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When looks can kill: the evolution of sexually dimorphic floral display and the extinction of dioecious plants

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Dioecious plants (with separate male and female individuals) more often have drab, inconspicuous flowers than related bisexual plants. Models indicate, however, that similar conditions favour the evolution of showy floral displays in dioecious and bisexual plants. One difference, however, is that dioecious plants may evolve floral displays that are sexually dimorphic. We show that males are more likely to evolve showy flowers than females in animal-pollinated plants, especially when pollinators are abundant. We demonstrate that this dimorphism places showy dioecious plants at a much higher risk of extinction during years of low pollinator abundance because pollinators may fail to visit female flowers. The higher extinction risk of showy dioecious plants provides an explanation for the fact that dioecious plants that do persist tend to have inconspicuous flowers and are more often wind pollinated. It may also help explain why dioecious plants are less species-rich than related bisexual plants.

Keywords: dioecy; extinction; floral display; sexual dimorphism

1. INTRODUCTION

A striking difference between plant and animal reproduction is that having separate sexes is rare among flowering plants (*ca.* 6%; Renner & Ricklefs 1995) but predominant among animals. Interestingly, it has been shown that dioecious plant families contain fewer species than hermaphroditic sister taxa in 79% of 28 paired comparisons (Heilbuth 2000). This result indicates that dioecious plants have a lower speciation rate or a higher extinction risk than non-dioecious plants, but the proximate explanation for this pattern remains a mystery. One potential explanation lies in the evolution of sexual dimorphism between male and female floral display. Unlike in animals, sexual selection in dioecious plants often involves a third party (pollinators). If selection favours showier males than females, a pattern common amongst dioecious species (Delph 1996; Eckhart 1999), pollinators will disproportionately visit males, which reduces the chance that a female will ever be pollinated (Bawa 1980*b*).

A previous model of floral display in dioecious plants (Sakai 1993) found, however, that the evolution of attractive structures should proceed in much the same way in bisexual and dioecious plants. This result raises the intriguing question of why dioecious flowers are so often sexually dimorphic and less showy than bisexual flowers (Bawa 1980*a*; Charlesworth 1993; Richards 1997). This contradiction between Sakai's theoretical result and the empirical pattern may be due to the assumption made by Sakai (1993) that the costs of floral display were equal in males and females. One factor in the evolution of sexual dimorphism that has not been investigated, however, is that differences may exist between males and females in terms of the costs of floral display. The number of pollen grains exceeds that of ovules usually by several orders of magnitude (Willson 1979), so that increasing floral display might have less of a detrimental effect on the amount of pollen transferred to stigmata (an important component of male fitness) than on the number of ovules produced (an important component of female fitness). Indeed, it has been shown in *Wurmbea dioica* that pollen production increases rather than decreases with male floral size, even though ovule production declines with female floral size (Vaughton & Ramsey 1998). Even when pollen production does decline, the amount of pollen transferred by pollinators need not decrease to the same extent unless pollinators completely deplete the pollen available in the anthers. Whenever the reproductive costs of investment in floral display are lower in males than in females, we would expect sexual dimorphism in floral display between males and females to evolve according to Bateman's principle. Bateman's principle states that males should become showier than females whenever attractive structures contribute more to male reproductive success than female reproductive success (Bateman 1948). This theory has recently been tested by Ashman & Diefenderfer (2001), who found that a male-biased sex ratio decreased pollen limitation, which decreased selection for petal size in females but not in males. We demonstrate that selection generally favours a greater allocation of resources to attractive display in male plants than female plants, especially when pollinators are abundant. The presence of abundant pollinators sets up a scenario where females are not pollen limited, causing selection to act on floral display in a manner similar to that observed in populations with a male-biased sex ratio. We then show that the extinction risk of a dioecious plant increases substantially with the level of sexual dimorphism.

