

Jack and Jill in the Pulpit

For some small plants, the burden of being female is just too much to bear

by Paulette Bierzychudek

Jack-in-the-pulpit, *Arisaema triphyllum*, is a perennial forest herb that is endowed with one of the rarest of all plant breeding systems. During each flowering season, a jack-in-the-pulpit plant behaves like a member of one sex or the other, producing either male or female flowers. Plants are not fixed as males or females for their entire lives, however, and an individual has the option each year of performing as a member of either sex. This breeding system, more common in animals than in plants, has been termed sequential hermaphroditism. In common parlance, jack-in-the-pulpit can change sex: "Jack" can become "Jill," and vice versa.

Common in the understory of deciduous forests throughout the eastern half of the United States from Maine to Florida, jack-in-the-pulpits thrive in moist, species-rich woods. They come into bloom just as the canopy is leafing out in the spring, somewhat after the peak of the wildflower display. Each plant produces one or two deep green, tripartite leaves. A stalk bearing a tall, graceful pulpit or hooded inflorescence, grows from the junction of the leaves. The pulpit, a complicated structure characteristic of the arum family, Araceae, consists of many flowers surrounded by a modified leaf called a spathe. This leaf may have a variety of color patterns, ranging from solid green to green with longitudinal stripes of sharp white or exotic purplish brown.

The spathe surrounds and forms a hood over a columnar spadix, a fleshy spike whose base is covered with dozens of tiny, simple male or female flowers. Each male flower is a cluster of creamy white or purplish anthers, which open to release large quantities of pollen; the pollen then collects at the base of the chamber created by the spathe. Female flowers are green spherical structures, each topped by a stigma and containing several ovules, or potential seeds.

Pollen is carried from male to female flowers by tiny fungus gnats that flit from plant to plant. Hardly the traditional pollinator, these flies possess no special structures for the transport of pollen, but a few grains cling to their sparse coats of hairs and bristles. Jack-in-the-pulpits, for their part, have none of the attractive devices normally associated with pollinator reward--no nectar or bright color, for example. They apparently attract fungus gnats by means of deception. Something about the inflorescence--its color or odor--may resemble the mushrooms on which fungus gnats mate and lay eggs. Once they have flown into the open top of the spathe, the flies are trapped, unable to fly in the narrow chamber or to walk up the smooth walls.

A subtle sexual dimorphism in jack-in-the-pulpits makes pollen transfer from males to females possible. On male plants, where the spathe overlaps itself at the base of the chamber, there is a gap just large enough to allow the gnats to escape and carry some of the male's pollen with them. The spathe of each female inflorescence overlaps smoothly, leaving no escape hole. By the end of the flowering period the chambers of most female pulpits contain dead gnats. The pulpit "traps" bear some resemblance to the traps of such insectivorous pitcher plants as *Darlingtonia* or *Sarracenia*, but there is no evidence that jack-in-the-pulpits absorb any nutrients from the trapped flies. The trap simply seems to insure that the flies will thrash around in the chamber long enough to lose any pollen they might be carrying.

During the course of the summer, the fruits of successfully pollinated flowers enlarge within the spathe's covering. Eventually the swelling berries become large enough to burst out of the enclosing leaf, and by late summer they begin to turn red. Ripe berries contain one to several seeds in a watery, sweetish matrix surrounded by a bright scarlet skin.

Herbivory is not a serious problem for jack-in-the-pulpit since the leaves and the corm (thick, underground stem) contain crystals of calcium oxalate, a mechanical irritant that deters a wide range of potential herbivores, mammals and insects alike. Only snails and slugs, apparently resistant to the effects of the crystals, feed on the foliage with any regularity. The damage they do is minor, however, and usually occurs at the end of the growing season, when foliage is already beginning to die back for the winter. *Arisaema*'s most serious enemy is a rust, a fungus disease that arrives via airborne spores and spreads throughout the plant, causing the development of deformed leaves and inflorescences, interfering with photosynthesis, and causing early senescence and eventual death.

A perennial, *Arisaema* grows slowly, probably because of the low levels of light available in the forest understory. Large (knee-high) plants may be twenty or more years old. At the end of a summer, a plant's one or two leaves are the same size as when they developed in the spring, and no new ones have been added. Instead of being used to form new leaves, the sugars formed by photosynthesis over the course of the season are stored as starch in the underground corm, providing fuel reserves for next season's leaf or leaves and inflorescence. By the end of the growing season, the plant has made certain developmental "decisions," presumably on the basis of the amount of stored material: whether to produce one or two leaves and whether to produce a male or female inflorescence or none at all. If a corm is removed from the ground in September and dissected, leaf and inflorescence organs can be seen, and the sex of next year's flowers easily identified.

