The number of competitors providing pollen on a stigma strongly influences intraspecific variation in number of pollen apertures

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ABSTRACT

Variation in the number of pollen apertures has been widely described among and within angiosperm species. Apertures are weak points of the pollen wall where the pollen tube germinates. Pollen aperture heteromorphism (pollen grains with different numbers of apertures in a single individual) is common in flowering plants, whereas polymorphism (among-individual variation) is rare. Previous work on *Viola* has shown that pollen with few apertures has a better survival rate, whereas pollen with more apertures germinates faster. Here we develop game-theoretic models of competition between several pollen donors. These show that heteromorphism can be a stable strategy for all finite numbers of competitors per stigma for some parameter values where one pollen type germinates faster but has lower longevity. In contrast, polymorphism is not stable in pairwise contests (two pollen donors). When more than two pollen donors interact on stigmas, polymorphism can be stable for certain parameter values.

In both heteromorphism and polymorphism, selection operating on the number of pollen apertures is an example of soft selection if each flower in a population produces a fixed number of seeds, regardless of the average fitness of the particular pollen composition present on its stigma. This results in stigma-level and population-level frequency dependence, which makes stable heteromorphism and polymorphism possible. Selective scenarios vary among stigmas due to variation in the pollen present. Thus, a particular pollen type may be more fit than average on some stigmas but less fit on others. As a pollen strategy increases in frequency in a population, the frequency of different kinds of pollen contests shift. This may result in the pollen strategy's fitness advantage being lost at an intermediate frequency, resulting in heteromorphism or polymorphism. Low numbers of pollen donors per stigma result in greater variance in pollen composition among stigmas, resulting in a broader parameter range for stable heteromorphism or polymorphism. For any number of pollen donors per stigma, the conditions for polymorphism are a more restrictive subset of those for heteromorphism. We

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show that heteromorphism can invade a polymorphic population, whereas heteromorphism is stable against polymorphism, thus explaining why polymorphic species are rare.

Keywords: game theory, heteromorphism, pollen competition, polymorphism, soft selection, two-level frequency dependence.

INTRODUCTION

In higher plants, pollen (the male gametophyte) is extremely diversified and its morphology can be family-, genus- or even species-specific. Many morphological characters are involved in this diversity, both for the pollen grain itself (size, shape, ornamentation and pollen wall structure) and for its apertures (number, size, shape and structure). The apertures have a crucial role in fertilization as the pollen grain hydrates and the pollen tube is usually initiated through these apertures. Variation in the number of pollen apertures has been widely described among and within angiosperm species. Within species, it is more often found within individual plants (heteromorphism; Till-Bottraud *et al.*, 1994), with the genetic variation being expressed in morph proportions produced by individuals (Till *et al.*, 1989; Dajoz *et al.*, 1991; Mignot *et al.*, 1994), rather than among individual plants (polymorphism, each plant being homomorphic) (Till *et al.*, 1989; Dajoz *et al.*, 1991; Mignot *et al.*, 1994). The evidence to date shows that the number of apertures is determined sporophytically (Bateson, in Crane and Lawrence, 1952; Baker, 1966; Ahokas, 1975; Charlesworth and Charlesworth, 1979; Mignot, 1995).

The functional consequences of aperture number have been investigated in a heteromorphic species, *Viola diversifolia* Gingins (Beck.). A high number of apertures resulted in more rapid germination but lower longevity (Dajoz *et al.*, 1991, 1993). Such differences in viability and germination rate are likely to occur in other species (partial evidence in *Viola calcarata*; Till-Bottraud *et al.*, 1999) and may help explain the evolution of aperture number in angiosperms.

To clarify how selection may operate on aperture number, Till-Bottraud *et al.* (1994) developed game-theoretic models of the evolution of pollen aperture number using the theoretical framework of sexual selection applied to male–male competition. These models consider how selection operates on a pollen donor that interacts with other members of its population on a series of flowers to which pollen has been delivered simultaneously. The most significant result is that selection can result in pure 3-aperturate, pure 4-aperturate or mixed evolutionarily stable strategies (Maynard Smith, 1982). The mixed evolutionarily stable strategy corresponds to heteromorphism with all plants producing both types of pollen. However, selection cannot easily maintain a standard genetic polymorphism with each pollen morph produced on a different plant (homomorphism).

In a survey of over 200 plant species, one-third were found to be heteromorphic (Mignot, 1995). Polymorphism was very rare (six species) and was always associated with heterostyly, where it is one component of the syndrome linked to mating type. Thus, the natural history of aperture number is consistent with predictions of the published models.

In these models, only pairwise contests were considered: competition occurred between two donors on a stigma, with each plant participating in a series of such pairwise contests. However, pairwise contests are not the only possibility, since pollen from more than

two pollen donors can arrive simultaneously on a stigma (see Erickson and Adams, 1989; Morris *et al.*, 1994). To derive a more realistic model of pollen competition, we relax the assumption of pairwise contests and study the influence of the number of pollen donors per stigma on the stability of heteromorphism and polymorphism. Changing the number of pollen donors per stigma has mostly quantitative effects on the conditions for pollen heteromorphism. However, increasing the number of pollen donors per stigma qualitatively alters the prediction for polymorphism: polymorphism cannot evolve in the model with two donors, but with more than two it can. Moreover, we show that the instability of polymorphism for two competitors is due to the simplifying assumption that all competitors provide the same number of pollen grains. Our exploration of the number of pollen donors per stigma also clarifies how flowers structure male competition into local arenas, giving rise to multi-level frequency dependence.

THE MODELS

We assume that pollen grains compete with one another on stigmas and styles for access to ovules and that all ovules are fertilized, whatever the composition of the pollen load on the stigma. Pollination is assumed to be random. Each pollen donor on a particular stigma is assumed to supply an equal amount of pollen simultaneously. The age of pollen, and thus its age-dependent fitness characteristics, are discrete with two possible states. It can be either 'young' (from a freshly dehisced anther) with a probability t ($0 < t < 1$) or 'old' (from an anther that dehisced the previous day) with a probability $1 - t$. Thus, this model builds on the discrete time models of Till-Bottraud *et al.* (1994). The competitive advantage (relative fitness) of 3-aperturate pollen is set to 1, regardless of age. The competitive advantage of 4-aperturate pollen relative to 3-aperturate pollen at fertilization is m (> 1). This value not only includes how much faster 4-aperturate pollen grains germinate, but also what fertilization advantage this provides. This fertilization advantage, due to faster germination, is the benefit gained from a higher number of apertures. The viability of 4-aperturate pollen when old is v ($0 < v < 1$) compared to 3-aperturate pollen, which shows no decrease in viability with age. Thus, the relative success of 4-aperturate pollen is m when young and mv when old (Table 1). Only the case where $m > 1$ and $mv < 1$ is of interest, since if $m < 1$ the 3-aperturate grains will always win and if $mv > 1$ the 4-aperturate grains will always win.

Heteromorphism

In the heteromorphic model, we assume that all plants can produce two types of pollen simultaneously and that the variation in morph proportions has at least a partially additive

Table 1. Fitness parameters of individual 3- and 4-aperturate pollen grains used in the models (see The Models section).

	Germination ability	Survival when old	Global fitness	
			Young	Old
Probability			t	$1 - t$
3-aperturate	1	1	1	1
4-aperturate	m (> 1)	v (< 1)	m	mv

genetic basis. To calculate the conditions for a heteromorphic evolutionarily stable strategy (ESS), we computed the paternal fitness of a mutant or migrant pollen donor that produces a proportion p of pollen grains with three apertures, which is poised to invade a population of plants that produce a proportion p' of pollen grains with three apertures:

$$W(p, p') = \sum_j a_j F_j(p, p') = \sum_j a_j \frac{W_j(p)}{W_{totj}(p, p')} \quad (1)$$

Because the mutant genotype is assumed to be initially at very low frequency, it is assumed to compete always against resident plants, which all produce the proportion p' of 3-aperturate pollen grains. However, each competing plant can contribute young or old pollen to a stigma. The sum in (1) is over the j situations corresponding to the different possible combinations of ages of the opponent's pollen and the two possible states of the mutant pollen (young or old). a_j is the probability of each situation occurring on a stigma assuming random mating.