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2. EVOLUTION OF SEXUALLY DIMORPHIC FLORAL DISPLAY

In animal-pollinated plants, the evolution of floral display is constrained by a resource allocation trade-off between display, which affects a plant's attractiveness to pollinators (A), and reproductive structures, such as pollen, ovules and seeds. This resource trade-off may occur at the whole plant level or at a per-flower level, although we will consider the former. Assuming that a constant amount of energy is allocated to flowers, we use a population genetic model to investigate the evolution of the fraction of floral resources, R ($0 \leqslant R \leqslant 1$), devoted to display versus reproductive structures. If $R = 0$, then floral display is minimal, and if $R = 1$, floral display is maximally showy but the flowers can produce no gametes or offspring. We assume that even a low allocation to floral display can attract pollinators to some extent ($A = 1$) but that the relative attractiveness of a plant increases linearly with the energy allocated to floral display, i.e. $A = 1 + cR$, where c is a conversion constant that measures how much attractiveness (in terms of pollinator visits) increases per unit resource. If c is large (much greater than 1), then the plant receives far more visits when it invests more resources in display. Throughout this paper, we assume that investment in floral display always increases attractiveness ($c > 0$). Estimates of c can be obtained from the slope of a regression line relating attractiveness (A) to the proportion of resources allocated to display (R) within a species. Empirical studies have examined the relationships between floral display and reproductive structures and between visitation rates and floral display. The first relationship allows one to estimate R for different plants and has been measured by Vaughton & Ramsay (1998) in *W. dioica*. The second relationship allows attractiveness to be related to a measure of floral display and has been estimated in studies such as Ashman & Diefenderfer (2001) for *Fragaria virginiana* and Bond & Maze (1999) for *Leucodendron xanthoconus*. Estimating both relationships within a single species would allow one to convert the measure of floral display into an estimate of R, which can then be used in a regression analysis to estimate c. The efficiency with which pollinators are attracted to a plant by an increased investment in floral display may differ between males (c_m) and females (c_f), a possibility that we allow in the most general version of the model.

In our model, the attractiveness of a plant relative to the average level of attractiveness within a population determines the probability that a pollinator visits the plant (see below). In addition, we must specify the relationship between investment in reproductive structures and fitness once a pollinator visit has occurred. Given that a pollinator visits a female plant, it is reasonable to assume that resource allocation to ovules and seeds will be linearly related to the number of offspring produced, i.e. fitness. Given that a pollinator visits a male plant, one would also expect that the pollinator will leave with more viable pollen grains if the male plant invests more in stamens and pollen. Consequently, investing more in reproductive structures should increase male fitness via a pollinator. This relationship need not be linear, however. If ample resources are devoted to reproductive structures (low R) and excess pollen is produced, a slight reduction in pollen production may have little effect on the amount of viable pollen that would attach to a pollinator. Conversely, if few resources are devoted to reproductive structures (high R), the same slight reduction in pollen production may cause a much more substantial reduction in the amount of viable pollen carried off by a pollinator. To model the resource allocation trade-off in males in a general way, we assume that the amount of viable pollen attaching to a pollinator follows a hyperbolic function of R: $(1 - R)/((1 - R) + aR)$, where a is a shape parameter. Depending on the value of a, this hyperbolic function allows for a large spectrum of possible trade-offs between male fitness through a pollinator and allocation to reproductive structures. When $a = 1$, there is a linear trade-off in males between floral display and reproductive success through a pollinator, as in females. Values of a near 1 might be expected for taxa that package pollen into a relatively small number of pollinia such as orchids and milkweeds. When $a = 0$, pollen is always produced in excess regardless of how little a male plant devotes to reproductive structures, an extreme and unlikely case. For intermediate values of a ($0 < a < 1$), fitness through a pollinator drops off slowly as a male invests more in floral display when R is low (a substantial fraction of resources devoted to stamens and pollen) but drops off more rapidly when R is high (few resources devoted to stamens and pollen).

For plants with annual or perennial life histories, we examine the evolution of floral display when pollinators are either extremely abundant or limiting. Pollinator abundance is known to vary drastically both spatially and temporally (Herrera 1989; Eckhart 1992; Utelli & Roy 2000; Thompson 2001), and it may have a strong influence on the evolution of male and female floral display. When pollen is not limiting, investing only in ovules and fruits maximizes female fitness, while investing in floral display can increase a male's fitness by attracting more pollinators than other males (Bateman 1948; Bell 1985; Ashman 2000; Ashman & Diefenderfer 2001). In the case of abundant pollinators, we assume that all females are fertilized, while in the case of pollinator limitation we assume that seed production increases linearly with the number of pollinators carrying pollen to female flowers. To simplify the analysis, we assume that pollinators only carry pollen from one flower to the next (i.e. female flowers are fertilized by a pollinator only if the pollinator last visited a male). Simulations indicate that pollen carry-over has an effect similar to increasing the total number of pollinator visits (Heilbuth 2001).

