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*The American Naturalist*, Vol. 144, No. 3. (Sep., 1994), pp. 395-411.

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*The American Naturalist* is currently published by The University of Chicago Press.

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## SELECTION ON POLLEN MORPHOLOGY: A GAME THEORY MODEL

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Submitted November 20, 1992; Revised September 27, 1993; Accepted September 30, 1993

*Abstract.*—Variation in pollen aperture number has been widely described among and within angiosperm species, and fossil data indicate that aperture number has increased over geological time. Within species, variation in aperture number is very often found within individual plants (heteromorphism), with the genetic variation being expressed in morph proportions produced by individuals. We present models of the evolution of pollen aperture number motivated by previous results on *Viola diversifolia* in which higher aperture number results in more rapid germination and lower longevity. The models demonstrate that under certain conditions selection results in a mixed evolutionarily stable strategy (ESS), in which all plants produce all types of pollen. In contrast, selection cannot easily maintain a standard genetic polymorphism with each pollen morph produced on a different plant. These predictions match the available evidence on patterns of natural variation in pollen aperture number. The models and data lead to an unusual evolutionary prediction: a population-level increase in the mean number of pollen apertures should occur by a progressive increase in the proportion of higher aperture-number morphs produced on individual plants, rather than by an increase in the proportion of individuals that consistently produce pollen with different aperture numbers.

Plant species vary markedly with respect to pollen morphology and physiology (Erdtman 1966; Layka 1976; McNeill and Crompton 1978; Hoekstra 1983), and the fossil record shows an evolutionary increase in aperture number in angiosperms since the Mesozoic (Walker and Doyle 1975; Van Campo 1976). The ancestral condition in seed plants is to have pollen grains with one aperture, and this condition was retained by early lines of angiosperms (including monocots). Recent evidence suggests that a shift from one to three apertures occurred once, or at most a few times, in the line(s) leading to the vast majority of angiosperm species (Donoghue and Doyle 1989). Subsequently, there have been numerous shifts from three to four or more apertures as well as a reduction in aperture number.

Because the aperture is the place at which pollen tubes are initiated as well as pollen and stigma interact, it seems logical to hypothesize that this increase in aperture number has led to a higher probability of quick germination. This hypothesis cannot be tested at the interspecific level and requires intraspecific polymorphism. Since population-genetics models usually consider polymorphism between

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individuals with selection or drift acting on alternative types, we might expect to find polymorphic situations in which different plants of the same species produce different pollen morphs. Instead (except for cases of heterostyly), when pollen morph polymorphism has been observed, it has always occurred within plants, with the genetic variation being expressed as differences in morph proportions produced by individuals. In a survey of 186 species from families described as "polymorphic" by Erdtman (1966), we found approximately 30% of species with some level of heteromorphism (different morphs in all flowers of the same plant), the remaining species being homomorphic (one morph in a species) (Till et al. 1989; Dajoz et al. 1991; Mignot et al., in press).

One potentially confusing subtlety of plant life cycles is that pollen grains are actually haploid organisms (gametophytes) that produce the male gametes. Yet pollen morphology is determined by the diploid parent (the sporophyte; Baker 1966; Heslop-Harrison 1971; Charlesworth 1979). Thus, pollen variation of the kind described above does indeed represent a parental heteromorphism, not a genetic polymorphism among pollen grains.

In this article we explore models of natural selection on pollen grain aperture number. We use game theory (Maynard Smith 1982) to distinguish between cases in which selection results in a mixed evolutionarily stable strategy (ESS) *sensu stricto* (i.e., all individuals exhibit more than one strategy) and a polymorphism at the population level. The ESS approach (and the concept of strategy) has previously been applied to plants in a number of other situations, including dispersal (Hamilton and May 1977), sexual allocation (Charnov 1982), and defense against herbivores (Till-Bottraud and Gouyon 1992).

In our models the selection of pollen grain aperture number is driven by competition between pollen grains during germination and subsequent pollen tube growth (see Mulcahy 1979). Pollen competition can be an important selective force occurring at this stage of the life cycle; faster-growing pollen genotypes are more likely to fertilize ovules and transmit their traits to subsequent generations (Mulcahy 1974; Mulcahy and Mulcahy 1975; McKenna and Mulcahy 1983; Snow and Spira 1991).

Our models assume two physiological consequences of having a greater aperture number: faster germination and reduced pollen longevity (with consequent benefits and costs for successful gametophytic competition for ovules). These assumptions are motivated by the biology of *Viola diversifolia* (Gingins) Becker (Dajoz et al. 1991). Individual pollen grains have either three or four apertures, and grains with four apertures germinate faster than those with three, which thus provides a potential competitive advantage. However, the survival of four-aperturate pollen declines more rapidly. Variation in the proportions of the different pollen morphs has a genetic basis in *Viola diversifolia* as demonstrated by a significant family effect on the proportions of the two morphs in maternal progenies from natural crosses (Dajoz et al. 1993).