$F_j(p, p')$ gives the fraction of a flower's seeds fathered by the mutant genotype for each possible age combination of pollen. This fraction is given by the ratio of mutant fertilization success ($W_j(p)$) to total fertilization success, that is mutant plus residents ($= W_{totj}(p, p')$). The sum gives the mean success of the mutant in siring seeds in a resident population as the mean proportion of seeds sired.

Strategy p^* is an ESS if an individual with any other strategy $p \neq p^*$ cannot invade the population. This is true when the value of p that maximizes the fitness of a mutant is the same as the actual population value, p'. Otherwise, selection would tend to move the population value towards the fitness-maximizing value, which is itself a function of the population value. Thus, the necessary condition (ensuring a fitness maximum, minimum or saddle point) is that:

$$\left.\frac{\partial W(p, p')}{\partial p}\right|_{p = p' = p^*} = 0$$

This equation gives ESS candidates, p^*, implicitly as a function of the model parameters. The ESS proportion p^* was determined for various numbers of competitors and combinations of the parameters. Whenever a solution was found where $0 < p^* < 1$, this value was also unique. As the function is continuous and differentiable, p^* is the fitness maximum if some p greater than 0 has greater fitness than $p = 0$ in a population with $p' = 0$ and some p less than 1 has greater fitness than $p = 1$ in a population with $p' = 1$. These conditions can be calculated as:

Condition 1: $\partial W(p, p')/\partial p|_{p = p' = 0} > 0$

Condition 2: $\partial W(p, p')/\partial p|_{p = p' = 1} < 0$

Condition 1 ensures that the *pure* 4-aperturate strategy is not an ESS, thus guaranteeing the production of at least some 3-aperturate pollen grains ($p^* > 0$). Condition 2 ensures that the *pure* 3-aperturate strategy is not an ESS, thus guaranteeing the production of at least some 4-aperturate pollen grains ($p^* < 1$).

The formulae for two competitors per stigma are given in Till-Bottraud *et al.* (1994). The general equations for any number of pollen donors per stigma are given in Appendix 1. Here we develop the fitness equations for three competitors per stigma as an illustration (the pollen donor with proportion p of 3-aperturate pollen grains is confronted with two opponents producing proportion p' of 3-aperturate pollen):

$$W(p, p') =$$

$$\frac{t^3(p + m(1-p))}{p + m(1-p) + 2(p' + m(1-p'))} + \frac{t^2(1-t)(p + m(1-p))}{p + m(1-p) + p' + m(1-p') + p' + mv(1-p')} +$$

$$\frac{t(1-t)t(p + m(1-p))}{p + m(1-p) + p' + mv(1-p') + p' + m(1-p')} + \frac{t(1-t)^2(p + m(1-p))}{p + m(1-p) + 2(p' + mv(1-p'))} +$$

$$\frac{(1-t)t^2(p + mv(1-p))}{p + mv(1-p) + 2(p' + m(1-p'))} + \frac{(1-t)t(1-t)(p + mv(1-p))}{p + mv(1-p) + p' + m(1-p') + mv(1-p')} +$$

$$\frac{(1-t)^2t(p + mv(1-p))}{p + mv(1-p) + p' + mv(1-p') + p' + m(1-p')} + \frac{(1-t)^3(p + mv(1-p))}{p + mv(1-p) + 2(p' + mv(1-p'))}$$

Each term corresponds to a different possible permutation of young and old pollen deposition from each competitor. The permutations of t and $1 - t$ give the probability of occurrence of each of these permutations (i.e. a_j from equation 1). Each permutation has been written separately with the condition of the mutant pollen donor (with morph proportion p) first, then one opponent and then the other. The remaining ratio in each term gives F_j, the proportion of ovules fertilized by the pollen donor with morph proportion p in that type of encounter. The numerator gives the fertilization success of the mutant donor, whereas the denominator gives the total fertilization success of all three competitors summed in the same order as the probabilities of young and old pollen. Note that some permutations have the same outcome and can be combined. The actual number of pollen grains from each competitor cancels out, since it is assumed to be the same.

The ESS morph proportion, p^*, is given implicitly by

$$0 = (1-t)^2[2p^*(1-mv) + 2mv]\left[\frac{t(1-m)}{[p^*(3 - m(2v+1)) + m(2v+1)]^2} + \frac{(1-t)(1-mv)}{[3p^*(1-mv) + 3mv]^2}\right] +$$

$$2t(1-t)[p^*(2 - m(v+1)) + m(v+1)]\left[\frac{t(1-m)}{[p^*(3 - m(v+2)) + m(v+2)]^2} + \right.$$

$$\left. \frac{(1-t)(1-mv)}{[p^*(3 - m(2v+1)) + m(2v+1)]^2}\right] +$$

$$t^2[2p^*(1-m) + 2m]\left[\frac{t(1-m)}{[3p^*(1-m) + 3m]^2} + \frac{(1-t)(1-mv)}{[p^*(3 - m(v+2)) + m(v+2)]^2}\right] \quad (2)$$

Condition 1, which guarantees that the ESS involves producing some or all 3-aperturate pollen grains, is:

$$m < \frac{2v(1-t)^2\left[\frac{t}{(2v+1)^2}+\frac{(1-t)}{(3v)^2}\right]+2t(1-t)(v+1)\left[\frac{t}{(v+2)^2}+\frac{(1-t)}{(2v+1)^2}\right]+2t^2\left[\frac{t}{9}+\frac{(1-t)}{(v+2)^2}\right]}{2v(1-t)^2\left[\frac{t}{(2v+1)^2}+\frac{v(1-t)}{(3v)^2}\right]+2t(1-t)(v+1)\left[\frac{t}{(v+2)^2}+\frac{v(1-t)}{(2v+1)^2}\right]+2t^2\left[\frac{t}{9}+\frac{v(1-t)}{(v+2)^2}\right]} \quad (3)$$

Condition 2, which guarantees that the ESS involves producing some or all 4-aperturate pollen grains, is:

$$tm + (1-t)mv > 1 \quad (4)$$

For the general equations (Appendix 1), when the number of pollen donors per stigma (N) is infinite, condition 1 reduces to the opposite of condition 2 (equation 4). This implies that heteromorphism cannot exist.

Polymorphism

The conditions for polymorphism can be developed by assuming that a fraction x of the pollen donors in the population produce only 3-aperturate pollen, while others $(1 - x)$ produce only 4-aperturate pollen. Aperture number is assumed to exhibit additive genetic variance. To derive a general formula, we need to write the fitness equation of a mutant pollen donor that is confronted with pollen from the resident population. The paternal fitness of a pollen donor that produces 3-aperturate pollen is calculated as the average, over all pollinations, of the proportion of seeds fathered:

$$W_3 = \sum_i^Z P_i \sum_j F_{ij}(3) = \sum_i^Z P_i \left(\sum_j a_{ij} \frac{W_j(3)}{W_{\text{tot}ij}} \right) \quad (5)$$

This sum averages over the i different possible combinations of pollen donors (opponents with 3- or 4-aperturate pollen plus the 3-aperturate pollen donor in question). For a total of Z pollen donors per stigma, there are Z such combinations and P_i is the probability of each such combination. $F_{ij}(3)$ is the fraction of ovules on a flower that are fertilized by the 3-aperturate pollen donor in question. This fraction depends on the combination i of 3- and 4-aperturate pollen on a stigma and on the particular combination j of young and old pollen. The number of ovules per flower is assumed to be equal and thus cancels out. a_{ij} is the probability of the jth age combination for the ith combination of 3- and 4-aperturate opponents. The paternal fitness of a pollen donor that produces 4-aperturate pollen is obtained by substituting $F_{ij}(4)$ and $W_j(4)$ into this equation.

