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BEYOND FLORAL BATEMANIA: GENDER BIASES IN SELECTION FOR POLLINATION SUCCESS

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Abstract.—For over a decade, Bateman's principle has been used to argue that the showy petals and sweet nectar of flowers are evolutionarily more male than female—that they are adaptations principally for promoting the export of pollen rather than the setting of seed. Here we present alternative views. (1) We question whether the assumptions of Bateman's principle have been generally upheld for angiosperms. (2) We present a path model that contradicts Bateman's principle by asserting that floral attractiveness characters might well affect fitness more deterministically through female than through male function. (3) We envision an episodic selection scenario that has the same outcome as Bateman's principle but is based specifically on the ecology and mechanics of pollination. In the end, we recognize that selection on the displays and rewards of flowers is probably often gender biased (one way or the other), but we warn against reflexive invocation of Bateman's principle, which is neither the only nor the best way to think about the problem.

The attributes of animal-pollinated flowers are elaborately suited for attracting and exploiting pollinators. To Sprengel (1793), the match between flowers and visitors was an exquisite testimony to the genius of the creative deity. To Darwin (1877), it was an example of the ability of natural selection to mold organic form with uncanny precision. Since Darwin, not all workers have so fully embraced adaptationist explanations of floral form, but landmark works like that of Grant and Grant (1965) on pollination in the phlox family have contributed to a general consensus that pollination ecology is the principal architect of flowers.

Historically, there have been several ways of thinking about floral adaptations. Darwin and many followers concentrated on characters that influence the likelihood of self- versus cross-pollination. Others considered the mechanical fit or "harmony" of flowers and their visitors (see Faegri and van der Pijl 1979). These outlooks gradually grew to consider rates of visitation as well as the quality of pollination. In the agricultural literature of the mid-twentieth century, it became well established that levels of natural pollination are often insufficient for maximum seed set, and importing honey bees to increase visitation rates became standard practice (see Robinson et al. 1989). Likewise, evolutionary biologists of

the time typically considered selectively favored and unfavored floral phenotypes to differ primarily in that the former received more pollen and set more seed. Although seldom, if ever, stated, selection was implicitly treated as acting through female function. However, since many plants are hermaphrodites, there is a potential for selection through both female function (seed production) and male function (seed siring). Although the distinction was enunciated by Horovitz and Harding (1972), it did not receive widespread attention until the publication of Janzen's (1977) and Willson's (1979) provocative articles. These authors stressed the importance of male function in interpreting floral characters, and their articles led to a quick and widespread acceptance of the idea (now suddenly obvious) that selection through male function can indeed be potent. The field of plant reproductive biology subsequently underwent a fundamental change.

New theory was developed. Willson (1979), Charnov (1979), and many other authors applied Bateman's (1948) comments on sexual selection to the male and female components of hermaphroditic plants. Bateman's principle has been variously stated. For instance, it is said that intrasexual selection acts more on male function than on female function or, alternatively, that the variance among individuals in male reproductive success exceeds the variance among individuals in female reproductive success. This in turn arises as a consequence of a difference in the numbers of male and female gametes, which set upper bounds on male and female reproductive success, respectively. The plant literature most often focuses on the factors that limit reproduction: male reproductive success is said to be limited by competition with other flowers for the services of pollinators, while female success is said to be limited by resources (Charnov 1982 and many since then).

The view that characters like petals and nectar are principally male gained partial empirical support from Queller's (1983) study of pollinaria removal and fruit set. The view was then explored most generally by Bell (1985) in a very influential article that included both theoretical arguments and experimental results relating measures of male and female reproductive success to attractiveness. Bell (p. 263) discussed his experiments on male function as equivocal, but the view that petals are male became an exciting plausibility to many naturalists, including ourselves. That excitement was further promulgated by the finding that petal color predicted number of seeds sired, but not number of seeds set, in an experimental population of *Raphanus* (Stanton et al. 1986, 1989).

We do not now dispute that Bateman's principle (or something like it) is true in some cases, but we are concerned that it is being treated as generally, or even axiomatically, true. More recent empirical studies call for a more sophisticated answer to the question, What, if any, is the gender bias of selection on characters of floral attractiveness? (and by attractiveness we mean both advertisements and rewards sensu Waser 1983). We first review the evidence for resource-limited female function and pollinator-limited male function. Second, we develop an argument for why one might imagine selection on attractiveness to actually be more female than male. Third, we present a contrary argument by which flowers might be (somewhat) more male after all but for reasons much more complicated than the litany of Bateman's principle.