Upon examination, these dormant corms reveal a clear pattern, one that is also evident when inspecting flowering plants in the spring. Large, two leaved plants almost invariably bear female inflorescences; smaller, one-leaved plants usually behave like males; and the smallest plants produce no inflorescence at all. This pattern is so striking that a person with some experience can accurately predict the sex of most plants from several yards away on the basis of their size alone.

If a medium-sized male plant has a profitable year, from a photosynthetic standpoint, then in the fall it will produce primordia for two large leaves and a female inflorescence. If, however, it has managed only to replace the reserves it used from last year, but not add to them, the plant will once again form male flower primordia and only one leaf. And if the plant has had a particularly bad year--if, for example it was cut down or trampled not long after emergence--it is likely not to flower at all in the succeeding year. No state is irreversible, and a new decision is made every year. Even a very large female plant that has suffered severe damage for several years running can be induced to produce smaller leaves and to flower as a male. With time and good conditions, the plant is likely to regain its large size and female status. So change among jack-in-the-pulpits is far from a rare phenomenon. In successive years, as many as 50 percent of all the plants large enough to produce flowers switch from one sex to the other.

Why are there no females among the small plants and no males among the large ones? The relationship between the size of plants and their sex provides some clues about the possible reason for the evolution of this sex-changing behavior. The pattern of large females and smaller males is not uncommon in the animal kingdom and is thought to be an adaptation related to the greater reproductive effort, or cost, that females must sustain. An egg usually contains a larger supply of nutrients and stored energy than does a sperm. In addition, females often carry and nourish developing embryos in their bodies for an extended period of time, and they are more likely than the males to engage in the care and feeding of the offspring after birth. For these reasons, large size is

advantageous for females. Males can also be subject to selection for large size, especially in species where competition for females is involved, and this can reduce male--female size differences. Even in these species, however, females must often be larger than males before they achieve sexual maturity.

Among plants, the costs of reproduction may also be greater for females than for males. To test this hypothesis, I measured the reproductive effort of male and female jack-in-the-pulpits, using the weight of each plant part as an estimate of the amount of energy required for its production. A male inflorescence tends to represent a fairly constant proportion of a plant's total biomass, about 8 percent. Because this structure withers and disappears soon after the flowering period, it does not have to be supported by the plant for very long.

The story is different for females. After flowering, females must also supply the developing embryos with food (endosperm), protection (seed coat), and fruit flesh to attract potential seed dispersers--all over the course of the growing season. Thus, while a female inflorescence alone is no more costly to produce than a male one, the cost rises if seeds are produced. Furthermore, jack-in-the-pulpit seeds are large and heavy, and seed size is constant rather than flexible, so the cost of producing a set number of seeds will always be greater for a small plant than it is for a large one. The production of five seeds, for example, represents a reproductive effort of as little as 10 percent for a very large female and about 20 percent for an average-sized female. Extrapolating from the mathematical relationship between plant size and reproductive effort, I have predicted that if a tiny plant the size of a male were to function as a female, the production of five seeds would entail a reproductive effort of 30 percent.

Other perennial species of forest herbs average a reproductive effort of about 5 percent. For reasons that are not clear, jack-in-the-pulpits expend considerably more energy than this on reproduction--8 percent for males, 10 percent or more for fruiting females. A reproductive effort as high as 30 percent is seen only in a few species of annuals, which die at the end of the growing season. Presumably, no perennial plant could invest 30 percent of its biomass in reproduction and still have sufficient reserves for surviving the winter and producing new leaves the following spring.

In the face of this high cost of female reproduction, sex changing is probably a better option than dioecism, the condition of having individuals with separate, fixed sexes. If jack-in-the-pulpit were to behave as a typical dioecious plant, the males would attain flowering size after only a few years, but the females would need to wait many years before they became large enough to flower and produce seeds. Because mortality chances are high for small plants, few females would survive to reproductive size. Sex changing allows plants to reproduce sooner and more often; they can be fathers whenever they are too small to be mothers.

Comparing the relative merits of sex changing and dioecism may be of little help in understanding the origin of jack-in-the-pulpit's reproductive behavior, however, since sex changing appears to have evolved, not from dioecism, but from a monoecious condition in which individual plants produce both male and female flowers. While dioecism is unknown in the family Araceae, monoecism is extremely common.

The genus *Arisaema* is a large one, containing more than a hundred species, most of them native to the temperate and semitemperate forests of China, Japan, and India. In some species, an individual reproduces as a male when it is small, but as the plant grows larger, its inflorescence contains first a few and then, with each succeeding year, more and more female flowers. Even the largest plants, though, bear male as well as female flowers. Developmentally, these plants begin life as males and eventually become monoecious.

