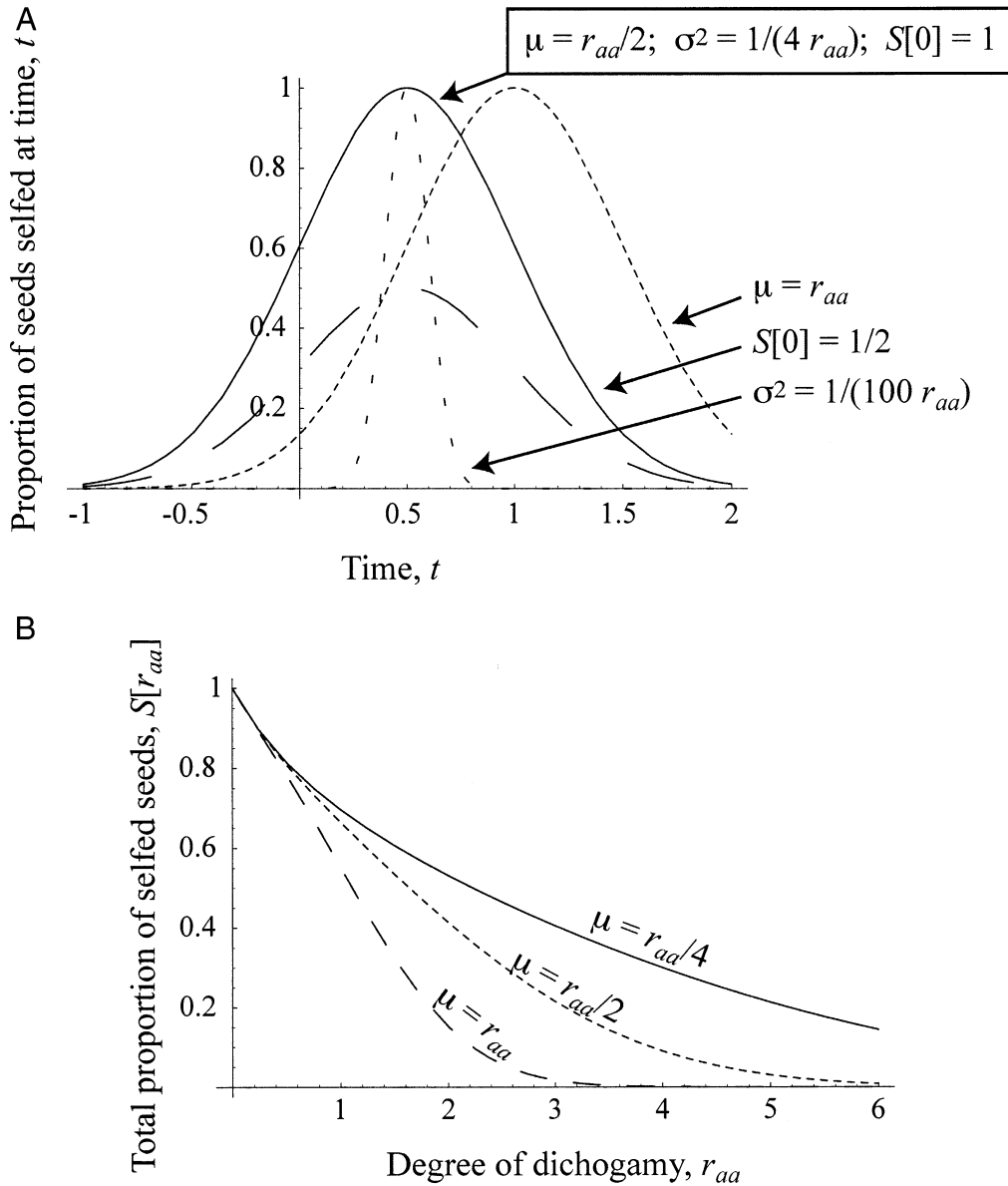To illustrate the combined effects of anther-stigma inter-