We modelled the evolution of floral display by considering the fate of a new allele that changes the fraction of energy allocated to attraction from R_m^* to R_m in heterozygous males and from R_f^* to R_f in heterozygous females. Because we assume that the fate of the new allele is determined while it is rare, the value of R in homozygotes for the new allele may be ignored. The floral display locus is assumed to be autosomal and unlinked to any loci that determine sex. The fraction of males is assumed to remain constant at σ within the population. The probability that a pollinator visits a new flower type depends on its attractiveness ($1 + c_f R_f$ for a female, $1 + c_m R_m$ for a male) relative to the average level of attraction in the population ($1 + cR^* = 1 + (1 - \sigma)c_f R_f^* + \sigma c_m R_m^*$). If pollinators are common, then all female flowers are eventually pollinated, so that the fitness of a female bearing the new allele depends only on how much energy she devotes to reproductive structures and offspring, which is $(1 - R_f)/(1 - R_f^*)$ relative to other females. If pollinators are limiting, then the fitness of females bearing the new allele also depends on the probability that the pollinator visits them after first visiting a male, which is $(1 - \sigma)(1 + c_fR_f)/(1 + cR^*) \times \sigma(1 + c_mR_m^*)/(1 + cR^*)$ assuming that the new floral display allele is rare. This differs from the probability of successful pollination of the remaining females by a factor $(1 + c_fR_f)/(1 + c_fR_f^*)$. Let δ be an indicator variable of pollinator limitation that equals 0 if pollinators are overabundant and 1 if pollinators are limiting. The relative fitness of a female bearing the new floral display allele, W_f, is then

$$W_f = \frac{1 - R_f}{1 - R_f^*}\left(1 - \delta + \delta\frac{1 + c_fR_f}{1 + c_fR_f^*}\right). \tag{2.1}$$

Whether or not pollinators are common, the fitness of a male is always assumed to depend on the number of pollinator visits and is therefore proportional to its attractiveness relative to other males, $(1 + c_mR_m)/(1 + c_mR_m^*)$. Male fitness also depends on the fraction of ovules that are fertilized by its pollen if the pollinator next visits a female flower, which is assumed to be proportional to $(1 - R_m)/((1 - R_m) + aR_m)$. Thus the relative fitness of a male bearing the new display allele, W_m, is

$$W_m = \frac{1 + c_mR_m}{1 + c_mR_m^*}\,\frac{\dfrac{1 - R_m}{1 - R_m + aR_m}}{\dfrac{1 - R_m^*}{1 - R_m^* + aR_m^*}}. \tag{2.2}$$

Because every offspring will have exactly one mother and one father, the representation of the allele in the next generation depends on the average fitness of the allele in males and females and does not depend on the sex ratio. Thus, the frequency of the floral display allele (q) changes from one season to the next (q') according to the recursion

$$q' = (1 - g)\left(\frac{W_f}{2} + \frac{W_m}{2}\right)q + g, \tag{2.3}$$

where g is the probability of surviving to the following season as an adult for perennial species. Because the change in allele frequency is linear in q while the allele is rare, its general solution is straightforward to calculate; according to this solution, q will increase as time passes if and only if $(W_f + W_m)/2$ is greater than one. At this point, we can determine the value of investment in floral display that cannot be invaded by any mutation with a different investment into attractive features. If there is such a combination of R_f^* and R_m^*, it represents an evolutionarily stable strategy (ESS). It can be shown that the ESS of equation (2.3) is the strategy that maximizes $W_f + W_m$, subject to the constraint that $0 \leqslant R_f^*, R_m^* \leqslant 1$ and that this ESS is convergence stable. The results described below were obtained by finding this maximum. Notice that the fate of the floral display allele and the ESS depend only on $W_f + W_m$ and not on the degree of perenniality (g). According to the general solution of equation (2.3), the degree of perenniality affects the rate at which a new floral display allele spreads per year, but not whether it spreads.

It may not always be possible for floral display to evolve independently in males and females. Thus, we first explored the case where mutations have the same effect on resource allocation in males and females, that is, we constrained R_f to equal R_m and R_f^* to equal R_m^*. One important special case where allocation to floral display must be, by definition, equal in male and females is when the population consists of out-crossing hermaphrodites with bisexual flowers. Rederiving equation (2.3) confirms that the dynamics and hence the ESS are identical for a bisexual population and for a dioecious population constrained to have identical floral display in males and females (not shown). Given that resource allocation is forced to be equal in males and females, there is no investment in floral display at ESS ($R^* = 0$) if $c_m + \delta c_f \leqslant 1 + a$ (i.e. if the increase in attractiveness is too low relative to the decrease in ovule and pollen production) and otherwise solves

$$\frac{c_m}{1 + c_mR^*} + \frac{\delta c_f}{1 + c_fR^*} + \frac{1 - a}{1 - (1 - a)R^*} - \frac{2}{1 - R^*} = 0. \tag{2.4}$$