#### THE MODELS

As with most game theory models, we will not specify the exact genetic mechanism but assume that "there is some additive genetic variance" (Maynard Smith

1982, p. 4). Indeed, we do not know the precise genetic mechanism for aperture number variation in *Viola diversifolia* or any other species.

We develop three models: a discrete-time homomorphic model in which each plant produces only one pollen type and the pollen arriving on a stigma can be either “young” or “old,” a discrete-time heteromorphic model in which each plant produces a proportion of two pollen morphs, and a continuous-time heteromorphic model in which the age of pollen arriving at a stigma (and its age-dependent physiological consequences) can vary continuously. Our models consider selective events that occur when pollen from a plant has been delivered to a series of flowers, simultaneously with pollen from another plant. Each stigma receives an equal amount of pollen from the focal plant and one other member of the population. On any particular stigma, a pollen donor competes with one other individual, though in the aggregate it competes with a variety of individuals, because it produces many flowers and delivers pollen to many stigmas during a flowering season.

We make no assumption about pollinator limitation in the sense of the number of flowers actually pollinated, except when speculating as to how this might affect pollen delivery times. For example, although a low proportion of flowers pollinated because of low pollinator activity might be correlated with delays in pollen pickup and the delivery of older pollen, we do not consider this scenario. We do, however, assume that, when a flower is pollinated, there is more than enough pollen to fertilize all the ovules. This assumption has two simplifying implications. First, single-parent pollinations have no selective impact and can be ignored (i.e., faster germination will be of no benefit, nor will reduced viability be a cost in single-parent pollinations). Second, in simultaneous multiparent pollinations of a stigma, there will be enough pollen so that competition occurs. We assume that this is frequent enough to be of selective importance but unlikely enough that it seldom involves more than two pollen donors. The reasonableness of these assumptions is discussed below.

The absolute fitness accruing to a plant from pollination of a particular stigma equals the proportion of seeds fathered times the number of seeds in the fruit. If we assume that each fruit produces the same number of seeds (or at least that the number of seeds is independent of the pollen type that fertilizes the ovules), then the total paternal fitness of a plant exhibiting a particular pollen morphology can be modeled as the average, over all pollinations, of the proportion of seeds fathered.

#### *The Discrete-Time Homomorphic Model*

A fraction  $x$  of the plants in the population produce pollen with three apertures (and  $1 - x$  plants produce four-aperturate pollen), and aperture number in a plant exhibits additive genetic variance. On day  $D$ , an equal amount of pollen from two plants arrives on the stigma. It can be either young (from a freshly dehisced anther, day  $D$ ) with a probability  $t$  ( $0 \leq t \leq 1$ ) or old (issued from an anther that dehisced on  $D - 1$ ) with a probability  $1 - t$ . The competitive advantage (relative fitness) of four-aperturate pollen is  $m$  ( $>1$ ) at fertilization, which includes how much faster four-aperturate pollen grains germinate and whatever fertilization advantage this provides. The cost of higher aperture number is that the viability

of old four-aperturate pollen is reduced by a factor  $v$  ( $0 \leq v \leq 1$ ), compared to three-aperturate pollen, which does not lose viability with age. On the whole, we set the success of three-aperturate pollen to one (independent of age) and the relative success of a four-aperturate pollen to  $m$  when young and to  $mv$  when old. Only the case where  $mv < 1$  is of interest, since otherwise four-aperturate pollen grains are more successful than three-aperturate pollen grains regardless of age, and the pure four-aperturate strategy will be the ESS.

We assume that the proportions of individuals give the probabilities of encounters (see Maynard Smith 1982). Total paternal fitness will be the sum of fitness accruing to the pollen donor in question from each type of event weighted by its probability of occurrence.

Given these assumptions, the paternal fitness of a plant that produces three-aperturate pollen is calculated as the average, over all pollinations, of the proportion of seeds fathered:

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

Since the actual number of pollen grains landing on each stigma is assumed to be the same for both pollen donors, it cancels from the equation. The competing plant has a probability  $x$  of being three-aperturate (and  $1 - x$  of being four-aperturate). In the first term of the equation ( $x/2$ ), the three-aperturate pollen from the focal plant is competing with three-aperturate pollen from an other plant in the population, and pollen from each plant has a 50% chance of winning, regardless of pollen age. In the second term, the three-aperturate pollen is confronted with four-aperturate pollen from the other plant. This pollen can be either young (probability  $t$ ), and then the three-aperturate pollen grains win in one out of  $1 + m$  cases (as each four-aperturate pollen grain is  $m$  times better than a three-aperturate grain); or it can be old (probability  $1 - t$ ), and then the three-aperturate pollen grains win in one out of  $1 + mv$  cases (as this time each four-aperturate pollen grain is  $mv$  times "better").

Similarly, the paternal fitness of a plant that produces four-aperturate pollen is

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

The evolutionary change in  $x$  will have the same sign as the average paternal fitness difference between plants producing three- and four-aperturate pollen grains:

$$W_3 - W_4 = \frac{t}{1 + m} + \frac{1 - t}{1 + mv} - 0.5.$$

Notice that this fitness difference does not depend on  $x$ , so that no polymorphic state can be evolutionarily stable. Three-aperturate pollen will be the ESS for all values of  $x$  when

$$\frac{t}{1 + m} + \frac{1 - t}{1 + mv} > 0.5,$$

and four-aperturate pollen will be the ESS when the inequality is reversed (aperture number will be selectively neutral if  $W_3 - W_4 = 0$ ).

