Bringing the Male Side of Plant Sex into Focus

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The first American Naturalist *appeared in March 1867. In a countdown to the 150th anniversary, the editors have solicited short commentaries on articles from the past that deserve a second look.*

When the editor-in-chief solicited historical perspective pieces based on old articles from *The American Naturalist*, I initially assumed that nothing that had happened during my scientific career would be "old enough." On reflection, I realized that my current students see the 1970s as I saw the 1930s! My choice became easy because it let me focus on two 1970s articles from *The American Naturalist* that transformed the field I work in, realigned my own thinking, and showed me the direction of the next 30 years of my work.

The first of these articles—just a note, in fact—made such an impression that I remember exactly where I read it. I was at a wobbly table in a rundown shack at the Rocky Mountain Biological Lab (RMBL) in Crested Butte, Colorado, and yes, it was a physical journal issue that had been delivered by actual mail. I was at RMBL to frantically collect data on flower visitors and phenology to investigate the extremely 1970s question of whether plant-pollinator communities showed an organized structure of niche partitioning driven by plants competing for pollinators. Measuring niche overlaps was the most popular thesis topic of an uncritical generation of grad students, but I had hoped to go further than most such studies by measuring the pollination success of focal populations at the same time as measuring how much "competition" they faced. That forced me to consider what "pollination success" meant and how to measure it. At that time, pollination ecology remained largely an offshoot of agriculture, in which context "pollination success" was conceived and measured without a second thought as fruit and seed set. Of course, evolutionists were concerned with floral biology, applying selection for outcrossing as their universal intellectual solvent, but that way of thinking was barely integrated with community ecology. Questions nagged. Responses to competition for pollinators might be numerical or evolutionary. I was very interested in both sorts of responses, but the literature I was reading was not helping me very much. I felt convinced that the fates of pollen grains mattered, but I could not articulate exactly why. I had an undefined sense that a plant population could respond evolutionarily to differential selection pressures from pollinators, even if all plants were getting enough pollen to set full crops of seeds, but I did not see a mechanism for this. Nevertheless, my brain was primed to recognize the relevance of Dan Janzen's quirky note in *The American Naturalist*, "On Optimal Mate Selection by Plants," which begins,

> 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. (Janzen 1977, p. 365)

Only two sentences in, and I suspected that this argument would take me somewhere new. Despite some dubious grammar or copyediting, the end of the second paragraph confirmed my suspicion:

> 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. (p. 366)

"Gene donors and gene receivers." Bookkeeping of fitness for hermaphrodites simply requires separate male and female accounts. Had I possessed the excitable Mediterranean temperament of Archimedes, I might have leapt naked from my bath—crying "ηὕρηκε!" instead of "ηὕρηκα!" of course—but I lack the requisite immodesty,

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and RMBL lacks bathtubs. Nevertheless, my thoughts were whirling as I worked my way through Janzen's assertions and tested their explanatory power on my prejudices and paradoxes. Not everything he said rang true. For example, he presumed that a plant could upgrade the quality of its pollination service simply by investing more resources, which glosses over a tremendous amount of practical pollination ecology. Still, the main message—that selection would necessarily reflect a flower's success at donating pollen in addition to receiving it—not only made sense but was blindingly obvious and consequential ... in retrospect.

Janzen wrote breezily and brashly. Surely, he must have been aware that staid senior colleagues would tend to harrumph at such images as pollen grains raping stigmas by circumventing incompatibility reactions. Perhaps he chose his vivid language precisely for its annoyance value, but I prefer to think that his main motive was to draw a forcible parallel between the reproductive biology of sessile, hermaphroditic plants and the behavioral ecology of animals. He had already published descriptions of anthesis in the journal *Behaviour* (Janzen 1968), surely a provocative choice of platform in those bygone days when zoologists and botanists still occupied separate universes. It does not seem that Janzen's article affected many others as powerfully as it did me; I was certainly conditioned to be receptive, partly because Janzen and Monte Lloyd had taught me as an impressionable undergraduate at the University of Chicago and partly because of my own efforts to grapple with the evolutionary implications of pollination. My impression is that the article was initially written off in some circles as an unscholarly rant, partly for its informal assertiveness and partly for Janzen's chutzpah in publishing an ideas piece with no literature citations whatsoever. Even for the *Naturalist*, that must have seemed a stretch of scholarly decorum.