FIG. 3. Selfing rate as a function of time and degree of dichogamy (Gaussian model). (A) The solid curve illustrates the case where the maximum amount of selfing occurs at $\mu = r_{aa}/2$ with $\sigma^2 = 1/(4r_{aa})$ and $S[0] = 1$, and the remaining curves alter one of these parameters at a time. The degree of dichogamy is one standard deviation between mean ovule and pollen presentation ($r_{aa} = 1$). (B) The total proportion of selfed seeds $S[r_{aa}]$ as a function of dichogamy (r_{aa}) when $S[0] = 1$ and $\sigma^2 = 1/r_{aa}$. The extent of anther-stigma interference follows a similarly shaped curve (see Appendix 2).

ference and selfing, Figure 6 plots the ESS when inbreeding depression is 0.75. In this case, some dichogamy is favored unless there is no selfing and no anther-stigma interference (i.e., $C[0] = 0$, $S[0] = 0$). The highest degree of separation is predicted to evolve when $C[0] = 1$, regardless of the amount of selfing, illustrating our finding that anther-stigma interference is a strong force driving the evolution of dichogamy.

DISCUSSION

Our model explores several aspects of the reproductive biology of hermaphroditic flowering plants and their role in the evolution of dichogamy. The results stemming from our model confirm that inbreeding depression plays an important role in

the evolution of dichogamy, as with other plant mating systems (Lloyd 1979; Lande and Schemske 1985; Charlesworth and Charlesworth 1987; Holsinger 1991; Barrett 2002; Porcher and Lande 2005). Dichogamous species often exhibit high inbreeding depression (e.g., Aizen and Basilio 1995; Routley and Husband 2003). Furthermore, Husband and Schemske (1996) estimated inbreeding depression in a survey of 62 natural plant populations and found a range of −0.15 to 0.92. Thus, it is reasonable to assume that inbreeding depression can be high enough to affect the evolution of dichogamy.

We also confirmed that anther-stigma interference plays an important role in the evolution of dichogamy. Indeed, in the absence of self-fertilization, we found that anther-stigma in-
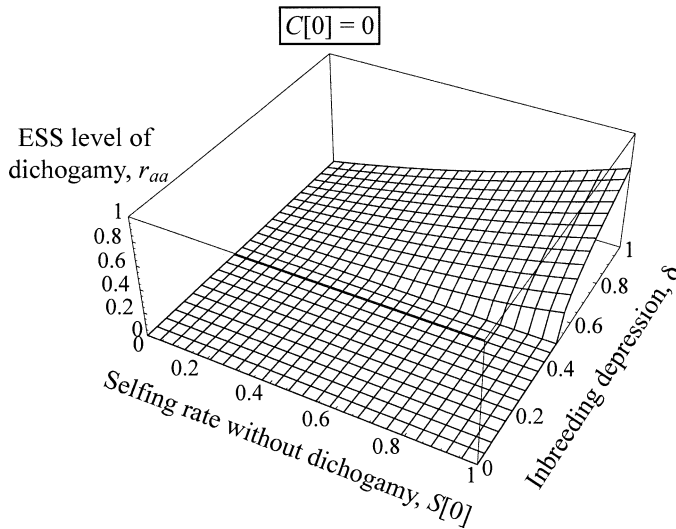
$C[0] = 0$

FIG. 4. The ESS degree of anther-stigma separation as a function of inbreeding depression (δ) and selfing ($S[0]$) when there is no anther-stigma interference ($C[0] = 0$), where $S[0]$ is the amount of selfing when $r_{aa} = 0$ (i.e., under adichogamy) for $\mu = r_{aa}/2$ and $\sigma^2 = 1/r_{aa}$. Increasing dichogamy causes a reduction in the selfing rate according to the function $S[r_{aa}]$. Height on the z-axis indicates the number of standard deviations between pollen production and ovule availability at the ESS (as illustrated in Fig. 2).

$C[0] = 0.5$

FIG. 5. The ESS degree of dichogamy as a function of inbreeding depression (δ) and the selfing rate in the absence of dichogamy ($S[0]$), when anther-stigma interference equals $C[0] = 0.5$, $\mu = r_{aa}/2$ and $\sigma^2 = 1/r_{aa}$.

terference alone can drive the evolution of dichogamy. This result is supported by evidence that dichogamy has evolved and is maintained in several self-incompatible species (Lloyd and Yates 1982; Bertin 1993; Cesaro et al. 2004; Routley et al. 2004).