DOUBTS ABOUT THE BATEMANIAN ASSUMPTIONS

Field biologists have spent considerable effort in assessing whether female reproductive success (fruit or seed production) can be increased by elevating the level of pollination. When it cannot, female function is thought to be limited by maternal resources, and the consequences for selection are as outlined by Johnston (1991, p. 1500): "Wherever seed production is resource limited . . . there will be competition among plants for male success, causing selection on traits influencing pollen dissemination. When seed production is pollen limited, on the other hand, there will be less competition among potential sires but stronger selection on characters influencing pollen receipt."

Bateman's principle applies only if seed production is limited by resources rather than by mating success. Although early compilations of studies were interpreted as supporting the generality of resource limitation for female function (e.g., Willson and Burley 1983), there is now reason for caution in drawing this conclusion.

1. Fruit set in some species is pollinator limited not just occasionally, but chronically, even when tested in different years and places, for example, in *Cypripedium acaule* in New Brunswick (Plowright et al. 1980; Barrett and Helenurm 1987), Massachusetts (Primack and Hall 1990), and Tennessee (Cochran 1986). Numerous cases of pollen limitation have been reported in various taxa. Useful reviews are presented by Bierzychudek (1981), Bawa and Webb (1984), Zimmerman and Pyke (1988), and Karoly (1992). Although the experimental requirements for a conclusion of pollinator limitation are onerous and many early studies are inadequate, some of the more recent studies meet stringent criteria.

2. A new review by Young and Young (1992) raises doubts about the general validity of the pollen-supplementation technique most commonly used to infer resource limitation. Pollen is typically added to the stigmas of some plants, and their fecundity is compared against that of open-pollinated plants that did not receive supplemental pollen. A nonsignificant difference between the treatments is commonly taken to indicate resource limitation, but Young and Young found that in a surprising number of tests the supplemented flowers were actually less fecund than the controls. They discuss possible reasons why such manipulations can be detrimental to the supplemented flowers. Regardless of the causes, their survey indicates that interpreting pollen-supplementation experiments may be less straightforward than has been presumed.

3. In a number of cases, a plant species appears to be pollinator limited in some natural situations and resource limited in others: *Veronica cusiskii* (Campbell 1987), *Lysimachia quadrifolia* (McCall and Primack 1985), *Calathea ovan-densis* (Horvitz and Schemske 1988), *Lobelia cardinalis* (Devlin and Stephenson 1987; Johnston 1991), *Mimulus guttatus* (Dudash and Ritland 1991), *Encyclia krugii* (Ackerman 1989), *Trillium ovatum* (M. Mesler, unpublished manuscript), and *Erythronium grandiflorum* (J. Thomson, unpublished data). Indeed, Haig and Westoby (1988) suggest that selection should balance a plant's allocations to pollinator attraction and seed provisioning to the point where both effects can be considered limiting, even though "most pollen-addition experiments should fail

to cause major increases in seed set" (p. 758). Other work (Galen et al. 1985) found that seed set in *Clintonia borealis* responded when pollination and resources were both increased but not to a unilateral increase in either one, a result consistent with the Haig-Westoby proposal.

4. Perhaps our most important concern is that most tests of pollinator limitation take place in situations especially favorable for pollination, that is, in large dense study populations. Such populations may have very different pollinator service from those in marginal, sparse, or isolated areas. Typically, they will receive higher visitation rates because of the foraging preferences of pollinators (Thomson 1981, 1982; Johnston 1991). Large populations may be less affected by interspecific competition for pollination (see, e.g., Campbell and Motten 1985, but see also Thomson 1980 and Lavery and Plowright 1988). Also, the spectrum of pollinators may differ (Stanton et al. 1991, 1992). Isolated populations may lose the services of particular pollinators, as has been proposed to explain the breakdown of heterostyly in various taxa (Barrett 1988). Pollination in marginal populations may generate selection pressures that differ in strength and direction from those in large, heavily visited populations (Stanton et al. 1991).

All of these considerations lend force to Johnston's (1991, p. 1502) conclusion that "we still do not know whether pollen limitation is a common feature of plant populations."