To get a better sense of the behaviour of the ESS value of R^* when resource allocation is constrained to be equal in males and females, we now assume that the efficiency of converting resources into attractiveness is the same in males and females ($c_m = c_f = c$). If pollen is not easily depleted by pollinators (a small), the ESS is *ca.* $1/2(1 - a - 1/c)$ when pollinators are abundant ($\delta = 0$) and $2/3(1 - a - 1/(2c))$ when pollinators are limiting ($\delta = 1$). If, on the other hand, pollen transferred by pollinators declines linearly with increasing investment in floral display ($a = 1$), the ESS is *ca.* $1/3(1 - 2/c)$ when pollinators are abundant ($\delta = 0$) and $1/2(1 - 1/c)$ when pollinators are limiting ($\delta = 1$). As in these two examples, it can be shown that, in general, showier displays are expected to evolve when pollinators are rare than when they are common. Furthermore, as floral display becomes more efficient (c rises) or as pollen becomes cheaper (a declines), more energy is devoted to showiness at ESS (R^*) up to a maximum of one-half in populations with ample pollinators and two-thirds in pollinator-limited populations. In summary, when sexual dimorphism is impossible, the predicted ESS is the same for dioecious and bisexual species. Furthermore, as one might expect, showier flowers are expected at ESS when pollinators are rare, attractiveness increases rapidly with investment in floral display, and pollen is cheap.

The evolutionarily stable allocation to attractive structures changes dramatically when mutations can arise that have different effects on male and female flowers (R_m and R_f, respectively). Although quantitative genetic studies of floral traits in dioecious (or gynodioecious) species have found strong positive genetic correlations between males (or hermaphrodites) and females (e.g. in *Silene latifolia* (Meagher 1999) and *F. virginiana* (Ashman 1999)), dimorphism for floral traits was observed in 85% of 436 unisexual speces studied by Delph (1996). The mere presence of so many sexually dimorphic species suggests that mutations that affect floral display differently in males and females can, and often do, occur. If pollinators are abundant and every flower receives multiple visits ($\delta = 0$), all females will be pollinated, and there is no selection to increase floral display in females ($R_f^* = 0$). Selection still

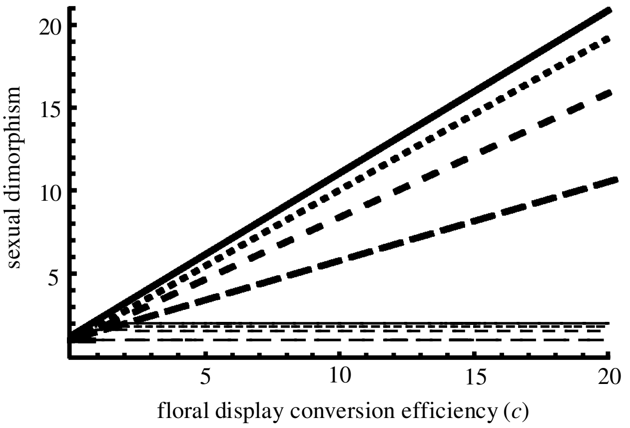

Figure 1. The extent of sexual dimorphism at the ESS (D^*) measured as the ratio of male to female attractiveness $(1 + c_m R_m^*)/(1 + c_f R_f^*)$. Here, for simplicity, we assume that $c_m = c_f = c$. The population evolves to be much more sexually dimorphic for floral display when pollinators are abundant (thick upper curves) than when pollinators are scarce (thin lower curves), when pollen is abundant (a low), and when it is easy to increase the attractiveness of a flower (c high). (solid lines, $a = 0$; short dashed lines, $a = 0.01$; middle length dashed lines, $a = 0.1$; long dashed lines, $a = 1.0$) Sexual dimorphism is a useful property because it can be measured in natural populations as the ratio of pollinator visits to males versus females. (To obtain D^*, this ratio should be divided by $\sigma/(1 - \sigma)$ in populations with an unequal sex ratio.)

acts on males to increase display due to the fact that they benefit from being visited more often than other males. We found that male investment in attractiveness evolves towards $R_m^* = 0$ if $c_m \leqslant a$ (i.e. if the increase in attractiveness is too low relative to the decrease in pollen production) and otherwise evolves towards