Overall, we determined that the evolution of dichogamy depends on the balance of its advantages (i.e., reduced production of inbred seeds and decreased anther-stigma interference) and disadvantages (i.e., loss of fitness via selfed ovules and production of skewed sex ratios at different points in time). Clearly, the contributions of selection to avoid self-fertilization and anther-stigma interference depend on the mating system and degree of anther-stigma interference. For example, Harder and Aizen (2004) found that dichogamy does not promote outcross siring success in *Alstroemeria aurea* and therefore they suggested that the avoidance of self-fertilization is responsible for the evolution of dichogamy in this species.

Predictions

Our model predicts that both anther-stigma interference and selfing avoidance drive the evolution of dichogamy within a single species. In a broad survey of 588 angiosperm species, Bertin (1993) found that dichogamy was equally common among self-compatible and incompatible species. This observation suggests that anther-stigma interference has been the key force in the evolution of dichogamy because, as our model confirms, inbreeding depression should more strongly favor dichogamy in self-compatible species but have no impact in self-incompatible species. A specific testable prediction is that self-incompatible species displaying dichogamy should be more sensitive to anther-stigma interference than self-compatible species, particularly those subject to strong inbreeding depression. Furthermore, our ESS analysis (Figs. 4–6) illus-
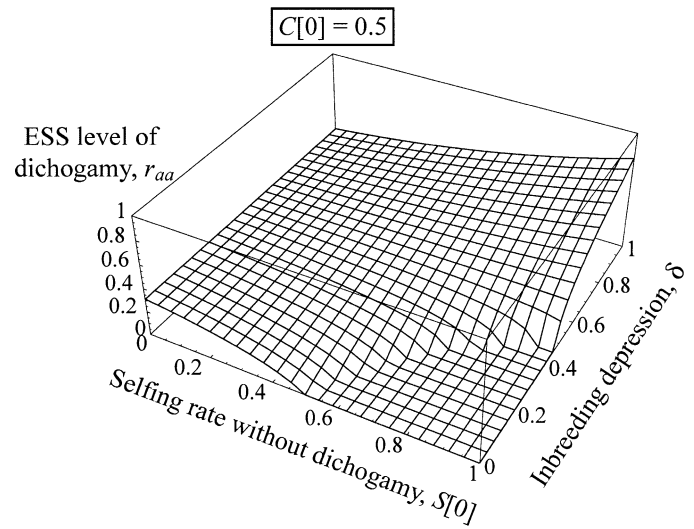
trates that more dichogamy is predicted in groups with greater potential for anther-stigma interference (i.e., higher $C[0]$).

We also predict that sex-ratio selection on the mismatch between pollen and ovule availability should counter the evolution of dichogamy to equalize the sex ratio at every point in time. Medan and Bartoloni (1998) simulated the effects of sex ratio selection on different genotypes of plants; their simulation results also indicated that selection favored those genotypes (or genotypic combinations) that had the most overlap in male and female function. Plants might mitigate the lost mating opportunity associated with dichogamy by producing a series of flowers over time, where individual flowers (particularly the earliest and latest, which tend to suffer the greatest loss of mating opportunity) only represent a small fraction of the plant's overall investment in reproduction. If this is true,
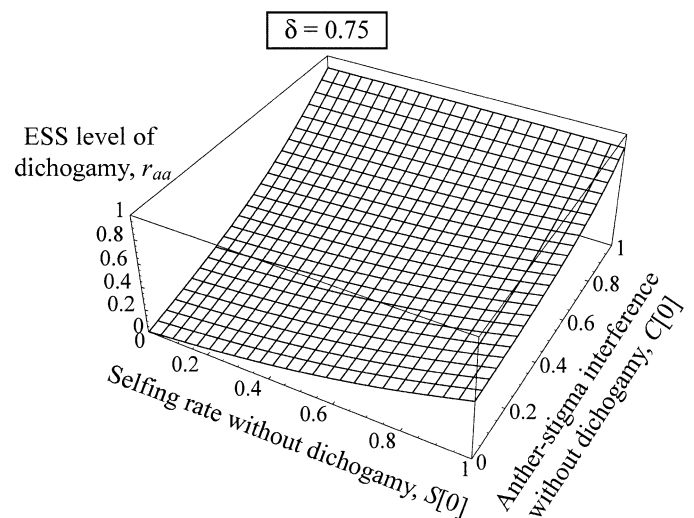
$\delta = 0.75$