Moreover, resource-limited female function is not the only assumption of Bateman's principle. It is also assumed that male function is pollinator limited—that flowers are in competition to receive more visits in order to have more of their pollen exported. Yet, just as seed set can conceivably be either visitor limited or not, so can pollen removal be either visitor limited or not. Bateman's principle is realized only when pollen removal is visitor limited but seed set is not (Stanton and Preston 1988). There has been relatively little empirical effort on how often and under what circumstances pollen removal is limited by visitation rather than by pollen production. At the grossest level, there are cases in which some flowers are not visited at all and have pollen to be taken away (*Viola*, Beattie 1969; *Catalpa*, Stephenson 1982; *Erythronium*, Thomson and Thomson 1992). Also, for *Asclepias* with pollen in pollinia, far less than 100% of the pollinaria are typically removed, which supports an assertion of pollinator-limited male function (Willson and Price 1977; Morse and Fritz 1983; Queller 1983). On the other hand, our studies on plants with granular pollen suggest that, when pollinators are plentiful, they quickly remove all the pollen that can be removed (*Impatiens*, Wilson and Thomson 1991; *Raphanus*, Stanton et al. 1992; *Sidalcea*, T. Ashman, unpublished data; *Drosera*, P. Wilson, unpublished data). This casts some doubt on the idea that pollen removal is generally more limited by pollinators than is seed set.

Bateman (1948) focused on variance in male and female reproductive success, arguing that greater variability in the reproductive success of one gender permits greater sexual selection on the traits of that gender. Two plant studies address this issue, although neither directly presents variances in number of progeny. In *Chamaelirium luteum*, Meagher (1986) found that the variance in number of mates was 37.8 for males and 4.9 for females. In contrast, Devlin and Ellstrand (1990) found that the range in proportion of seeds parented was 15-fold for male function

(0.004–0.060) and nearly 200-fold for female function (0.001–0.094) in *Raphanus sativus*. If the situation in *Chamaelirium* is the general rule, selection may indeed have a greater opportunity to act through male function, but, as we shall explain, an inequality in variance is not all there is to an inequality in selection.

MALE AND FEMALE PATHS TO FITNESS

The models of floral evolution that popularized Bateman's principle are evolutionarily stable strategy formulations (see, e.g., Charnov 1982; Lloyd 1984; Charnov and Bull 1986; Charlesworth and Charlesworth 1987). As such, they do not consider the issue of how precisely variation in an attractiveness character, such as petal size, translates into variation in male and female reproductive success. In stable strategy models, these relationships are summarized by mathematical functions with no scatter. Empirical studies are now finding very imprecise linkages between phenotype and success.

Male reproductive success is very difficult to measure in most populations. Accordingly, many workers have measured components of male reproduction rather than estimating paternity itself. These components include (among others) visitation rate, pollen removal, and pollen delivery. Although component measures incompletely represent fitness and can be misleading (Wilson and Thomson 1991), they are useful for understanding mechanisms and for putting upper bounds on the degree of determinacy we might expect between different steps in the reproductive process. For instance, we previously found a positive relationship between the number of pollen grains presented by a single *Erythronium grandiflorum* flower and the number of those grains that were delivered to other flowers' stigmas during subsequent visits (Thomson and Thomson 1989). Although the relationship was significant, it displayed considerable scatter ($R^2 = 0.37$ for a linear fit).

The few studies of paternity that have been accomplished seem to be consistently finding that success through male function is only weakly related to even gross plant characters. The tightest relationship yet reported is for paternity as a function of staminate strobilus production in wind-pollinated white spruce ($R^2 = 0.61$; Schoen and Stewart 1986). For insect pollination, Meagher (1991) detected no relationship ($R^2 = 0.07$) between an index of male plant size and progeny sired in *Chamaelirium luteum*. Although R^2 values are not reported for relationships between paternity and flower number, described by Devlin and colleagues for *Raphanus sativus*, their graphs do show very pronounced scatter (Devlin and Ellstrand 1990; Devlin et al. 1992). In the same species, another study (Stanton et al. 1992) was unable to predict patterns of pollen dissemination from the amount of pollen removed at a donor flower. Flowers with discrete pollinia might be expected to show closer coupling between reproductive success and attractiveness characters than those with granular pollen, yet even in *Asclepias* realized paternity is only weakly related to the number of flowers possessed by a donor plant ($R^2 = 0.12$; Broyles and Wyatt 1990), and the corresponding relationship for female success is tighter ($R^2 = 0.41$).