The 4-aperturate strategy can increase when rare in a 3-aperturate population when the fitness of a 4-aperturate plant with 3-aperturate opponents is greater than that of a 3-aperturate plant with 3-aperturate opponents – that is, when $W(4, 3) > W(3, 3)$, where $W(4, 3)$ and $W(3, 3)$ stand for W_4 and W_3 respectively when $x = 1$ (condition 1).

The 3-aperturate strategy can increase when rare in a 4-aperturate population when $W(3, 4) > W(4, 4)$, where $W(3, 4)$ and $W(4, 4)$ are W_3 and W_4 respectively when $x = 0$ (condition 2). A stable polymorphism can evolve only if there are parameter values for which both of these conditions are satisfied. The evolutionary change in x will have the same sign as the difference in average paternal fitness between pollen donors producing 3- and 4-aperturate pollen grains ($W_3 - W_4$) and the value of x at any polymorphic equilibrium is obtained by equating W_3 and W_4.

We illustrate this model by developing the fitness equations for three pollen donors per stigma:

$$W_3 = \frac{x^2}{3} + 2x(1-x)\left(\frac{t}{2+m} + \frac{1-t}{2+mv}\right) + (1-x)^2\left(\frac{t^2}{1+2m} + \frac{2t(1-t)}{1+m+mv} + \frac{(1-t)^2}{1+2mv}\right)$$

The first term of the equation ($x^2/3$) describes all the stigmas on which the 3-aperturate pollen from the pollen donor in question finds itself in competition with 3-aperturate pollen from its two opponents assuming random pollination. This occurs with probability $P_i = x^2$. All pollen is 3-aperturate, so age is irrelevant. Since the pollen load is homogeneous, the donors fertilize equal fractions of the ovules giving the donor in question one-third of them. The second term describes the case where the 3-aperturate pollen is confronted with 3-aperturate pollen from one opponent and 4-aperturate pollen from the other. The probabilities of the different combinations of 3- and 4-aperturate pollen (p_i) are given by the terms x and $(1-x)$. Here, the age of the 4-aperturate pollen (first young, then old) matters. The third term describes the cases where the 3-aperturate pollen is confronted with 4-aperturate pollen from its two opponents (where pollen from the two opponents could both be young, one could be young and one old, or both could be old). The probabilities of the different age combinations of pollen (a_{ij} in equation 5) are given by the powers of t and $(1-t)$. The fraction $F_{ij}(3)$ of ovules in a flower that are fertilized by 3-aperturate pollen is given by the terms with m and v. The number of pollen grains landing on each stigma is assumed to be the same for all donors, so it cancels from the equation.

The paternal fitness of a pollen donor that produces 4-aperturate pollen can be derived similarly, yielding:

$$W_4 = \frac{(1-x)^2}{3} + 2x(1-x)\left(\frac{t^2m}{1+2m} + \frac{(1-t)^2mv}{1+2mv} + \frac{2t(1-t)(m+mv)}{1+m+mv}\right) + x^2\left(\frac{tm}{2+m} + \frac{(1-t)mv}{2+mv}\right)$$

Condition 1:
$$\frac{tm}{2+m} + \frac{(1-t)mv}{2+mv} > \frac{1}{3} \tag{6}$$

Condition 2:
$$\frac{t^2}{1+2m} + \frac{2t(1-t)}{1+m+mv} + \frac{(1-t)^2}{1+2mv} > \frac{1}{3} \tag{7}$$

The value of x at equilibrium is determined by setting W_3 equal to W_4:

$$x^* = \frac{1/3 - t^2/(1+2m) - 2t(1-t)/(1+m+mv) - (1-t)^2/(1+2mv)}{2t/(2+m) + 2(1-t)/(2+mv) - 1/3 - t^2/(1+2m) - 2t(1-t)/(1+m+mv) - (1-t)^2/(1+2mv)} \tag{8}$$

The formulae derived for two pollen donors per stigma are developed in Till-Bottraud *et al.* (1994). The general equations (for any number of pollen donors per stigma) are given in Appendix 2. When N is infinite, condition 1 reduces to:

$$tm + (1-t)mv > 1 \tag{4}$$

Condition 2 reduces to the same, with the inequality reversed (see proof in Appendix 2).

Can heteromorphism invade a stable polymorphism?

We computed the paternal fitness of a heteromorphic pollen donor (that produces a proportion p of pollen grains with three apertures) in a polymorphic population (with x homomorphic 3-aperturate and $(1 - x)$ 4-aperturate individuals) in the case of three pollen donors per stigma:

$$W(p, x) = x^2\left(t\frac{p + m(1-p)}{p + m(1-p) + 2} + (1-t)\frac{p + mv(1-p)}{p + mv(1-p) + 2}\right) +$$
$$2x(1-x)\left(t^2\frac{p + m(1-p)}{p + m(1-p) + 1 + m} + t(1-t)\frac{p + m(1-p)}{p + m(1-p) + 1 + mv} +\right.$$
$$\left.(1-t)t\frac{p + mv(1-p)}{p + mv(1-p) + 1 + m} + (1-t)^2\frac{p + mv(1-p)}{p + mv(1-p) + 1 + mv}\right) +$$
$$(1-x)^2\left(t^3\frac{p + m(1-p)}{p + m(1-p) + 2m} + t(1-t)^2\frac{p + m(1-p)}{p + m(1-p) + 2mv} +\right.$$
$$2t^2(1-t)\frac{p + m(1-p)}{p + m(1-p) + m + mv} + (1-t)t^2\frac{p + mv(1-p)}{p + mv(1-p) + 2m} +$$
$$\left.2(1-t)^2t\frac{p + mv(1-p)}{p + mv(1-p) + m + mv} + (1-t)^3\frac{p + mv(1-p)}{p + mv(1-p) + 2mv}\right) \quad (9)$$

A heteromorphic strategy p can increase when rare in a polymorphic population if it provides a higher paternal fitness than the homomorphic strategies (remember that, when the population has reached the stable polymorphic frequency, the fitness of all homomorphic individuals is equal to 1/3 for three pollen donors on a stigma). Therefore, polymorphism is not stable if we can find at least one heteromorphic p strategy, such that $W(p, x^*) > W(0, x^*) = W(1, x^*) = 1/3$.

Can polymorphism invade a stable heteromorphism?

Using equation (1), we can compute the paternal fitness of a homomorphic 3- or 4-aperturate pollen donor in a population at the evolutionarily stable heteromorphic strategy, $W(1, p^*)$ and $W(0, p^*)$ respectively, and compare them to the paternal fitness of a heteromorphic pollen donor $W(p^*, p^*)$. Heteromorphism is stable if $W(1, p^*)$ and $W(0, p^*) < W(p^*, p^*)$.