*The Heteromorphic Models*

To calculate the ESS for pollen heteromorphism, we computed the total paternal fitness of a plant that produces a proportion  $p$  of pollen grains with three apertures and  $1 - p$  pollen grains with four apertures when it occurs in a population of plants that produce a proportion  $p'$  of pollen grains with three apertures ( $W(p, p')$ ). In this case, the variation in morph proportions is assumed to have a partially additive genetic basis. All the biological assumptions and parameter definitions from the previous model still apply, except those regarding the distribution of pollen morphs within and among plants (see the list of symbols in App. A).

*Discrete-time.*—Total paternal fitness is again calculated as the average, over all pollinations, of the proportion of seeds fathered.

On each stigma we assume that four independent events are possible: young pollen grains from two plants arrive simultaneously on the stigma (probability  $t^2$ ), young pollen grains from a plant in question and old pollen grains from a second plant arrive simultaneously on the stigma (probability  $t[1 - t]$ ), old pollen grains from a plant in question and young pollen grains from a second plant arrive simultaneously on the stigma (probability  $[1 - t]t$ ), or old pollen grains from both plants arrive simultaneously on the stigma (probability  $[1 - t]^2$ ).

We then have

$$\begin{aligned}
 W(p, p') = & \frac{t^2[p + m(1 - p)]}{p + m(1 - p) + p' + m(1 - p')} \\
 & + \frac{t(1 - t)[p + m(1 - p)]}{p + m(1 - p) + p' + mv(1 - p')} \\
 & + \frac{(1 - t)t[p + mv(1 - p)]}{p + mv(1 - p) + p' + m(1 - p')} \\
 & + \frac{(1 - t)^2[p + mv(1 - p)]}{p + mv(1 - p) + p' + mv(1 - p')}.
 \end{aligned}$$

Each term corresponds to a different possible combination of young and old pollen deposition with its probability of occurrence. The ratio in each term gives the proportion of ovules fertilized by the individual with morph proportion  $p$  in that type of encounter. Here again, the actual number of pollen grains from each plant cancels out because it is assumed to be the same. The numerator gives the number of fertilizations achieved by this individual, while the denominator gives the number of fertilizations achieved by both pollen parents. Note that since the individual under consideration (with morph proportion  $p$ ) occurs in a population characterized by morph proportion  $p'$ , it will always compete with a pollen parent with morph proportion  $p'$ .

Strategy  $p^*$  is an ESS if an individual with strategy  $p \neq p^*$  cannot invade the population. This is true when the fitness-maximizing value of  $p$  is the same as

the actual population value  $p'$ . Otherwise selection would tend to move the population value toward 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

$$\begin{aligned} \frac{\partial W(p, p')}{\partial p} \Big|_{p=p'=p^*} &= 0 \\ \Rightarrow t^2(1-m)[p^*(1-mv) + mv][p^*(2-m-mv) + m + mv]^2 \\ &+ (1-t)^2(1-mv)[p^*(1-m) + m] \\ &\times [p^*(2-m-mv) + m + mv]^2 \\ &+ 4(1-t)[(1-m)(1-mv)(2p^* - 1) + 1 - m^2v] \\ &\times [p^*(1-mv) + mv][p^*(1-m) + m] = 0. \end{aligned}$$

This equation (a third-order polynomial in  $p^*$ ) gives ESS candidates,  $p^*$ , implicitly as a function of the other parameters. To ensure that  $p^*$  is an ESS, we must confirm that it is a maximum (i.e., we must show that  $\partial W(p, p')/\partial p|_{p'=p^*} > 0$  for  $p < p^*$  and  $\partial W(p, p')/\partial p|_{p'=p^*} < 0$  for  $p > p^*$ ).

The ESS proportion  $p^*$  was determined for various combinations of the parameter values ( $0 < v \leq 1$ , with a step of 0.05;  $0 \leq t \leq 1$ , with a step of 0.1;  $1 < m \leq 2$ , with a step of 0.1;  $2 \leq m \leq 5$ , with a step of 0.5;  $6 \leq m \leq 40$ , with a step of 1; and  $45 \leq m \leq 100$ , with a step of 5). For each combination we graphically verified that  $p^*$  was a fitness maximum. For all combinations of the parameters tested, the ESS is a unique global fitness maximum.

The conditions for a heteromorphic ESS are that some  $p$  greater than zero have greater fitness than  $p = 0$  in a population with  $p' = 0$  and that some  $p$  less than one have greater fitness than  $p = 1$  in a population with  $p' = 1$ . These conditions are given by  $\partial W(p, p')/\partial p|_{p=p'=0} > 0$  and  $\partial W(p, p')/\partial p|_{p=p'=1} < 0$ , which yield

$$m < 1 + \frac{(1-t)(1-v)[(1+v)^2(1-t) + 4vt]}{t^2v(1+v)^2 + (1-t)^2v(1+v)^2 + 8v^2t(1-t)}$$

and

$$m > \frac{1}{t + v - vt}.$$

These inequalities give the upper and lower threshold values of the competitive advantage of faster germination,  $m$ , that are necessary for a heteromorphic ESS as a function of  $t$  and  $v$  (table 1; fig. 1).