$$R_m^* = \frac{c_m - \sqrt{a c_m (1 - a + c_m)}}{c_m (1 - a)}. \qquad (2.5)$$

If $c_m = 1$ and $a = 0.05$, the proportion of resources allotted to attractiveness is 72% for males but 0% for females at the ESS. The extent of sexual dimorphism (D^*) in floral attractiveness, measured as the ratio of male to female attractiveness $(1 + c_m R_m^*)/(1 + c_m R_f^*)$, is illustrated in figure 1. As long as pollinators are abundant, extreme sexual dimorphism is expected to evolve whenever floral attractiveness is easily enhanced by additional investment in display (c_m large). In our model the sex ratio does not explicitly affect the level of sexual dimorphism (D^*). Extreme sex ratios may, however, determine whether fertilization is assured ($\delta = 0$; expected under an extremely male-biased sex ratio) or limiting female reproductive success ($\delta = 1$; expected under an extremely female-biased sex ratio). Because our results indicate that sexual dimorphism is more extreme when fertilization is assured (i.e. pollinators are abundant; $\delta = 0$), our results are consistent with those of Ashman & Diefenderfer (2001), who found that a male-biased sex ratio increased selection for sexual dimorphism. If, however, factors other than the sex ratio of the plant determine whether pollinators are abundant or limiting, such as climate, altitude, or abundance and diversity of other plant species, then the sex ratio will not influence the level of sexual dimorphism at ESS, as we have shown.

Investment in male display still evolves towards equation (2.5) when pollinators are rare. In females, however, whenever reproductive success is pollinator limited ($\delta = 1$), there is selection for investment in attractiveness to ensure fertilization. The evolutionarily stable investment in attractive structures for females is now greater than zero as long as $c_f > 1$, and investment evolves towards $R_f^* = 1/2 - 1/(2c_f)$. The extent of sexual dimorphism is consequently much smaller (figure 1), with the attractiveness of male plants being at most twice that of females (when a is small) unless males are more efficient at converting resources into floral display ($c_m > c_f$).

By and large, the above results imply that male display should evolve to be more attractive to pollinators than female display. Only if pollinators are scarce ($\delta = 1$) and females are much more efficient at converting resources into attractive floral displays (i.e. c_f is sufficiently greater than c_m that $1 + c_f R_f^* > 1 + c_m R_m^*$) would we expect females to be more attractive. If $c_m > c_f$, as may be the case if pollinators are attracted to anthers and pollen as well as petals, then sexual dimorphism with showier males can be even greater. There are, however, two important cases where sexual dimorphism is not expected to evolve. First, if the gain in attractiveness per investment in floral display is too low ($c_m \leqslant a$ and $c_f \leqslant 1$), the ESS predicts no investment in attractive structures in either sex whether pollinators are rare or abundant. Second, if pollinators are limiting, if the potential fertility cost to males of allocating resources to display is linear as in females ($a = 1$), and if the efficiency of producing attractive floral displays is the same in both sexes ($c_m = c_f = c$), then the ESS investment in display is equal in males and females and equal to the ESS investment for bisexual flowers (i.e. $1/2 - 1/(2c)$). This second set of limiting conditions corresponds most closely to the assumptions made by Sakai (1993). Notice that, even if the cost to males of allocating resources to display is linear as in females ($a = 1$), sexual dimorphism can still evolve when pollinators are abundant, because of the asymmetry in the benefits of attracting pollinators for males and females (Bateman 1948). Attracting more pollinators than other males can increase the siring success of a male even if it transmits less pollen per pollinator, whereas investing in attractive structures has only costs and no benefits for females when pollinators are plentiful and fertilization is assured. Thus, except in the above limiting cases, sexual dimorphism is expected to evolve under a wide variety of biologically reasonable conditions.

When sexual dimorphism does evolve, do males become more showy, females less showy, or both compared with an equivalent non-dimorphic or bisexual species? To address this question, we compared the ESS solutions for the allocation to floral display of males (R_m^* obtained from equation (2.5)), females ($R_f^* = 0$, when $\delta = 0$; $R_f^* = 1/2 - 1/(2c_f)$, when $\delta = 1$), and non-dimorphic or bisexual populations (R^* from equation (2.4)). If resource allocation to floral display increases attractiveness to the same extent in males and females ($c_m = c_f = c$), if $0 \leqslant a \leqslant 1$ and if $c \geqslant 0$, then it can be shown that R_f^* is always less than or equal to R^* (constrained to be equal in males and females), which in turn is less than or equal to R_m^*. Thus, sexual selection in dioecious species tends to drive the evolution of more floral display in males and less floral display in females than would be predicted at ESS for a similar bisexual species.

