A Note on Optimal Mate Selection by Plants

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A NOTE ON OPTIMAL MATE SELECTION BY PLANTS

Call the genetic programming for stigmas, seeds, and other parts of the seed-producing machinery the "female" part of the plant and the genetic programming for anthers and other parts of the pollen donating machinery the "male." Forget for the moment that these two programs may overlap in large to small part. The central and largely unaddressed question in plant reproductive biology is, How many of which fathers does a female want for any given seed crop and how many offspring in which seed crops does a male wish to sire? I would argue

that in either case the answer is not a maximum number but rather some optimal number and optimal distribution. Further, I would argue that the optimal numbers and distribution of fathers and mothers are very unlikely to be the same for the female and male and that the conflict leads to differential pollen acceptance, monoecy, and dioecy. Here I do not deal with the terribly difficult question of what environmental circumstances select for what numerical values of optimal outcrossing. Rather, I am concerned with expected differences between the sexes in optimal parentage mixtures and how a plant might produce these differences.

Not all pollen donors are of equal status, and neither are all pollen receivers. If they are not all of equal status, and this can be seen by examination of any plant population, then there must be some distribution of kinds of individuals. This distribution should strongly influence which kinds of pollen vectors give the most for the money, so to speak. If, for example, most of the trees acting as females in a population are rather flimsy specimens, with an occasional robust individual having huge seed crops and contributing many individuals to future generations, then a very different kind of pollen vector will be selected for by the trees acting as males than if all individuals are roughly equal in seed reproductive potential. In short, plants are not trying to maximize outcrossings but rather to optimize it. In doing so they perform courtship displays, rape, promiscuity, and fickleness just as do animals. I feel that pollination biology has lost sight of the fact that plants are gene donors and gene receivers and that these two activities are not necessarily complementary, compatible, or directed toward the same end.

To elaborate these generalizations, begin by examining the conditions of optimal female programming of an iteroparous plant (e.g., a tropical rain-forest tree). First, her fitness will not be maximized by having all possible males in the area sire her seeds but rather some optimal number. There are at least four reasons: (a) many males may be flowering but too young, sick, crippled, etc., to have demonstrated that their genotypes will ultimately be among those with the highest fitness in the area; (b) given a desired amount of heterogeneity of mutants and recombinants appropriate for the amount of temporal-spatial heterogeneity in the habitat, this heterogeneity will likely be contributed by some average number or fraction of the males in the area rather than by all of them; (c) the cost of getting some pollen from all males in the habitat may be much greater than the return in slightly increased heterogeneity of offspring over that which would be obtained by a moderate-sized subset of the males; and (d) the appropriate mix of parental heterogeneity may even be contributed by a very badly imbalanced distribution of males (her fitness may even be highest if most of her offspring are fertilized by her own male and only a few by outside males).

Second, if we restrict ourselves to considering only those males that are in a class that she regards as "acceptable," it is clear that a number of males contributing to a seed-crop/expenditure-on-pollen-capture curve will have a form like that in figure 1. At small expenditures of resource, perhaps no pollen-bearing vectors will reach the stigmas (a). As the floral display becomes more
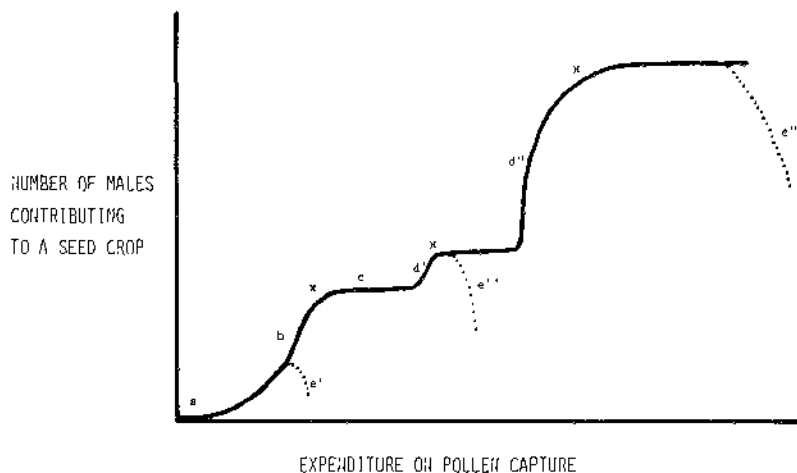
FIG. 1.—A theoretical relationship between the expenditure of resources by the female portion of the plant in capturing pollen and the number of male plants that contribute to the seed crop of that female plant (see text for details).