RESULTS

Heteromorphism

Heteromorphism can be an ESS for any finite number of competitors. Equations (4) and (3) or (A2) give the threshold values of the parameters between which there is a heteromorphic ESS. Note that the protection threshold for the 4-aperturate strategy (equation 4) remains unchanged with the number of competitors. When the competitive advantage of

4-aperturate pollen (m) is smaller than the threshold value, the ESS is the pure 3-aperturate strategy; when it is greater, the 4-aperturate strategy is maintained. The threshold values for the protection of 3-aperturate pollen is represented for two to six competitors in Figs 1 and 2, and the ESS values (p^*) are given in Fig. 3. For values of the competitive advantage of 4-aperturate pollen (m) greater than the threshold, the pure 4-aperturate strategy is an ESS. Between these two thresholds, heteromorphism is an ESS. The threshold curve for the protection of 3-aperturate pollen becomes lower and closer to the threshold curve for the protection of 4-aperturate pollen as the number of competitors increases. Thus, the parameter space for which a mixed ESS exists becomes smaller as the number of competitors increases. The parameter space in which the 4-aperturate strategy is the ESS gets larger as the number of competitors increases and the parameter space in which the 3-aperturate strategy is an ESS remains the same. When the number of competitors is infinite, the thresholds are superposed and there is no heteromorphic ESS.

When the viability of old 4-aperturate pollen grains is high (Fig. 1b), all the thresholds are very close to each other. Heteromorphism is stable for a large range of competitive advantage of 4-aperturate pollen (m) values, or of the probability of rapid delivery (t), only when the viability of older 4-aperturate pollen is very low (Fig. 1a; note the change in scale between Fig. 1a and 1b).

Polymorphism

With two pollen donors per stigma, no stable polymorphism is obtained, and the ESS strategy is either pure 3- or pure 4-aperturate pollen (Till-Bottraud *et al.*, 1994). However, we show here that, when there are more than two donors, a stable polymorphism is possible for certain parameter values.

The range of parameter values (competitive advantage of faster germination, m; survival, v; and age probability, t) for each strategy was obtained from the conditions for the maintenance of a strategy in a population consisting primarily of the other strategy (equations 6 and 7 for three donors; equations B1 and B2 for any number of donors). With two donors, the two conditions are exactly symmetrical (Fig. 4), but when there is a finite number of donors greater than two (e.g. 3 in Fig. 4), the threshold values for the protection of each strategy are different. When the competitive advantage of 4-aperturate pollen (m) is smaller than the first threshold value (protection of the 4-aperturate), the 3-aperturate strategy is an ESS; when it is greater than the second value (protection of the 3-aperturate), the 4-aperturate strategy is an ESS; and between the two, a stable polymorphism is possible. The values of competitive advantage of 4-aperturate pollen for which a polymorphism is maintained are always smaller than the threshold value of the two strategies in the pairwise contests (Fig. 4). The parameter space in which the 4-aperturate strategy is an ESS becomes larger as the number of donors increases, while that of the 3-aperturate strategy becomes smaller. As the number of donors increases, both threshold values decrease and tend to the same fixed limit (equation 4, Fig. 4). The polymorphic zone first increases as the number of donors increases, then becomes smaller, and disappears when the number of donors approaches infinity.

A comparison with the results of the heteromorphic model shows that, for any number of donors (shown for three donors in Fig. 5), the polymorphic domain is smaller than, and included within, the heteromorphic domain. Note that the limit value (when the number of donors is infinite) is the same in both models.

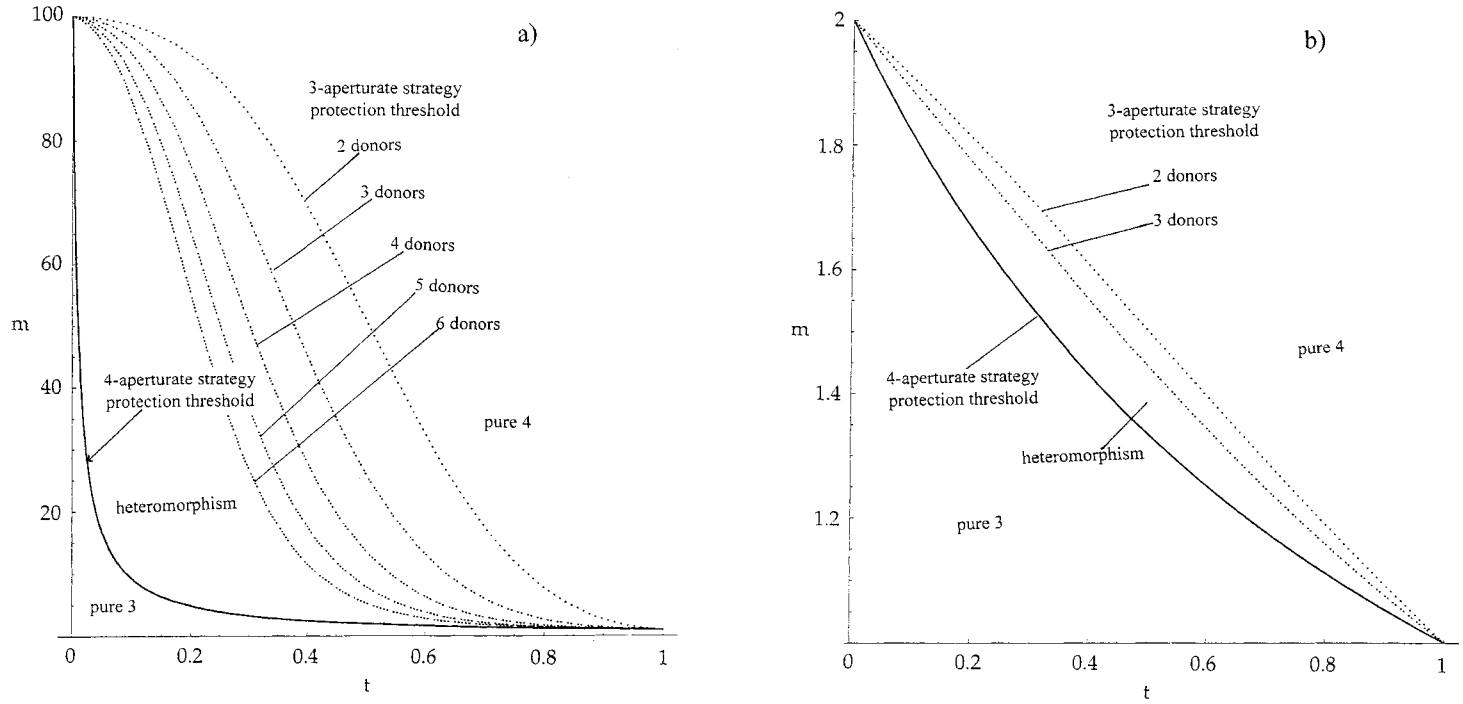

Fig. 1. Heteromorphism. Threshold values of the parameters (m and t) for the protection of the 3-aperturate, 4-aperturate and mixed (heteromorphic) strategies for two to six pollen donors per stigma. Solid line = protection threshold of the 4-aperturate strategy (equation 4). Dotted lines = protection thresholds of the 3-aperturate strategy (equation A2) for various numbers of donors. The number of points grouped together increases with the number of donors (1 point = 2 donors; 5 points = 6 donors). 'pure 3' (or 'pure 4') = area in which only pure 3-aperturate (or 4-aperturate) pollen grains can be maintained. (a) $v = 0.01$, (b) $v = 0.5$.