The underlying causes of the weak linkage between phenotype and reproduc-

tive success are clarified by tracing the paths through which variation affects fitness via pollen grains and via ovules, as shown in figure 1. Selection through male function on floral characters occurs to the extent that variance in those characters explains variance in fitness via the siring of seeds (w_δ). As an approximation, consider the strength of selection to be the extent to which petal size predicts success at the flower having its sperm fertilize eggs (*right path* on fig. 1). Selection through female function on floral characters occurs to the extent that variance in the characters explains variance in fitness via the setting of seed (w_φ). Consider this to be the extent to which petal size predicts success at the flower having its eggs fertilized by sperm (*left path*). The path diagram assumes that attractiveness characters can only affect fitness by influencing how much pollen is removed or how much is received. The rest of the diagram represents the usual steps in the life cycle of angiosperms.

In path analysis, the degree to which the value of one variable directly predicts the value of another variable is termed a path coefficient (p value). Path coefficients are standardized regression coefficients that range from -1 to $+1$, and path coefficients that are in a causal chain are multiplicative. Hence, the overall predictive relationships between the floral attractiveness character and male and female fertilization successes are the product of the path coefficients between each component stage: $p_\delta = p_a p_b p_c$ and $p_\varphi = p_x p_y$. Because the male path to reproductive success has more steps than the female path, the causal relationship between attractiveness and male success is predisposed toward being weaker. This predisposition runs contrary to Bateman's principle.

What actually matters, however, is not the number of steps per se, but the strength of the component coefficients. Bateman's principle could be restated in path-analytic terms as saying that p_y is very small because the effect of ovule production dominates in determining the number of fertilized ovules, whereas p_a is not so constrained. This would make p_x much less important than p_a if it could be assumed that $p_b p_c$ is near 1. This cannot be assumed for plants. The parallel situation in animals would be when copulation success only weakly affects fertilization success. The idea that petals are male was made tangible in large part by studies that used pollen removal as a surrogate of male fitness (e.g., Willson and Rathcke 1974; Willson and Price 1977; Queller 1983; Bell 1985; Cruzan et al. 1988; Piper and Waite 1988). This is a risky substitution, as pointed out by Snow (1989) and reinforced by other studies (Campbell 1989; Thomson and Thomson 1989; Broyles and Wyatt 1990; Stanton et al. 1991; Wilson and Thomson 1991). In fact, pollen transfer by insects is a messy operation. In assessing the overall asymmetry of selection, all the component path coefficients need to be considered. Unfortunately, there is no system for which we have empirical knowledge of all parts of the path diagram.

We have actively been trying to measure p_a and p_x in several species under a variety of conditions. Sometimes they are statistically distinguishable from zero, meaning that floral morphology can at least weakly determine the amount of pollen removed and deposited, but often the relationships are weaker than one might have expected from reading the classical pollination literature (e.g., Clements and Long 1923).