efficient at obtaining pollen (and presumably more expensive), the number of males contributing should increase (b). There should, however, come a time when most of the males within "pollinator radius" have contributed some pollen, and therefore more expenditure on floral traits does not yield more parents (c). It may be paid, however, since higher expenditures may yield more pollen from particular individually acceptable parents. Then, as the floral expenditure continues to rise, the plant may become attractive to new sets of pollinators that move longer distances, and thus the number of contributing males may again rise (d', d"). This may occur at several levels and to several degrees, depending on the kinds of vectors.

If simple numbers of fathers are what matter to a female, then I expect most pollination systems to be perched at the shoulders of the curve (x). However, if quality of the fathers counts a great deal as well, then I expect most pollination systems to be scattered along the curve. This is because the female may then pay a great deal to obtain a small number of specific fathers. It is notable that there is no information in the literature on wild plants that would allow examination of these two expectations.

At any point on the curve, the floral reward may become so great that the number of parents contributing to the seed crop begins to decline (e', e", e'"). This is the case where a territorial animal, such as a male hummingbird or colony of stingless bees, finds the floral resource sufficiently valuable that it defends it and excludes other visitors. This restriction of visits may well be selected for, if such expenditure is cheaper or more reliable than the many more classical ways that certain animals can be prevented by plants from reaching the flower crop, or that visits can be held to a small number.

In building a model such as this one, I assume that a female makes a physiological decision that she has, or on the average has, a fixed amount of resources

for maturing seeds in a given year. Of course, over evolutionary time a genome may evolve such that all the seeds she can make are pollinated, if only with her own pollen. Within broad limits, the number of seeds set is therefore not a measure of pollinator efficiency. She may make a full complement of seeds and be quite inefficiently pollinated, or she may set 50% of her seed crop and be very efficiently pollinated. The real measure of pollinator efficiency is to what degree the actual parentage of her seed crop matches with the optimal parentage for that seed crop. If she is genetically fixed for obligatory outcrossing to make, say, 10,000 seeds and she does not get that much foreign pollen in a specific year, she might well fail to make her 10,000 seeds, and then we may say she is inefficiently pollinated. However, if this is a regular occurrence over evolutionary time she should evolve to where the difference is made up by self-pollination, but even here she has several options. It may well be that 10,000 seeds based partly on selfing give her a lower fitness than 8,000 seeds based entirely on outcrossing. If her current floral display gives her only enough foreign pollen for 6,000 seeds she may well expend 2,000 seeds' worth of resources to get enough additional pollen for a total of 8,000 outcrossed seeds, rather than selfing 4,000 seeds.

How can she physiologically manipulate the parentage of her clutch? One easy way is to produce a large number of flowers with normal stigmas in all of them and allow pollination to occur by foreign pollen as it comes in. If enough arrives early in the life of the inflorescence to set a full complement of seeds, then the remainder of the perfect flowers on her plant are simply serving as males or pollen donors (see below). Furthermore, if many more flowers are cross-pollinated per inflorescence than fruits can be matured per inflorescence, she can at a later time choose the best ones by selective fruit or flower abortion. (Abortion of perfect flowers is a common event in trees with large flower crops and small fruit crops.) If little foreign pollen is arriving, as the termination of the inflorescence approaches she may become physiologically receptive to her own pollen, or to fruits developing from the same. On a very short time scale such behavior is found in flowers that move their anthers onto their stigmas late in the day, well after the outcrossing animals have had their go. She may also rig the hormonal and nutrient traits of the stigma and style such that her own pollen grows much slower than certain foreign pollen. Finally, if far too little foreign pollen arrives and she is not programmed to self, she may simply store the nutrients for a bigger flower or seed crop the following year, when the vectors' arrival patterns may be more optimal. If this happens regularly, there is ordinary selection favoring the tree that facultatively selfs, makes fewer bigger seeds, makes progressively bigger floral displays as mentioned at the end of the previous paragraph, etc.