FIG. 6. The ESS degree of dichogamy as a function of anther-stigma interference ($C[0]$) and selfing ($S[0]$), when there is strong inbreeding depression, $\delta = 0.75$, for $\mu = r_{aa}/2$ and $\sigma^2 = 1/r_{aa}$.

we predict that there should be a positive correlation between the degree of dichogamy and the duration of the flowering season. That said, the maximum amount of dichogamy must certainly be constrained by floral longevity (Shoen and Ashman 1995), which might obscure any association between dichogamy and length of the flowering season. Nevertheless, there is evidence that the extent of dichogamy is reduced in species with shorter flowering seasons (Mazer et al. 2004).

Moreover, we predict that sex-ratio selection should be reduced or absent in heterodichogamous species (i.e., those that exhibit polymorphic populations of equal numbers of protandrous and protogynous individuals). Heterodichogamous species avoid costly anther-stigma interference and inbreeding depression without the associated cost of mismatched pollen and ovule presentation schedules, and it should therefore be quite common (Wells and Lloyd 1991). For unknown reasons, heterodichogamy is relatively rare in natural systems, although its frequency may be underestimated because it is difficult to detect (Renner 2001).

Furthermore, our model generates specific predictions about the degree of anther-stigma separation that should evolve under specific conditions (see Figs. 4–6). A study by Routley and Husband (2005) demonstrated that the timing of anther dehiscence and stigma receptivity in dichogamous *Chamerion angustifolium* is heritable and that selection can produce rapid changes in male-phase duration in this species. Our model predicts that even when dichogamy is strongly favored (i.e., high anther-stigma interference and high inbreeding depression), sex-ratio selection ensures that anther dehiscence and stigma receptivity will show substantial overlap in the population. This finding is consistent with the fact that dichogamy is rarely complete in nature (Lloyd and Webb 1986). Indeed, an analysis of a dataset of dichogamous species (R. Bertin, unpubl. data) indicates that for more than two-thirds of the families in the dataset ($N = 124$) every sampled species exhibits flowers with overlapping anther dehiscence and stigma receptivity.

Future Directions

The model we have developed here could be further developed to make predictions concerning the conditions that favor one form of dichogamy over the other (i.e., protandry or protogyny). Our model makes no direct predictions about which form of dichogamy evolves. The specific functions we tested (Gaussian) are unimodal and symmetrical and therefore favored protandry or protogyny equally. Future explorations using functions with skew might be useful for elucidating the processes that drive protandry and protogyny. It is also likely that the form of dichogamy that evolves is constrained by factors other than those considered here, such as floral developmental pathways and the types of mutations available. For example, it has been suggested that protandry may evolve more easily as a by-product of floral development (Wyatt 1983). Conversely, protogyny requires a reversal in the order of whorl development and therefore the mutations required to evolve protogyny may be less likely to occur.

Furthermore, our model does not allow for evolution of inbreeding depression in response to changes in dichogamy. Based on previous models of selfing and outcrossing, the impact of this omission should depend on the genetic basis of inbreeding depression. Allowing inbreeding depression to evolve should have little impact when inbreeding depression is caused primarily by numerous partially recessive deleterious mutations at loosely linked loci where selection is weak against mutants (see Uyenoyama and Waller 1991). In this case, purging of deleterious mutations is a slow process that has little impact on the evolution of selfing rates. Nevertheless, there is evidence that mutations of large effect also contribute substantially to inbreeding depression (Husband and Schemske 1996). Further studies of the evolution of dichogamy that explicitly track strongly selected mutations are thus warranted.

Finally, our model should be extended to include reproductive assurance, which is hypothesized to play a role the evolution of dichogamy (Herlihy and Eckert 2002; Kalisz et al. 2004). Reproductive assurance has been invoked to explain the evolution of protogyny instead of protandry because the presentation of the stigma before anthers enables self-pollination to occur after a period of time where outcrossing is possible (reviewed by Goodwillie et al. 2005). Because we assume all ovules are fertilized, we have omitted reproductive assurance as a potential factor. Future modifications should relax this assumption to explore the role of reproductive assurance in the evolution of dichogamy.

