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Phenological assortative mating in flowering plants: the nature and consequences of its frequency dependence‡

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ABSTRACT

It has long been supposed that variation in mating phenology leads to assortative mating, but its inherent frequency dependence has not been examined. When plants in a population vary in their flowering schedule, the phenotypic (and genetic) composition of the mating pool changes over the season; this causes phenological assortative mating even if pollen is exchanged at random during each interval of the season. Phenotype frequencies govern this temporal shift in the mating pool and this makes phenological assortative mating frequency dependent. We studied phenological assortative mating in four steps. First, we derived a method to estimate the phenotypic correlation between mates from flowering schedules; this correlation, symbolized by ρ, is the standard measure of assortative mating. Next, in a one-locus, two-allele system, we showed that the correlation between mates decreases as one or the other allele approaches fixation, but increases as the population deviates from Hardy-Weinberg proportions. Third, we showed that unlike assortative mating based on fixed preferences, the level of phenological assortment in one generation influences the level of assortment in the next, such that ρ reaches an equilibrium value that depends on allele frequencies. Finally, we contrasted the effects of frequency-dependent, phenological assortative mating on directional selection to the effects of fixed levels of assortative mating. When allelic effects were additive, frequency dependence slightly accelerated the selection response, compared with a fixed ρ. When one allele was dominant, phenological assortment slightly decelerated the selection response. Similarities between assortative mating through phenology and through habitat preference can cause the latter also to be frequency dependent.

Keywords: flowering phenology, genetic variance, natural selection.

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‡ This paper is dedicated to Dr Jules Lerner in honour of a lifetime of distinguished teaching.

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INTRODUCTION

Flowering time in plants is a textbook example of a trait subject to assortative mating (e.g. Hartl and Clark, 1989; Lynch and Walsh, 1998; Hedrick, 2000; Conner and Hartl, 2004). The logic is clear – early bloomers will mate with other early bloomers more often that late bloomers, and vice versa. Despite the central place of flowering time in the plant's life history, the effect of assortative mating on flowering time evolution has received scant consideration (Ennos and Dodson, 1987; Fox, 2003). The limited evidence available confirms that plants mate with phenologically similar individuals more frequently than random (Gutierrez and Sprague, 1959; Ennos and Dodson, 1987; Lyons and Mulley, 1992; LeBuhn, 2004), but the prevalence, intensity and consequences of phenological assortative mating are basically unknown.

Assortative mating does not change allele frequencies, but it does change genotype frequencies by bringing together alleles with similar phenotypic effects (Lewontin *et al.*, 1968; Barton and Turelli, 1991; Lynch and Walsh, 1998). In the single-locus case, it reduces heterozygote frequency (Wright, 1921; Crow and Kimura, 1970). This inflates genetic variance in the assortative trait, relative to panmixia, which in turn accelerates the selection response. The strength of assortative mating is measured by the phenotypic correlation between mates, symbolized by ρ.

Fox (2003) noted, but did not develop, the inherent frequency dependence of phenological assortative mating. This is not the case with simple models of assortative mating based on mate choice behaviour. Those models assume a single mating pool wherein potential mates encounter one another at random; the probability that an encounter ends in mating depends upon a fixed bias for phenotypically similar mates (e.g. Wright, 1921; O'Donnald, 1960; Karlin and Scudo, 1968; Scudo and Karlin, 1968; Moore, 1979; Nagylaki, 1992). Formally, the assorting trait is the criterion for assortment, but not its cause. When all genotypes are equally 'choosey', the phenotypic correlation between mates holds to a constant value. Starting from Hardy-Weinberg equilibrium, a constant level of assortative mating, over the generations, inflates genetic variance in the criterion trait to a new equilibrium level (Crow and Kimura, 1970; Barton and Turelli, 1991).

Sewell Wright noted that while it is simplest to assume that the strength of assortative mating, ρ, is fixed, 'actually it would be likely to rise as σ_P^2 (*the phenotypic variance*) rises' (Wright, 1969, p. 280). In short, the likelihood of mating within one's own type depends on the availability of alternative types. This sort of frequency-dependent mating emerges from variation in flowering phenology (Fox, 2003). Phenology is not a criterion for mate choice; rather, variation in phenology directly causes non-random mating (Kirkpatrick, 2000; Fox, 2003). When flowering time varies, the population divides into a seasonal succession of mating pools. Even if individuals mate randomly within each succeeding pool, the shifting pool structure ensures that individuals encounter phenotypically (i.e. phenologically) similar mates more often than if all flowered synchronously (Ennos and Dodson, 1987; Fox, 2003). As the phenotypic variance in flowering time increases, so do the frequencies of early × early and late × late matings.

We hypothesized that, when starting from Hardy-Weinberg equilibrium, a frequency-dependent correlation between mates would lead to greater inflation of genetic variance than a fixed correlation. Variation in flowering phenology in the initial generation will cause a base level of assortment. The inflated genetic variance in the subsequent generation would increase phenotypic variance, which in turn would amplify assortative mating, which would then further inflate genetic variance. The end result could be an equilibrium level of genetic variance substantially higher than if assortment was fixed at the base level.

We explore frequency dependence in phenological assortative mating in four steps. As a practical matter, first we show how ρ, the phenotypic correlation between mates, is determined by variation in the flowering schedule. Next, we explore the sensitivity of ρ both to genotype frequencies and to the structure of the flowering schedule. Third, we determine if the equilibrium value of ρ depends on allele frequency. Finally, we contrast the effect of frequency-dependent phenological assortative mating on directional selection with the effect of fixed levels of assortment. We present our findings in the context of flowering phenology for annual plants, but with suitable adjustments they could apply to any semelparous species where individuals differ in mating schedule (e.g. Craig *et al.*, 1993). The logic also applies to some cases where habitat selection induces assortment.

MATING SCHEDULES AND THE CORRELATION BETWEEN MATES

Fox (2003) showed that many types of phenological variation lead to assortative mating. We show that any one of these can be summarized by a standard statistic from population genetics, the phenotypic correlation between mates (Fisher, 1918; Wright, 1921; Barton and Turelli, 1991; Lynch and Walsh, 1998). For trait z,

$$\rho = \frac{\mathrm{cov}\,(z_{\mathrm{m}}, z_{\mathrm{f}})}{\sigma^2\,(z)} = \frac{\sum_i \sum_j \{\Phi_{ij}\,(z_i - \bar{z})(z_j - \bar{z})\}}{\sum_i X_i\,(z_i - \bar{z})^2} \tag{1}$$

where i and j are the phenotypic classes of the mother and father, respectively, in a mating pair, X_i is the population frequency of the i-th phenotypic class, and Φ_{ij} is the proportion of all matings where the mother has phenotype i and the father phenotype j. Under random mating, the Φ_{ij}'s are simply products of the i-th and j-th class frequencies, and the numerator becomes zero. If z is a phenological trait, such as flowering time, variance in z causes $\Phi_{ij} > X_i^2$, thus causing $\rho > 0$.

The ρ statistic has two alternative interpretations, depending on properties of the phenotypic distribution. If maternal and paternal phenotypes are bi-variate normal, ρ predicts the phenotype of the 'average male' for a randomly selected female (Weis and Kossler, 2004). Expressing phenotypes as deviations from the mean, and assuming equal variance for the two sexes,

$$(z^* - \bar{z}) = \rho\,(z_i - \bar{z}) \tag{2}$$

where z_i is the phenotype of female i, z^* is the expected phenotype of her mate, and $\bar{z}$ is the population mean phenotype. This holds because $\rho = \mathrm{cov}(z_{\mathrm{m}}, z_{\mathrm{f}})/\sigma^2(z)$, which is the slope of the regression of fathers over mothers. When the two sexes have the same phenotypic variance, ρ also predicts the 'average mother' for a given father.

A second interpretation applies when phenotypes fall into a few discrete categories. According to this view, used in single-locus models (e.g. Wright, 1921; O'Donald, 1960; Crow and Kimura, 1970), ρ is the proportion of matings that are 'assortative'. The remaining proportion, $1 - \rho$, are random. This interpretation is verified by re-arranging equation (2) to

$$z^* = \rho z_i + (1 - \rho)\,\bar{z} \tag{3}$$

In words, for randomly selected mother i, fraction ρ of her matings will be to fathers with phenotypes identical to her own, and fraction $1 - \rho$ will be to randomly selected fathers, whose expected phenotype, by definition, is the population mean.

The phenotypic correlation between mates can result in a genetic correlation, termed the marital correlation (Fisher, 1918; Wright, 1921) and symbolized as m. The two are related by the equation $m = \rho h^2$, where h^2 is the heritability of the assorting trait; this identity assumes no genotype–environment correlation (Wright, 1921, 1969).