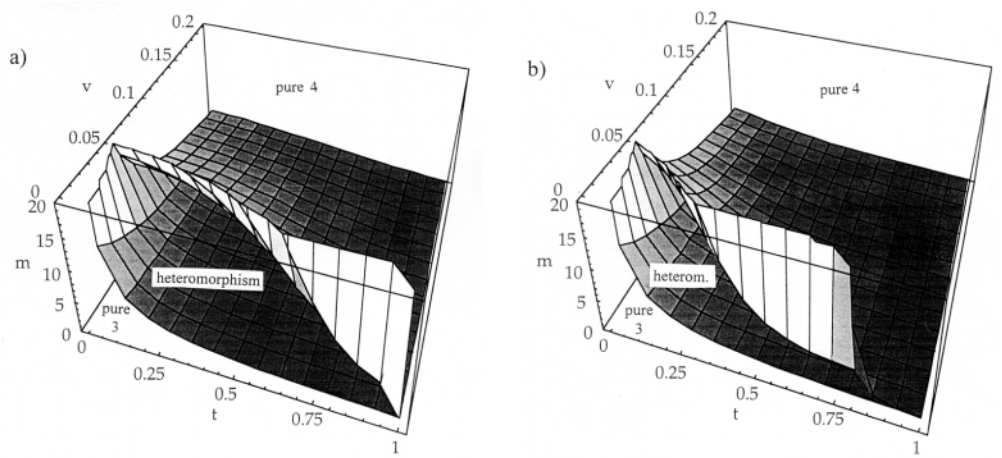

Fig. 2. Threshold values of the parameters (m, t and v) for the protection of the 3-aperturate, 4-aperturate and heteromorphic strategies: (a) two pollen donors per stigma; (b) six donors.

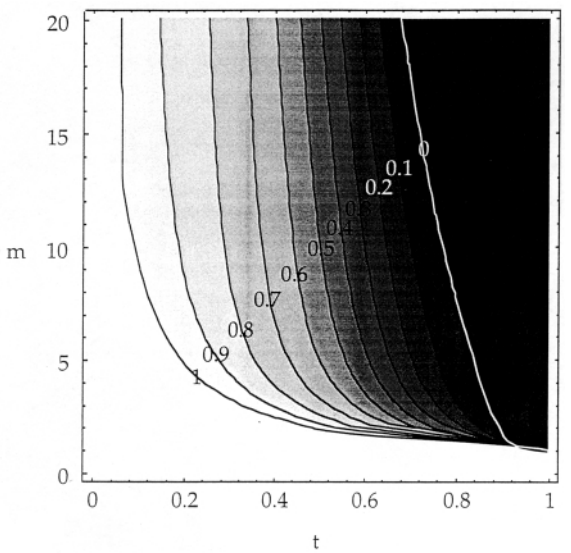

Fig. 3. Value of the ESS proportion of 3-aperturate pollen grains (p^*) as a function of m and t for two pollen donors per stigma ($v = 0.01$).

Can heteromorphism invade a stable polymorphism?

We numerically computed male fitness of a heteromorphic individual producing a proportion $p = x^*$ of 3-aperturate pollen grains in a stable polymorphic population $W(p, x^*)$ (equation 9), using Mathematica (Wolfram, 1996), for $v = 0.0005$, $v = 0.001$, $v = 0.005$, $v = 0.01$, $v = 0.05$, $v = 0.1$, $v = 0.5$ and $v = 0.8$. Within the range of m and t values where

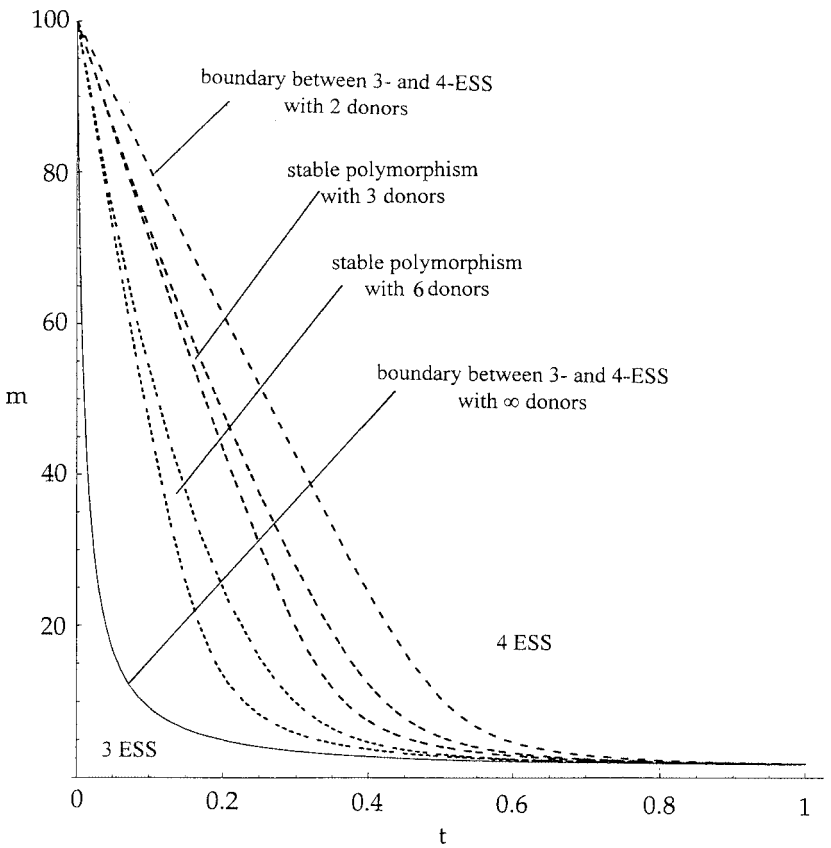

Fig. 4. Polymorphism. Threshold values of the parameters (m and t) for the protection of the 3- and 4-aperturate strategies for 2, 3, 6 and an infinite number of pollen donors per stigma ($v = 0.01$). Solid line = protection threshold of the 3- and 4-aperturate strategies for an infinite number of donors. Dashed lines = the protection thresholds of the 3- and 4-aperturate strategies for various numbers of pollen donors per stigma. The number of dashes grouped together increases with the number of pollen donors per stigma (1 dash = 2 donors; 2 dashes = 3 donors; 5 dashes = 6 donors).

polymorphism is stable, $W(p, x^*)$ is always greater than 1/3. As $W(p, x^*)$ is continuous for v, this result should be valid for all values of v. Therefore, heteromorphism can invade a stable polymorphism in the case of three pollen donors competing on a stigma.

Can polymorphism invade a stable heteromorphism?

$W(1, p^*)$, $W(0, p^*)$ and $W(p^*, p^*)$ were numerically compared for three, four and six competitors, and for values of $v = 0.005$, 0.01, 0.05, 0.1 and 0.5, using Mathematica (Wolfram, 1996). Within the range of m and t values where heteromorphism is stable, the ESS heteromorphic strategy is always better that the homomorphic strategies, showing that heteromorphism cannot be invaded by pure strategies. Again, as $W(p, p^*)$ is continuous for v, this result should be valid for all values of v.