In conclusion, our model offers insight into the interacting forces that shape the evolution of dichogamy in hermaphroditic plant populations. Dichogamy is predicted to evolve in the presence of strong inbreeding depression, anther-stigma interference, or a combination of these forces. The existence of traits that mitigate the negative effects of housing anthers and stigmas in close proximity such as herkogamy or a long flowering season should reduce the fitness benefits of dichogamy. These reproductive traits differ widely among species of plants. Even when dichogamy evolves, our model makes it clear that substantial levels of dichogamy are selected against by sex-ratio selection. If ovules are produced within a population long before pollen, mutants that produce pollen early will be able to take advantage of the skewed sex ratio and spread. Again, the strength of sex-ratio selection will depend on the species. For example, continuously flowering plants should have equal sex ratios across the year regardless of the level of dichogamy, allowing for greater levels of dichogamy to evolve. Consequently, the specific forces driving selection for and against dichogamy will depend on the ecology and genetic background of the species of interest.

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APPENDIX 1: STABILITY ANALYSIS

We performed a local stability analysis of the equilibrium ($\hat{R} = 1$) by analyzing the equations $D' = N'_{AA}/N'$, $H' = N'_{Aa}/N'$, assuming that D and H were close to zero. Replacing R with $1 - D - H$, we performed a Taylor expansion of both D' and H', keeping only linear terms D and H in the expansion.

This procedure generates linear recursions in D and H that are accurate near $\hat{R} = 1$. These recursions can be written in matrix form as

$$\begin{pmatrix} D' \\ H' \end{pmatrix} = \mathbf{M} \begin{pmatrix} D \\ H \end{pmatrix},$$

where

$$\mathbf{M} = \begin{pmatrix} \dfrac{(1 - \delta)S[r_{AA}]}{(1 - \delta)S[r_{aa}] + (1 - S[r_{aa}])} & \dfrac{(1 - \delta)\dfrac{S[r_{Aa}]}{4}}{(1 - \delta)S[r_{aa}] + (1 - S[r_{aa}])} \\[4ex] \dfrac{(1 - S_{AA}) + \displaystyle\int_{-\infty}^{\infty} \dfrac{V_{AA,t}(1 - C_{AA})}{V_{aa,t}(1 - C_{aa})} O_{aa,t} F_{[t]}\, dt}{(1 - \delta)S[r_{aa}] + (1 - S[r_{aa}])} & \dfrac{(1 - \delta)\dfrac{S[r_{Aa}]}{2} + \dfrac{(1 - S[r_{Aa}])}{2} + \displaystyle\int_{-\infty}^{\infty} \dfrac{V_{Aa,t}M[r_{Aa}, t]}{2V_{aa,t}M[r_{aa}, t]} O_{aa,t} F_{[t]}\, dt}{(1 - \delta)S[r_{aa}] + (1 - S[r_{aa}])} \end{pmatrix}. \qquad \text{(A1)}$$

When selfing is absent ($S[0] = 0$), the first row consists of zeros because the *AA* genotype is not produced at an appreciable frequency.

To evaluate the integrals in **M**, we assumed that the *A* allele caused only a small change in the amount of dichogamy. That is, we assumed that $r_{AA} - r_{aa} = O(\varepsilon)$ and $r_{Aa} = r_{aa} = O(\varepsilon)$, where ε is small. The eigenvalue of **M** can then be written in terms of the effect of allele *A* as $\lambda = 1 + (r_{AA} - r_{aa})X + (r_{Aa} - r_{aa})Y + O(\varepsilon^2)$, where *X* and *Y* are terms of order one, that is, they involve only parameters for the resident *aa* population (e.g., r_{aa}) and do not contain terms involving the *AA* and *Aa* genotypes. To find *X* and *Y*, we substituted the above equation for λ into the characteristic polynomial of **M** and took the Taylor Series with respect to ε. Because an accurate approximation for λ must cause the characteristic polynomial to be zero (by the definition of an eigenvalue), we set each term in the Taylor Series to zero and solved for *X* and *Y*. This procedure is an example of a perturbation analysis, and it resulted in equation (7).