As stated above, variation in flowering phenology divides the populations into a temporal succession of mating pools, and this induces assortative mating (Ennos and Dodson, 1987; Fox, 2003). At one extreme, the mating probability between two phenotypic classes, Φ_{ij}, will equal zero if they contribute to non-overlapping sets of mating pools (as would occur if class i comes into flower only after class j completes flowering). At the other extreme, Φ_{ij} will be high if the two classes contribute equally to the same set of mating pools. Mating probabilities depend upon flowering schedules of potential mates. Assume a plant population wherein individuals fall into one of several phenological classes, each individual produces an equal number of flowers over its lifetime, and all flowers have the same success through male and female function. Each day a phenotypic class produces a characteristic number of flowers that last for that day only. Thus the composition of the mating pool can change daily. Under these conditions

$$\Phi_{ij} = \sum_{d=1}^{D} \theta_{id}\, v_{dj} \tag{4}$$

where i and j denote phenotypes of the mother and father respectively, θ_{id} denotes the proportion of all flowers produced by the population over the entire season that were open on plants of phenotype i on day d, and v_{dj} represents the proportion of all flowers producing pollen on day d that are on plants of phenotype j.

FREQUENCY DEPENDENCE OF THE CORRELATION BETWEEN MATES

The remainder of this paper applies equations (1) to hypothetical flowering schedules to explore the dependence of ρ on genotype frequencies. We assume a single locus that determines 'mean flowering day' (e.g. a genotype producing a single flower on days 1, 2 and 3 of the flowering season has a mean flowering day of 2). The model can apply to any other phenological trait, or any trait correlated to a phenological trait. Assume two alleles, e and l, which cause early and late flowering, respectively. Additional simplifying assumptions include: (1) flowering schedules are determined solely by genotype; (2) all genotypes produce the same total number of hermaphroditic flowers; (3) all genotypes have a flowering period of equal length, D; (4) every day, each genotype matures a characteristic number of flowers, which are active for that day only; (5) all flowers have the same chance of donating pollen and the same chance of setting seed; and (6) during each day mating is random among the open flowers. The strength of assortative mating depends not only on genotype frequencies, but also on the size of the genetic effect on mean flowering day – the greater the phenological difference between the *ee* and *ll* genotypes, the greater the assortment. We have organized our presentation to show how genotype frequencies affect the relationship of ρ to the size of the genetic effect.

Additive allelic effects

We start with the case of additive allelic effects. Suppose that the mean flowering day for opposite homozygotes differs by *d* days, and heterozygotes are intermediate. We define the difference between the early and late homozygotes as $\delta = d/D$ (i.e. the delay in flowering as a proportion of the flowering period). The phenotypic effect of the *l* allele is thus $\frac{1}{2}\delta$. By convention, we define the phenotypes of the *ee, el* and *ll* genotypes as 0, $\frac{1}{2}\delta$ and δ, respectively. The frequencies of the *e* and *l* alleles are *p* and *q*, respectively.

Fox (2003) classified phenological assortative mating as 'standard' or 'cryptic'. Standard assortment occurs when the genotypes vary in their day of first (and last) flowering. When they do, there are periods in the season when one or more genotypes are out of the mating pool (Fig. 1A). Cryptic assortment can occur even if all individuals start and stop flowering on the same days; if classes reach peak flowering on different days (Fig. 1C), within-class mating will occur more frequently than random.

Figure 1 shows hypothetical examples of flowering schedules for the *ee, el* and *ll* genotypes that result in assortative mating that is standard, cryptic and a mixture of the two. In all three cases, $\delta = 0.4$ (i.e. the genotypes differ in mean flowering day by the same amount in each case). In the standard case (Fig. 1A), genotypes produce the same number of flowers every day of their flowering period, and so assortment is caused only by differences in the day of first flowering. There is an 80% overlap between the *el* genotype and each homozygote, and a 60% overlap between the two homozygotes.

In the mixed case (Fig. 2B), the three genotypes have flowering schedules with shapes derived from a binomial distribution ($n = 9$, $P = 0.5$). Although the *l* allele delays the start of flowering by the same amount as in the standard case, the potential for assortment is greater.

During the middle of the season when all genotypes are in flower, their relative contributions to the mating pool change day by day (Fig. 1B), leading to some cryptic assortment. The overlap between each homozygote and *el* is 68%, and 27% for opposite homozygotes. Empirical studies suggest that mixed assortment, similar to that in Fig. 1B, is the most common situation in nature (Pors and Werner, 1989; Meagher and Delph, 2001; Buide *et al.*, 2002; Mahoro, 2002; Weis and Kossler, 2004).

Under the purely cryptic case (Fig. 1C), the genotypes start and stop flowering on the same days, but differ in the day of peak flowering. These schedules also follow binomial distributions ($n = 9$, and $P = 0.277$, 0.5 and 0.722 for the *ee, el* and *ll* genotypes, respectively). The flowering schedules for the *ee* and *el* genotypes have a 66% overlap, while those for the *ee* and *ll* genotypes have a 23% overlap, which is comparable to that for the mixed case. Note that in the cryptic case, $\delta < 1$ by definition because mean flowering day for the *ee* and *ll* must fall within the same time period of *D* days.

Assuming equal frequency of the *e* and *l* alleles ($p = q = 0.5$) and Hardy-Weinberg genotype frequencies, the phenotypic correlations between mates for the standard, mixed and cryptic cases in Fig. 1 are $\rho = 0.28$, 0.47 and 0.50, respectively.

Before illustrating the frequency dependence of ρ, we review how allele frequencies and departures from Hardy-Weinberg expectations determine genotype frequencies. The frequencies of the *ee, el* and *ll* genotypes are designated as *E, M* and *L* (early, middle and late), respectively. Assortative mating can reduce heterozygote frequency, and this reduction is quantified by Wright's (1969) inbreeding coefficient, $F = (2qp - M)/2qp$. Thus, the genotype frequencies are:

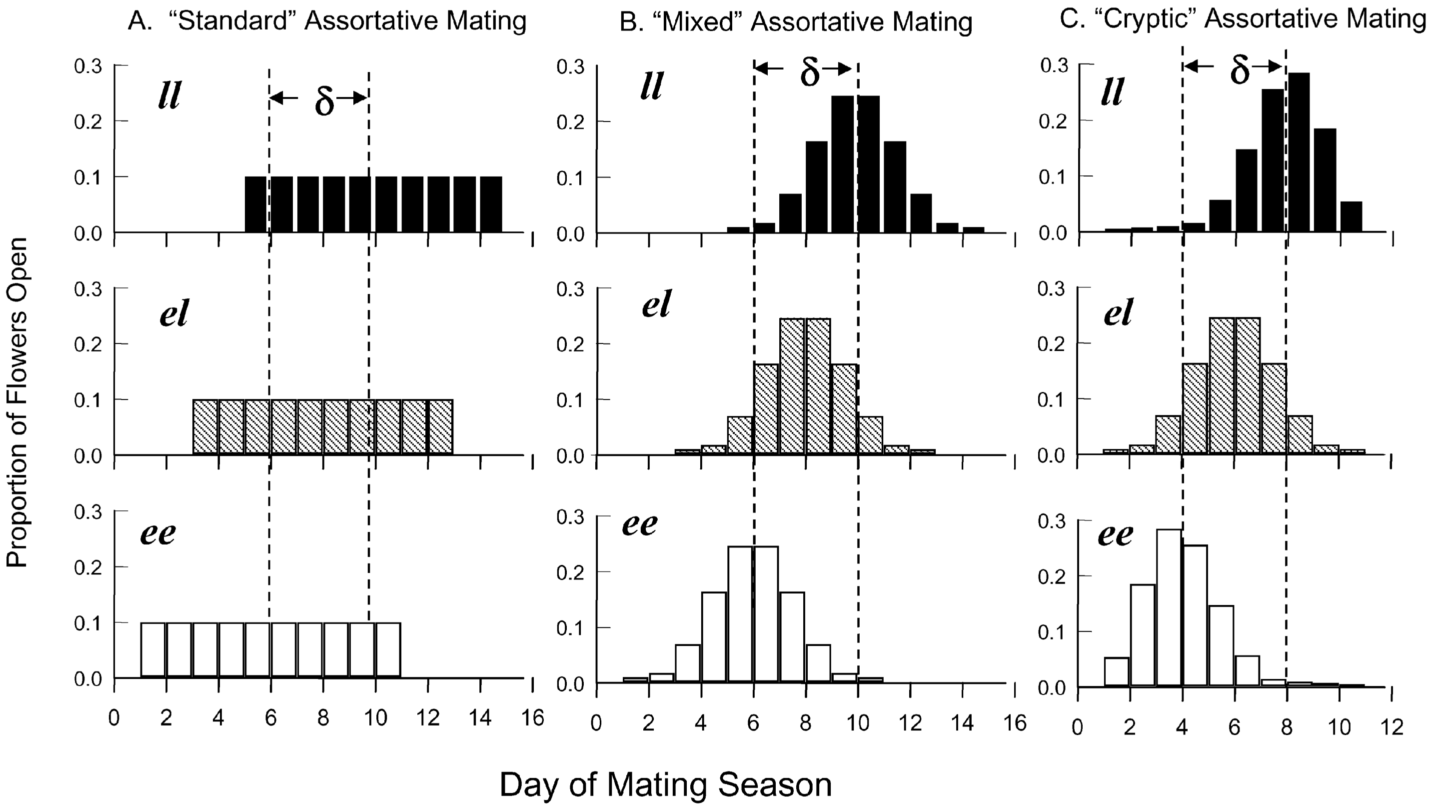

Fig. 1. Hypothetical flowering schedules for three plant genotypes. All genotypes flower for *D* days. The mean flowering day for the *ll* genotype is *d* days after the *ee*. The proportional delay in flowering for *ll* is $d/D = \delta$. (A) The standard scenario in which assortment occurs solely due to variation in the day of first and last flowering. (B) In the mixed scenario, assortment occurs not only due to differences in the start and stop days for flowering, but due to daily variation in flower production. (C) In the cryptic scenario, all genotypes start and stop flowering at the same time, but assortment nonetheless occurs because they differ in daily flower production.

$$E = q^2 + qpF$$

$$M = 2\,pq(1 - F)$$

$$L = p^2 + qpF$$

The phenotypic mean is $\bar{z} = q\delta$, and the phenotypic variance is $\sigma_P^2 = 2qp(1 + F)(½\delta)^2$. (Because there are no environmental effects or dominance, $\sigma_P^2 = \sigma_G^2$.) Thus, the variance increases with the square of the phenotypic effect of l (i.e. $½\delta$) and with the deviation from Hardy-Weinberg (F) but decreases as one allele approaches fixation (p or $q \to 1$).

Figure 2 plots the relationship of ρ to δ under a range of values for q, assuming the standard, mixed and cryptic cases. Note that when $\delta = 0$, the mating schedules of all genotypes overlap completely and so $\rho = 0$.

Consider the standard case. Figure 2A shows that if genotypes are held to Hardy-Weinberg proportions ($F = 0$), ρ has a bi-phasic response with the break-point at $\delta = 1$. Below the break-point, all three genotypes have some overlap in flowering, and so the steeper increase in ρ in this lower region reflects the progressive reduction in all between-genotype matings. Above $\delta = 1$, the flowering schedules of the homozygotes no longer overlap, and so the weaker increase in ρ in this upper region reflects only reduced mating between the heterozygotes and homozygotes. If $\delta \geq 2$, there is no overlap and so assortment is perfect, $\rho = 1$. When one allele is at very high frequency (p or $q \to 1$), ρ approaches zero; most individuals will be homozygous for the common allele and so the population mean is close to that homozygote's phenotypic value. Matings between individuals of the rare homozygote contribute the most to the covariance, but these matings are infrequent. As a consequence, the covariance between mates (numerator of equation 1) approaches zero.

Assortative mating is less sensitive to allele frequencies when the population deviates from Hardy-Weinberg proportions, although ρ increases more strongly with δ (Fig. 2A *vs* 2B). At $F = 1$, there are no heterozygotes, and so all matings are between homozygotes.

The relationship of ρ to δ under the mixed and cryptic cases is similar to that under the standard case (Figs. 2C–F). There is a decelerating increase in the correlation between mates, ρ, when the l allele has a strong effect on flowering time (high values of δ). Also, the correlation between mates is perfect when $\delta > 1$ if heterozygotes are absent ($F = 1$). Under the mixed and cryptic cases, a genotype's mating opportunities are concentrated within a few days of its peak flowering. Even a small offset in peak flowering can greatly decrease the opportunities for two genotypes to mate with one another. The starkest difference of the mixed and cryptic cases from the standard case is their greater sensitivity to allele frequency. For instance, when one allele is very rare, assortment is negligible unless δ is large (see Fig 2B). This also comes from concentrating mating opportunities into just a few days.

Dominance

With complete dominance there are only two phenotypes, the *ee* and the *el*/*ll* classes. This makes the response of ρ to allele frequency similar to the $F = 1$ additive case. With standard assortative mating, $\rho = \delta$ because each class is alone in the mating pool for proportion δ of its flowering period. This is true regardless of allele frequencies or heterozygosity.

With mixed assortment, the relationship of ρ to δ remains sigmoidal (Fig. 3A *vs* 2C). However, dominance causes an asymmetry in the relation of ρ with q not seen in the additive case (Fig. 5A). When the recessive allele is common, say $p = 0.9$, the frequency of

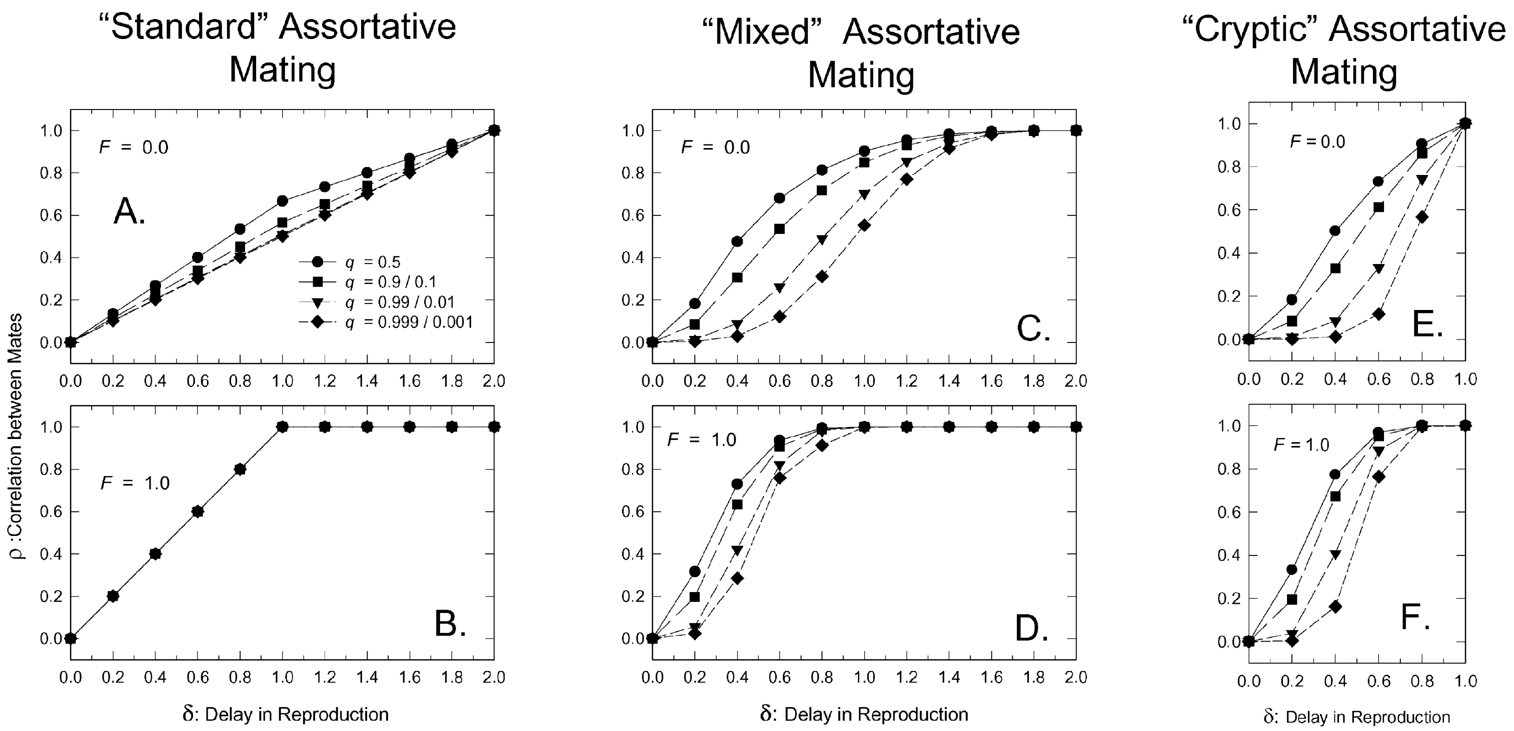

Fig. 2. The phenotypic correlation between mates, ρ, as a function of reproductive delay, δ, allele frequency, q, and departures from Hardy-Weinberg proportions, F, assuming additive allelic effects. (A) Standard assortative mating with heterozygotes at Hardy-Weinberg proportions ($F=0$). (B) Standard assortment, heterozygotes absent ($F=1$). (C, D) Mixed assortment, at the same F values. (E, F) Cryptic assortment at the same F values.

