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THE EVOLUTION OF GENDER SPECIALIZATION FROM DIMORPHIC HERMAPHRODITISM: PATHS FROM HETERODICHOGAMY TO GYNODIOECY AND ANDRODIOECY

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Abstract.—Several different pathways for the evolution of dioecy from hermaphroditism have been invoked and analyzed. These have largely considered either the spread of male- or female-sterility mutations in a monomorphic hermaphroditic population (i.e., the evolution of gynodioecy or androdioecy, respectively) or the gradual divergence in sex allocation of two classes of individuals, one that becomes increasingly male and the other that becomes increasingly female in functional gender (the paradioecy pathway). Here we assess the conditions under which male- or female-sterility mutations may invade and spread in a heterodichogamous population, that is, a dimorphic population composed of protandrous and protogynous individuals. Our model is formally applied to heterodichogamous populations, but the ideas we explore may also apply to the evolution of separate sexes in distylous species, where plants are either long- or short-styled. The model predicts that, under many circumstances, conditions for the evolution of gynodioecy and androdioecy in a heterodichogamous population are the same as those for their evolution from monomorphic populations. However, if one or the other of the two morphs are already somewhat specialized in their functional gender, as might occur if the quality or quantity of seed set is time dependent, the conditions for the invasion of males or females are relaxed. In particular, androdioecy can evolve more easily under such circumstances in heterodichogamous populations than in monomorphic hermaphroditic populations.

Key words.—Dioecy, distyly, functional gender, protandry, protogyny, sex allocation.

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Dioecy has evolved repeatedly from hermaphroditism and occurs in approximately 7% of angiosperm genera and 6% of species (Yampolsky and Yampolsky 1922; Renner and Ricklefs 1995; Sakai and Weller 1999). The selective mechanisms thought to have driven these transitions can broadly be summarized in terms of the benefits of inbreeding avoidance by unisexual individuals relative to self-fertile hermaphrodites (Lloyd 1975; Charlesworth and Charlesworth 1978; Thomson and Barrett 1981a), the benefits of sexual specialization (Charnov et al. 1976; Givnish 1980; Bawa and Beach 1981; Niklas 1985; Seger and Eckhart 1996), or the combined benefits of both outcrossing and specialization (Charlesworth and Charlesworth 1981; Freeman et al. 1997; Charlesworth 1999; Barrett 2002). Whereas the endpoint of any evolutionary transition to dioecy will always be a population of obligately outcrossing gender specialists, the paths by which this endpoint is reached are many and varied (Lloyd 1980; Ross 1982; Renner and Ricklefs 1995; Barrett 2002; Dorken and Barrett 2004). These will depend on numerous factors, including the life history (Bawa 1980; Lloyd 1982; Dorken and Barrett 2003), details of the biology of pollination and seed dispersal (Bawa 1980, 1982; Givnish 1980; Charlesworth 1993; Wilson and Harder 2003; Wolf and Takebayashi 2004), and the genetic system possessed by the hermaphroditic ancestors (Miller and Venable 2000; Pannell et al. 2004).

The evolution of dioecy from hermaphroditism is thought to have most commonly followed one of two different paths (Charlesworth 1999; Barrett 2002): (1) an initial spread of a male-sterility or a female-sterility mutation is followed by a reduction of the opposite sexual function in the remaining hermaphrodites (the gynodioecy and androdioecy pathways, respectively) (Lloyd 1974, 1977; Charlesworth and Charlesworth 1978; Charlesworth 1999); or (2) the genders of two classes of individual in the population gradually diverge, one becoming increasingly male and the other becoming increasingly female (the monoecy-paradioecy pathway, so named because the ancestral population is most likely to comprise monoecious individuals rather than those with perfect bisexual flowers; Lewis 1942; Lloyd 1980; Ross 1982; Renner and Ricklefs 1995; Webb 1999). There is a good deal of evidence for both the gynodioecious and the monoecy-paradioecy pathways (but for caveats regarding the latter see Dorken and Barrett 2004), and the theoretical conditions for the evolution of gynodioecy, in particular, are well understood (reviewed in Charlesworth 1999). In contrast, androdioecy is unlikely to evolve from hermaphroditism, because the conditions for the invasion and spread of males among hermaphrodites are severe (Lloyd 1975; Charlesworth and Charlesworth 1978; Charlesworth 1984; Pannell 2002). Specifically, females can invade a partially inbreeding hermaphroditic population with relative ease if inbred progeny suffer sufficient inbreeding depression; in contrast, males must always disperse at least twice as much pollen as hermaphrodites—and often substantially more if selfing rates are high—if they are to coexist with hermaphrodites (Lloyd 1975; Charlesworth and Charlesworth 1978; Charlesworth 1984).

The principles outlined in the previous paragraph apply to ancestral hermaphroditic populations in which all individuals are phenotypically identical. However, dioecy may also evolve from populations that are monomorphic in gender but dimorphic in floral morphology or phenology (Ross 1982;

Webb 1999). The possible evolution of dioecy from distyly, where populations comprise long- and short-styled morphs that mate disassortatively, was considered at some length by Darwin (1877) and has since been the subject of several empirical and theoretical studies (Ornduff 1966; Lloyd 1979; Beach and Bawa 1980; Ross 1982; Wyatt 1983; Muenchow and Grebus 1989; Webb 1999). Thus, in distylous populations dioecy may evolve simply through the gradual gender specialization by each morph as either male or female (Lloyd 1979). Whereas the respective morphs of many distylous species show no tendency toward dioecy, the evolution of gender specialization, and ultimately of completely separate sexes, is known to have occurred in several families independently, usually through the feminization and masculinization of long-styled and short-styled morphs, respectively (Darwin 1877; Baker 1958; Ross 1982). Despite good comparative and morphological evidence for the evolution of dioecy from distyly, the selective mechanisms responsible for the transition are not well established. One idea is that a shift in the pollination biology of distylous populations may disrupt the complementarity of pollen transfer between the two morphs, so that one receives more pollen than it disperses and vice versa, eliciting the evolution of a corresponding emphasis of the more profitable gender in each morph (Ornduff 1975; Lloyd 1979; Beach and Bawa 1980; Bawa and Beach 1981; Muenchow and Grebus 1989; Barrett 1992). Another is that dioecy may evolve in response to selection to avoid self-fertilization in self-compatible populations (Ornduff 1966).

Dioecy may also evolve from populations that are dimorphic for the timing of pollen release and stigma receptivity, that is, from heterodichogamy, where hermaphrodites in a population vary in the timing of their male and female phases of reproduction, such that individuals in their male phase mate with those in their female phase, before switching genders and mating reciprocally (Darwin 1877; de Jong 1976; Lloyd 1979; Kubitzki and Kurz 1984; Dommée et al. 1990; Webb 1999; Pendleton et al. 2000; Renner 2001). Less attention has been focused on this pathway, but heterodichogamy is phylogenetically widespread, occurring in 17 genera across 11 families of angiosperms, and there is now good evidence that it has evolved toward dioecy in several independent angiosperm lineages (reviewed in Pendleton et al. 2000; Renner 2001).

Three rather different manifestations of heterodichogamy are known (reviewed in Renner 2001). The first type includes populations in which all individuals are uniformly protandrous or protogynous, but two morphs occur that differ in terms of when they commence flowering during the day, such that, for example, some individuals flower as males in the morning and females in the afternoon, while others, which open their flowers later in the day, flower as males in the afternoon and as females the following morning. This type is known in several species of the Lauraceae, for instance, a family in which dioecy appears to be derived from dichogamy (Kubitzki and Kurz 1984). However, the selective mechanism for this putative transition to dioecy is not yet understood.

The second and third types both include populations in which protandrous and protogynous individuals co-occur. In the second type, the male and female phases of perfect hermaphroditic flowers are separated over the single day on which they are open, with protandrous and protogynous individuals flowering in their male and female phases in the morning, respectively, and in the complementary phase in the afternoon. In the genus *Alpinia*, these temporal differences in sexual function also correspond to reciprocal movement of the stigmatic surface through a vertical axis during the course of the day (Li et al. 2001; Zhang et al. 2003). In these species, differences in pollen:ovule ratios between the two morphs indicate the evolution of a degree of gender specialization (Wang et al. 2004).