When most four-aperturate pollen grains survive because of either rapid arrival at stigmas (high  $t$ ) or little loss of viability with age (high  $v$ ), the competitive advantage resulting from faster germination need not be great for them to fertilize ovules successfully. As either  $t$  or  $v$  approaches one, there will be no cost of producing four-aperturate pollen, and even a small competitive advantage ( $m >$

TABLE 1  
 RANGE OF VALUES OF THE COMPETITIVE ADVANTAGE OF FOUR-APERTURATE POLLEN ( $m$ ) FOR WHICH THE ESS IS A MIXED STRATEGY IN THE  
 DISCRETE-TIME HETEROMORPHIC MODEL

VIABILITY OF FOUR-APERTURATE POLLEN	PROBABILITY THAT POLLEN IS YOUNG						
	1	.9	.8	.6	.4	.2	0
.00	1	1.11-∞	1.25-∞	1.67-∞	2.50-∞	4.98-∞	.01-∞
.10	1	1.01-1.41	1.22-2.06	1.56-4.17	2.17-6.83	3.57-8.94	5.26-9.59
.20	1	1.09-1.26	1.19-1.60	1.47-2.49	1.92-3.51	2.78-4.40	3.57-4.74
.30	1	1.07-1.18	1.16-1.40	1.39-1.90	1.72-2.44	2.27-2.94	2.70-3.15
.40	1	1.06-1.13	1.14-1.27	1.32-1.59	1.56-1.91	1.92-2.23	2.17-2.37
.50	1	1.05-1.09	1.11-1.18	1.25-1.39	1.43-1.61	1.67-1.81	1.82-1.91
.60	1	1.04-1.06	1.09-1.13	1.19-1.26	1.32-1.40	1.47-1.54	1.56-1.60
.70	1	1.03-1.04	1.06-1.08	1.14-1.17	1.22-1.26	1.32-1.34	1.37-1.39
.80	1	1.020-1.025	1.04-1.05	1.09-1.10	1.14-1.15	1.19-1.20	1.22-1.23
.90	1	1.010-1.011	1.020-1.022	1.042-1.044	1.064-1.067	1.087-1.089	1.099-1.100
1.00	1	1	1	1	1	1	1

NOTE.—When  $m$ , the competitive advantage of four-aperturate pollen, is less than the lower value in the table, the ESS is a pure three-aperturate strategy. When  $m$  is greater than the higher value, the ESS is a pure four-aperturate strategy.



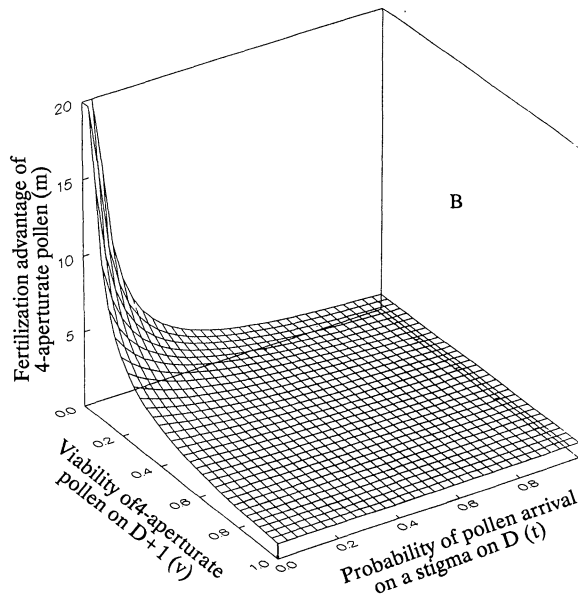
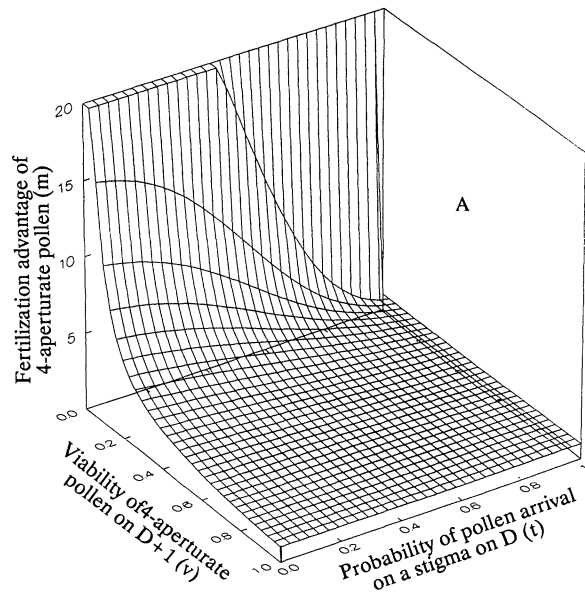


FIG. 1.—Upper (A) and lower (B) boundaries of the parameter space in which the ESS is a mixed strategy in the discrete-time heteromorphic model. For values of  $m$  (the competitive advantage of four-aperturate pollen) greater than the upper boundary, all pollen is four-aperturate; for values of  $m$  less than the lower boundary, all pollen is three-aperturate.  $D$ , Day of anther dehiscence.