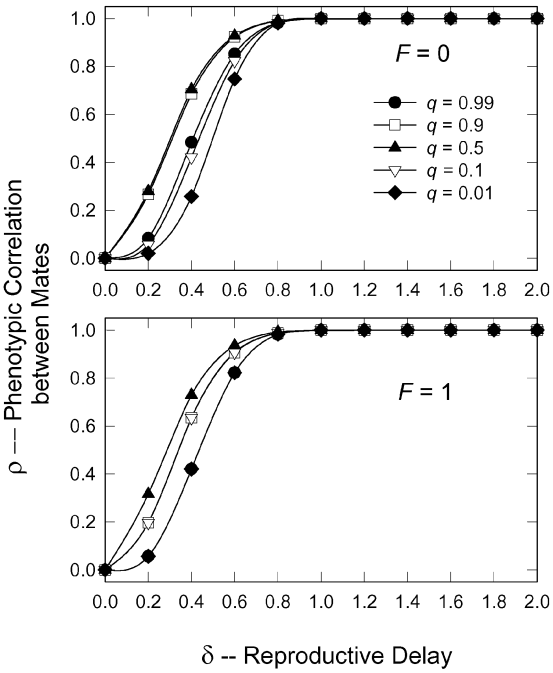

Fig. 3. The phenotypic correlation between mates, ρ, as a function of reproductive delay, δ, allele frequency, q, and departures from Hardy-Weinberg proportions, F, assuming complete dominance and mixed assortment.

the recessive phenotype is of the same order of magnitude, $E = 0.81$. When the recessive allele is rare, say $p = 0.1$, the recessive phenotype can be an order of magnitude rarer, $E = 0.01$, or more. Thus, when the recessive is rare, almost all of the potential mates encountered by recessive homozygotes will be of the dominant phenotype (unless flowering delay is large). When $F = 1$, the symmetry in the relationship between ρ and q is restored (Fig. 3B) because allele frequencies and phenotype frequencies are identical. Comparing Figs. 3A and 3B with Figs. 2C and 2D shows that with dominance, departure from Hardy-Weinberg has little influence on ρ. Frequency dependence under dominance for the cryptic case was very similar to the mixed case (data not shown).

ASSORTATIVE MATING AND EQUILIBRIUM GENOTYPE AND PHENOTYPE FREQUENCIES

Not only does assortment respond to heterozygote frequency, heterozygote frequency is changed by assortment. Thus, the relationship of ρ to δ is not constant. We show that feedback between assortment in one generation and assortment in the next leads to an equilibrium correlation between mates that depends on allele frequency. We examine two starting conditions. The first is a single population starting at Hardy-Weinberg proportions. The second starts with the merger of two populations fixed for opposite alleles, such as when isolated populations come into secondary contact.

Allelic effects additive

We start by reviewing the effect of constant levels of assortative mating on heterozygote frequencies. Following Haldane (1924) and others (e.g. Nagylaki, 1992), and assuming additivity, one generation of assortative mating changes genotype frequencies as follows:

$$E' = \rho\{E + \tfrac{1}{4}M\} + (1-\rho)\{E(E + \tfrac{1}{2}M) + \tfrac{1}{2}M(E + \tfrac{1}{2}M)\} \tag{5a}$$

$$M' = \rho\tfrac{1}{2}M + (1-\rho)\{E(\tfrac{1}{2}M + L) + \tfrac{1}{2}M(E + M + L) + L(\tfrac{1}{2}M + E)\} \tag{5b}$$

$$L' = \rho\{L + \tfrac{1}{4}M\} + (1-\rho)\{\tfrac{1}{2}M(L + \tfrac{1}{2}M) + L(L + \tfrac{1}{2}M)\} \tag{5c}$$

The right-hand side of each equation consists of two parts; the first denotes offspring produced by assortative matings and the second denotes those due to random mating. Although genotype frequencies can change in this model, allele frequencies do not. Starting at Hardy-Weinberg proportions, heterozygote frequency declines for several generations because only half of the offspring from $el \times el$ matings are heterozygous. However, this loss of heterozygotes through segregation is balanced by $ee \times ll$ matings when

$$\tfrac{1}{2}M\rho + \tfrac{1}{2}M^2(1-\rho) = 2EL(1-\rho) \tag{6}$$

which brings the population to equilibrium. Remembering that the frequency of heterozygotes is a function of F, it has been shown (Crow and Kimura, 1970) that for a constant level of assortative mating, at equilibrium,

$$\rho = \frac{2\hat{F}}{1+\hat{F}} \qquad \text{and} \qquad \hat{F} = \frac{\rho}{2-\rho}$$

where the circumflex indicates the equilibrium value. The phenotypic and genetic variances also reach equilibria of $2qp(1+\hat{F})(\tfrac{1}{2}\delta)^2$ (these expressions apply to m, the genetic correlation between mates, but since the genetic and phenotypic correlations are identical in our scenario, we can substitute ρ for m).

We adjusted the model given by equations (5a–c) to accommodate phenological assortative mating, where ρ increases with F. This created the feedback between the level of assortment in one generation and that in the next. Starting at Hardy-Weinberg proportions ($F = 0$), an initial level of assortative mating, ρ_0, decreases heterozygote frequency in the next generation, which increases F. With fewer heterozygotes (and more homozygotes), the frequency of within-homozygote matings goes up, making $\rho_1 > \rho_0$. Eventually, the loss of heterozygotes by segregation is balanced by mating between opposite homozygotes (equation 6). The equilibrium value of $\hat{F}$ reached at this point is greater than that reached when ρ is fixed at ρ_0. An equilibrium correlation between mates, $\hat{\rho}$, is also reached. The value of $\hat{\rho}$ depends on δ, the relative delay in *ll*'s mean flowering day, and on allele frequencies.

Before attempting an analytical result for $\hat{\rho}$ in relation to δ, it is helpful to illustrate the dynamics of ρ numerically. We applied recursion equations (5a–c), assuming the mixed case (Fig. 1B; $\delta = 0.4$) and $q = p = 0.5$. The frequency of each mating combination, Φ_{ij}, was calculated by equation (4), and the correlation between mates, ρ, by equation (1). Two starting genotype frequencies were used; one assumed heterozygotes present in Hardy-Weinberg proportions ($F = 0$) and the other assumed heterozygotes were absent ($F = 1$). The values of ρ_0 for these conditions were 0.47 and 0.73, respectively. We then calculated ρ_t each generation and found the new genotype frequencies. For comparison, we repeated the calculations holding ρ fixed at the values of 0.47 and 0.73.

The frequency dependence of phenological assortative mating caused the correlation between mates to converge on a value of 0.58, regardless of the starting value (Fig. 4A). Under fixed levels of assortative mating, heterozygotes came to stable frequencies in less than seven generations (values the same to four decimals), with a higher $\hat{M}$ for the higher ρ_0 value. In contrast, under phenological assortative mating, the two starting conditions converged on a single, stable heterozygote frequency by nine generations (Fig. 4B). Incidentally, this result indicates that the level of assortment observed when two populations first come into secondary contact would overestimate the barrier to introgression caused by phenological differences.