Finally, in the third type of heterodichogamy, the male and female phases are separated over the entire flowering season, rather than over single days as in *Alpinia*; these species are usually monoecious, with unisexual flowers (e.g., *Acer*: de Jong 1976; *Juglans*: Gleeson 1982; *Thymelea*: Dommée et al. 1990; and *Grayia*: Pendleton et al. 2000). In species of the genus *Acer*, for example, each of the two sexual phases may last for up to three weeks, with limited temporal overlap (Sato 2002; G. Gleiser, M. Verdú, and J. R. Pannell, unpubl. ms.). In *Acer*, sexual specialization and dioecy have evolved repeatedly from heterodichogamy, apparently via androdioecy (de Jong 1976; Gleiser and Verdú 2005).

In some dioecious or subdioecious species that have evolved from heterodichogamy, the distribution of genders suggests that males arose from protandrous individuals and females from protogynous individuals (Miglia and Freeman 1996; Pendleton et al. 2000; Sato 2002), whereas in others the reverse seems likely (Dommée et al. 1990; El-Keblawy et al. 1996). As in the pathway from distyly, the selective mechanisms responsible for the transition from heterodichogamy to dioecy are not well understood. One possibility is that dioecy may evolve as a direct result of benefits of gender specialization, either through male or female function, or both. Here, for example, it has been suggested that individuals that specialize as males may reap high fitness rewards by attracting a disproportionate number of pollinators (G. Gleiser and M. Verdú, unpubl. ms.), although the costs of a large floral display in terms of reduced pollen carry-over to other individuals in the population may be expected to offset such benefits (Klinkhamer et al. 1994). Another possibility is that gender specialization may be driven by an asymmetry in the availability of ovules and in seed production between the two morphs over the reproductive season (Pendleton et al. 2000).

The idea that ovule availability and seed production may differ between the morphs of heterodichogamous populations is conceptually similar to the hypothesis of asymmetrical levels of pollen flow between the morphs of distylous populations. However, whereas asymmetrical pollen flow in distylous populations is thought to result from differences in the way pollinators contact stigmas and anthers in flowers of the two morphs (Beach and Bawa 1980; Muenchow and Grebus 1989), this seems unlikely to be the case in heterodichogamous populations in which flowers of the two morphs are morphologically similar. One obvious idea is that gender asymmetry may result from temporal differences in pollinator abundance. For instance, if the seed production becomes pollen limited toward the end of flowering, then individuals that flower in their male phase early on will necessarily become functionally male biased, and those that flower in their male phase later will correspondingly become female biased. To our knowledge, there is as yet no evidence for this mechanism.

In heterodichogamous populations in which male and female phases of reproduction segregate early or late in the reproductive season, asymmetrical functional gender might also result through difference in resource availability as the season progresses. There is some evidence for this mechanism. For example, the failure of protandrous plants to produce mature seed in the heterodichogamous species *Grayia brandegei* has been attributed to limited water availability later in the season (Pendleton et al. 2000). Similarly, in *Acer opalus*, seeds produced later in the season were smaller that those produced earlier (G. Gleiser, M. Verdú, and J. R. Pannell, unpubl. ms.), so that the female function of protandrous individuals might be expected to be reduced compared to that of protogynous individuals. As Pendleton et al. (2000) reviewed in their discussion, a decline of female function toward the end of the flowering season has been observed in several temperate species, probably as a result of reductions in soil moisture levels and photosynthetic capacity as the season progresses (e.g., Thomson and Barrett 1981b; Ashman and Baker 1992). Thus, the conclusion reached by Pendleton et al. (2000, p. 513) that selective pressure on the female function may be driving sexual specialization and the evolution of dioecy in *G. brandegei* may be applicable to the evolution of separate sexes from heterodichogamy more generally.

Despite the recognized importance of distyly and heterodichogamy as ancestral states in the evolution of dioecy in several families and genera, there are no formal models in the literature to identify threshold conditions for progression along this evolutionary pathway. Here we present a model for the evolution of dioecy from heterodichogamy, incorporating a mechanism for the sexual specialization by allowing for the gradual reduction in a capacity for seed production by individuals as the season progresses. We apply our model formally to heterodichogamous populations in which protandrous and protogynous individuals flower as males and females, respectively, early in the reproductive season and as females and males, respectively, toward its end (see Discussion for an evaluation of empirical examples that correspond to this scenario). However, some of the ideas we explore may also apply to the evolution of sexual specialization and separate sexes under any mode of heterodichogamy, as well as to distylous species, where plants are either long- or short-styled.

We first assess the conditions that would allow male- or female-sterile mutations to invade and spread in a heterodichogamous population, accounting for the possibility that these sterility mutations occur in either a protandrous or a protogynous individual. We then consider the frequency that males or females should expect to reach following their invasion. Although the potential for self-fertilization is likely to be low in heterodichogamous populations with low to zero temporal overlap between male and female functions, we incorporate this possibility into the model, both for completeness and because models for the evolution of dioecy via gynodioecy and androdioecy have focused on the implications of partial selfing for the spread of males or females (e.g., Charlesworth and Charlesworth 1978). Throughout, we refer to males resulting from a female-sterility mutation in protandrous and protogynous individuals as ''protandrous males'' or ''protogynous males,'' respectively. Similarly, we refer to individuals resulting from male-sterility mutations in the two different morphs as ''protandrous females'' and ''protogynous females,'' as appropriate.

MODEL AND RESULTS

Assume that a large population comprises protandrous and protogynous phenotypes (morphs) at frequencies f_a and f_g, respectively, and let f_m and f_f be the frequencies of males and females following their invasion into the population (see below). Let the male and female phases of individuals of each morph i be characterized by two potentially overlapping density functions of time, $p_i(t)$ and $c_i(t)$ respectively, such that the area under each of the curves p and c sums to one. Also, let λ_i and γ_i be the total absolute amount of pollen and ovules produced by morph i, respectively, and define $r_m = \lambda_m/\lambda_a$ and $r_f = \gamma_f/\gamma_a$; r is thus the pollen and seed production of males and females, respectively, relative to that of hermaphrodites; note that we assume that $\gamma_g = \gamma_a$. Within a given time increment, δt, the amount of pollen dispersed by individuals of morph i, and the number of ovules made available for fertilization, are thus given by the products $\lambda_i p_i(t)\delta t$ and $\gamma_i c_i(t)\delta t$, respectively.

We assume that the density functions p and c follow a normal distribution with standard deviation σ. Let time $t = 0$ represent the midpoint of the flowering season. Then protandrous individuals have their male flowering peaks at time $t = -z$, protogynous individuals have their male peak at time $t = z$, and the female function of protandrous and protogynous individuals peaks at times $t = z$ and $t = -z$, respectively. In integrating the male and female fitness functions over the flowering period, we will assume that flowering in the population commences and ends at times $T_0 = -(z + 3.29\sigma)$ and $T_1 = z + 3.29\sigma$, respectively. We thus truncate the flowering distribution by ignoring the small contributions made by individuals prior to T_0 and after T_1; this amounts to integrating over 99.9% of the full male and female distributions for all phenotypes. Figure 1 shows the effect of z in our model on the distribution of flowering in a heterodichogamous population.

We assume that all ovules are fertilized (i.e., there is no pollen limitation), and that pollen grains dispersed between times t and $t + \delta t$ compete on an equal basis to cross-fertilize receptive ovules in flowers of other individuals within the same time increment. Thus, at time t, individuals of morph i will fertilize a competitive share, $\pi_i(t)$, of all receptive ovules in the population that have not been self-fertilized:

$$\pi_i(t) = \frac{\lambda_i p_i(t)}{P(t)}, \tag{1}$$

where $P(t) = \Sigma_i f_i \lambda_i p_i(t)$ is the total amount of pollen produced by the population at time t.