1) will result in a four-aperturate ESS. Also, the range of values of  $m$  yielding a mixed ESS (pollen heteromorphism) is very narrow if either  $t$  or  $v$  is high. As either approaches one, the range shrinks to zero, and any competitive advantage ( $m > 1$ ) results in a four-aperturate ESS. However, with some probability that pollen will be old upon arrival at stigmas, a decrease in  $v$  increases both the threshold value and the range of the competitive advantage that result in heteromorphism. This conclusion is intuitive since a greater competitive advantage of four-aperturate pollen is required for it to be advantageous in the face of larger fitness losses through viability problems. The range of competitive advantage yielding a heteromorphic ESS increases as  $v$  decreases because low  $v$  and high  $m$  mean that there are two mutually exclusive ways to have high fitness: produce four-aperturate grains and arrive early, or produce three-aperturate grains and arrive late.

As  $v$  declines and  $m$  increases, these alternatives become more and more successful in their respective spheres (early vs. late arrival) and less successful under the wrong circumstances. As long as a fair proportion of both early and late pollinations occur, producing only one pollen type means having little chance of success in a large proportion of stigmas encountered, and greater fitness can be achieved by producing both types and thus having access to ovules in all pollination events. For this reason, the greatest range of conditions favoring heteromorphism occur with intermediate values of  $t$ , the probability that pollen arrives on the first day (intermediate  $t$  gives the highest variance in opportunities). Note that for low viability of older pollen and intermediate to low probability of first-day pollination, the range of conditions for pollen heteromorphism can be quite large. Indeed, if viability of older pollen is zero (and  $t < 1$ ), four-aperturate pollen will never be the ESS, and a threshold in competitive advantage separates the region favoring a three-aperturate ESS versus a heteromorphic ESS. Also note that as long as  $v$ ,  $t < 1$ , some values of competitive advantage give a heteromorphic ESS.

*Continuous-time.*—We formulated a version of the preceding model using the same assumptions except that the parameter values are described by continuous functions of time (see App. B). As with the previous model, the greatest range of conditions for heteromorphism tend to result when pollen arrival is most delayed (fig. 2). Likewise, a more rapid loss of viability of four-aperturate pollen results in a higher threshold competitive advantage and a broader range of four-aperture competitive advantages required for heteromorphism. These results are very similar to those of the discrete heteromorphic model.

#### DISCUSSION

Our homomorphic model indicates that no stable polymorphism can be maintained in which plants in a population show polymorphism for producing either three- or four-aperturate pollen. In contrast, the heteromorphic models, whether discrete or continuous, show that under some conditions a mixed ESS is favored by selection (i.e., at the ESS, all plants in a population will produce both types of pollen). Moreover, the continuous- and discrete-time models agree as to what

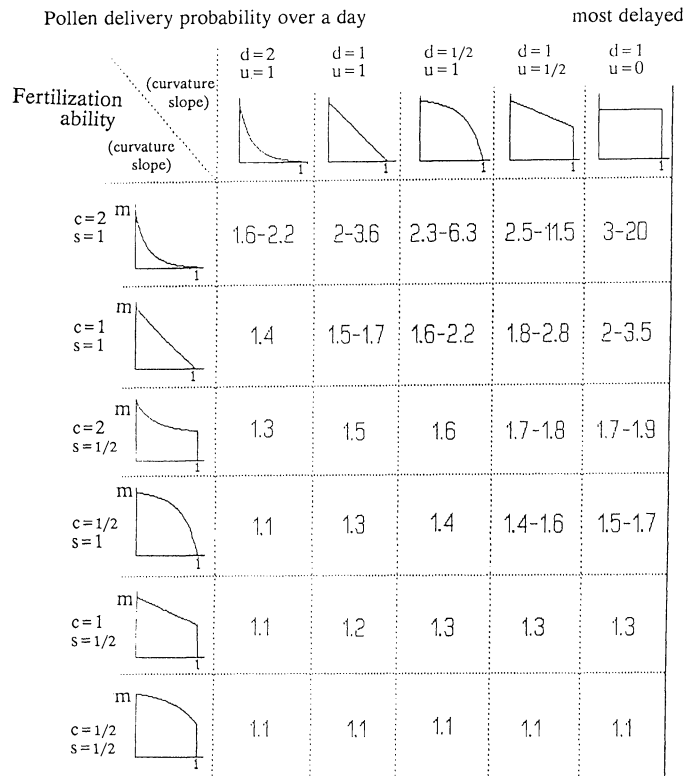


FIG. 2.—Range of values of the competitive advantage of four-aperturate pollen ( $m$ ) for which the ESS is a mixed strategy in the continuous-time heteromorphic model. When  $m$ , the competitive advantage of four-aperturate pollen, is less than the lower value in the table, the ESS is a pure three-aperturate strategy. When  $m$  is greater than the higher value, the ESS is a pure four-aperturate strategy.

situations promote pollen heteromorphism (compare table 1 and fig. 2). The conditions for heteromorphism are most easily met when there is a fairly high proportion of both young and old pollen delivered to stigmas simultaneously, the competitive advantage due to faster germination of four-aperturate grains is high, and the viability of older four-aperturate pollen is low.