How else may a female determine the number of males that contribute to her seed crop? The ways are well known but not generally thought of in this context. Figure 1 gives us one way—vary the amount of resources presented to the vector community. Second, she may vary the amount of time, and kinds of pollen to which the stigma is receptive. Of course, there should be strong selection favoring male traits that allow it to rape the flower on both counts (see
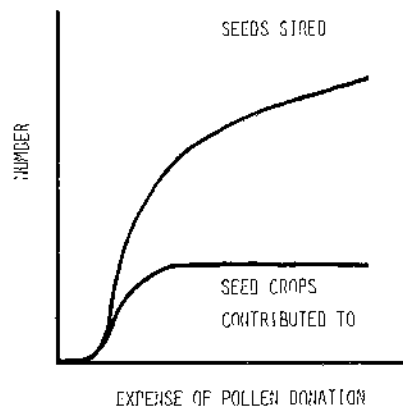
Fig. 2.—A theoretical relationship between the expense of donating pollen by a male plant and (*a*) number of seed crops contributed to and (*b*) number of seeds sired.

below). Third, she may have compatibility genes that automatically eliminate a certain subset or fraction of the males within pollinator radius (including her own male). Fourth, she has the various morphological, behavioral, and physiological qualitative traits that exclude or make her less attractive to specific pollinators, pollinators that may on average produce too large or too small numbers of parents for a seed crop. For example, an oak may have her stigmas receptive only on the most violently windy days, thereby maximizing the chance of getting pollen from many distant males rather than the four immediately adjacent.

How does the female evaluate the courtship displays presented by the males? Again, I suspect one primary way is to select for flower types that are attractive and available to those particular vectors that are most likely to come from the highest-quality males in the habitat. For example, if she is a canopy-member tropical rain-forest tree, perhaps her stigmas should be accessible only to those large bees that visit the largest nectar crops of the healthiest mature trees. She may have her stigmas available during a short time of day or season, a time that may be accurately hit by only the more robust males when releasing pollen. If wind pollinated, perhaps her stigmas should be receptive only on the days when the healthiest and most robust trees will be releasing pollen.

The male has somewhat different problems. In some habitats his fitness may be maximum if he sires a maximum number of seeds, in others if he is a contributor to a maximum number of seed crops, and yet in others if he fathers some optimal number of each. That the former two goals are not identical may be seen in figure 2. The maximum possible number of seed crops to which he contributes with the available pollen vectors will be attained long before the maximum number of seeds that can be sired. Furthermore, quite different pollinators may achieve high values on the X axis for the two different functions. Depending on the pollinators, the rate of rise of the two curves may be very different. Certain pollinators should be very good at taking pollen to a large

number of seed crops but pollinating only a small percentage of the flowers, while others may be very good at pollinating many flowers but do it primarily in only a few tree crowns. Furthermore, upward steps are expected as in figure 1, d' and d''.

In some cases, as with the female, I expect to find that the number of seeds sired or the number of seed crops contributed to decreases with increasing cost of reproduction (as in fig. 1, e', e'', and e'''). This is more complex than with the female, since pollen, as well as nectar, is a commodity. The production of much pollen may result in territoriality by vectors or attraction of specialized pollen eaters, with the result of lowered pollen flow, even when the pollen was not produced to attract vectors. Even a reduction such as this may be selected for (just as with the female) if the smaller numbers of pollen movements are to qualitatively superior seeds or seed crops. For example, the optimal pollen receivers may be those few females growing within a "seed's-throw" of new and uninvaded habitat.