Let $\rho_i(t) = \lambda_i p_i(t) + xP(t)$ be the total density of pollen around an individual of morph i at time t, where the introduction of x (with $x < 1$) accounts for the fact that pollen dispersed by a given individual will tend to be more concentrated in the local pollen pool than pollen produced by

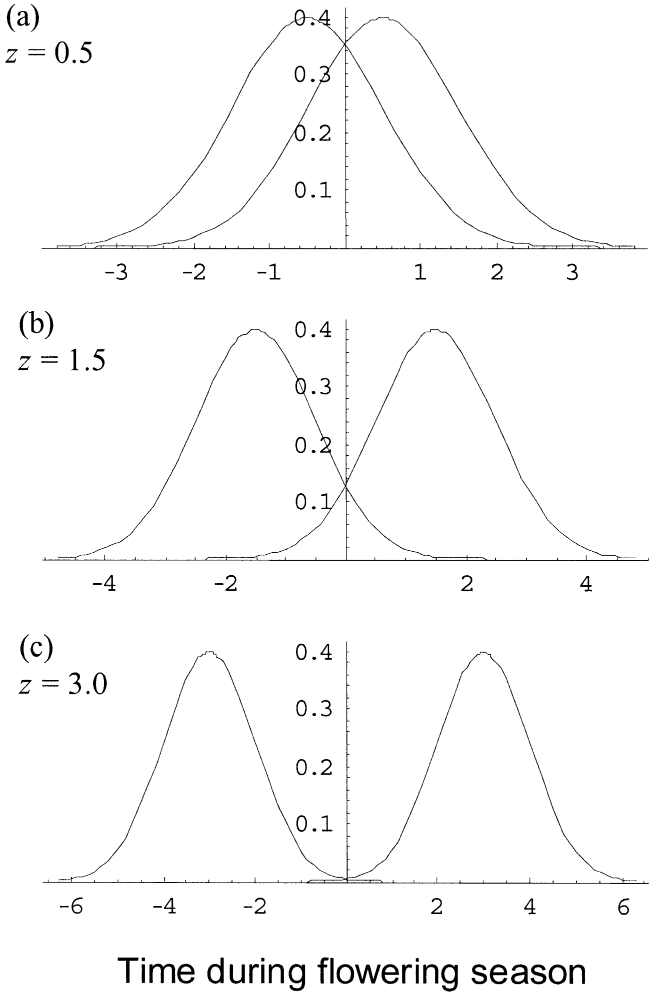

FIG. 1. The distribution of flowering over time (i.e., functions p and c) assumed in the model of a heterodichogamous population with (a) low ($z = 0.5$), (b) medium ($z = 1.5$), and (c) high levels of dichogamy ($z = 3.0$). In each plot, time $t = 0$ marks the midpoint of flowering, and $T_1 = -T_0$. The first and second curves in each plot correspond to the distribution of male and female or to female and male flowering for protandrous or protogynous individuals, respectively. In the numerical integrations, flowering was assumed to commence at times (a) $T_0 = -3.79$, (b) $T_0 = -4.79$, and (c) $T_0 = -6.29$.

other individuals in the population. Note that increases in the parameter x reflect increases in the density of outcross pollen in the local pollen pool, through increased plant density, for instance, and that this will reduce the selfing rate. This behavior is consistent with what is known about density-dependent pollen limitation and selfing rates from observations of natural populations (Kunin 1993; Karron et al. 1995; Pannell 2001; Knight 2003; Ashman et al. 2004; Davis et al. 2004). Assuming that self and outcross pollen compete on equal terms to fertilize each ovule, the selfing rate of ovules produced by individuals of morph i at time t is given by

$$S_i(t) = \frac{\lambda_i p_i(t)}{\rho_i(t)}. \tag{2}$$

Seeds produced by self-fertilization at time t will reduce the siring opportunities for other plants in the population that are in their male phase at that time. We thus write the total number of ovules available for outcrossing at time t as

$$\Gamma(t) = f_\mathrm{a}\gamma_\mathrm{a}c_\mathrm{a}(t)[1 - S_\mathrm{a}(t)] + f_\mathrm{g}\gamma_\mathrm{g}c_\mathrm{g}(t)[1 - S_\mathrm{g}(t)] + f_\mathrm{f}\gamma_\mathrm{f}c_\mathrm{f}(t). \tag{3}$$

We assume that seeds produced by selfing might suffer from inbreeding depression, and we account for this in our model by letting their probability of reaching reproductive maturity equal to $(1 - d)$ times that of seeds fertilized by outcross pollen at the same point in time. Finally, we allow for the possibility that seeds produced early in the reproductive season may be better provisioned with resources than those produced later in the season by incorporating a term $v(t)$ for viability of seeds fertilized at time t. There is substantial evidence for this kind of temporal effect on seed size (e.g., Fenster 1991; see also Discussion). For simplicity, let us assume that $v(t)$ is given by

$$v(t) = 1, \qquad \text{for } k = 0 \tag{4a}$$

$$v(t) = k(T_0 - t) + 1, \qquad \text{for } k > 0,\ t < (1 + kT_0)/k \tag{4b}$$

$$v(t) = 0, \qquad \text{for } k > 0,\ t \geq (1 + kT_0)/k, \tag{4c}$$

that is, the viability of outcrossed seeds falls linearly with time at rate $k \geq 0$ from a value of unity at $t = T_0$ to an eventual value of zero, if $k > 0$, at $t = (1 + kT_0)/k$. The effect of k on $v(t)$ is shown in Figure 2.

With the above assumptions, the female and male components of fitness accruing to individuals of morph i over the reproductive season, summed over small increments of time between T_0 (when flowering first commences) and T_1 (when flowering ends), and the total fitness of morph i, can be written, respectively, as

$$w_{f,i} = \int_{T_0}^{T_1} \gamma_i c_i(t) v(t)[S_i(t) - 2S_i(t)d + 1]\,\mathrm{d}t, \tag{5a}$$

$$w_{m,i} = \int_{T_0}^{T_1} \pi_i(t) v(t) \Gamma(t)\,\mathrm{d}t, \quad \text{and} \tag{5b}$$

$$w_i = w_{f,i} + w_{m,i}. \tag{5c}$$

To find the conditions under which female- or male-sterility mutations can invade and spread in a heterodichogamous population at equilibrium, we used numerical integration of equations (5a–c) to find f_a and f_g, subject to the condition $w_\mathrm{a} = w_\mathrm{g}$, and we evaluated the parameter space at this equilibrium for which w_m or $w_\mathrm{f} > w_\mathrm{a} = w_\mathrm{g}$ when f_m or $f_f = 0$, that is, for which males or females could invade from rarity. We considered the invasion of female- or male-sterility mutations affecting both protandrous and protogynous morphs.

Figure 3 shows the threshold value of r that would allow a protandrous male mutant or a protogynous female mutant to invade a heterodichogamous population at equilibrium (assuming $\lambda_\mathrm{g} = \lambda_\mathrm{a} = \gamma_\mathrm{g} = \gamma_\mathrm{a} = 1$). Recall that r is the ratio of the amount of pollen or seeds produced by males or females, respectively, relative to that produced by the other two morphs. In an outcrossing population ($x \gg 1$), the conditions for the invasion of males and females are equivalent (Fig. 3a,b); when female function is unaffected by the timing