#### *Empirical Values of the Parameters for the ESS*

*Viability.*—Loss of viability with time is likely to be common; however, data concerning pollen loss of viability over time are scarce and do not, as yet, allow comparison of different pollen morphs. Our data would suggest that the viability of second-day four-aperturate pollen is about half of that of second-day three-aperturate pollen ( $v = 0.5$ ) in *Viola diversifolia* (Dajoz et al. 1993). Some species show little or no loss of viability over 24 h (*Brassica napus*: Dumas et al. 1983; *Monarda fistulosa*: Cruden et al. 1984); however, pollen from Gramineae, Com-

positae, or *Erythronium grandiflorum* loses viability over a few hours (Goss 1968 [in Hoekstra 1983]; Ladyman and Taylor 1988; Thomson and Thomson 1992).

*Pollination.*—In good pollination conditions, the chance of rapid pollen delivery is probably very high; however, when the weather is variable, this chance will fall rapidly. In *Viola diversifolia*, which grows on alpine scree above 2,000 m, very few pollinators were observed in the field, and pollination is probably very bad; thus,  $t$  is probably low ( $< 0.5$ ). Examples of both high and low rates of visitation by insects can be found (e.g., bumblebees visit *Aralia hispida* and *Penstemon strictus* about every 2 min during most daylight hours on a fair day, while *Erythronium grandiflorum* only receives about one visit per day; J. D. Thomson, personal communication). However, the most relevant parameter for our model is the timescale in which pollen viability declines compared to pollination rate. This parameter is even harder to estimate, and, although pollination may seem very efficient, pollen may still be delivered in an old stage if its viability declines even more rapidly. In *V. diversifolia*, the timescale in days (as used in the discrete-time model) seems appropriate.

Our models make no assumptions as to whether pollination is a limiting factor, but, rather, we assume that when pollen from at least two parents lands on a stigma, there is enough for competition to occur (and when pollen from only one parent lands on a stigma, there is at least enough to fertilize all the ovules). In most species investigated, the amount of pollen delivered to individual flowers appears to be sufficient for pollen competition to occur (e.g., *Asclepias exaltata*: Queller 1983; *Epilobium canum*: Snow 1986; *Phlox drummondii*: Schlichting and Devlin 1989). In other species, pollen is a limiting factor for seed set (see Bierzychudek 1981 for a review; Galen et al. 1985; Snow 1986), and pollen competition may not always occur. However, three caveats are in order. Even if seed set is limited by low pollen loads, there still may be competition among pollen grains if ovules vary in quality, for example, because of position effects (Marshall and Ellstrand 1988). In such cases there could still be a fitness advantage to fast germination and fertilization of the better ovules. Also, in some species, when pollination is insufficient (usually fewer pollen grains than ovules), the fruit fails to develop (e.g., *Campsis radicans*: Bertin 1982; *Cochlospermum vitifolium*: Bawa and Webb 1984; *Lysimachia quadrifolia*: McCall and Primack 1985). If some pollination events result in saturation levels of pollen and some do not, selective events in the ones that do have the larger influence on fitness. This is because the absence of competition can be associated with incomplete seed or fruit set.

In cases in which pollen loads are low, three-aperturate grains will generally be favored more than predicted by our models. If single-donor pollinations do not fertilize all the ovules, single-donor pollinations must be considered in the overall selection problem. Selection in single-donor fruits with low pollen loads will unilaterally favor three-aperturate grains because rapid germination of four-aperturate grains confers no competitive advantage. With inadequate pollen loads (fewer pollen grains than ovules), the lower viability of older four-aperturate grains would mean fewer ovules fertilized. Low pollen loads on stigmas with two simultaneous donors will likewise tend to favor three-aperturate pollen grains more than our models predict. Even when four-aperturate grains have the potential to

win a larger fraction of the fertilizations, in this scenario they are not numerous enough to fertilize all the ovules, and three-aperturate grains can still fertilize.