Two years later, Mary Willson published "Sexual Selection in Plants" (Willson 1979), also in *The American Naturalist*. It was a much more decorous, respectable, and undeniably scholarly piece that cited 107 more articles than Janzen's did. (Willson's was evidently the fourth article to cite Janzen's.) Her main tack differed. Rather than using novel but elusive terms such as "optimal female programming," she explicitly evoked the existing concepts of sexual selection in animals—competition and mate choice—and applied them to hermaphroditic plants. Also, she explicitly adopted an allocational viewpoint and implicitly an evolutionarily stable strategy viewpoint (citing Charnov et al. 1976). Despite the differences in approach, though, she converged on and reinforced Janzen's main themes that male and female functions might conflict and that the literature on the behavioral ecology of animals held keys to understanding how selection shaped floral phenotypes.

If Janzen's article could be discounted as a quirky sermon, Willson's could not. In particular, rather than claiming as Janzen did that plants might be optimizing outcrossing rather than maximizing it, she threw down a gauntlet by claiming that sexual selection offered an alternative explanation to outcrossing—a competing explanation—for some major evolutionary trends in plants, particularly the evolution of separate sexes. If Janzen seemed to be "coming from left field," Willson was coming from another field—a respectable and established one. Botanists' faith in the evolutionary potency of selection for outcrossing came directly from Darwin but so did sexual selection. Willson's tart characterization of outcrossing-based explanations as "knee-jerk responses" simply demanded critical evaluation. Do these new ideas hold up? Must we discard old views or just tweak them?

A number of research programs swiveled around this point, mine among them. Conceptual models and more formal theory blossomed. Gender became a continuous variable rather than a set of categories. Sex allocation theory rose to prominence. Interference and conflict between the two sex roles of hermaphrodites were identified as selective forces to be reckoned with. Claims were made that selection through male function should be considered the major force shaping floral evolution. As an ecologist interested in mechanisms, I was particularly struck by Willson's warning that "the test of any possible reality in these suggestions is to be found in detailed (and excruciating! [...]) monitoring of pollen donation and seed production of marked individual flowers and plants" (Willson 1979, p. 784). From then to the present, a continuing thread of my research has been to account directly for the fates of pollen grains and to understand the consequences for evolution. Numerous other contemporary scientific careers, although divergent, trace back to similar roots. Modern studies do not always attempt to measure what has become known as "male fitness" because it is still an onerous task, but reviewers demand that subject be discussed at the very least.

Would these developments have happened if *The American Naturalist* had not published these two provocative articles? Probably so. Formidable thinkers such as David Lloyd, Kamal Bawa, Eric Charnov, Graham Bell, and many others were on the hunt. On the other hand, the basic insights offered by Janzen and Willson had been offered before, for example, by Horovitz and Harding in a 1972 article in *Heredity*:

> While a self-fertilising plant makes equal male and female gamete contributions to the next generation, so that male gamete contributions can be extrapolated from data on functional embryo sacs, this situation need not hold in outcrossing plants. Here the

> 1 : 1 ratio between male and female gametes obtains only at the level of the population and individuals or genotypes in the breeding entity can function more largely as male than as female parents, or *vice versa*, at each other's expense. (Horovitz and Harding 1972, p. 223)

Why did Janzen (1977) and Willson (1979) stimulate a flurry of activity and 500 citations, while Horovitz and Harding (1972) made little splash? I think that it is partly a matter of style. Janzen and Willson presented verbal arguments in broad, vivid strokes. Instead of considering "embryo sacs" and "the breeding entity," they introduced fresh, zoologically flavored terms such as "mate choice" and explicitly sought analogies and parallels outside the traditional bounds of plant population genetics. Horovitz and Harding stayed inside that tradition, presenting their insight as a refinement rather than a leap forward. They presented the big message about gender conflicts by deriving mathematical formulas for "female outcrossing rates" and "male outcrossing rates," while Willson was telling readers to look beyond outcrossing to see a bigger picture. Style aside, however, there is also the choice of journal. Janzen and Willson published in a journal concerned with "the conceptual unification of the biological sciences," and their arguments truly served that goal. Horovitz and Harding published in a journal concerned with, well, heredity. *The American Naturalist* has long been the most desirable place to publish an ambitious article promoting a new idea or a fresh synthesis, and its editors have been alert enough and risk-prone enough to accept visionary work. May the journal continue to fill that role as it moves into its fourth half-century!

In *The American Naturalist*

Janzen, D. H. 1977. A note on optimal mate selection by plants. American Naturalist 111:365–371.

Willson, M. F. 1979. Sexual selection in plants. American Naturalist 113:777–790.

Other Literature Cited

Charnov, E. L., J. Maynard Smith, and J. J. Bull. 1976. Why be an hermaphrodite? Nature 263:125–126.

Horovitz, A., and J. Harding. 1972. The concept of male outcrossing in hermaphrodite higher plants. Heredity 29:223–236.

Janzen, D. H. 1968. Reproductive behavior in Passifloraceae and some of its pollinators in Central America. Behaviour 32:33–48.