Our ESS predictions appear biologically realistic when compared with data on resource allocation in bisexual and dioecious species. In the hermaphroditic, self-incompatible *Ipomopsis aggregata* (Campbell 1992), the proportion of floral biomass that is invested in pollinator attraction (R) varies greatly but averages 44%. For the case where pollinators are limiting, the ESS values given by equation (2.4) would correspond to values of c between 1.47 (for $a = 0$) and 8.333 (for $a = 1$), which would predict that the flowers are between 1.65 and 4.67 times more attractive to pollinators than if no investment were made to floral display. Antos & Allen (1994) estimated the proportion of reproductive biomass allocated to pollinator attraction in males and females of *Oemelaria cerasiformis*. They estimated that 15% of reproductive biomass in males and 1% in females is devoted to floral display, considering only petals as an attractive structure. Taking these values as R^*_{m} and R^*_{f}, respectively, and assuming that $c_{\mathrm{m}} = c_{\mathrm{f}} = c$, this suggests that $c = 1.02$ and $a = 0.72$ using the ESS values given by equation (2.5) and $R^*_{\mathrm{f}} = 1/2 - 1/(2c_{\mathrm{f}})$ for the case where pollinators are limiting (because R^*_{f} is not zero). Accordingly, we would expect that males of *O. cerasiformis* should be 14% ($D^* = 1.14$) more attractive than females to pollinators, which consist mainly of thrips, beetles and honeybees. Indeed, males had significantly larger flowers than females, although the relative attractiveness to pollinators of males versus females was not determined. There are, of course, many caveats to this inference. Antos & Allen (1994) note that the hypanthium may also be considered a trait that functions in pollinator attraction, which would alter the above values of R^*. (If the hypanthium is included as a pollinator-attracting feature then males and females devote 60% and 4% to pollinator attraction, respectively. These values correspond to the following parameters of the model: $c = 1.09$; $a = 0.13$; $D^* = 1.58$). Alternatively, females may still invest in petals, not because pollinators are limiting, but because of some inherent constraint or because insufficient time has passed to reach the ESS with no investment in petals. (If we assume that $R^*_{\mathrm{f}} = 0$, we now only have one equation, (2.5), and two unknowns, c and a. If we vary a between 0 and 1 to solve for c using $R^*_{\mathrm{m}} = 0.15$ in equation (2.5), we predict that males should be between 0% and 20% more attractive to pollinators than females.) Furthermore, there may be differences between males and females in the efficiency by which they can increase attractiveness by investment in display ($c_{\mathrm{m}} \neq c_{\mathrm{f}}$). Finally, our analysis only considers the extreme cases where either pollinators are abundant or they limit female reproductive success; a more explicit accounting of the numbers of pollinators could yield different predictions. Nevertheless, this example shows how the model may be used to generate predictions about reproductive investments that can inform future experimental work.

3. EXTINCTION RISK OF SEXUALLY DIMORPHIC PLANTS

Once sexual dimorphism has evolved, it places a dioecious population (or deme) at a greater risk of extinction if pollinator abundance subsequently declines, because pollinators may fail to visit less attractive female plants. To assess this risk, we consider a patch of flowers fertilized by P pollinators that each visit V flowers. A conservative estimate can be made if we assume that the only risk of extinction arises from pollinators failing to visit females and that the population persists at carrying capacity even when only one female is fertilized (more realistic population dynamics would make sexually dimorphic populations more prone to extinction). The probability of extinction is then f^P, where f is the probability that a single pollinator fails to fertilize any females. Pollinator failure will occur whenever a pollinator first visits females and then males or visits only males (all other visit sequences result in at least one female being fertilized). In a population with a proportion σ of males, where males are D times more attractive than females, the probability of pollinator failure (f) equals

$$f = \sum_{i=0}^{V}\left(\frac{1-\sigma}{1-\sigma+\sigma D}\right)^{i}\left(\frac{\sigma D}{1-\sigma+\sigma D}\right)^{V-i} = \frac{\left(\frac{\sigma}{1-\sigma}D\right)^{V+1} - 1}{\left(1+\frac{\sigma}{1-\sigma}D\right)^{V}\left(\frac{\sigma}{1-\sigma}D - 1\right)}. \tag{3.1}$$

The extinction risk is minimized when

$$\left(\frac{\sigma}{1-\sigma}D\right),$$

which is the effective sex ratio in the eyes of pollinators, equals one. In populations with an even sex ratio, sexual dimorphism acts to skew the effective sex ratio, causing the extinction risk over 100 generations to be dramatically higher than in populations with equally attractive male and female plants (figure 2). For example, if 10 pollinators each visit four flowers, a local population with no sexual dimorphism has a very small probability of going extinct within 100 generations (0.0009), while a population with fourfold more attractive males has a 21% risk of extinction and a population with 10-fold more attractive males is almost certain to go extinct (0.999). Although these calculations assume that the number of visits per pollinator and the number of pollinators are constant, a stochastic model where the number of visits per pollinator is Poisson distributed and the number of pollinators per year is normally distributed with a coefficient of deviation C generates contour plots that are nearly identical to figure 2 for C values up to *ca.* 20%; with even more variation in the number of pollinators per year (higher C), extinction rates rise substantially, especially for sexually dimorphic species (data available upon request). Because perennial species can persist even when fertilization fails to occur within a year, perennial species have a dramatically lower extinction risk (see figure 2), which may explain the correlation between perenniality and dioecy among the dioecious species that have persisted (Renner & Ricklefs 1995).