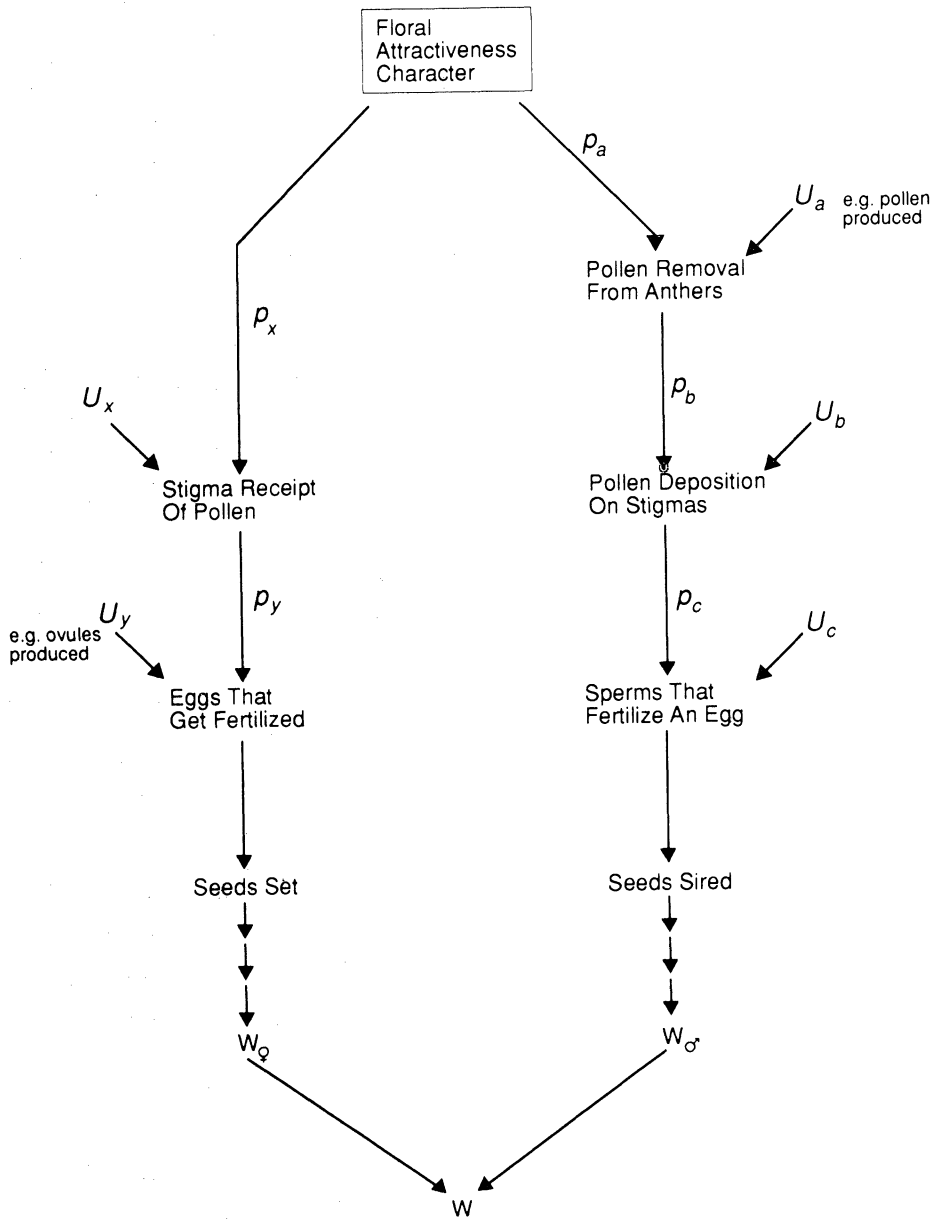


FIG. 1.—Path diagram showing the two ways in which a floral attractiveness character (such as petal size) can affect fitness. Values for p 's (like correlation coefficients) range from -1 to $+1$, which indicates how deterministic the associated arrow is. Along any path, p 's are multiplicative, so that the relationship between the character and sperms that fertilize an egg is $p_a p_b p_c$, whereas the relationship between the character and eggs that get fertilized is $p_x p_y$. The U 's represent unspecified independent factors.

The only direct measurements of p_b we have are the aforementioned *Erythronium* data. These relate the number of pollen grains removed from a virgin flower in the first bee visit to the number of those grains that were subsequently deposited on stigmas by that bee. In this controlled experiment, pollen removal predicted subsequent donation at the level of $p_b = 0.61$. We would expect to find yet lower values under less controlled conditions given the obvious sloppiness of (at least) granular pollinations, in which many pollen grains are surely lost from the system arbitrarily by being shaken to the ground or groomed into scopae. In a *Raphanus* study with radioactively labeled pollen (Stanton et al. 1992), a value of $p_b = 0.09$ was estimated (although admittedly this number includes considerable measurement error). Because p_b is a link in the male path that has no counterpart in the female path, it could have particular sway in making selection less potent in its action through male than through female function.

We find it more difficult to guess at what the strength and importance of p_c and p_y might be. When resources or constraints limit seed production and pollinators are in excess, then p_y will approach zero. Under such conditions, p_c might also be small, because fertilizing an ovule will not merely be determined by whether a flower's pollen grains get to a stigma (note, however, that p_y and p_c represent different relationships—the number of pollen grains on stigmas is doubtless partitioned among donors very differently than among recipients, so the variances are different and the two p values need not even be similar).