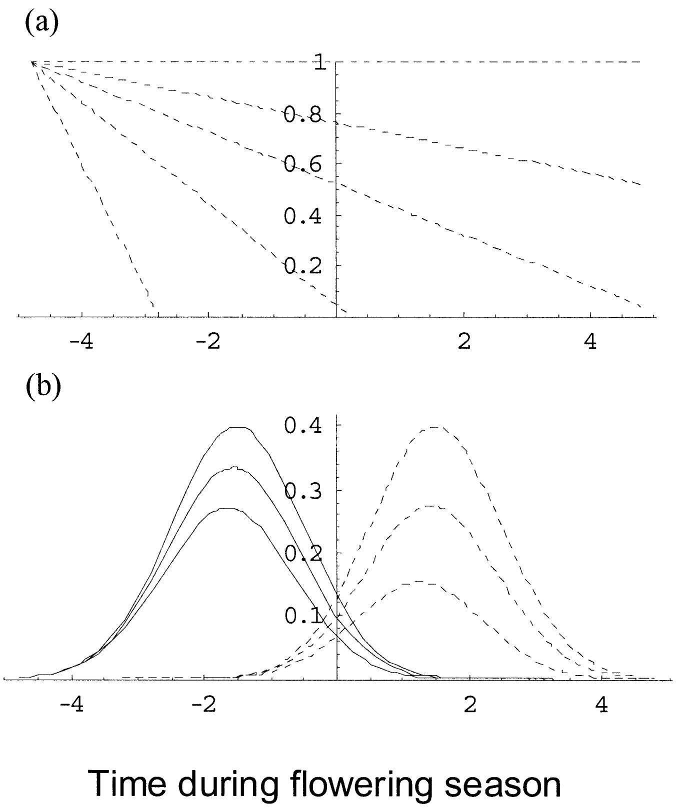

FIG. 2. The effect of delayed seed production during the flowering season on (a) the viability of seed produced by an individual at time t, modeled by function $v(t)$, and (b) the total numbers of successful seeds produced by protogynous individuals (solid curves) and protandrous individuals (dashed curves) in a heterodichogamous population with an intermediate degree of dichogamy ($z = 1.5$), modeled by the product $c(t)v(t)$. In (a), the series of curves with increasingly negative gradients correspond to values of $k = 0.0$, 0.05, 0.1, 0.2, and 0.5. In (b), the descending series of curves in each group correspond to value of $k = 0.0$, 0.05, and 0.1.

of flowering and allocation to seed maturation (i.e., $k = 0$), males and females must both produce at least twice as much pollen or seeds, respectively, as the heterodichogamous hermaphrodites. Partial overlap of the male and female phases of reproduction leads to potential self-fertilization. With increasing selfing (i.e., smaller x), males must produce an increasing amount of pollen to invade a population, relative to the pollen produced by hermaphrodites (Fig. 4a; see also Fig. 3b,c). In contrast, as long as seed-set is not pollen limited, the critical threshold of r_f for female invasion does not increase above two; indeed, if selfed progeny suffer from inbreeding depression, females will find it increasingly easy to invade a heterodichogamous population with increasing rates of selfing (Fig. 4a). These results are identical to those predicted by models of the invasion of males and females into monomorphic hermaphroditic populations (Lewis 1941; Lloyd 1974, 1975; Charlesworth and Charlesworth 1978; Charlesworth 1984).

In a heterodichogamous population in which $k > 0$, that is, in which seed produced later in the season is less likely to contribute to future generations, protandrous males and protogynous females will find it increasingly easy to invade and spread (Figs. 3, 4). In outcrossing populations, the effect of increasing k on male and female invasion is identical: the threshold level of pollen or seed production falls below 2.0 for male and female invasion, respectively, with the effect intensified in populations in which the temporal overlap between the male and female phases of individuals is decreased through greater temporal spread over the season (i.e., with increases in z; Fig. 3). With $k > 0$ and increases in the selfing rate (lower panels in Fig. 3; Fig. 4b), the contrast between male and female invasion outlined above still holds: males find it more difficult to invade a heterodichogamous population than females. Importantly, however, with k sufficiently high and the selfing rate sufficiently low, males may still invade a heterodichogamous population with $r_m < 2$ (Figs. 3, 4b).

The effect of reduced female function with progression through the flowering season is reversed for the invasion of protogynous males and protandrous females (Fig. 5). Males and females will find it increasingly difficult to invade a population with increasing k. Again, the conditions for the invasion of males are more severe than those for the invasion of females. Also, note that r is now always above two for both males and females if $d = 0$ (Fig. 5).

To establish the equilibrium frequency of protandrous, protogynous, and male individuals following male invasion, we ran the following recursion equations until phenotype frequencies remained unchanged between generations to order 10^{-3}:

$$f_i' = f_i w_i \Big/ \sum_j f_j w_j, \tag{6}$$

where f_i and f_i' are the frequency of the ith phenotype in generations t and $t + 1$, respectively, and division by the summation term ensures that frequencies at $t + 1$ sum to one. To check that the frequencies found were globally stable, we performed our calculations using the following three contrasting initial conditions: $f_a = f_g = 0.495$, $f_u = 0.01$; $f_a = f_u = 0.495$, $f_g = 0.01$; and $f_g = f_u = 0.495$, $f_a = 0.01$ (where f_u refers to either f_m or f_f, as appropriate).

The results for a range of parameter values are presented in Figures 6 and 7 for the case of protandrous male and protogynous female invasion, respectively. The salient and most consistent result across all parameter combinations investigated is that the invasion of protandrous males into a heterodichogamous population occurs through the replacement of the protandrous hermaphroditic phenotype, and that the frequency of the protogynous phenotype remains reasonably close to 0.5 with small k. Similarly, the invasion of protogynous females occurs through the replacement of the protogynous hermaphrodites, with the protandrous phenotype remaining reasonably close to 0.5 when k is small. This result follows from our assumption that protandrous males disperse their pollen at the same time as do protandrous hermaphrodites, that is, males are competing directly with the protandrous phenotype to pollinate ovules that are largely produced by protogynous individuals (as found in *Acer*, Sato 2002; G. Gleiser, M. Verdú, and J. R. Pannell, unpubl. ms.). Similarly, females contribute to the same temporal ovule pool as protogynous hermaphrodites.