A general analytical solution for the relationship of $\hat{\rho}$ to δ is not possible because parameters for the shape of the flowering schedule must enter into the equation; since flowering schedules can take a variety of shapes, no single set of additional parameters is suited to all cases. However, when flowering schedules are 'flat', as in our standard case (Fig. 1A), no shape parameters are needed. We derived an analytical solution for the relationship of $\hat{F}$ to δ, and from that, $\hat{\rho}$ to δ, for the one-locus, two-allele scenario, assuming

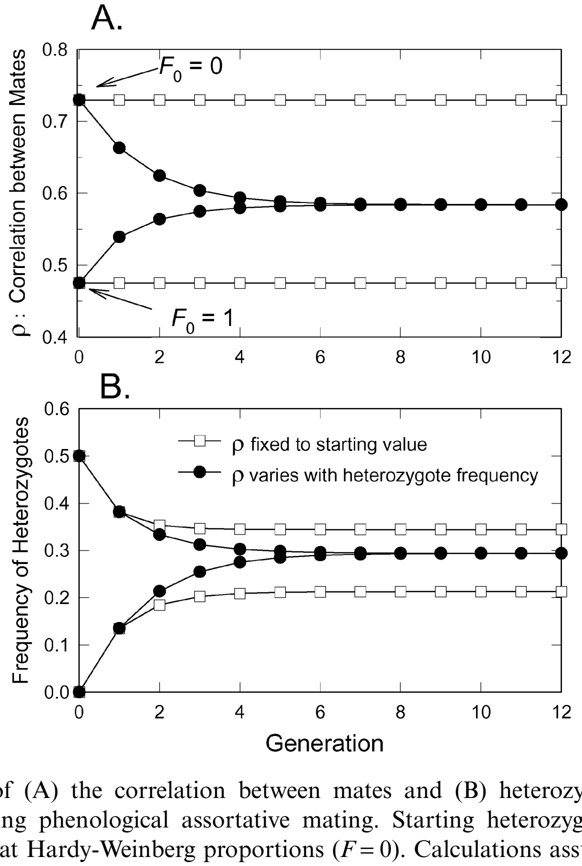

Fig. 4. Trajectories of (A) the correlation between mates and (B) heterozygote frequencies, for populations undergoing phenological assortative mating. Starting heterozygote frequencies were either zero ($F = 1$) or at Hardy-Weinberg proportions ($F = 0$). Calculations assume that $q = 0.5$, that alleles have additive effects and that the mixed-assortment scenario applies (Fig. 1B). For comparison, we display results holding ρ fixed at the starting values.

the flowering schedules for the standard case, $\delta \le 1$, and $q = p = 0.5$. At these frequencies, the two homozygotes deviate from the population mean flowering day by $|\,½\delta\,|$, whereas the heterozygote deviates by 0.

With the standard case, the flowering season can be divided into five periods (Fox, 2003), during which one, two or all three genotypes are in flower (Fig. 1A). The mating frequency for each mother–father genotypic combination, Φ_{ij}, depends on the proportional representation of each genotype during each of the periods. Under these conditions,

$$\rho = \frac{1}{E(-½\delta)^2 + L(½\delta)^2}\left\{\begin{array}{l} E\left[½\delta + ½\delta\left(\dfrac{E}{E+M}\right) + (1-\delta)E\right](-½\delta)^2 \\ + L\left[½\delta + ½\delta\left(\dfrac{L}{M+L}\right) + (1-\delta)L\right](½\delta)^2 \\ + E[(1-\delta)L](-½\delta)(½\delta) \\ + L[(1-\delta)E](½\delta)(-½\delta) \end{array}\right\} \tag{7}$$

The first two quantities enclosed by the curved brackets are the within-type mating probabilities for the homozygotes (Φ_{ii} and Φ_{jj}) times the product of their deviations from the phenotypic mean. The second two quantities are the between-type probabilities (Φ_{ij} and Φ_{ji}) times the product of their deviations. For example, the first term gives the frequency of *ee* × *ee* matings. The E before the square brackets is the probability that a randomly drawn mother is *ee*. Inside the brackets, $½\delta$ of all her matings occur during the first period of the season, when the probability of encountering an *ee* father is 1. Another $½\delta$ of her matings occur when both *ee* and *el* are available, during which time the probability of an *ee* father is $E/(E + M)$. The remaining $1 - \delta$ of her matings occur when all genotypes are available, when the probability of an *ee* father is $E/(E + M + L) = E$. During this last period, the probability of an *ee* mother mating with an *ll* father is L, as shown by the third term within the curved brackets. The *ll* genotype shows complementary relationships. Terms for heterozygotes disappear because their deviation from the mean is zero. Expression (7) simplifies because $E = L$. With the restriction that $\delta \le 1$,

$$\rho = ½\delta\left\{1 + \left(\frac{E}{E+M}\right)\right\} \tag{8}$$

(Note that when $\delta > 1$, *ee* and *ll* mating schedules do not overlap and so heterozygotes lost by segregation cannot be replaced, and by necessity $\hat{\rho} = 1$.)

Using equation (8), we can find the equilibrium correlation between mates, $\hat{\rho}$, in relation to the delay in mean flowering day, δ. Rewrite genotype frequencies in terms of $\hat{F}$ as follows:

$$\hat{\rho} = ½\delta\left\{1 + \left(\frac{\hat{E}}{\hat{E}+\hat{M}}\right)\right\} = ½\delta\left\{1 + \left(\frac{q^2 + pq\hat{F}}{(q^2 + pq\hat{F}) + (2pq(1-\hat{F}))}\right)\right\}$$

where $\hat{E}$ and $\hat{M}$ are the equilibrium frequencies of the *ee* and *el* genotypes, respectively. Remembering the condition that $q = p$, the expression simplifies to

$$\hat{\rho} = ½\delta + \left\{\frac{½\delta(q^2 + q^2\hat{F})}{3q^2 - q^2\hat{F}}\right\} \tag{9}$$

Substituting $2\hat{F}/(1+\hat{F})$ for $\hat{\rho}$, this simplifies and rearranges to

$$\delta = \frac{3\hat{F} - \hat{F}^2}{1 + \hat{F}} \tag{10}$$

Further rearrangement gives $\hat{F}$ – and thereby $\hat{\rho}$, $\hat{M}$, $\hat{\sigma}_G^2$ and $\hat{\sigma}_P^2$ – in terms of δ:

$$\hat{F} = \frac{3 - \delta - \sqrt{\delta^2 - 10\delta + 9}}{2} \tag{11}$$

Figure 5 shows the relation of $\hat{\rho}$ to δ for the specified conditions. For comparison, we also indicate the correlation when $F = 0$ and $F = 1$. When flowering time differences are small, $\hat{\rho}$ changes little from that expected under Hardy-Weinberg frequencies. As the proportional delay in flowering increases, $\hat{\rho}$ increases at an accelerating rate, reaching $\hat{\rho} = 1$ when $\delta \geq 1$.

Analytical solutions for $\hat{\rho}$ assuming other flowering schedule shapes (e.g. our mixed and cryptic cases) may be possible, but given the complexity of the solution for the simplified scenario, they are unlikely to reveal clear principles. We numerically established the equilibrium values of $\hat{\rho}$ for other scenarios. Assuming the flowering schedules in Fig. 1, we calculated $\hat{\rho}$ for the same selected values of q and δ used in Fig. 2. We plot the results in Fig. 6, which shows that the equilibrium correlation between mates is relatively insensitive to allele frequency under standard phenological assortment (Fig. 6A) but much more sensitive when assortment is mixed or cryptic (Figs. 6C and E). For comparison, Figs. 6B, D and F show that $\hat{\rho}$ can be as strong as that seen when heterozygotes are absent, especially when allele frequency is intermediate ($q \sim 0.5$). The inflation in genetic variance caused by assortment will similarly be greater.

Dominance

As we show above, for the standard case (Fig. 1A), with dominance, the correlation between mates (ρ) equals the relative delay in *ll*'s mean flowering day (δ) regardless of phenotype frequencies. Remembering that $m = \rho h^2$, and that h^2 changes with both q and F in the case of

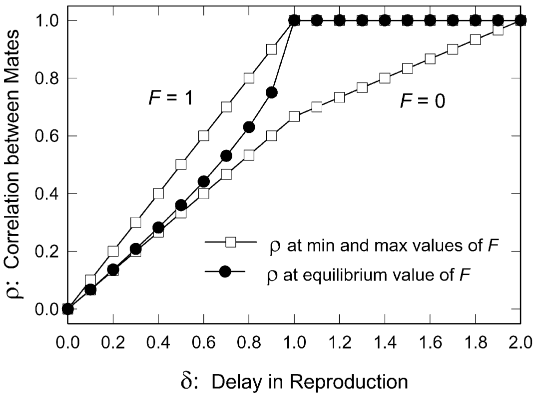

Fig. 5. Equilibrium correlation between mates, $\hat{\rho}$, in relation to δ, the proportionate delay in *ll*'s mean flowering day. Calculations use equation (11) to calculate $\hat{F}$, and from there, $\hat{\rho} = (2\hat{F}/1 + \hat{F})$; assumes standard assortment (Fig. 1A), and $p = q = 0.5$. For comparison, the ρ at $F = 0$ and $F = 1$ are indicated.