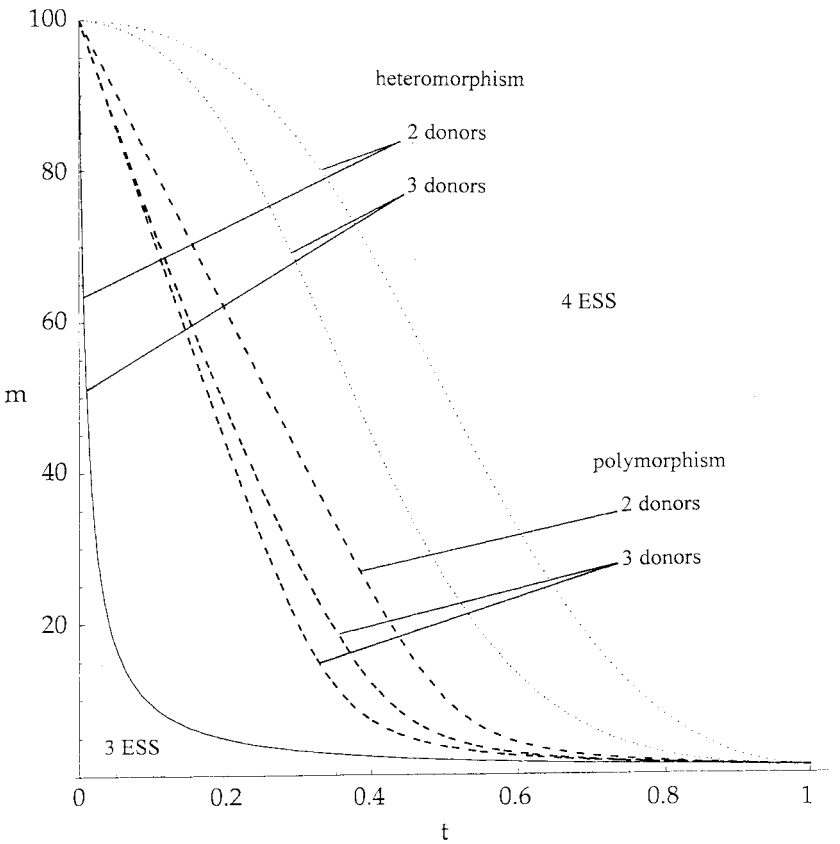

Fig. 5. Comparison of the conditions on m and t for a stable polymorphism and heteromorphism with two and three pollen donors per stigma ($v = 0.01$). Solid line = protection threshold of the 3- and 4-aperturate strategies for an infinite number of donors in both models, dots = heteromorphism, dashes = polymorphism.

DISCUSSION

In classical population genetic models with infinite population size, the parameter values for which a strategy or genotype is favoured are typically found by comparing its fitness to the population average fitness. In our scenario, this would mean that either 3- or 4-aperturate grains would win on all stigmas depending on whether $tm + (1 - t)mv$ was less than or greater than 1. Neither heteromorphism nor polymorphism could evolve. Competing against the population average is equivalent to having an infinite number of pollen donors so that each individual stigma reflects the overall composition of the population.

In real pollination systems, however, pollen grains landing on a stigma do not compete in a completely mixed fashion against the average composition of the whole population. Rather, individual stigmas act as local arenas structuring competition among subsamples of pollen donors, much like the case of local mate competition (Hamilton, 1967). To the extent that the number of seeds produced by each flower is fixed and independent of the

pollen composition on the stigma (as our models assume), pollen competition operates under soft selection (selection occurring within patches, while the total contribution of each patch to the metapopulation is independent of the mean fitness of patch residents; Christiansen, 1975). The outcome of local competition depends on the particular composition of the pollen arriving on a stigma, which varies from flower to flower. Since different competitive scenarios will arise on different stigmas due to the local frequency of 3- and 4-aperturate pollen grains and the proportions of those that are young and old, a pollen type that is inferior on average may be superior on some stigmas. If such stigmas are frequent enough, this pollen type may be maintained. The fitness benefits accruing to the locally superior pollen type saturate with increasing frequency on a stigma (stigma-level frequency dependence). This occurs because, at high frequency, the locally superior strategy competes more with itself and less with the locally inferior strategy for the fixed number of ovules. The frequencies at which different pollen types occur on stigmas depend, in part, on their frequencies in the population at large. There may be parameter values at which a particular pollen strategy has higher fitness when rare in the population (and thus on stigmas) but have lower fitness when common. Thus, frequency dependence on stigmas creates frequency dependence in the population, which can result in heteromorphic or polymorphic ESSs. The random variation among stigmas in pollen composition, which creates the opportunities for grains that are inferior on average to win, is greater when the number of pollen donors is low.

It makes intuitive sense that polymorphism or heteromorphism can evolve under some subset of conditions for which 4-aperturate grains are better competitors when young, but worse when old. Such conditions would include the possibility of either morph being better 'on average'. Yet our results are asymmetric, with polymorphism and heteromorphism only evolving when 4-aperturate grains are better on average. Strategies involving 3-aperturate grains can invade when 4-aperturate grains are better on average because, with few pollen donors, there is high variance in pollen composition on stigmas and there are 'refuge' stigmas with mostly inferior old 4-aperturate grains. Since the performance of 3-aperturate grains does not vary with age, strategies involving 4-aperturate grains can only invade when 4-aperturate grains are better 'on average'.

Heteromorphism

In the heteromorphism model, all plants can produce both pollen types in various proportions and heteromorphism can be stable for all finite numbers of pollen donors. The boundary conditions between pure 3-aperture and heteromorphic ESSs do not change with the number of pollen donors per stigma and correspond to the boundary between pure 3- and pure 4-aperturate pollen for models in which plants compete against the population average strategy. However, reducing the number of pollen donors from infinity changes the boundary conditions for pure 4-aperturate pollen and lets heteromorphic plants invade the domain where the 4-aperturate grains are better on average.

As mentioned above, a finite number of pollen donors per stigma creates variance in pollen composition among stigmas, which increases as the number of competitors decreases. However, in the heteromorphic model, the most important aspect of this variance is in the frequencies of young and old pollen. Because the mutant and resident aperture number variants can have very similar pollen type ratios, a small number of pollen donors does not necessarily result in high variance among stigmas in the proportions of 3- and

4-aperturate grains. Thus, it is the variation among stigmas in the proportions of young and old pollen, not 3- and 4-aperturate grains, that drives the evolution of heteromorphism.

Because we assume that pollen age does not affect the fitness of 3-aperturate grains, the boundary between the pure 3-aperturate ESS and heteromorphic ESSs does not change with the number of pollen donors. This is because, in a pure 3-aperturate population, stigmas that by chance have a high proportion of old 3-aperturate grains do not create refuges where pollen donors that produce a few 4-aperturate grains can invade. However, the number of pollen donors does affect the position of the boundary between the pure 4-aperturate ESS and heteromorphic ESSs. This is because stigmas that by chance have a high proportion of old 4-aperturate grains create refuges where pollen donors that produce a few 3-aperturate grains can invade, even when their fitness is lower on average.

This co-existence of 3-aperturate grains despite lower mean fitness can be thought of in terms of a trade-off between mean and variance. The more variable specialist 4-aperturate grains can only win or co-exist as heteromorphism when they have a higher mean fitness. However, the generalist 3-aperturate grains can co-exist as part of a heteromorphic strategy despite lower mean performance, because of their lower variance in performance. Circumstances like this are similar to bet-hedging because they involve a trade-off between mean and variance, but are not considered to be bet-hedging *sensu stricto* because the variance is spatial (among stigmas) rather than temporal (among years) (Seger and Brockmann, 1987).

Polymorphism

This model assumes that each plant can produce only one type of pollen. Because mutant and resident aperture numbers produce totally different pollen types, the variance among stigmas created by a finite number of pollen donors acts both through the frequencies of young versus old pollen and the proportions of 3- and 4-aperturate grains. There are two main types of contests: homogeneous contests between plants that produce the same type of pollen and heterogeneous contests between plants, some of which produce different types of pollen. Because seed production per flower is assumed to be independent of pollen source, pollen types have equal fitness across the different types of homogeneous contests and these do not affect the evolutionary outcome. The outcome depends only on what happens in heterogeneous contests and the proportions of the different kinds of heterogeneous contests.