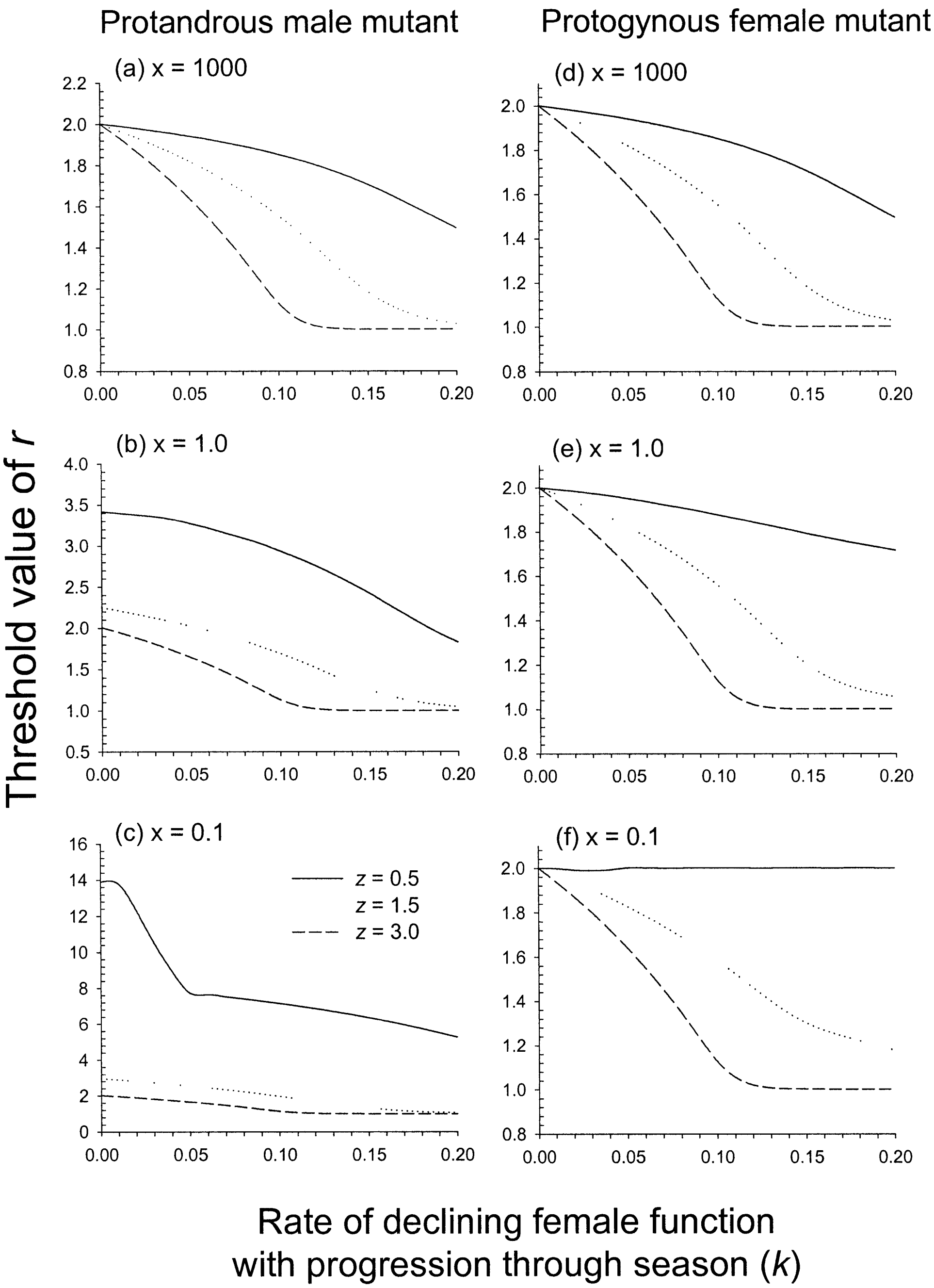

FIG. 3. The threshold value of r (the pollen production of males or seed production of females, relative to that of hermaphrodites) above which protandrous males (a, b, c) or protogynous females (d, e, f) can invade a heterodichogamous population. r is plotted as a function of k, the rate of declining female function with progression through the flowering season. Curves are shown for several values of z (the degree of overlap between male and female functions within each morph) and x (a parameter that regulates the extent to which outcross pollen contribute to the pollen pool around receptive stigmas and that thus affects the selfing rate, which increases with decreasing x; see text for details). In all panels, inbreeding depression, $d = 0$.

It is clear from Figures 6 and 7 that a polymorphic equilibrium with all three phenotypes is maintained for a broad range of parameter values. In other words, the invasion of protandrous males or protogynous females into a heterodichogamous population will not necessarily replace one or other of the hermaphrodite phenotypes completely. It is also clear that when progeny viability is independent of the time of seed set ($k = 0$), the degree of heterodichogamy has little effect on the relative frequencies of the three phenotypes (cf. Figs. 6a and 6d; Figs. 7a and 7d); rather, increases in r lead to an increased frequency of unisexuals and a concomitant reduction in the frequency of the hermaphroditic morph with which it is mainly competing during mating. With large r, the population tends toward functional dioecy.

When progeny produced later in the season are less viable than those produced early ($k > 0$), the invasion of unisexuals

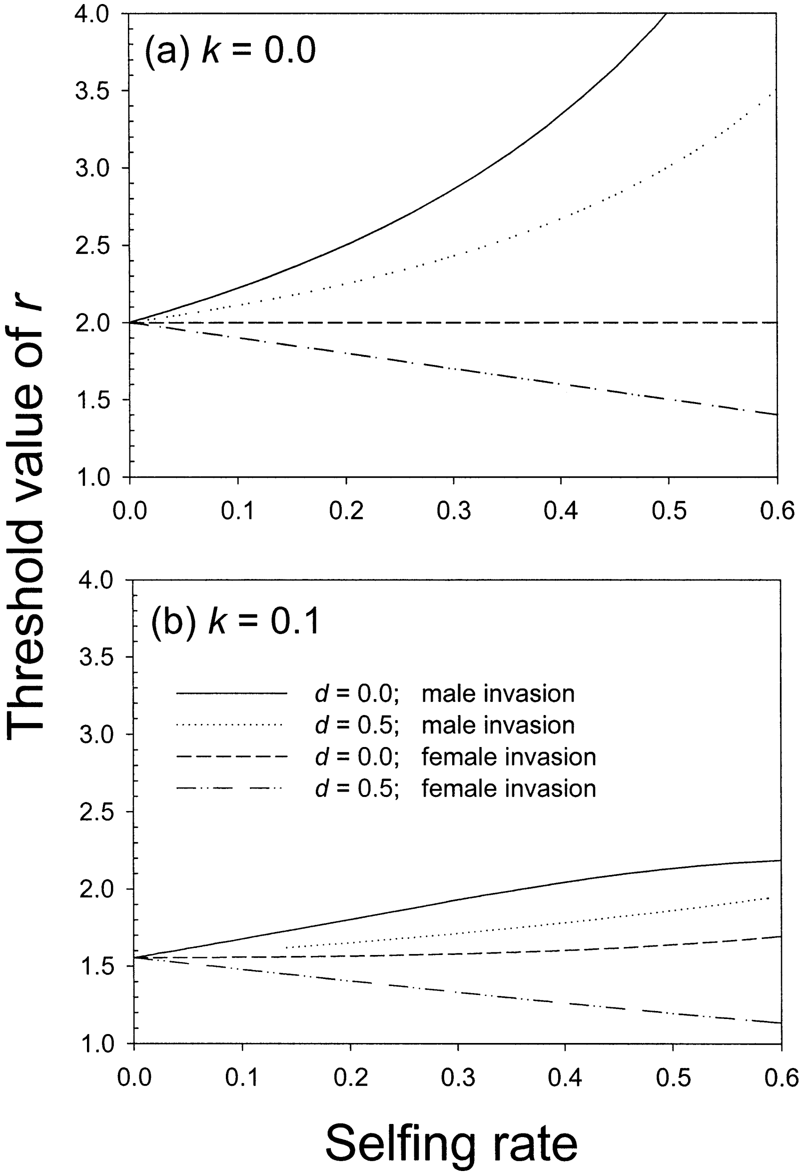

FIG. 4. The threshold value of r (the pollen production of males or seed production of females, relative to that of hermaphrodites) above which males or females can invade a heterodichogamous population. r is plotted as a function of the selfing rate. (a) $k = 0$ (female fitness independent of the timing of flowering); (b) $k = 0.1$ (female fitness declines with progression through the flowering season; see Fig. 2). Curves in each panel are shown for both male and female invasion, and for two values of inbreeding depression, d. In all panels, $z = 0.5$.

when r is intermediate in value causes not only a decline in the frequency of the competing morph, but also in an increase in the frequency of the other morph above 0.5. This effect is not surprising. In the case of male invasion, for instance, the fitness of the protogynous phenotype will be less adversely affected by the reduced viability of later-produced seed than the protandrous phenotype when $k > 0$. Protandrous individuals are thus less competitive through both male function (in competition with males that produce more pollen) and female function. Similar reasoning follows for the case of female invasion. Finally, when $k > 0$, an increased degree of dichogamy allows the invasion of unisexuals with a lower value of r. It also renders the population more susceptible to the evolution of dioecy, in which males or females coexist at an equal frequency with (functionally female) protogynous or (functionally male) protandrous hermaphrodites, respectively (cf. Figs. 6c and 6f; Figs. 7c and 7f).

Note that with male or female invasion, the protogynous and protandrous morphs, respectively, may increase in frequency above 0.5 for large values of k when r_m or r_f have intermediate values (Figs. 6, 7). This result may seem counterintuitive, especially in the case of female invasion (Fig. 7), because an increase in k is expected to decrease female fitness more intensively in the protandrous than in the protogynous and female morphs. However, the rapid replacement of the protogynous morph by females with increasing r_f, for example, will shift the functional gender of the protandrous morph toward increased maleness, that is, away from female function that is compromised by positive *k*. This illustrates the frequency dependence of hermaphroditic functional gender and fitness in the face of unisexual invasion.