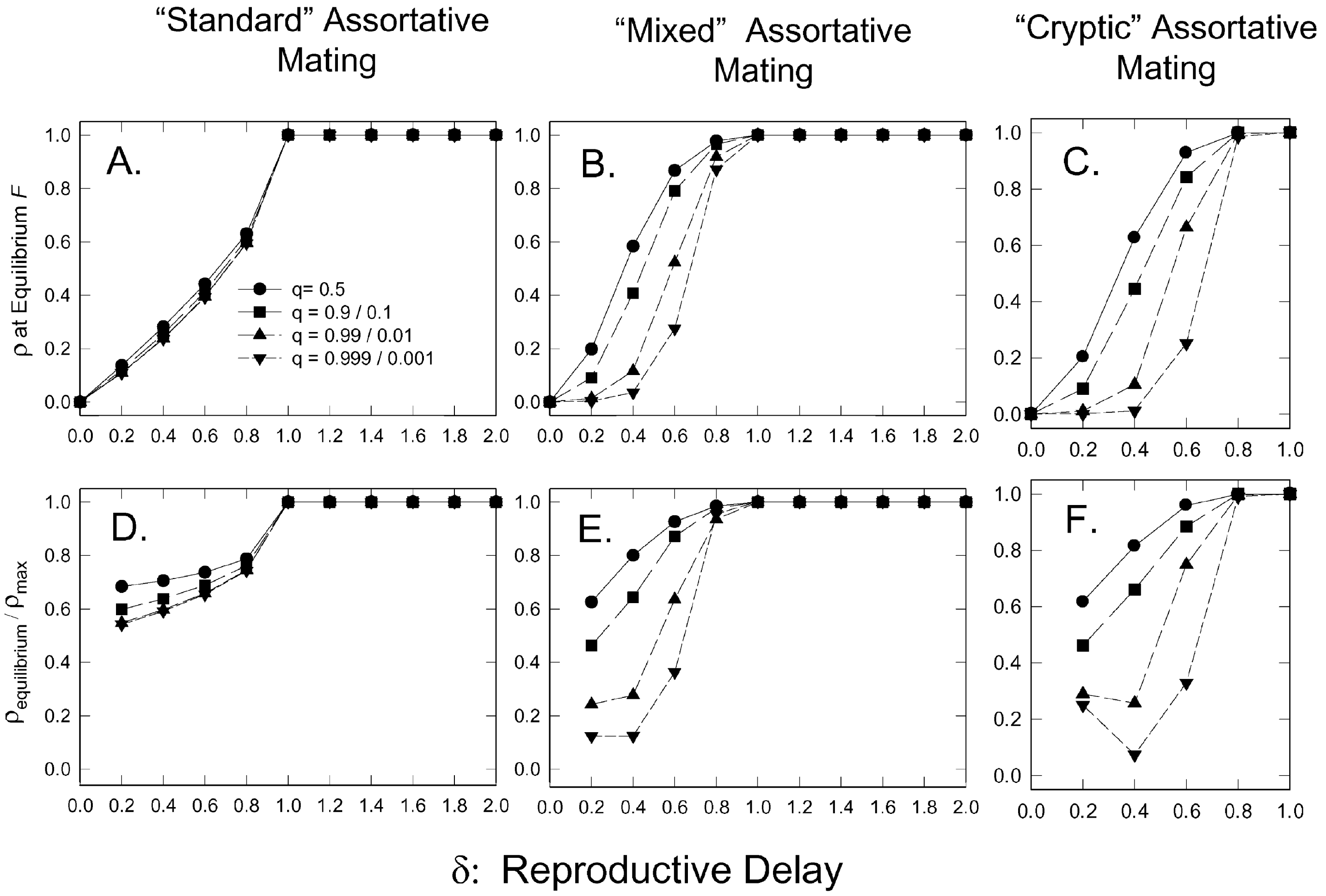

Fig. 6. The equilibrium value of ρ, the phenotypic correlation between mates, as a function of δ, the proportional delay in *ll*'s mean flowering day. (A–C) $\hat{\rho}$ for the standard, mixed and cryptic cases illustrated in Fig. 1. (D–F) The ratio of $\hat{\rho}$ to $\rho_{\max}$; that is, the equilibrium correlation between mates as a proportion of the correlation when heterozygotes are absent. The greater this ratio, the greater the amplification of genetic variance, compared with assortative mating with a fixed intensity of ρ_0.

dominance, we can see that genetic assortment remains, as always, frequency dependent. The genetic correlation between mates comes to an equilibrium derived by Wright (1921):

$$\hat{m} = \rho \hat{h}^2 = \delta \hat{h}^2 = \frac{2\hat{F}}{1 + \hat{F}}$$

where $\hat{h}^2$ is the heritability at equilibrium (see Crow and Kimura, 1970, p. 131).

Turning to dominance in the mixed and cryptic cases, we iterated modifications of equations (5a–c) at different values of δ and q, starting at Hardy-Weinberg proportions. The results (not shown) indicate that although assortative mating reduced heterozygote frequency to an equilibrium level (i.e. F increased from zero to $\hat{F}$), the difference between ρ_0 and $\hat{\rho}$ was minimal at any given combination of δ and q.

PHENOLOGICAL ASSORTATIVE MATING AND DIRECTIONAL SELECTION

Assortative mating accelerates directional selection on the assorting trait by increasing its genetic variance (e.g. Wright, 1921; O'Donald, 1960; Nagylaki, 1992; Fox, 2003). The frequency dependence of phenological assortative mating presents an interesting situation. A new flowering time mutation by definition will be rare, and so it will not initially induce strong assortative mating. If the mutation is beneficial, it will spread by selection at an initial rate similar to panmictic expectations. As it spreads, the intensity of assortative mating will increase, which will then accelerate the selection response. But, as the favourable allele reaches high frequency, assortment will again decline and so too will the selection response.

Does this dynamic affect the long-term selection response? To find out, we calculated trajectories of the allele frequency for *l* under a number of conditions. We modified the recursion equations (5a–c) by including terms for the relative fitness of each genotype, $w_i = W_i/\bar{W}$ (see Nagylaki, 1992). We varied δ (the difference in mean flowering day between *ee* and *ll*) and the fitness differential between homozygotes. A large δ could have either a small or a large effect on fitness. We also varied the dominance relationships between *e* and *l*. The calculations followed q from 0.01 to 0.99 starting at Hardy-Weinberg frequencies. Note that although assortative mating was frequency dependent, selection intensity was not.

For comparison, we also ran the recursion equations using a fixed ρ. We wanted to decouple the variation in assortment caused by frequency dependence *per se* from the overall magnitude of assortment. The most relevant constant value of ρ for this comparison is the mean ρ in the corresponding frequency-dependent case. After iterating the recursion equations for a given combination of fitness differential, dominance and δ values, we calculated the average value of ρ over the generations it took for q to increase from 0.01 to 0.99. We then iterated the recursion equations assuming *l* had the same influence on fitness but that assortment was fixed at a value $\bar{\rho}$. We also obtained trajectories under random mating.

The general patterns are typified by the three cases illustrated in Fig. 7. Here the absolute fitnesses of *ll* and *ee* were 1.05 and 0.95, respectively, and $\delta = 0.4$. We used the flowering schedules for the mixed case (Fig. 1B).

When alleles have additive effects, the correlation between mates, ρ, reaches its maximum when $q = 0.5$ (Fig. 2), and this is also the allele frequency at which the genetic variance in fitness can reach its highest value (Crow and Kimura, 1970). Thus, we suspected that intense