In figure 2, the total number of pollinator visits to the plant population is low ($PV < 250$). Such a scenario is unlikely to describe pollinator visitation over the entire range of a plant species, unless this range is quite restricted

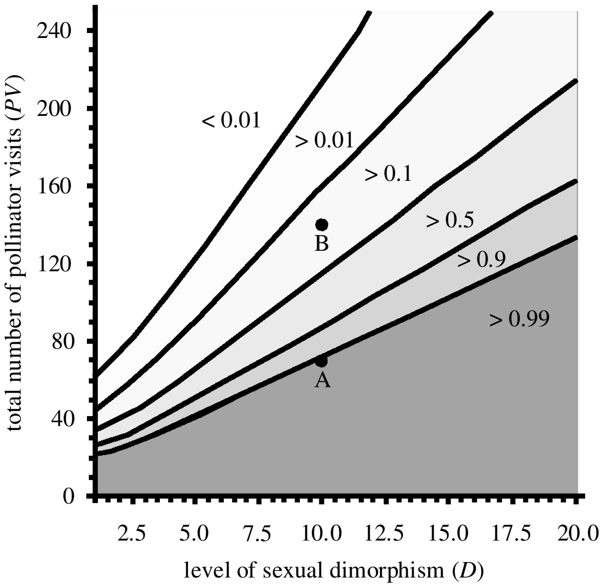

Figure 2. The extinction risk of sexually dimorphic plants. The contours indicate the probability that a population goes extinct within 100 years. The total number of pollinator visits made by P pollinators that each visit two flowers ($V = 2$) is shown on the y-axis. The x-axis measures the degree of sexual dimorphism (D), with the left-hand edge representing equally showy male and female flowers ($D = 1$). For plant species that persist for multiple years, G, without producing seeds (i.e. perennials and plants with a seed bank), PV should be multiplied by G in calculating extinction risk. For example, points A and B indicate the extinction risks of an annual ($G = 1$) and biennial ($G = 2$) species, respectively.

and/or pollinators have undergone a drastic decline in numbers. Nevertheless, the above scenario may be quite realistic for local populations (demes). This suggests that dioecious populations with extensive sexual dimorphism may be more likely to go extinct in, and are less likely to colonize, locations where pollinator abundance is currently low. Thus, dimorphic dioecious populations would be more likely to have smaller and more fragmented ranges, both of which are associated with a higher risk of extinction at a species level (e.g. Barrett & Kohn 1991; Kéry *et al.* 2000). For example, recent studies on a hermaphoditic annual species, *Clarkia concinna concinna*, have shown that separating patches by as little as 100 m can generate such severe pollinator limitation as to cause the extinction of a patch (Groom 2001). Dynamics such as these might be what is occurring in the Mediterranean dioecious species *Ruscus aculeatus* (Martinez-Palle & Aronne 2000), which is so severely pollen limited as to set, on average, only 3% of its fruit; this is probably due to a decrease in the pollinators that accompanied the region's switch from tropical to a Mediterranean climate. Direct observations of pollinator visits to *R. aculeatus* flowers, in which males have white flowers that are approximately twice as large as the greenish-brown flowers on females, are non-existent at present but would be very useful for discerning the contribution of pollinator dynamics to the extinction vulnerability of this species.