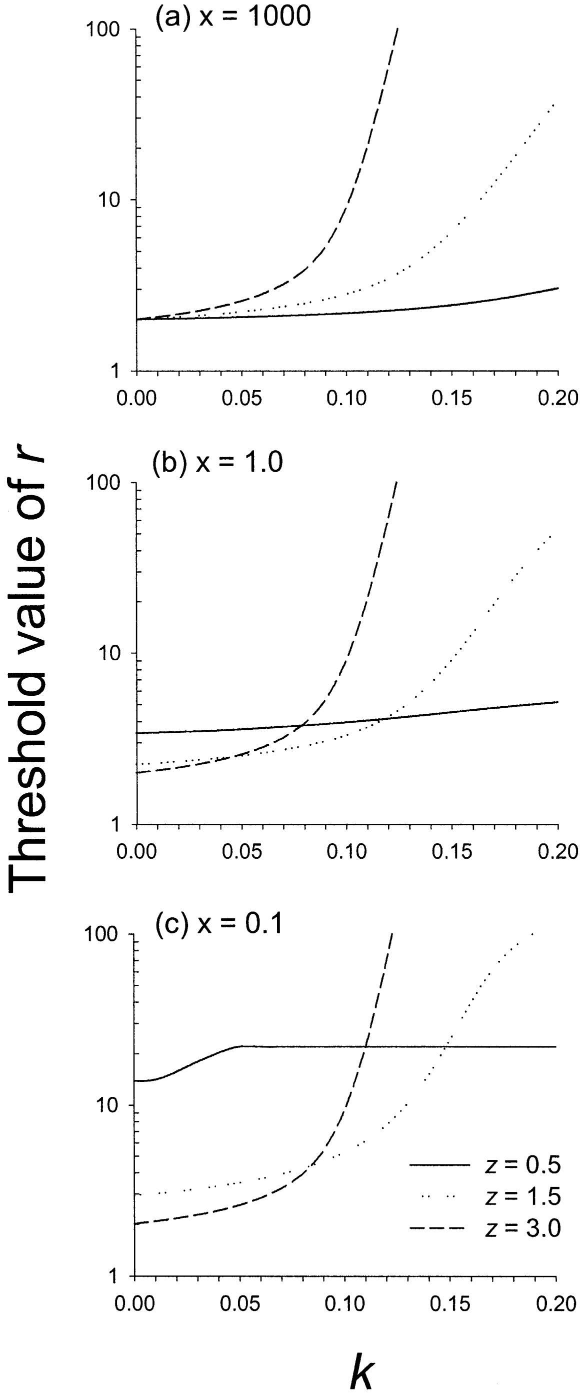

FIG. 5. The threshold value of r (the pollen production of males or seed production of females, relative to that of hermaphrodites) above which protogynous males (a, b, c) or protandrous females (only panel a) can invade a heterodichogamous population (note that the conditions for male and female invasion illustrated in panel a are identical). r is plotted as a function of k, the rate of declining female function with progression through the flowering season. Curves are shown for several values of z (the degree of overlap between male and female functions within each morph) and x (a parameter that regulates the extent to which outcross pollen contribute to the pollen pool around receptive stigmas and that thus affects the selfing rate, which increases with decreasing x; see text for details). The curves in (a) illustrate the conditions for protandrous female invasion under any rate of selfing, that is, for any x, whereas x affects male invasion; see text for details. In all panels, inbreeding depression, $d = 0$.

DISCUSSION

We have analyzed conditions for the invasion and spread of male- or female-sterility mutations in a heterodichogamous population, focusing on two particular selective causes. First, we asked how selection to avoid the potentially detrimental effects of inbreeding depression might favor the spread of gender-sterility mutations in partially selfing heterodichogamous populations. Second, we asked how the invasion of gender-sterility mutations might be influenced by a shift in the functional gender of heterodichogamous morphs, for example, as a result of differential resource availability during the course of the flowering and fruiting season. Both of these forces can be construed as a cause of gender specialization. Below, we discuss each mechanism in turn, before discussing the importance of gender specialization in evolutionary pathways from combined to separate sexes in general.

Selfing and Inbreeding Depression

In a heterodichogamous population in which the two morphs are functionally equivalent in terms of gender, conditions for the invasion and spread of males or females are essentially the same as those for invasion into a monomorphic hermaphroditic population. In particular, in the absence of selfing, males must sire at least twice as many offspring and females must produce at least twice as many seeds as hermaphrodites (Lloyd 1975; Charlesworth and Charlesworth 1978; Charlesworth 1984). In partially selfing populations, the minimum male fertility threshold for males always rises above two, because males are effectively excluded from competing for self-fertilized ovules. If these ovules suffer reduced fitness through the effects of inbreeding depression, the invasion criteria for males are somewhat relaxed, but never sufficiently so for the threshold to fall below two (Lloyd 1975; Charlesworth and Charlesworth 1978; Charlesworth 1984). In contrast, self-fertilization by hermaphrodites in the absence of inbreeding depression has no effect on the invasion criteria of females, as long as seed-production is not pollen limited, as assumed here. If selfed progeny have reduced fitness than outcrossed progeny, then the seed production threshold for the invasion of females falls below two (Lloyd 1975; Charlesworth and Charlesworth 1978). This well-established result for the spread of male- versus female-sterility mutations has been invoked to explain both the relatively higher incidence of gynodioecy over androdioecy in nature (Charlesworth 1984), as well as the hypothesis that the evolution of separate sexes has often been driven by selection to avoid inbreeding via a gynodioecious path (Charlesworth and Charlesworth 1978; Charlesworth 1999).

Gender Specialization

Our model introduced a parameter that has not been used in models for the evolution of separate sexes from hermaphroditism before, that is, the rate of declining female function with progression through the flowering and fruiting season,

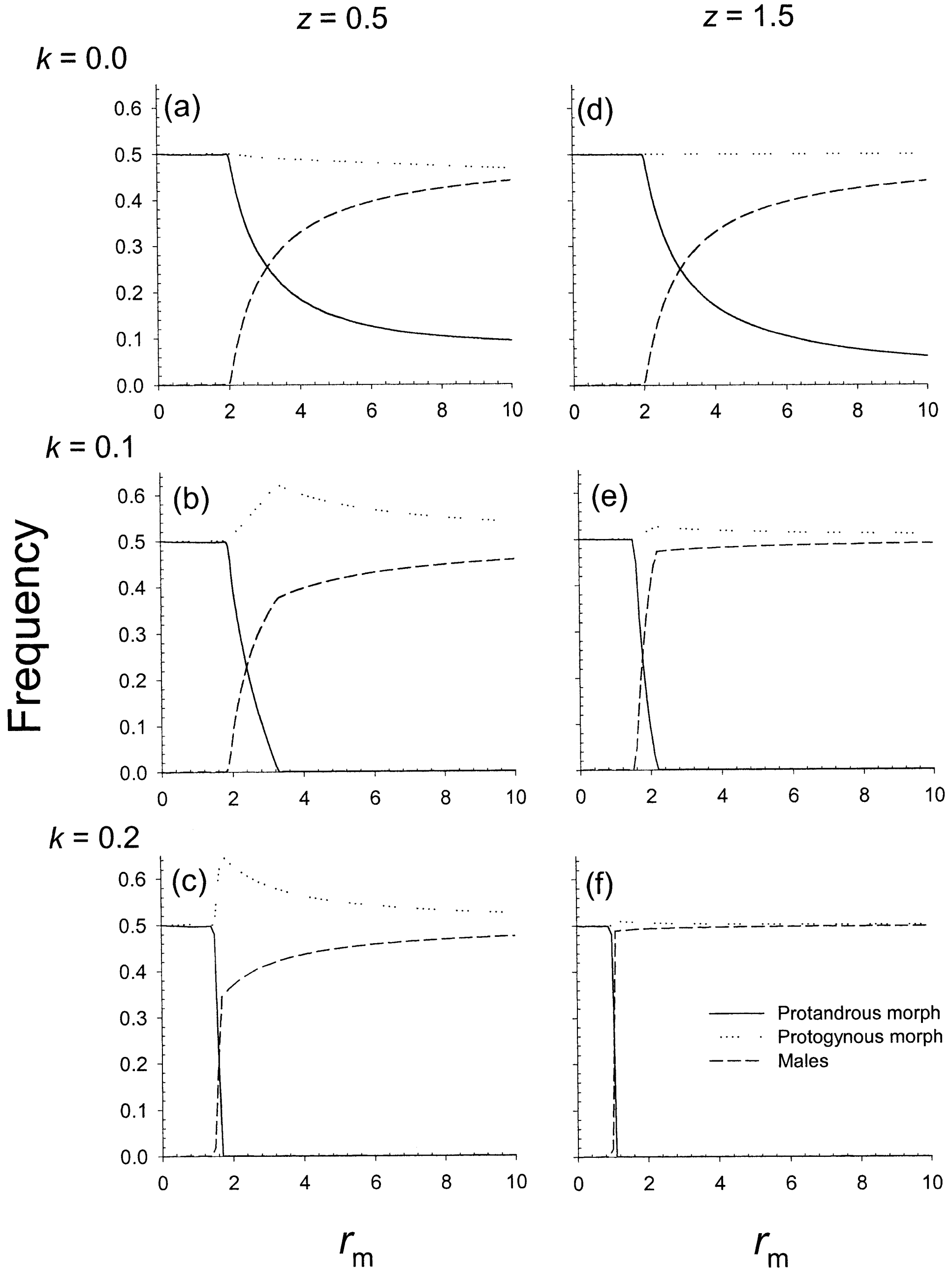

FIG. 6. The equilibrium frequency of protandrous males and protandrous and protogynous hermaphrodites, plotted as a function of r_m, the pollen production of males relative to that of hermaphrodites. The left- and right-hand panels show curves for a low ($z = 0.5$) and an intermediate degree of dichogamy ($z = 1.5$), respectively. Panels (a) and (c) show curves for the situation where seed viability is independent of the time of seed set ($k = 0$); panels (b) and (e) show curves for an intermediate rate of decline in seed viability with the time of seed set ($k = 0.1$); panels (c) and (f) show curves for a rapid decline in seed viability with the time of seed set ($k = 0.2$). In all curves, inbreeding depression, $d = 0$.

