Sex choice and the size advantage model in jack-in-the-pulpit (*Arisaema triphyllum*)

(sex change/reproductive success/demography/protandry)

DAVID POLICANSKY

Gray Herbarium, Harvard University, 22 Divinity Avenue, Cambridge, Massachusetts 02138

ABSTRACT   *Arisaema triphyllum* is a perennial herb whose sex and size often change from one growing season to the next. The proportional gain in reproductive success (RS) with size is much greater for female (carpellate) plants than it is for male (staminate) plants. I constructed *RS*–size curves for males and females; the curves intersect at a point t = 398 mm. According to theory derived from the size advantage model, t is the point below which the plants should be male and above which they should be female. Plots of size–frequency distributions of males and females show that below 380 mm the proportion of males is greater than the proportion of females, whereas above that point the proportion of females is greater than the proportion of males. Thus prediction and observed results are in very close conformity.

Many animals (1–3) and some plants (4–10) are known to change from male to female or vice versa during their lifetimes, but only recently has much attention been paid to understanding their life histories (11–15). The most widely accepted explanation for sex change is the "size advantage" model of Ghiselin (11). He suggested that if an organism reproduced more "efficiently" as one sex, say male, when small, and more efficiently as a female when large, then a genotype changing from male to female with increasing size would be favored. This model was extended and formalized and its consequences were analyzed by Warner (12). A refinement he made was that the *rate* of increase of reproductive success (RS; = m_x) with increasing size for each sex was important. In other words, an important question is whether the sexes gain RS in the same proportion with increased size. Because every zygote has equal genetic input from its male parent and its female parent, the average male and the average female have equal RS (if there are equal numbers of the two sexes). Thus, if RS increases in greater proportion with size for females than for males, for example, plotting RS versus size for the two sexes will yield two intersecting curves as in Fig. 1. In this case smaller individuals have greater RS as males and larger individuals have greater RS as females. An individual changing from male to female on reaching size t, the size at which the RS–size curves intersect, has the maximal lifetime RS and will be more fit than either a pure male or a pure female. Thus a prediction of the size advantage model is that females (in this case) will be as large or larger than size t, whereas males will be that size or smaller. In this paper I report results of a field study of the jack-in-the-pulpit, *Arisaema triphyllum* (subspecies *triphyllum*), in which this prediction is confirmed. Thus the size advantage model has now been tested by construction of *RS*–size curves for males and females, and the model has now been applied to a plant.
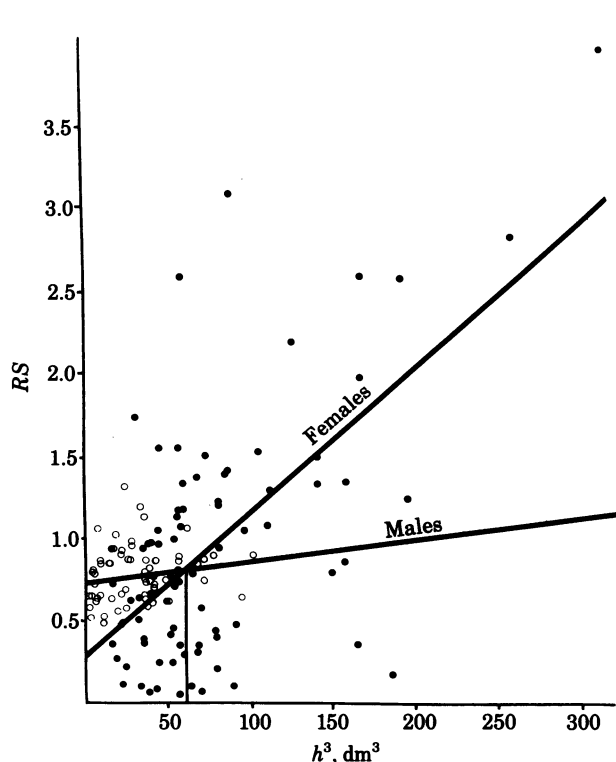
FIG. 1.   *RS* for males (○, n = 63) and females (●, n = 80) versus h^3. The coordinates of the point in quotation marks are 373, 4.44. The lines are the calculated regressions. Almost all male flowers had four anthers; there was no correlation between the size of the plant or the number of flowers (average 49.5) and the size of the anthers (which reflects the amount of pollen produced). About half of all females produced seeds. The average height of the 80 females in the sample, all of which produced seeds (average 51.9), was 414 mm, as compared with 411 mm for all females. Because of attrition due to mortality and loss of markers there were fewer plants in 1979 than earlier. To give the sex ratio for each year equal weight I used the average of F/M for the 3 years rather than the total number of females (814) divided by the total number of males (1224).