An important result of this model is that stable polymorphism cannot exist with either two or an infinite number of pollen donors per stigma, but can exist for any finite number of donors greater than two. This is due to the lack of variance in the frequency of pollen types in heterogeneous contests with either two or an infinite number of donors. With only two donors, all heterogeneous contests consist of 50 : 50 mixtures of 3- and 4-aperturate grains, although age may vary. At this single frequency, either 3- or 4-aperturate grains will win on average regardless of the frequency of 4- and 3-aperturate morphs in the population. Whichever wins on average with 50 : 50 mixtures on stigmas will be the ESS for the population, because only heterogeneous contests result in differential fitness. Thus, while local frequency dependence exists in the two-donor model, local frequency does not vary in the contests that count. With an infinite number of pollen donors, there are only heterogeneous contests, all of which occur at the population frequency of pollen morphs and at the population frequency of young and old 4-aperturate pollen. All contests are the same and

will be won by either 4- or 3-aperturate grains depending on which one is better on average, but not depending on the proportions of the two variants. With three pollen donors or more, several types of heterogeneous contests occur in frequencies that depend on the proportions of the different morphs and polymorphism can be stable.

Another noteworthy difference between our two models is in the position of the pure 3-aperturate ESS boundary. In the heteromorphic model, the boundary between conditions for a pure 3-aperture ESS and a mixed ESS is independent of the number of pollen donors and is equal to the boundary between the condition under which 3- or 4-aperturate grains are better on average (Fig. 1). In the polymorphic model, the position of the boundary between a 3-aperture ESS and a mixed ESS depends on the number of pollen donors. Furthermore, for numbers of pollen donors less than infinity, the conditions for a pure 3-aperture ESS extend well into the domain where 4-aperturate grains are better on average (Fig. 4).

In the heteromorphic model, a heteromorphic strategy can involve the production of a very small proportion of 4-aperturate grains, which does not provide a refuge for 3-aperturate grains to invade unless they are better on average. However, in the polymorphic model, a 4-aperturate pollen donor produces all 4-aperturate grains. Even if the proportion of 4-aperturate plants in the population is very small, 4-aperturate grains will be fairly common in heterogeneous contests when the number of pollen donors per stigma is small. Thus, in the polymorphic model, when there are small numbers of pollen donors per stigma, random high local frequencies of old 4-aperturate grains in heterogeneous contests will permit 3-aperturate plants to take over under some conditions where pure 4-aperturate grains are better on average. Similarly, limitations on the values pollen type frequencies can take on stigmas explains why the conditions for polymorphism are more restrictive than for heteromorphism at the boundary between the pure 4-aperture ESS and mixed ESSs.

Biological implications

The relevance of the model parameters to pollen aperture evolution in natural systems was discussed for the two-competitor models in Till-Bottraud *et al.* (1994). There it was mentioned that the most relevant issue is the time scale at which pollen viability declines compared to the speed with which pollen is picked up and delivered. Species for which pollen longevity is low and the pollination ecology results in long lags between pollen production and delivery should evolve a low number of pollen apertures. High pollinator activity with rapid pollination combined with high pollen longevity will favour a high number of apertures. Variable time from pollen production to delivery, combined with a high fitness advantage of one morph and low viability of the other, will promote the production of more than one pollen type. It was argued that although some of these parameters are hard to measure and only limited data exist, the conditions favouring the production of multiple pollen types are likely to be fairly common in nature.

This paper has explored the effects of the number of pollen donors. The general effect of an increase in pollen donors per stigma is to favour the pure 4-aperturate specialist strategies, both in heteromorphic and polymorphic models. In the heteromorphic model, the pure 3-aperture domain remains constant, whereas it decreases in the polymorphic model. The heteromorphic or polymorphic domains decrease with the number of pollen donors. Moreover, for a given number of donors, the parameter space in which polymorphism is stable is much smaller than that for heteromorphism.

The large qualitative difference between two and three donors in the polymorphic model is probably not relevant biologically: even with two donors, several types of heterogeneous contests with different pollen type frequencies are possible if the donors provide variable amounts of pollen on the stigmas. The number of pollen grains from one plant has been observed to decrease exponentially in the course of a pollinator's visits (Thomson and Plowright, 1980; Thomson *et al.*, 1986; Morris *et al.*, 1994). The last plant visited by the pollinator provides a large amount of pollen to a given stigma, the second-to-last provides less, and so on. Each plant, depending on its order in the pollinator's visits, will provide a different amount of pollen to different contests. In wind-pollinated species, the nearest plants usually sire more offspring than plants located further away (Erickson and Adams, 1989), and undoubtedly provide more pollen grains. So even with two pollen donors per stigma, we expect to find a large array of heterogeneous contests under natural conditions. Thus polymorphism could theoretically be found for any finite number of donors greater than one.

The number of pollen donors per stigma can be seen as another parameter related to pollinator activity, together with the chance of rapid pollen delivery. Indeed, if pollinators are very active, they will visit many flowers in a short time and deposit viable pollen from many plants on the same stigma. The result of an increase in pollinator activity is to favour the specialist 4-aperturate pollen type both through competitor number and the speed of pollen delivery.

In natural situations, the number of pollen donors on a stigma is difficult to assess directly, but it can be estimated from pollen carry-over data or from paternity analyses of single fruits. The former (Table 2) are likely to provide an over-estimate of the number of donors on a stigma: if pollen from a given plant can be transported up to the xth stigma of a visitation sequence, most of the intervening plants should also provide pollen to that stigma. The latter (Table 3), giving the number of successful donors, will usually provide an under-estimate. Few donors (typically between two and six for insect-pollinated species, slightly more for hummingbird-pollinated ones) provide a lot of pollen grains to a single stigma. Thus the infinite pollen donor model, although theoretically revealing, is unrealistic. Two pollen donors on a stigma are necessary for pollen competition to occur, but the number of donors is never very high, so that the conditions for heteromorphism or polymorphism should easily be obtained in nature. This, of course, requires that the other characteristics of pollen and pollinators be in the range for heteromorphic or polymorphic ESSs: (i) that the time of pollen collection in relation to that of anther dehiscence is variable and (ii) that the viability decay of multi-aperturate pollen is much greater than that of few-aperturate pollen (during the time interval of possible pollen collection).

Even if the conditions in which we can find polymorphism are much more restricted than for heteromorphism, our models still predict that polymorphic species could exist. Yet, in a survey of over 200 species, no purely pollen-polymorphic species were found (Mignot, 1995). In the models, polymorphism is stable in a range of parameters where heteromorphism is also a stable strategy. However, we have shown that at least for the case of three pollen donors on a stigma, polymorphism can be invaded by heteromorphic strategies, whereas the reverse is not possible. This suggests that polymorphism can always be replaced by heteromorphism. Heteromorphism can be obtained by slight modifications of the developmental processes acting during meiosis (Ressayre *et al.*, 1998) and a large number of the heteromorphic species in Mignot (1995) have a largely dominant pollen type and small

Table 2. Pollen carry-over data from the literature

Plant species	Pollinator	Experimental conditions[a]	N_{max}[b]	N (more than 5 PG)[c]	N of flowers observed[d]	Reference
Echium vulgare	*Bombus*	dye + emasc.	32	5	32	Rademaker *et al.* (1997)
Ranunculus bulbosus	bees	effective CO	5	5	>30	Mogie and Stamp (1995)
Lithophragma parviflorum	insects	effective CO	6	3–6	?	Pellmyr and Thompson (1996)
Brassica napus	*Bombus*/*Apis*	dye, field	20/10	5.6/4.5	20	Cresswell *et al.* (1995)
Lotus corniculatus	*Bombus*	dye, natural	64 (11 plants)	5 plants	88 plants	Rasmussen and Brodsgaard (1992)
Ipomopsis agregata	hummingbirds	natural/dye	>35/30	30/20	35/30	Morris *et al.* (1994)
Delphinium nelsonii	*Bombus*	emasc.	30	20	35	Morris *et al.* (1994)
Linaria vulgaris	*Bombus*	emasc.	>10	>10	10	Morris *et al.* (1994)
Erythronium grandiflorum	*Bombus*	natural	20	5	20	Morris *et al.* (1994)

[a] natural = natural population, dye = dye was used as an analogue of pollen, emasc. = anthers from the recipient flowers were emasulcated, field = experimental array, effective CO = pollen was assessed as being carried over when seeds were formed after the pollinator visit.
[b] Maximum number of flowers to which pollen (or dye) was carried over.
[c] Number of flowers to which more than 5 pollen grains (or 10 dye particles) were transported (estimated from the carry-over curves in the references).
[d] Number of flowers in a sequence.