The reproductive strategy of some other species comes closer to that of *Arisaema triphyllum*. The plants in this second group pass through three size related stages: male, monoecious, and

female. Finally, the majority of the species have a reproductive strategy like *Arisaema triphyllum*'s; here the monoecious stage has been entirely eliminated. While the phylogenetic relationships within this rather large genus are still unclear, it seems safe to assume, on the basis of the reproductive biology of the rest of the family that the sex-changing species represent an evolutionary advance over the monoecious ones.

Whether the loss of the monoecious stage carries with it a selective advantage and, if it does, what that advantage might be are not clear. No information is available about whether the monoecious species of *Arisaema* are capable of self-fertilization. Certainly, self-fertilization is impossible for members of this third group; jack-in-the-pulpit females can never produce seeds unless pollen from a separate male plant arrives via fungus gnats. There are several possible advantages to avoiding self-fertilization, but in jack-in-the-pulpit, these theoretical advantages must be weighed against a clear disadvantage--the meager seed production of females in some locations. Although a typical female has thirty to fifty flowers and each flower contains four to six ovules, the average plant at my study sites in upstate New York produced fewer than ten seeds per year. Many plants produced no seeds at all. This poor performance is not a result of energetic constraints: when I pollinated jack-in-the-pulpits by hand with a camel's-hair brush, using pollen from neighboring males, these same females regularly produced from fifty to two hundred seeds. *Arisaema*'s pollinators appear to be so inefficient and unreliable that the probability of fertilization for any individual female flower is extremely low.

I was surprised by this finding; pollinators rarely limit the seed production of plants so severely. But jack-in-the-pulpit and its fungus gnats are different from the stereotypic flower and its faithfully cooperative pollinator partner. Since flies receive no reward for pollinating jack-in-the-pulpit flowers and will die in female pulpits, natural selection favors flies that are the least effective and efficient pollinators; these are the ones that will survive to mate and lay their eggs. Any fly that successfully transports pollen from a male to a female inflorescence dies without reproducing, and any genes that might influence that propensity are lost from the fungus gnat gene pool. How, then, could anything but a haphazard, chancy relationship between *Arisaema triphyllum* and its pollinators be expected? The obvious solution would be for *Arisaema* to modify its pollination syndrome in order to attract the services of more effective pollinators. Why has this not occurred?

Before I can begin to answer this question, more information is needed. Do all *Arisaema* species exhibit the same degree of pollinator limitation or is *A. triphyllum*, one of only two *Arisaema* species in North America, exceptional in this respect? Perhaps jack-in-the-pulpit has not always been so poorly pollinated. Fungus gnats may be less common today than in presettlement days, now that the forest that once covered all of eastern North America exists only as small patches. If this relatively recent environmental change has lowered jack-in-the-pulpit's seed production, adaptive modifications may occur with time and seed set may improve. If however, jack-in-the-pulpit's behavior is different from that of its Asian relatives and has been for a long time, then this meager seed production suggests that evolution may have a difficult time revamping a basic plan once it has become established. *Arisaema*'s reproductive behavior does seem conservative: all the species that have been studied are pollinated by tiny flies. and all possess inflorescences very similar in structure to those of *A. triphyllum*.

Before Darwin's time, natural historians believed that the components of the natural world were all part of a master plan. They expected efficiency and perfection of design, sought examples of such efficiency, and marveled at the wisdom of Providence when they found them. In more recent times, we have sometimes had a similar regard for natural selection. We often expect to find organisms that are perfectly adapted to their environments, and certainly many of them seem to be, sometimes in amazing ways. The leaf-mimicking butterfly, complete with insect damage. and the

provisioning by some acacias of special nectaries and food bodies for their ant protectors are examples of the power of natural selection. But natural selection operates under various constraints that can sometimes prevent the attainment of the optimal design.

First, because no year is exactly like any other year, no environment exactly like any other environment, there maybe no one "best" design. The design that natural selection favored at one time or in one particular place is unlikely to be perfectly suited for that environment forever or once the organism has dispersed to a new place. Second, drawing the theoretically best design from a species' limited genetic repertoire may not be possible. Genes with unrelated functions may be closely linked, making it impossible for selection to improve on one aspect of an organism's design without interfering with another. Finally, when a structure or a behavior is being modified by natural selection for a new function, a total overhaul is never possible. The old design must be altered to serve the new role, and such remodeling is unlikely to result in the most efficient, streamlined form conceivable.

Some such constraint may be responsible for jack-in-the-pulpit's low levels of seed production. Reconstructing the co-evolutionary history of the jack-in-the-pulpit and the fungus gnat may prove elusive, but the plant's apparent maladaptiveness appears to be a testimony to the often overlooked limitations of natural selection.

Paulette Bierzychudek is an assistant professor in the Department of Biology at Pomona College.