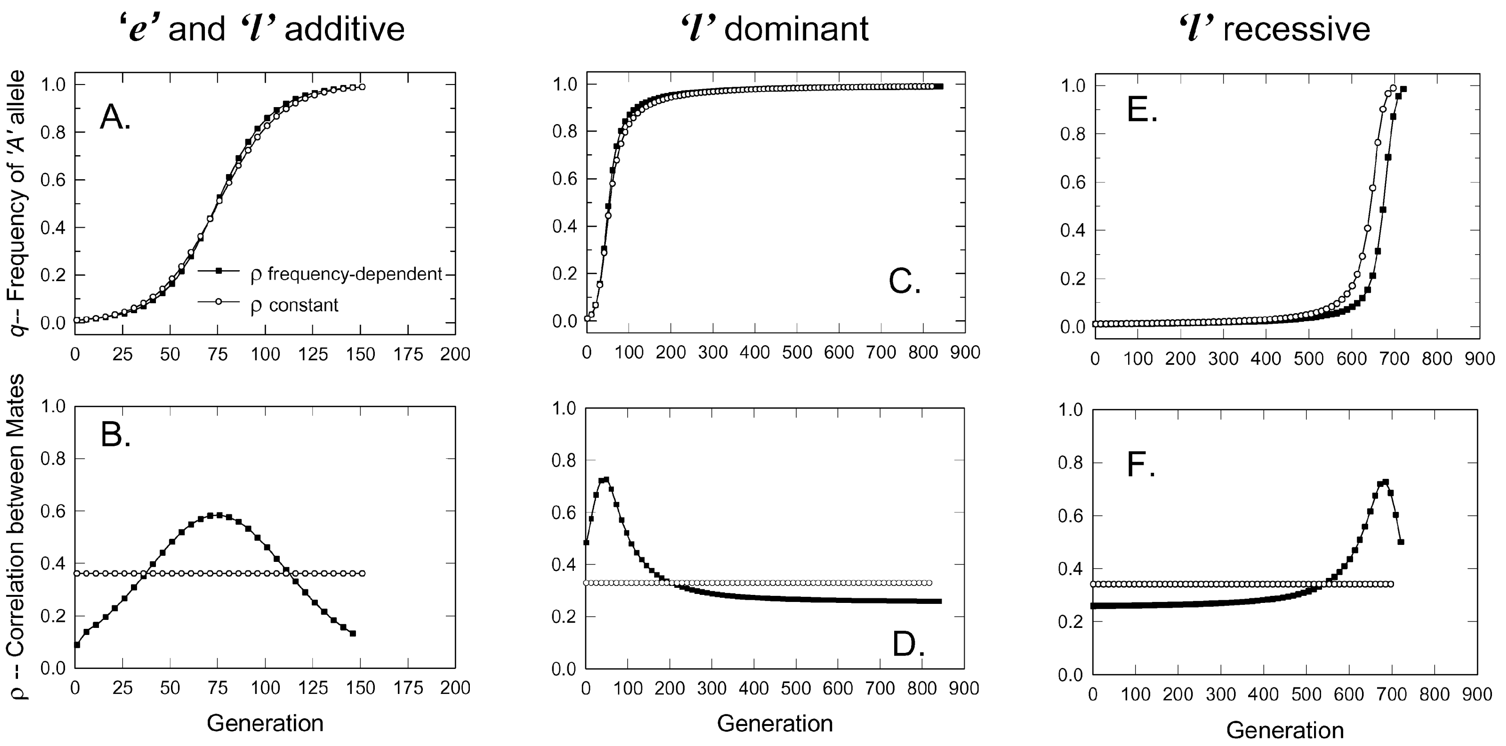

Fig. 7. Trajectories for the frequency of allele *l* under selection and assortative mating. All cases span the number of generations needed for q to increase from 0.01 to 0.99. Absolute fitnesses are 1.05 and 0.95 for the *ll* and *ee* genotypes, respectively. The proportional delay in mean flowering day, δ, is 0.4. (A, B) Trajectories assume additive allelic effects. Under phenological assortment, ρ is frequency dependent and increases to a maximum at $q = 0.5$. For comparison, we display the trajectory where ρ is held constant at the average value observed for the frequency-dependent case. (C, D) Trajectories assuming *l* is dominant. Under phenological assortment, ρ reaches a maximum at $q = 0.3333$. (E, F) Trajectories assuming *l* is recessive. Under phenological assortment, ρ reaches a maximum at $q = 0.6667$.

assortative mating at the time of the maximum selection response would cause allele frequency to reach 0.99 in fewer generations than in the corresponding case of fixed assortment.

Under random mating, the transition required 185 generations. Both fixed and frequency-dependent assortative mating accelerated this transition by at least 17%. Our suspicion that frequency-dependent assortment had the greater effect was supported (Figs. 7A and 7B), but the acceleration was trivially small (150 *vs* 153 generations). When assortment is fixed at $\bar{\rho}$, there is less acceleration of the selection response when alleles are at intermediate frequency, but greater acceleration when one or the other allele is rare. Thus, the net effects of fixed and frequency-dependent assortment on selection response are equivalent.

With dominance, the time for transition from $q = 0.01$ to 0.99 required 1120 generations under random mating. Assortative mating accelerated this transition by as much as 26%. When the favoured allele was dominant, we expected the transition time under phenological assortative mating to be slower than under fixed assortment. Under fixed assortative mating, *ee* individuals always mate disproportionately with other *ee*'s, and as a result they produce more offspring that express the deleterious effect of the *e* allele. Under frequency-dependent assortative mating, however, the frequency of $ee \times ee$ matings drops as *e* becomes rare, and so most copies of *e* are 'concealed' from selection in heterozygotes. The results supported our prediction (Figs. 7C and D), but the effect on transition time was weak. It took 848 generations for q to go from 0.01 to 0.99 under frequency-dependent assortative mating, which was only 2.5% longer than the corresponding fixed assortative mating situation (827 generations).

A complementary result was expected when *l* was recessive. Here the beneficial effects of *l* are masked in the heterozygote. Figure 7F shows that for phenological assortative mating, the correlation between mates is initially very low, keeping the frequency of *ll* individuals low and preventing its beneficial effects from being exposed. The modest value of ρ under fixed assortative mating was sufficient to produce enough *ll* homozygotes to accelerate the spread of the *l* allele. The transition of q from 0.01 to 0.99 required 730 generations under phenological assortative mating, which was 4.6% longer than the 698 generations required under fixed assortment (Fig. 7E). These compare to 1052 generations under random mating.

DISCUSSION

Phenological assortative mating

Variation in flowering schedule leads to assortative mating. Factors that increase the phenotypic variance in mean flowering day also increase the intensity of assortment. Genotype frequencies influence the correlation between mates in two ways. First, when one allele is rare, the rarer homozygote has few opportunities to mate within-type, leading to weak assortment. At intermediate allele frequencies (e.g. $q = p = 0.5$), both homozygotes have many opportunities to mate within-type, intensifying assortment. Second, departures from Hardy-Weinberg equilibrium increase the opportunities for within-type matings by homozygotes regardless of allele frequency. This sets up feedback between the level of assortment in one generation with that in the next. The feedback fades to zero when the population reaches an equilibrium heterozygote frequency.

The frequency dependence of phenological assortative mating alters directional selection trajectories. In the one-locus, two-allele case, ρ increases as allele frequencies approach 0.5, and so assortment inflates genetic variance at the point when that variance is already high. This causes a transitory acceleration of selection response. However, we found that when the overall level of assortment is de-coupled from this frequency-induced effect, phenological assortative mating causes only a modest effect on long-term selection response. In fact, when one or the other allele is dominant, the selection response is slower compared with the case where p is held at the appropriate fixed value.

We focused on a single phenological trait, mean flowering day. However, real flowering schedules vary in many components, such as days of first and last flowering, and the skew or kurtosis of the schedule (e.g. Pors and Werner, 1989; Meagher and Delph, 2001; Buide *et al.*, 2002; Mahoro, 2002; Weis and Kossler, 2004), and these components may be correlated. The between-mate correlation matrix for schedule components should have frequency-dependent variation. Assortment by the individual component traits will inflate not only the genetic variance in each, but also the genetic covariance between them (Gianola, 1982). A multi-locus model to explore the effects of gametic phase disequilibrium (Barton and Turelli, 1991; Lynch and Walsh, 1998), as induced by phenological assortative mating, on the genetic variance/covariance structure of the flowering schedule would be interesting.

Phenological assortative mating and other forms of selection

Using a one-locus, two-allele model, Fox (2003) found that the outcomes of stabilizing and disruptive selection can be qualitatively different under assortative mating than under random mating. For instance, heterozygote superiority does not inevitably lead to stable polymorphism, as expected for panmixia. When the fitness of one homozygote exceeds that of the other, moderate assortative mating can allow the favoured allele to go to fixation. This occurs because selection reduces the frequency of the less-favoured homozygotes and assortment reduces frequency of the heterozygote. Curiously, the population mean fitness may fall in the process because the most fit genotype, the heterozygote, disappears (Fox, 2003). Assortative mating can also alter the outcome of disruptive selection. When both homozygotes have the same fitness, random mating leads to fixation of whichever allele is at initially higher frequency. With unequal fitness for the homozygotes, the less fit allele can still go to fixation if its initial frequency is high enough. Assortative mating narrows the range of initial conditions that allow fixation of the less favoured allele; strong assortment can prohibit its fixation (Williams and Sarkar, 1994; Fox, 2003). Williams and Sarkar (1994) showed in a two-locus model that assortative mating can allow populations to cross so-called adaptive valleys without a drop in population mean fitness (because assortment reduces the frequency of the least fit genotype). Although we have not made an extensive study of it, our model indicates that the frequency dependence of phenological assortative mating produces only minor differences in the time it takes to reach equilibrium under stabilizing and disruptive selection compared with corresponding constant levels of assortment. This is in line with our results on directional selection.

Frequency dependence in other forms of assortative mating

Due to the complexity of mate choice, we suspect assortative mating is seldom a fixed quantity. Wright (1969) suggested that as the phenotypic variance for a trait increases, the strength of assortment would probably also increase. As assortment increases the frequency of extreme phenotypes, they will be more and more likely to encounter and mate with one another. This intensified assortative mating further increases the frequency of extreme phenotypes.