*Number of competitors.*—We assumed that each flower in which competition occurs receives pollen from two donors. A particular donor with many flowers may pollinate many stigmas and thus compete with many other pollen donors over a flowering season, yet the arena of competition is each individual gynoeceum. Although a receptive stigma may experience more than two visits, contributions from different donors must arrive within a short time of each other to compete (e.g., within 15 min in wild radish; Marshall and Ellstrand 1988). The assumption of two pollen donors is probably not far from reality in many cases. Thomson and Plowright (1980) and Thomson (1986) have shown that most of the pollen is transported to the next two or three flowers, with an average of six flowers to which the pollen of one plant is transported, and that the amount of pollen from a single donor decays rapidly over the course of a bumblebee visit to an inflorescence (Galen and Plowright 1985; Thomson et al. 1986). These data suggest that very few donors provide a lot of pollen grains to a single stigma. For hummingbird pollination, the number of plants and the amount of pollen is larger (Waser and Price 1982). The available evidence from natural multiple paternity of individual fruits indicates that two is the modal number of pollen parents, except in species with one seed per fruit and species with pollinia or pollinia-like packaging (e.g., *Asclepias*, *Acacia*) in which case it is one (N. C. Ellstrand, personal communication). In cases of pollinia, the second most common number of pollen parents is two (Broyles and Wyatt 1990). Note that species with pollinia are likely to have saturation pollen loads with a single donor, which fulfills our requirement for no selection in single-donor pollinations. Thus, it would seem that our assumption of two pollen donors is quite reasonable for modeling purposes. It is also the simplest hypothesis for the model. We are currently working on an extension of these models to include a variable number of competitors. In the heteromorphic model, an increase in the number of competitors just reduces the parameter space in which a mixed ESS is favored. In the homomorphic model, stable polymorphism can be maintained as soon as there are three or more competitors (I. Till-Bottraud, P.-H. Gouyon, B. Godelle, and D. L. Venable, unpublished manuscript).

It is true that many angiosperm species produce only one seed per fruit (Kress 1981) and thus have only one pollen parent per fruit. Our model must be slightly modified to deal with these plants. Rather than calculating the proportion of seeds fathered in individual fruits, we must calculate the probability that the seed will be fathered by a particular pollen donor. If individual plants deliver pollen to many flowers over a season, this situation amounts to much the same thing. Our models require no special modification for these cases.

Another simplifying assumption of the models was that equal amounts of pollen arrive from the different donors, which is unlikely to be strictly true. As long as the proportions are not totally unbalanced (i.e., large amounts of pollen grains from two or more pollen donors), it should have very little effect on the predictions of the model.

*Competitive advantage of four-aperturate pollen due to rapid germination.*—This parameter is very hard to estimate. Although it is possible to measure the

germination rates,  $m$  is the fertilization advantage achieved by faster germination. We have no genetic markers to determine what type of pollen grain fertilizes the ovules (remember that both types are produced by the same plant). However, we suspect that this parameter can take on very high values. Four-aperturate grains germinating just a little faster (say, 1.1 times faster) may be able to reach all the ovaries before the other type of pollen, which would result in  $m$  being infinite. Indeed, empirically based models of Thomson (1989) and Mulcahy (1983) suggest that it is not difficult for variation in germination time to strongly determine fertilization success. With the parameter values suggested for *Viola diversifolia* ( $v = 0.5$ ;  $t < 0.5$ ), our model predicts that heteromorphism is the ESS for a range of values of  $m$  between one and two, which seems quite plausible.

In sum, we have made a variety of simplifying assumptions to arrive at analytically tractable models for the evolution of pollen aperture number. While such simplification is desirable in a general heuristic model, it does restrict the applicability under some specific circumstances. However, we argue that our assumptions are likely to be quite reasonable for a broad range of plant species. Furthermore, there is no one simple way to broaden the applicability of the model because, in specific settings, the assumptions could be modified in many different, more or less independent ways. The probability distribution of pollen loads could vary in mean, variance, and higher moments. Details of floral and vector biology affect the likelihood of single versus simultaneous multiple pollen donors to a flower. We leave these potentially enlightening modifications for future work in specific systems when the empirical details are more fully understood.

Our model predicts different stable strategies, depending on the details of pollination ecology and pollen physiology. In species with low pollen longevity and pollination systems that result in long lags between anther dehiscence and pollination, selection will favor and maintain low pollen aperture number. In contrast, very rapid and efficient pollination and high viability favor a high number of apertures. Finally, variable times from anther dehiscence to pollen delivery times as well as high fitness advantage but low viability of one morph promote more than one type of pollen. The latter phenomenon may be quite frequent, as several species produce two or more pollen types per plant (Till et al. 1989; Dajoz et al. 1991; Mignot et al., in press).

In some species, pollinator activity differs between populations (e.g., *Campsis radicans*: Bertin 1982; *Trientalis borealis*: Anderson and Beare 1983; *Lysimachia quadrifolia*: McCall and Primack 1985), between different flower colors (*Raphanus raphanistrum*: Stanton et al. 1986), and during the flowering season (*Claytonia virginica*: Motten et al. 1981; *Sidalcea oregana*: Ashman and Stanton 1991). Under these scenarios of differential pollination ecology characteristics, our models predict different ESS proportions of the different types.