Although we do not have a complete set of coefficients, it is easily conceivable that selection through the male path might be systematically weaker than that through the female path. If so, floral extravaganzas might be considered evolutionarily more female than male.

GENDER ASYMMETRIES IN VARYING SELECTION REGIMES

We now turn around and present a view that again emphasizes male function in the way that selection acts on attractiveness characters. It does so for reasons that emerge from the ecology and mechanics of pollination as well as from the difference in numbers between pollen grains and ovules. The dynamics we envision are engendered by spatial or temporal variation in pollination intensity. We imagine that plants experience situations in which pollination is ample as well as situations in which pollination is meager, and we suspect that there are radical differences in the shape of selection between the good and the marginal times. Such contextualism can be seen in Campbell's (1989) study of pollen-analogue transfer in *Ipomopsis*: she found enormous site-to-site and year-to-year changes in the selection gradients relating pollen-analogue donation and receipt to floral characters.

Consider first the situation in which pollination is ample. We envision systems in which there is little selection for increased attractiveness through either male or female function, since additional visits would not remove additional pollen after it is all gone, nor would additional visits produce more seed after enough is deposited for all ovules to be fertilized. True, increased pollen-tube competition might still produce more vigorous progeny from flowers with greater stigma loads

(Mulcahy 1974; Stephenson et al. 1992), but this effect seems to be weak in nature (see review by Walsh and Charlesworth [1992]) and probably saturates rapidly with mixed pollen loads. Contrasting instances also exist in which excessive visitation is actually harmful to female function (Young 1988). On the male side, one can imagine further complications. For instance, there are probably systems in which, when pollinators are abundant, there is intense male-male competition among flowers to be first in having pollen grains removed so that they will be ahead in a race to reach stigmas, grow pollen tubes, and fertilize ovules. Despite the potential for such added complexities, we imagine that many plants under some circumstances receive enough visits for selection on attractiveness characters to be negligible.

Although ample pollination should relax selection on attractiveness characters like petal size, nectar production, and alluring coloration, other floral characters like stamen length, floral tube depth, and anther dehiscence schedules can still be under strong selection. Flowers that present their pollen in such a way that a larger proportion of it is transferred to receptive stigmas will have a greater reproductive success. Consider one scenario for pollen dispensing strategies (from Harder and Thomson 1989 and Harder 1990). When visitation is ample, we expect there to be a general male fitness advantage associated with gradual pollen presentation. This claim is based on the assumption that the number of pollen grains that reach stigmas is a decelerating function of the number removed in a single visit (fig. 2A): if a few grains are removed in a visit, then a high proportion of them will make it to stigmas; if many grains are removed in a visit, then a low proportion of them will be delivered. The number of grains removed in a visit is thus partially governed by the flower's schedule of pollen presentation, and plants have many mechanisms by which pollen is presented gradually (reviewed in Harder and Thomson 1989). We posit that, when pollination is ample, there can be strong selection through male function for gradual pollen presentation, because a high visitation rate linearizes the relationship between total number of grains removed and the total number subsequently deposited (compare fig. 2B and C). We further believe that there is no analogous general rule for female function and pollen receipt—even when visitation is superabundant, a flower may as well receive all the pollen it needs for full seed set in a single visit. In fact, if female tissue is choosing pollen grains by letting them race in their growth down the style, then selection should have favored simultaneous pollen receipt.

We now imagine that these plants that have been molded by strong intrasexual selection to present their pollen gradually (but without any such selection to receive pollen gradually) find themselves in a situation in which pollination is meager and contested. Individual plants with particularly showy, nectar-rich flowers get more visits than plants with small, low-reward flowers. Selection for attractiveness in this situation is at its strongest. When visits are few, every potential visit that would remove pollen or increase seed set is an opportunity for selection to act. Because pollen presentation is gradual but stigma receptivity is not, it takes more visits to fully remove pollen than to fully provide for seed production. In other words, once gradual pollen presentation becomes established, visitor-limited pollen removal is more prolonged than visitor-limited seed