The model of extinction risk that we have explored is clearly an over-simplification. In particular, females usually need more than one pollinator visit to fertilize all of their ovules (Burd 1994; Larson & Barrett 1999), sexes can become spatially segregated due to different ecological tolerances (Meagher 1984), pollinator visitation rates can decrease as patch size decreases (Ashman 2000), and population persistence almost certainly depends on the number of females fertilized and the number of seeds produced (e.g. Groom 2001). Incorporation of these factors would all generate higher extinction rates for sexually dimorphic dioecious populations. Furthermore, the assumption of independent visits is often violated because pollinators are prone to visit more than one flower on the same plant (Richards 1997; Utelli & Roy 2000). The tendency for multiple visits may place monoecious species, which have separate male and female flowers on the same plant, at a lower risk of extinction than dioecious species. Monoecious species can also be sexually dimorphic (van der Pijl 1978; Delph 1996), sometimes to an even greater degree than dioecious species (e.g. dioecious males (or hermaphrodites in gynodioecious species) are visited more often than females by a factor of 1.5 in *W. dioica* (Vaughton & Ramsey 1998), two in *F. virginiana* (Bell 1985), three to four in *S. dioica* (Carlsson-Granér *et al.* 1998), and four in *Antennaria parviflora* (Bierzychudek 1987), while in the monoecious *Begonia urophylla* and *B. tonduzii* male flowers are visited more often by factors of 8.6 and 15.4, respectively (LeCorff *et al.* 1998). The increased likelihood that pollinators visit female flowers after being attracted to male flowers on the same plant may explain why monoecious groups have: (i) more showy members than dioecious groups (e.g. members of Musaceae and Begoniaceae) and (ii) unlike dioecious plants, no association with higher extinction rates or lower speciation rates (Heilbuth 2000).

4. DISCUSSION

Interestingly, extant dioecious plants are often dramatically different from their hermaphroditic relatives in the degree of floral display (Bawa & Opler 1975; Bawa 1980*a*; Charlesworth 1993). This observation is odd in light of a previous model (Sakai 1993), which showed that floral display evolves under similar conditions in dioecious and bisexual plants. Our model demonstrates, however, that the evolution of floral display in dioecious plants will be accompanied by the evolution of sexual dimorphism to a moderate extent when pollinators are rare and to an even greater extent when pollinators are abundant. Under most circumstances, females will evolve to be less showy and males more showy than a similar bisexual species. The level of dimorphism can be extreme (figure 2), depending on the extent to which pollinators are abundant (δ), the degree to which pollinator attraction is increased by investment in floral display (c), and the costs of increasing floral display in terms of the dispersal of viable pollen (a).

Other studies have also found that sexual dimorphism for floral display could evolve for different reasons than explored in this paper. Ashman (1999) noted that male and female floral traits may have different heritabilities and may respond differently to selection even when the selective forces are the same. Delph (1996) proposed that genetic correlations between petal and stamen development could also cause sexual dimorphism. Furthermore, in a model similar to ours but where the trade-off between floral display and potential fertility was constrained to be equal in males and females (akin to $a = 1$ and $\delta = 1$ in our model), Sakai (1993) found that sexual dimorphism could evolve if flowers are near their maximum possible size. Dioecious plants often have small, inconspicuous flowers, however, which suggests that flower size is not typically constrained in the way that Sakai's model of sexual dimorphism requires (Bawa 1980*a*).

Whatever the means by which a population becomes sexually dimorphic for floral display, dioecious demes are at a much higher risk of extinction whenever local pollinator availability is low. Pollinator limitation would also hinder the range expansion of a species by reducing their ability to persist in areas with few pollinators, which could decrease speciation rates. For example, in dioecious *Dombeya* spp. on La Réunion, sexually dimorphic species tend to be more narrowly distributed than species with similar-sized male and female flowers (L. Humeau, T. Pailler and J. D. Thompson, unpublished data). Dioecious plants that are genetically constrained to have low floral display or that have dependable and diverse pollinator pools are more likely to persist, which could explain the observed correlation between drab floral display and dioecy.

Our hypothesis, that dioecious species that evolve showy floral displays will tend to be sexually dimorphic and consequently suffer a higher risk of extinction, provides a parsimonious explanation for several patterns observed among extant dioecious organisms: (i) dioecious species do evolve sexual dimorphism for flower number and flower size (Lloyd & Webb 1977; Delph 1996; Eckhart 1999); (ii) in animal-pollinated plants, pollinators often visit males at a higher rate than females (Bierzychudek 1987; Delph & Lively 1992; Burd 1994; Carlsson-Granér *et al.* 1998; LeCorff *et al.* 1998); (iii) surviving dioecious species are typically polyphilic (pollinated by a wide variety of insects) (Bawa 1980*a*, 1994; Richards 1997; Ashman 2000) or abiotically pollinated (pollinated via wind or water) (Renner & Ricklefs 1995), either of which reduces the risk of pollinator limitation; (iv) the higher extinction risk of showy dioecious species is consistent with the observation that those dioecious species that do persist tend to have small, inconspicuous flowers (Bawa 1980*a*; Lloyd 1982; Heilbuth 2001); and (v) it is also consistent with the fact that, unlike in animals, plants with separate sexes are rare (Heilbuth 2000). The fact that these trends are consistent with our hypothesis does not, however, prove that they are caused by the mechanisms we have outlined in this paper. Proving or disproving that our hypothesis underlies these trends awaits future empirical tests.

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