The models also predict that, in the case of two competitors, there cannot be a stable polymorphism involving pure strategies (one pollen morph per plant) in a population. We are currently developing more general cases (which would be too long to detail here). In the case of more than two competitors, preliminary results indicate that polymorphism can be maintained, but in a much reduced fraction of the parameter space compared to heteromorphism. Therefore, it seems

that the evolutionary increase in aperture number cited earlier should have frequently occurred either by saltational, rapid replacement of one pollen morph by another or else by a gradual increase in the proportion of one morph within plants of successive generations. Other scenarios in which mixed strategies are not equivalent to a mixture of pure strategies have been described (Maynard Smith 1982; Lloyd and Venable 1992). In the present analysis, this situation arises from the fact that selection on pure strategies (three-aperturate vs. four-aperturate) turns out to be frequency-independent so that selection favors, in an all-or-nothing fashion, the morph with the greatest average fitness. Selection on mixed strategies depends on the frequency of pollen morphs produced, and producing both morphs results in the highest fitness over a range of conditions.

As Dobzhansky (1973) stated, nothing in biology makes sense except in the light of evolution. Our approach describes another case of evolution of floral or pollen characteristics under pollination pressures or sexual selection: all the aspects of pollen ornamentation, production (Queller 1983), packaging, and flower phenology (particularly the timing of anther dehiscence) (Harder and Thomson 1989) have been shown to be highly influenced by pollination ecology and sexual selection. The question now remains, What other characters have we been ignoring that deserve a similar analysis?

#### ACKNOWLEDGMENTS

The authors wish to thank B. Godelle for help with the models. The article was much improved by comments from numerous colleagues, in particular D. Charlesworth, L. Harder, S. Maurice, X. Reboud, M. Stanton, and an anonymous referee. This work was supported in part by National Science Foundation grant BSR 91107324 to D.L.V. and was initiated while he was an invited professor in Orsay.

#### APPENDIX A

##### LIST OF SYMBOLS

###### DISCRETE-TIME MODELS

$D$	day of anther dehiscence
$m$	competitive advantage of four-aperturate pollen
$v$	second-day viability of four-aperturate pollen
$t$	probability of pollen arriving on $D$

###### *Homomorphic*

$x$	proportion of plants that produce pollen with three apertures
$W_3$	fitness of a plant that produces pollen with three apertures
$W_4$	fitness of a plant that produces pollen with four apertures

###### *Heteromorphic*

$p'$	proportion of three-aperturate pollen in the population
$p$	proportion of three-aperturate pollen in the mutant plant
$p^*$	ESS proportion of three-aperturate pollen in the population
$W(p, p')$	fitness of the mutant plant (with pollen proportion $p$ ) in a population with $p'$

## CONTINUOUS-TIME MODELS

$T$	age of the pollen grains
$P(T)$	probability that pollen from each plant arrives on the stigma $T$ time units after anther dehiscence
$u$	curvature of $P(T)$
$d$	slope of $P(T)$
$k$	the intercept of $P(T)$ (adjusted to make the sum of the distribution of $P(T)$ equal to one)
$F(T)$	fitness advantage of a four-aperturate pollen grain relative to three-aperturate pollen
$c$	curvature of $F(T)$
$s$	slope of $F(T)$
$W(p, p')$	same definition as for the discrete heteromorphic model

## APPENDIX B

## CONTINUOUS-TIME MODEL

In this model, the parameter values are described by continuous functions of time. The probability that pollen from each plant arrives on the stigma  $T$  time units after anther dehiscence is given by  $P(T) = k(1 - uT)^d$ . This functional form has parameters for intercept ( $k$ ), slope ( $u$ ), and curvature ( $d$ ) (see examples graphed in fig. 2). The intercept ensured that the total cumulative probability equaled one. The fitness advantage of a four-aperturate pollen grain relative to a three-aperturate pollen is given by  $F(T) = m(1 - sT)^c$ , which has the same functional form as  $P(T)$ . Varying the intercept  $m$  allows us to increase the competitive advantage of four-aperturate pollen without altering the slope or curvature, which describes the loss of viability over time (analogous to  $v$  from the previous model; see App. A for a summary of parameter definitions).

The total paternal fitness is again calculated as the average, over all pollinations, of the proportion of seeds fathered by a plant with morph proportion  $p$  in a population with morph proportion  $p'$ :

$$W(p, p') = \int_{T_1=0}^1 \int_{T_2=0}^1 \frac{P(T_1)P(T_2)[p + (1-p)F(T_1)]}{p + p' + (1-p)F(T_1) + (1-p')F(T_2)} dT_1 dT_2,$$

with  $T_1$  and  $T_2$  being the amount of time between anther dehiscence and pollination for the two pollen parents on each stigma. The integrals function analogously to the summations over all possible combinations of early and late pollination from the previous model. The ESS must satisfy  $\partial W(p, p')/\partial p = 0|_{p=p'=p^*}$ :

$$0 = \int_{T_1=0}^1 \int_{T_2=0}^1 \frac{P(T_1)P(T_2)[1 - F(T_1)][p + (1-p)F(T_2)]}{2p + (1-p)[F(T_1) + F(T_2)]} dT_1 dT_2.$$

The ESSs for several hundred combinations of the parameter values were calculated by successive approximation and graphic verification. Figure 2 presents the values of  $m$  (the competitive advantage of four-aperturate pollen due to faster germination) for which the ESS is a mixed strategy.

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