or k. With $k > 0$, seeds produced later in the season are less likely to reach reproductive maturity. This has two effects. First, $k > 0$ directly reduces the female fitness of individuals that tend to delay seed production toward the end of the reproductive season. In a heterodichogamous population, this implies a reduction in the female fitness of the protandrous morph. Second, $k > 0$ indirectly reduces the male fitness of individuals that disperse pollen toward the end of the flowering season, because the ovules they fertilize are less likely to mature. In a heterodichogamous population, this implies a reduction in the male fitness of the protogynous morph.

Because fitness in sexually dimorphic populations is frequency dependent, $k > 0$ in our model also causes an increase in the relative male and female fitness of protandrous and protogynous morphs in the population, respectively. It will also favor any strategy that accentuates its total allocation to reproduction, whether male or female, early in the season. This is essentially why a heterodichogamous population with

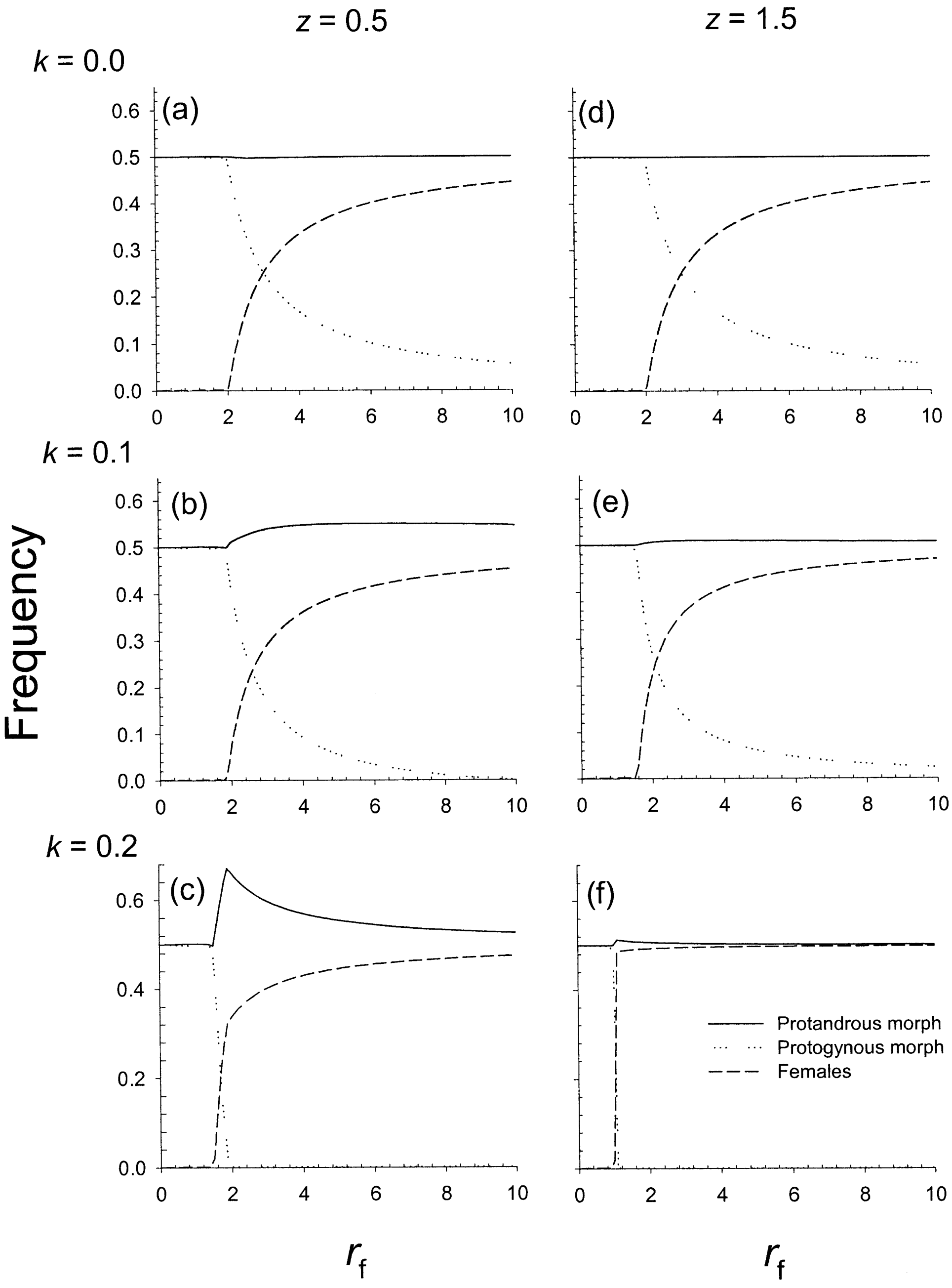

FIG. 7. The equilibrium frequency of protogynous females and protandrous and protogynous hermaphrodites, plotted as a function of r_f, the seed production of females relative to that of hermaphrodites. The left- and right-hand panels show curves for a low ($z = 0.5$) and an intermediate degree of dichogamy ($z = 1.5$), respectively. Panels (a) and (c) show curves for the situation where seed viability is independent of the time of seed set ($k = 0$); panels (b) and (e) show curves for an intermediate rate of decline in seed viability with the time of seed set ($k = 0.1$); panels (c) and (f) show curves for a rapid decline in seed viability with the time of seed set ($k = 0.2$). In all curves, inbreeding depression, $d = 0$.

$k > 0$ can be invaded relatively easily by protandrous female-sterility mutations or protogynous male-sterility mutations. It is also why conditions for the spread of female- or male-sterility mutations that affect protogynous or protandrous morphs, respectively, become increasingly severe with increasing *k*. These results are not surprising, and they parallel the intuitive prediction that, for example, it would be difficult for a short-styled female or a long-styled male to invade a distylous population in which long-styled individuals produce more seeds than short-styled individuals; in contrast, under such circumstances we should expect increased femaleness and maleness to be selected in long-styled and short-styled plants, respectively, as is indeed commonly found in distylous populations that have evolved toward dioecy (Ross 1982; Lack and Kevan 1987; Pailler et al. 1998; Webb 1999).

Data from Spanish populations of the heterodichogamous tree *A. opalus* strongly suggest that maleness has evolved in the protandrous morphs under conditions consistent with our models predictions. Here, seeds produced later in the season are smaller than those produced earlier, and the smaller seeds are likely to produce less competitive seedlings, suggesting that k is indeed greater than zero (G. Gleiser, M. Verdú, and J. R. Pannell, unpubl. ms.). An interesting contrast with *A. opalus* is provided by the shrub *Thymelea hirsuta*, in which k is likely to be $<$ zero; here, males have arisen from the protogynous morph, as we might expect (Dommée et al. 1990; El-Keblawy et al. 1996). This species starts to flower in autumn and therefore early fruit growth in protogynous individuals is limited by winter temperature. The later fruit growth in protandrous individuals thus benefits from optimal conditions in spring.