A. triphyllum is a sex-changing, perennial herb common in the deciduous forests of eastern North America. Its structure is simple, consisting of an underground storage organ (corm), one or two compound leaves, and one or no inflorescence. Typically the inflorescences in this study had about 50 male (staminate) or 50 female (carpellate) flowers; fewer than 1% had both male and female flowers at a frequency of at least 10%.

A. triphyllum is unusual among sex-changing organisms whose life histories have been studied in that it may change both its sex and its size in either direction from one season to the next.

Whereas most animals studied (1–3, 11–15) change only from small males to large females, or from small females to large males, *A. triphyllum* may change from a large female in one season to a smaller male in the next, or vice versa; some even become asexual after being male or female. I use the term "sex choice" to distinguish this complex pattern from the one in which there is a single, unidirectional change.

In May and June of 1977, I marked 597 male, 312 female, and 343 asexual plants with numbered, stake-wire flags in the Estabrook Woods, Concord, Massachusetts. The males and females represented all the sexual plants I could find within the study area. I recorded the height and sexual state of each plant during the growing seasons of 1977, 1978, and 1979. As an estimate of RS, I counted the flowers on each of 63 male inflorescences in 1979 and the seeds in each of 26, 36, and 18 berry clusters in 1977, 1978, and 1979, respectively. For each year I divided the number of seeds produced by each female in the sample by the average number of seeds produced per female in the sample; for males I divided the number of flowers on each inflorescence by the average number of flowers per inflorescence. This operation is important because it gives a method of determining an individual's relative RS—i.e., a method of comparing the RS of an individual with the average for its sex, and this is the crux of the test of the model. One can thus see whether a male or a female gains proportionally more in RS by being large.

If there are more males than females (as in this study) then the average male contributes less to the next generation than the average female (although of course the aggregate male contribution exactly equals the aggregate female contribution). I assumed for this study that the mean sex ratio (over time) and the RS values of males and females are in equilibrium. Thus, setting the average RS of a female at 1.0, the average RS of a male would be F/M, in which F and M are the numbers of females and males. In this study the observed ratio F/M varied between 0.58 and 1.23 in the 3 years, with a mean value of 0.79. I thus multiplied the RS of each male by 0.79 before performing the above operations.

Of the plants originally marked, 1224 were recorded as male

over the 3-year study, with mean height 336 mm (SD 67.8) and 814 were female with mean height 411 mm (SD 85.0). These heights are significantly different (Z = 21, P ≪ 0.001). Linear regression analysis of relative RS versus the cube of the height, h^3 (which is proportional to volume and was used as the best nondestructive estimate of size), for males and females yielded the equations RS = $0.0013h^3$ + 0.743; r^2 = 0.03; P(slope = 0) > 0.1 for males, and RS = $0.0090h^3$ + 0.256; r^2 = 0.45; P(slope = 0) < 0.001 for females (Fig. 1). (For females the 3 years are combined. The slopes of the regressions for each of the 3 years were 0.012, 0.009, and 0.011, respectively, all >0 at the 0.05 level of significance.) The intersection of the RS–size curves (t) corresponds to a height of 398 mm (if 0 slope is assumed for males, i.e., RS = 0.79, then t = 390 mm). The above method of estimation of t is equivalent to that used by Charnov *et al.* (16) when male RS, female RS, and sex ratio are in equilibrium. These authors maximized the product

$$\left[\int_0^t f(x)\cdot RS_m(x)dx\right] \cdot \left[\int_t^\infty f(x)\cdot RS_f(x)dx\right],$$

in which f(x) is the proportion of all individuals that are size x, $RS_m(x)$ is relative male RS at size x (i.e., the ratio of RS of a male of size x to the RS of an average male) and $RS_f(x)$ is relative female RS at size x. I performed this operation, using the $RS_f(x)$ function RS_f = $0.0090h^3$ + 0.256 and assuming male RS to be independent of size—i.e., $RS_m(x)$ = 1. When size intervals of 20 mm were used the maximal value of the product was between 380 and 400 mm, yielding at t of near 390 mm. Thus the two methods give the same result in this case.