Table 3. Paternity analyses data from the literature

Plant species	Compatibility system[a]	Pollinator	*N* fruits[b]	% MP[c]	Fathers[d]			*N* possible fathers	Reference
					2	3	4		
Asclepias exaltata	SI	hummingbird	103	12	12	0	0	55 (nat. pop.)	Broyles and Wyatt (1990)
Acacia melanoxylon	?	insects	196	12	12	0	0	? (nat. pop.)	Muona *et al.* (1991)
Glycine argyrea	SC	insects	40	60	52	8	0	>20 (nat. pop.)	Brown *et al.* (1986)
Trifolium repens	SI	*Apis*	?	100	50	25	25	4	Michaelson-Yeates *et al.* (1997)
		Bombus	(many)	90	30	50	10		
Phaseolus vulgaris	SC	hymenoptera	>6000	5.8	5.4	0.4	—	3	Ibarra-Perez *et al.* (1996)
				8.1	7.0	1.1	—		
Ipomopsis agregata	SI	hummingbird	30	100	up to 9	($\bar{x}$ = 4.44)		? (nat. pop.)	Campbell (1998)

[a] SC = self-compatible; SI = self-incompatible.
[b] Number of fruits analysed.
[c] Percentage of multiply sired fruits.
[d] Number of fruits with 2, 3 or 4 fathers. For *I. agregata*, the maximum and mean number of fathers per fruit are given. In *T. repens*, the experiment was repeated in two different years and the two results are given.

proportions of the other. Therefore, heteromorphism is easy to achieve when homomorphism is possible. In such circumstances, it is likely that heteromorphism would systematically win against polymorphism, explaining why no pollen-polymorphic species were found.

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APPENDIX 1: HETEROMORPHISM

The general formula for $N+1$ pollen donors (the mutant plant against N opponents) is:

$$W(p,p') = \sum_{i=0}^{N} C_N^i t^i (1-t)^{N-i} \times \left[\frac{t(p+m(1-p))}{p+m(1-p)+i(p'+m(1-p'))+(N-i)(p'+mv(1-p'))} + \right.$$
$$\left. \frac{(1-t)(p+mv(1-p))}{p+mv(1-p)+i(p'+m(1-p'))+(N-i)(p'+mv(1-p))} \right]$$

where i indicates the number of opponents that provide young pollen.

The ESS p^* is obtained from $\partial W(BA)/dq|_{q=q'=q^*} = 0$:

$$0 = \sum_{i=0}^{N} C_N^i t^i (1-t)^{N-i} [p^*(N-m(v(N-i)+i))+m(v(N-i)+i)] \times$$
$$\left[\frac{t(1-m)}{(p^*(N+1-m(v(N-i)+i+1))+m(v(N-i)+i+1))^2} + \right.$$
$$\left. \frac{(1-t)(1-mv)}{(p^*(N+1-m(v(N-i+1)+i))+m(v(N-i+1)+i))^2} \right] \quad \text{(A1)}$$

This equation gives ESS candidates, p^*, implicitly as a function of the parameters. The conditions for heteromorphism ($0 < p^* < 1$) to be an ESS (see text) are given by:

Condition 1: $\partial W(p, p')/\partial p|_{p=p'=0} > 0$ ($\mathrm{d}W(0) > 0$)

$$\Leftrightarrow m < \frac{\sum_{i=0}^{N} C_N^i t^i (1-t)^{N-i} (i + v(N-i))[t/(v(N-i)+i+1)^2 + (1-t)/(v(N-i+1)+i)^2]}{\sum_{i=0}^{N} C_N^i t^i (1-t)^{N-i} (i + v(N-i))[t/(v(N-i)+i+1)^2 + v(1-t)/(v(N-i+1)+i)^2]} \quad \text{(A2)}$$

Condition 2: $\partial W(p, p')/\partial p|_{p=p'=1} < 0$ ($\mathrm{d}W(1) < 0$) $\Leftrightarrow$ $tm + (1-t)mv > 1$ (4)

APPENDIX 2: POLYMORPHISM

The paternal fitness of a pollen donor that produces 3-aperturate pollen when it is confronted with N opponents from the population is:

$$W_3 = \sum_{i=0}^{N} C_N^i x^i (1-x)^{N-i} \sum_{j=0}^{N-i} C_{N-i}^j t^j (1-t)^{N-i-j} \left(\frac{1}{1 + i + mj + (N-i-j)mv} \right)$$

where i represents the number of opponents producing 3-aperturate pollen and $(N - i)$ is the number of opponents producing 4-aperturate pollen. Among these $(N - i)$ opponents, j provide young pollen and $(N - i - j)$ old pollen. As the individual fitness of 3-aperturate pollen is independent of its age, the numerator is 1.

Similarly, the paternal fitness of a pollen donor that produces 4-aperturate pollen is:

$$W_4 = \sum_{i=0}^{N} C_N^i x^j (1-x)^{N-i} \sum_{j=0}^{N-i} C_{N-i}^j t^j (1-t)^{N-i-j} \left(\frac{tm}{m + i + mj + (N-i-j)mv} + \frac{(1-t)mv}{mv + i + mj + (N-i-j)mv} \right)$$

In this case, the age of the 4-aperturate pollen from the pollen donor in question (numerator) must be taken into account.

The value of x^* can be obtained by equating W_3 and W_4. The 4-aperturate strategy will increase in frequency in a 3-aperturate population when $W(4, 3) > W(3, 3)$ (condition 1). That is, when

$$\frac{tm}{m+N} + \frac{(1-t)mv}{mv+N} > \frac{1}{1+N} \quad \text{(B1)}$$

The 3-aperturate strategy will increase in frequency in a 4-aperturate population when $W(3, 4) > W(4, 4)$ (condition 2). That is, when

$$\sum_{j=0}^{N} C_N^j t^j (1-t)^{N-j} \left(\frac{1}{1 + mj + (N-j)mv} \right) > \frac{1}{N+1} \quad \text{(B2)}$$

When N is infinite, the limit value of this equation is obtained as follows:

$$\text{(equation 4)} \Leftrightarrow \sum_{j=0}^{N} C_N^j \, t^j (1-t)^{N-j} \left(\frac{1}{1/(N+1) + mv(N/(N+1)) + m(1-v)\,(j/(N+1))} \right) > 1$$

$$\lim_{N\to\infty} \sum_{j=0}^{N} C_N^j \, t^j (1-t)^{N-j} \left(\frac{1}{1/(N+1) + mv(N/(N+1)) + m(1-v)(j/(N+1))} \right) =$$

$$\lim_{N\to\infty} \sum_{j=0}^{N} C_N^j \, t^j (1-t)^{N-j} \left(\frac{1}{mv + m(1-v)(j/N)} \right) = \lim_{N\to\infty} E\left(\frac{1}{mv + m(1-v)(j/N)} \right)$$

where j/N is the proportion of 1 outcomes following an N times repeated Bernoulli draw. Each trial is independent and identically distributed, and corresponds to a probability t (the probability of j 1's is thus $C_N^j \, t^j (1-t)^{N-j}$). Thus, following the law of large numbers,

$$= \frac{1}{mv + m(1-v)E(j/N)}$$

$$= \frac{1}{mv + m(1-v)t}$$

$$= \frac{1}{tm + (1-t)mv}$$