Evolution of Androdioecy and Gynodioecy

Perhaps the most significant prediction of our model concerns the conditions that would allow the invasion of a heterodichogamous population by males (female-sterile individuals), that is, the evolution of androdioecy. Models for the evolution of androdioecy from hermaphroditism have hitherto considered only the invasion and spread of males into a monomorphic hermaphroditic population (Lloyd 1975; Charlesworth and Charlesworth 1978; Charlesworth 1984). These models have shown that males must always disperse more than twice as much pollen as is dispersed by hermaphrodites, that is, $r_{\mathrm{m}} > 2$, potentially explaining the exceeding rarity of androdioecy in nature. In contrast, we have shown here that males can invade a heterodichogamous population more easily; in the limit of high k and thus where the female component of fitness is highly compromised in the protandrous morph, the critical threshold for male invasion falls as low as $r_{\mathrm{m}} > 1$. This is, of course, also the lower limit of r for the evolution of gynodioecy under a scenario of a high selfing rate and high level of inbreeding depression. The important conclusion is that the evolution of androdioecy is much more likely in a heterodichogamous population in which late seed and fruit maturation carries a penalty ($k > 0$), than in a hermaphroditic population that is monomorphic for functional gender. In this context it is interesting that, in contrast with the rarity and highly scattered distribution of androdioecy in the angiosperms in general (Pannell 2002), dioecy appears to have evolved repeatedly via androdioecy from a heterodichogamous ancestral state in the maple genus, *Acer* (de Jong 1976; Gleiser and Verdú 2005).

Of course, our model predicts that gynodioecy is in fact more likely to evolve in a partially selfing heterodichogamous population via the spread of protogynous females than androdioecy. This scenario may not be widely applicable to heterodichogamous populations if the selfing rate is kept low by the temporal separation of the sexes. However, even in a fully outcrossing heterodichogamous population, protogynous females are equally able to invade as protandrous males. Why then has dioecy apparently evolved via androdioecy in *Acer*? The answer remains unclear, but it is possible that elevated r_{m} may be easier to attain than elevated r_{f}. In other words, sexual specialization in male function may reap greater rewards than female specialization, for example, when the male fitness gain curve is accelerating or saturates less quickly than the female fitness gain curve. This situation may be obtained if limited seed dispersal results in strong local resource competition, or if specialist males are disproportionately attractive to pollinators (but see Klinkhamer et al. 1994; Bond and Maze 1999). In *A. opalus*, limited seeds are dispersed over short distances, implying substantial local resource competition (Gomez-Aparicio et al. 2005), and pollinators may be more attracted to larger numbers of male flowers (G. Gleiser and M. Verdú, unpubl. ms.).

Evolution of Sex Allocation and Complete Dioecy

Our model has considered only the spread of male- or female-sterility mutations in either the protandrous or the protogynous morph. Whether such major mutations have actually spread in heterodichogamous populations along their path to dioecy is not known. However, hypotheses for the evolution of separate sexes in both distylous and heterodichogamous populations have tended to invoke a gradual shift in gender to opposite extremes in each of the two morphs (Lloyd 1979), presumably through the fixation of a series of gender-modifying genes linked to the morph-determining locus. Conditions for the spread of a male-sterility mutation are known to be rather different from those favoring an incremental increase in female function in partially selfing populations but are equivalent to those for fully outcrossing populations (Ross 1982). Thus, it may be possible to generalize the predictions of our model here to the case of gradual gender adjustment if outcrossing can be assumed; this seems reasonable.

Our model also predicts the equilibrium frequencies of protogynous and protandrous individuals and males or females, following the invasion of a sterility mutation. Two points should be mentioned here. First, the unisexual variant will tend to replace its corresponding heterodichogamous morph, with the other morph maintaining its presence in the population at a frequency of approximately 0.5. For example, protandrous males will supplant protandrous hermaphrodites from the population, while the frequency of the protogynous morph remains largely unaffected. This is as we would expect, given that here, with sufficiently high r_{m}, the protandrous males will outdo the protandrous hermaphrodites in competition to fertilize ovules produced by protogynous individuals. Second, unless r is very high, the model predicts the maintenance of trimorphism under a wide range of conditions, that is, both heterodichogamous morphs can persist in the population with males or females, albeit with one morph at low frequency, as just explained. This prediction conforms to observations of *A. opalus* populations, where the protogynous occurs at a frequency of approximately 0.5 and the protandrous morph is less frequent than the male (G. Gleiser, M. Verdú, and J. R. Pannell, unpubl. ms.).

With increasing r, the equilibrium frequency of unisexuals approaches 0.5 and the population tends to dioecy. We defined r in our model as the relative pollen or seed production of males and females, relative to all heterodichogamous individuals. This definition served our purposes here, as the sex allocation of the protandrous and protogynous morphs was assumed to be equivalent. In a population responding to selection on the sex allocation, however, this latter assumption will not be realistic; rather, we should expect the less profitable gender in each morph to be reduced (Lloyd 1979), because, for example, selection will favor protogynous individuals with female-biased sex allocation (just as hermaphrodites may be selected to become increasingly male in gynodioecious and increasingly female in androdioecious populations; Seger and Eckhart 1996; Charlesworth 1999). In these cases, it would be appropriate to redefine r in our model in terms of the pollen or seed production of unisexuals relative to that of the morph with which they predominantly mate. A response to selection on the sex allocation of this morph would thus directly elevate r, reflecting a shift along a pathway toward increasingly separate sexes.

It is important to note that frequency-dependent selection on sex allocation acts simultaneously on the proportion of unisexual individuals in the population as well as on the sex allocation of the nondisplaced morph (and thus effectively also on r). Thus, the invasion of one class of gender specialists into a population will cause selection to act against that gender in the morph with which the invading specialist mates. Similarly, gender specialization by each of the morphs in a heterodichogamous population will both ease the conditions for invasion of a specialist in the respective opposite gender and allow its frequency to be increasingly elevated. The corollary of this is that an accelerating fitness gain curve in one sexual function establishes conditions for the evolution of increasing gender specialization in both morph classes simultaneously (Seger and Eckhart 1996). Whether the evolution of separate sexes begins with the establishment of a male- or female-sterility mutation, or with a gradual adjustment of the sex allocation of one or both of the heterodichogamous morphs, will therefore depend largely on the available mutations upon which selection can act. In this sense, and notwithstanding points made in the previous section, it is not clear from our model why androdioecy rather than gynodioecy has repeatedly been the intermediate stage in the evolution of dioecy in *Acer* (de Jong 1976; Gleiser and Verdú 2005)

Conclusion

Our model makes several predictions that underscore the role played by gender specialization in allowing males or females to invade a heterodichogamous population. The model makes use of a new parameter, k, that describes the differential environmental influences on female fitness (and thus on gender in general) on the two morphs; significantly, there is good direct and indirect evidence that $k > 0$ in natural plant populations, and that the conditions we have modeled may apply in nature. Estimates of k, or equivalent measures, from natural populations of heterodichogamous species would be valuable, particularly those showing a tendency toward gender specialization. Our most important conclusion is that gender specialization in heterodichogamous (and, by extension, probably in distylous) populations may allow the evolution of androdioecy under less stringent conditions than in populations that are monomorphic in gender. Detailed estimates of mating opportunities at different times of the reproductive season, as well as of relative pollen and seed productivities in species such as *Acer*, in which males cooccur with heterodichogamous hermaphrodites, would be useful in evaluating the likely importance of this path.

The framework we have introduced makes explicit the idea that mating opportunities can change during the course of a season, and that the functional gender of individuals and classes of individuals can therefore be time dependent (Ashman and Baker 1992; Sato 2002; Ehlers and Thompson 2004). This framework, which involves integration of the male and female components of fitness for each of several readily identifiable classes of individuals over a reproductive season, is heuristically useful. Our analysis here assumed a normal distribution for the shape of gender allocations in all morphs. However, as we show in a subsequent paper (G. Gleiser, M. Verdú, and J. R. Pannell, unpubl. ms.), the same framework can be generalized for the analysis of empirical data by measuring pollen dispersal and ovule availability for a sample of individuals over a series of time increments throughout a flowering season. Such an analysis requires no assumptions about the temporal distribution of sex allocation and is valuable not only for assessing the evolutionary stability of populations in which the gender of individuals may change over time, but also for documenting the temporal distribution of functional gender in natural plant populations.

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