According to the size advantage model, females should be as large as or larger than t—i.e., 398 mm—and males should be that size or smaller. The plot of size–frequency distributions of males and females (Fig. 2) shows that above 380 mm the proportion of females is greater than the proportion of males, whereas below that point the proportion of males is greater than the proportion of females. Thus the model has predicted a t (398 mm) extremely close to that observed (380 mm). The ex-
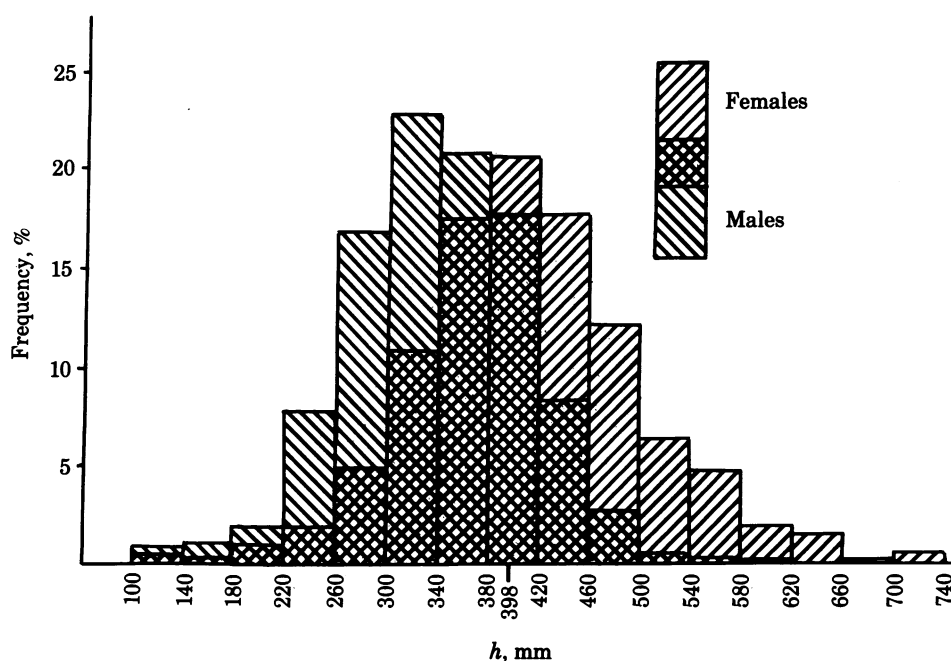

FIG. 2.   Size–frequency distributions of males and females. Data from 1977, 1978, and 1979 are combined.

istence of some females smaller than t and some males larger is likely related at least in part to the large yearly fluctuations in sex ratio.

As Charnov and Bull have pointed out (17), sex should be determined environmentally when environmental variations affect the RS values of the sexes differently, and where the organisms cannot choose their environments. Environmental variability can have both spatial and temporal components; it is temporal variability that favors sex choice. As noted above, *A. triphyllum* can change sex in either direction, and it can also change to being asexual from being male or female, and vice versa. It is noteworthy that when females become male or asexual in the following season they were smaller than before. This reinforces the results presented in Fig. 1 by showing that size rather than age is the important factor in determining sex, and it is through this factor that the action of the environment operates on sex choice.

1. Atz, J. W. (1964) in *Intersexuality in Vertebrates Including Man*, eds. Armstrong, C. N. & Marshall, A. J. (Academic, London), pp. 145–232.
2. Bacci, G. (1965) *Sex Determination*, International Series of Monographs in Pure and Applied Biology, Zoology 26 (Pergamon, Oxford).
3. Reinboth, R., ed. (1975) *Intersexuality in the Animal Kingdom* (Springer, Berlin).
4. Gregg, K. B. (1975) *Selbyana* 1, 101–113.
5. McArthur, E. D. (1977) *Heredity* 38, 97–103.
6. Heslop-Harrison, J. (1972) in *Plant Physiology*, ed. Steward, F. C. (Academic, New York), pp. 133–290.
7. Hibbs, D. E. & Fischer, B. C. (1979) *Bull. Torr. Bot. Club* 106, 222–227.
8. Schaffner, J. H. (1922) *Am. J. Bot.* 9, 72–78.
9. Maekawa, T. (1924) *J. Coll. Agr. Hokkaido Imp. Univ.* 13, 217–305.
10. Camp, W. H. (1932) *Ohio J. Sci.* 32, 147–151.
11. Ghiselin, M. T. (1969) *Q. Rev. Biol.* 44, 189–208.
12. Warner, R. R. (1975) *Am. Nat.* 109, 61–82.
13. Charnov, E. L. (1979) *Am. Nat.* 113, 715–734.
14. Charnov, E. L., Gotshall, D. W. & Robinson, J. G. (1978) *Science* 200, 204–206.
15. Warner, R. R., Robertson, D. R. & Leigh, E. G. (1975) *Science* 190, 633–638.
16. Charnov, E. L., Los-DenHartogh, R. L., Jones, W. T. & Assem, J. van den (1981) *Nature (London)* 289, 27–33.
17. Charnov, E. L. & Bull, J. (1977) *Nature (London)* 266, 828–830.