APPENDIX 2: GAUSSIAN SELFING AND ANTHER-STIGMA INTERFERENCE FUNCTIONS

We chose a selfing function based on the criterion that a greater degree of pollen and ovule overlap would have a higher selfing rate (i.e., selfing should decline with the value of r_x). Specifically, we modeled the selfing rate as a Gaussian function, where

$$S[r_x, t] = \exp\left\{\frac{-(t - \mu[r_{aa}])^2}{2\sigma[r_{aa}]^2}\right\} S[0]. \qquad \text{(A2)}$$

$S[r_x, t]$ has the shape of a normal distribution with a maximum selfing rate of $S[0]$, where $S[0]$ is the selfing rate for an adichogamous plant (i.e., $r_{aa} = 0$; Fig. 3A). When $S[0] = 0$, no selfed seeds are produced regardless of the degree of overlap of pollen and ovule presentation (e.g., a self-incompatible species). When $0 < S[0] < 1$, a species is partially self-compatible and when $S[0] = 1$, all seeds are produced by selfing unless dichogamy evolves. We defined $\mu[r_{aa}]$ to be the time at which the maximum selfing rate occurs (eq.

A2; Table 1; Fig. 3A), where we assume that $\mu[r_{aa}]$ and r_{aa} have the same sign and that $\mu[r_{aa}]$ is a linear function of r_{aa}. If selfing is at its highest rate when pollen and ovule overlap is greatest, $\mu[r_{aa}] = r_{aa}/2$. Conversely, if selfing is at its highest rate when pollen presentation is at its maximum, $\mu[r_{aa}] = r_{aa}$. Similarly, the temporal width (variance) of the selfing function is described by $\sigma[r_{aa}]^2$ (Table 1; Fig. 3A). The parameter $\sigma[r_{aa}]^2$ describes how rapidly selfing declines from its maximum, which we assume to be inversely proportional to the degree of dichogamy. As $\sigma[r_{aa}]^2$ approaches zero, selfing primarily occurs at points in time near $\mu[r_{aa}]$, whereas selfing occurs at roughly an equal rate at all points in time as $\sigma[r_{aa}]^2$ approaches infinity (Fig. 3A). For genotype *x*, the total fraction of selfed ovules over all points in time is described by the integral

$$S[r_x] = \int_{-\infty}^{\infty} \exp\left[\frac{-(t - \mu[r_x])^2}{2\sigma[r_x]^2}\right] S[0] F_{[t]}\, dt$$

(Fig. 2A). The derivative

$$\left.\frac{dS[r_x]}{dr_x}\right|_{r_x = r_{aa}} = \frac{-S[r_{aa}]\{1 + \sigma[r_{aa}]^2 + \mu[r_{aa}]^2(2 + 3\sigma[r_{aa}]^2)\}}{2r_{aa}(2 + \sigma[r_{aa}]^2)^2} \qquad \text{(A3)}$$

is always negative, indicating that the proportion of selfed ovules declines as a function of dichogamy.

We modeled anther-stigma interference by assuming that overlap in the timing of stigma elongation and anther dehiscence reduces pollen export for genotype *aa* by a constant factor, $C[r_{aa}] = \int_{-\infty}^{\infty} e^{-(t-\mu[r_{aa}])^2}/(2\sigma[r_{aa}]^2)C[0]F_{aa}\, dt$, at all points in time. Assuming that anther-stigma interference was constant over time allowed us to calculate the integrals in ρ. We chose this function for $C[r_x]$ so that the total amount of selfing and anther-stigma interference would decline in a similar fashion as a function of r_x. In particular, both anther-stigma interference, $C[r_x]$, and the total selfing rate, $S[r_x]$, are maximal when $r_{aa} = 0$, and their ratio, $C[r_x]:S[r_x]$, is given by $C[0]:S[0]$. Anther-stigma interference can thus be included in the model even when selfing is absent by setting $C[0] > 0$ and $S[0] = 0$ (e.g., in a self-incompatible species).