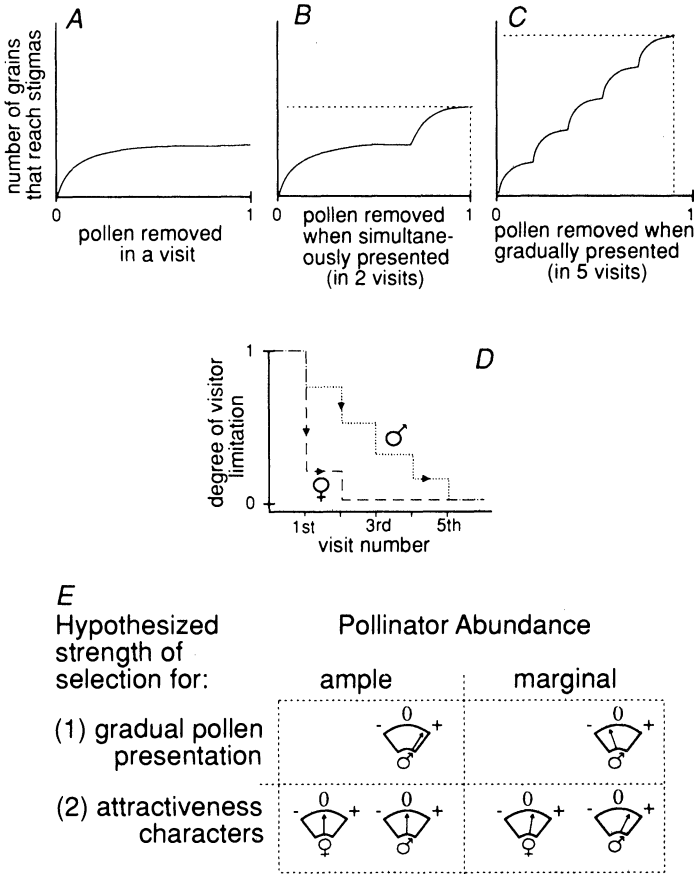


FIG. 2.—A–C, On the assumption that the number of pollen grains that successfully reach stigmas is a decelerating function of the number removed in a visit (A), then, when pollinators are plentiful, simultaneous pollen presentation (B) is a less fit strategy than gradual pollen presentation (C). D, When pollen presentation is gradual but stigma receptivity is not, pollen removal (δ function) is visitor limited until the fifth visit in this diagram, whereas seed set (φ function) ceases to be visitor limited after the second visit. E, Summary of hypothesized selection intensities. This model suggests a general gender bias toward male function in the strength of selection for attractiveness characters when pollinator abundance is marginal.

set (fig. 2D). It takes more visits to escape pollinator limitation of male function than pollinator limitation of female function, and thus there are more opportunities for selection to act on characters of attractiveness through male than through female function.

By this scenario, summarized in figure 2E, selection for attractiveness characters would indeed be (somewhat) more male than female. The asymmetry does not, however, arise directly from an inherent difference between male and female patterns of investment per gamete such as stated in Bateman's principle. Rather, it depends critically on pollination mechanics and ecology. In terms of pollination mechanics, diminishing male fitness returns (which are poorly studied but might

characterize most pollen delivery by insects) are necessary to set up a situation in which multiple visits are much better for male than for female function. In terms of pollination ecology, times of ample pollination are necessary for this potential advantage to be realized and incorporated into the phenotype via pollen-presentation characters, and then times of meager pollination are necessary to create a mismatch between the presentation schedule and the visitation rate. It is this mismatch that finally generates more selection on attractiveness characters through male than through female reproductive success.

CODA

Our two alternatives to Bateman's principle conflict, and we leave them unresolved. Both try to be general arguments, but one suspects that across the gamut of angiosperms every gender bias imaginable has probably been realized in the way selection acts on the floral features that attract pollinators. Both of our views are speculative, and they leave room for additional speculations. They are theories that were stimulated by our empirical experiences. We have spent years striving to measure the shape of the curves discussed by sex allocation theorists and striving to measure selection for male and female reproductive success. Our attempts have been humbling. Audiences have been known to laugh at our scatterplots. In the process of being forced to confront the sloppiness of animal pollination, we were led to incorporate stochasticity as a factor into our generalizations on how flowers evolve. Our path-diagram theory rests on the assumption that there is considerable randomness in the step between the number of pollen grains removed from a flower and the number that make it to stigmas. Our theory of the shifting shape of selection crucially relies on variation in the abundance of pollinators during the evolutionary history of a plant lineage. The two theories provide a conceptual framework beyond Bateman's principle by which to organize empirical studies and probe into fascinating general questions.

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