As with animals, the male portion of the genome differs from the female genome in that the investment per pollen grain (analogous to sperm) is much smaller, and further, once the pollen grain has been donated, there are no further costs to the male parent. This suggests that the male should be much more generous or sloppy per pollen grain than should the female per ovule. However, this may not be interpreted to mean that the pollen should be dumped on just any animal that just might happen to wander by a conspecific stigma at a later time. The male should be selected to put its pollen on those vectors that will yield an optimum number and distribution of offspring. For example, selection may favor pollen movement primarily to the healthiest female trees in the habitat (assuming of course that their robust phenotype is to some degree correlated with a robust genotype). While a male animal may choose to mate with any receptive female he happens upon at a small cost per mating, this is definitely not the same as putting pollen on any receptive insect that wanders across the flower. However, just as a male animal may wish to force himself on a female that is only marginally receptive, the male plant may well wish to effectively rape certain females in the area. He may do this by bombarding their stigmas with pollen, producing large pollen grains with special pollen tube growth abilities, producing pollen that is insensitive to the various physiological incompatibility barriers possessed by the stigma, and so forth. He may even produce biochemical mimics of compatible physiologies and do it in such a way that some other zygote is aborted in deference to his own as the fruits begin to develop. Once the pollen grain has arrived at the stigma, it has made an irreversible move. There should be very intense selection for it to get around whatever barriers the female may erect.

The male and female activities as described in the previous paragraphs may well be incompatible. For example, hummingbirds may regularly bring in pollen from an average of six different conspecifics per day for a particular plant's seed crop. Assume that this is the optimal amount from the viewpoint of the female part of the genome. The same birds likewise may take pollen to only six different conspecifics per day. However, from the male's viewpoint,

maximum fitness may be achieved by contributing pollen to 28 conspecifics, for example. In this case, the plant might choose to elevate the floral reward to where pollen is being taken to 28 conspecifics on the average at the cost of (*a*) getting perhaps 15 fathers for its seed crop and (*b*) some of its seed crop resources. Alternatively, it may strategically hold seed parentage at six by shortening the period of time that the stigma is receptive or available and raise pollen parentage by elevating the time that pollen and associated rewards are available.

As the male and female portions of the genome begin to manipulate their different parts of the flower in different ways, there should be times when it is more efficient to produce two different kinds of flowers on the same plant. A monecious plant can certainly be viewed as the outcome of this adaptive compromise. The female flowers may be specialized to obtain an optimal number and distribution of parents for the seed crop, and the male flowers are specialized to donate to an optimal number and distribution of seeds and seed crops. I would not suggest that this is the only driving force behind the evolution of dioecy in plants, but dioecy may be viewed as just carrying this process one step further. The dioecious plant is totally specialized at either donating pollen or receiving pollen and making seeds. Notably, some plants alternate back and forth between these two states over their lifespan, or start out with only the male programming active and later express their female programming when resources allow it.

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CORRELATION BETWEEN EGG SIZE AND DEVELOPMENTAL PERIOD

Underwood (1974) bases part of his criticisms of Vance's (1973*a*, 1973*b*) models of reproductive strategies in marine benthic invertebrates on the conclusion that an "absence of correlation between developmental period and egg size appears general." As evidence he uses prosobranchs, gastropods, holometabolous insects, thysanurans, and birds.

The purpose of the present note is to point out that this conclusion is not justified, because a correlation between egg size and developmental period is well documented in a variety of animals: amphipods (Steele and Steele 1973), copepods (McLaren 1966), decapods (Wear 1974), crustaceans in general (Steele and Steele 1975), tunicates (Berrill 1935), and frogs (McLaren and Cooley 1972). Moreover, the conclusion of Lack (1968) that in birds "the length of incubation