Even with fixed mate preferences, assortment can vary. For instance, McLain and Boromisa (1987) found that all male milkweed beetles strongly prefer large females. However, at high population densities, there is a strong size correlation between mates. When crowded, large-male aggression restricts small-male access to large females and this increases the frequencies of 'large × large' and 'small × small' matings. In plants, pollinator behaviour changes in response to the frequency of floral morphs and so can affect the strength of assortment (Jones, 2001; Smithson, 2001). Burley (1983) and Gimmelfarb (1988) have shown that a variety of mate-choice processes can give rise to a pattern of assortative mating. The conditional probabilities involved in mate choice are often likely to make assortment frequency- and density-dependent.

Some models of assortative mating have found that certain non-random mating patterns can lead to fixation of the common allele (Karlin and Scudo, 1968; Scudo and Karlin, 1968; Moore, 1979). These models add some biological realism to the discussion by recognizing that not all encounters between potential mates are equal and that some decisions can change an individual's chance of mating success. One genotype may be more 'choosy' than the others and end up with fewer matings. Such decision structures can give rise to frequency dependence, but as pointed out by Crow and Kimura (1970), these models incorporate reduced success for random matings and thereby conflate assortative mating with selective mating (Lewontin *et al.*, 1968).

Assortment in space and time

Assortative mating by habitat choice (Rice and Salt, 1990; Caillaud and Via, 2000; Schluter, 2001) may follow the same frequency dependence we showed for phenological assortment. Fox (2003) noted that temporal structure in the mating pool depresses heterozygote frequency in the same way as spatial structure – that is, the Whalund effect (Crow and Kimura, 1970). Felsenstein (1981), in a haploid model of sympatric speciation, showed that assortment varied with allele frequency (his diploid model appears to depend on fixed mating probabilities).

Figure 1 shows mating opportunities dispersed in time. This graph could be relabelled to represent genotypic differences in preference for some habitat factor. Suppose the factor is spatially autocorrelated and that juveniles freely disperse from their natal habitat, but then settle as adults in their preferred habitat. Frequency-dependent assortative mating for habitat choice will emerge even if adults choose mates at random from among their neighbours.

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REFERENCES

Barton, N.H. and Turelli, M. 1991. Natural and sexual selection on many loci. *Genetics*, **127**: 229–255.

Buide, M.L., Diaz-Peromingo, J.A. and Guitian, J. 2002. Flowering phenology and female success in *Silene acutifolia* Link ex. Rohrb. *Plant Ecol.*, **164**: 93–103.

Burley, N.T. 1983. The meaning of assortative mating. *Ethol. Sociobiol.*, **4**: 191–203.

Caillaud, C. and Via, S. 2000. Specialized feeding behavior influences both ecological specialization and assortative mating in sympatric host races of pea aphids. *Am. Nat.*, **156**: 606–621.

Conner, J.K. and Hartl, D.L. 2004. *A Primer of Ecological Genetics*. Sunderland, MA: Sinauer Associates.

Craig, T.P., Itami, J.K., Abrahamson, W.G. and Horner, J.D. 1993. Behavioral evidence for host-race formation in *Eurosta solidaginis*. *Evolution*, **47**: 1696–1710.

Crow, J.F. and Kimura, M. 1970. *An Introduction to Population Genetics Theory*. New York: Harper & Row.

Ennos, R.A. and Dodson, R. 1987. Pollen success, functional gender and assortative mating in an experimental plant population. *Heredity*, **58**: 119–126.

Felsenstein, J. 1981. Skepticism towards Santa Rosalia, or, why are there so few kinds of animals? *Evolution*, **35**: 124–138.

Fisher, R.A. 1918. The correlation between relatives on the supposition of Mendelian inheritance. *Trans. R. Soc. Edin.*, **52**: 399–433.

Fox, G.A. 2003. Assortative mating and plant phenology: evolutionary and practical consequences. *Evol. Ecol. Res.*, **5**: 1–18.

Gianola, D. 1982. Assortative mating and the genetic correlation. *Theor. Appl. Gen.*, **62**: 225–231.

Gimmelfarb, A. 1988. Processes of pair formation leading to assortative mating in biological populations: encounter-mating model. *Am. Nat.*, **131**: 865–884.

Gutierrez, M.G. and Sprague, G.F. 1959. Randomness of mating in isolated polycross plantings of maize. *Genetics*, **44**: 1075–1082.

Haldane, J.B.S. 1924. A mathematical theory of natural and artificial selection. Part II. *Proc. Camb. Phil. Soc., Biol. Sci.*, **1**: 158–163.

Hartl, D.L. and Clark, A.G. 1989. *Principles of Population Genetics*, 2nd edn. Sunderland, MA: Sinauer Associates.

Hedrick, P. 2000. *Genetics of Populations*, 2nd edn. Boston, MA: Jones & Bartlett.

Jones, K.N. 2001. Pollinator-mediated assortative mating: causes and consequences. In *Cognitive Ecology of Pollination: Animal Behavior and Floral Evolution* (L. Chittka and J.D. Thompson, eds.), pp. 237–258. Cambridge: Cambridge University Press.

Karlin, S. and Scudo, F.M. 1968. Assortative mating based on phenotype, II: Two autosomal alleles without dominance. *Genetics*, **63**: 499–510.

Kirkpatrick, M. 2000. Reinforcement and divergence under assortative mating. *Proc. R. Soc. Lond. B*, **267**: 1649–1655.

LeBuhn, G. 2004. Seasonal variation in reproductive traits in *Ipomopsis longiflora* (Polemonaceae), a desert annual. *Can. J. Bot.*, **83**: 401–408.

Lewontin, R., Kirk, D. and Crow, J. 1968. Selective mating, assortative mating and inbreeding: definitions and implications. *Eugen. Quart.*, **15**: 141–143.

Lynch, M. and Walsh, J.B. 1998. *Genetics and Analysis of Quantitative Traits*. Sunderland, MA: Sinauer Associates.

Lyons, E.E. and Mulley, T.W. 1992. Density effects on flowering phenology and mating potential in *Nicotiana alata*. *Oecologia*, **91**: 93–100.

Mahoro, S. 2002. Individual flowering schedule, fruit set, and flower and seed predation in *Vaccinium hirtum* Thunb. (Ericaceae). *Can. J. Bot.*, **80**: 82–92.

McLain, D.K. and Boromisa, R.D. 1987. Male choice, fighting behavior and assortative mating and the intensity of sexual selection in the milkweed longhorn beetle *Tetraopes teteraophthalmus* (Coleoptera: Cerambycidae). *Behav. Ecol. Sociobiol.*, **20**: 239–246.

Meagher, T.R. and Delph, L.F. 2001. Individual flower demography, floral phenology and life history in *Silene latifolia*. *Evol. Ecol. Res.*, **3**: 845–860.

Moore, W.S. 1979. A single-locus mass-action model of assortative mating with comments on the process of speciation. *Heredity*, **42**: 173–186.

Nagylaki, T. 1992. *Introduction to Theoretical Population Genetics*. Berlin: Springer-Verlag.

O'Donald, P. 1960. Assortative mating in a population in which two alleles are segregating. *Heredity*, **15**: 479–489.

Pors, B. and Werner, P.A. 1989. Individual flowering time in a goldenrod (*Solidago canadensis*): field experiment shows genotype more important than environment. *Am. J. Bot.*, **76**: 1681–1688.

Rice, W.R. and Salt, G.W. 1990. The evolution of reproductive isolation as a correlated character under sympatric conditions: experimental evidence. *Evolution*, **44**: 1140–1152.

Schluter, D. 2001. Ecology and the origin of species. *Trends Ecol. Evol.*, **16**: 372–380.

Scudo, F.M. and Karlin, S. 1968. Assortative mating based on phenotype, I. Two alleles with dominance. *Genetics*, **63**: 479–498.

Smithson, A. 2001. Pollinator preference, frequency dependence and floral evolution. In *Cognitive Ecology of Pollination: Animal Behavior and Floral Evolution* (L. Chittka and J.D. Thompson, eds.), pp. 259–273. Cambridge: Cambridge University Press.

Weis, A.E. and Kossler, T.A. 2004. Genetic variation in flowering time induces phenological assortative mating: quantitative genetic methods applied to a model population of *Brassica rapa*. *Am. J. Bot.*, **91**: 837–849.

Williams, S.M. and Sarkar, S. 1994. Assortative mating and the adaptive landscape. *Evolution*, **48**: 868–875.

Wright, S. 1921. Systems of mating. III. Assortative mating based on somatic resemblance. *Genetics*, **6**: 144–161.

Wright, S. 1969. *Evolution and the Genetics of Populations. Vol. 2: The Theory of Gene Frequencies*. Chicago, IL: University of Chicago Press.