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Simultaneous hermaphroditism and sexual selection

(sperm competition/pollination/male-female conflict/dioecy/double fertilization)

ERIC L. CHARNOV

Department of Biology, University of Utah, Salt Lake City, Utah 84112

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ABSTRACT Theory about the evolution of sexual behavior in dioecious species is based on the general assumption that egg production is limited by a female's ability to garner resources to make eggs, not by a lack of sperm to fertilize them. Reproductive success for males is thus limited by access to females (and their eggs). I suggest that egg production by simultaneous hermaphrodites also obeys this principle—that fertilized egg production by an individual is not limited by sperm availability, but by resources allocated to eggs. If true, this suggests that sperm competition (reproduction success through male function) and a form of male-female conflict have played important roles in the evolution of hermaphroditism.

In 1948 Bateman (1) proposed that natural selection operating on reproductive strategies would be expected to produce different results in males and females, for the following reasons. In terms of autosomal genes, males and females contribute equally to any zygote formed; thus the fitness of an average male equals that of an average female. However, female reproductive success is limited by ability to accrue resources to make offspring, rather than by the availability of sperm to fertilize eggs. Thus, male reproductive success is limited by the ability to gain access to eggs. Trivers (2) and Orians (3) have used these assumptions to construct a general theory of sexual and parental behavior, which includes situations where males would be selected to provide parental care (i.e., to invest more than just gametes in offspring).

While these authors (and others) have shown how useful these assumptions are, they restricted attention to dioecious organisms. Simultaneous hermaphroditism (SH), in which an individual reproduces through both sperm and eggs in each breeding season, is the dominant life form in higher plants (4-6) and is quite common in animals (7, 8), excluding arthropods and vertebrates. I propose here that "Bateman's principle" is also valid for these organisms—that fertilized egg production by an individual is limited not by the ability to get sperm, but by resources allocated to eggs. This is a strong assumption, and not all that I will discuss depends upon its perfect validity. However, if it is approximately true, then the theory outlined below has several important implications for reproductive biology. In earlier papers, my colleagues and I (9, 10) proposed several reasons for selection favoring SH over dioecy (including situations in which Bateman's principle is not true). This paper focuses attention on the role of sperm competition (reproductive success through male function) and male-female conflict.

Why be a hermaphrodite?

This section will develop implications of Bateman's principle in a general way using a graphical model. Suppose that we assign a hermaphrodite genotype a fitness of α through male function, and β through female, compared to fitnesses of 1 for both males and females (under outbreeding). Thus the her-

maphrodite produces β proportion as many eggs as a female, and is α times as competitive at fertilizing eggs as is a male. Both α and β depend upon how the hermaphrodite allocates its resources to male as opposed to female function. If we can specify the tradeoff between α and β , it is straightforward (10) to show that under natural selection: (i) for a hermaphrodite population, the equilibrium α, β (denoted α^*, β^*) is the pair that maximizes the product $\alpha^* \cdot \beta^*$. (ii) Such a population is stable to invasion by a gene that produces males provided $\alpha^* > 1/2$ (or a gene that produces females if $\beta^* > 1/2$). If both these conditions are met, SH is stable when compared to dioecy. Thus, hermaphroditism will be stable provided the individual has a reproductive success that is at least half that of both males and females. (iii) Dioecy will be favored over SH if and only if $\alpha + \beta < 1$ (for all possible α and β , given the tradeoff specified). If $\alpha + \beta > 1$ and either α^* or $\beta^* < 1/2$, then neither dioecy nor SH is stable, and the only stable population is a mixture of sexual types (10).

Now, let us combine these inequalities with Bateman's principle. Assume (for example) that mortality rates do not differ among males, females, and hermaphrodites and that each has R resources to allocate to reproduction. Following Heath (11), I assume that there exist two kinds of costs for reproduction. The first might be termed "a fixed or fertility-independent cost." It involves structures that must be built simply in order to reproduce, but which do not quantitatively affect the amount of reproductive success (other than allowing it to be greater than zero). The second cost involves the resources left after the fixed cost is paid. Allocation of these resources to reproduction increases the individual's reproductive success. A simple example would be the construction of a duct to transport gametes (a fixed cost) compared to resources put into the gametes themselves. Reproductive success should increase with resources put into gametes, but only after the duct is built. If the fixed cost is a for female function and h for male function, the female will have $R - a$ resources left after set-up, the male $R - h$, and the hermaphrodite $R - a - h$. As noted by Heath (11), the hermaphrodite must pay both male and female fixed costs, while each pure sex pays only one. This is the reason behind considering costs to be of two types. The dichotomy is a simple one and I use it here mostly for illustration (as we know almost nothing about relative magnitudes for the costs, or just what structures can be considered a fixed cost). Note that any fixed cost that is paid by all three types is simply included in the determination of R . In order to incorporate this idea into a model for α and β , I will assume as follows. Let r be the proportion of resources (left after the fixed costs are paid) that is allocated to male function. Under Bateman's principle, β is proportional to $1 - r$; fertilized eggs depend only upon resources diverted into eggs. Thus, we may set $\beta = (1 - r)b$. $b < 1$ refers to the fixed cost the individual pays for also reproducing through male function. For α , we need to specify how reproductive success

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Abbreviation: SH, simultaneous hermaphroditism.

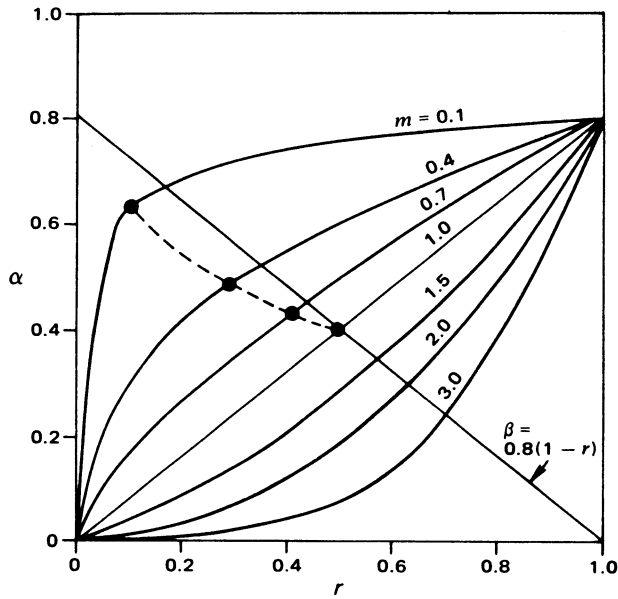


FIG. 1. A relation between male fitness (α) and the input of resources (r) to male function. Male fitness is given by $\alpha = 0.8r^m$; the curves are for various m . For $m < 1$, the curve is convex and tends to favor hermaphroditism. For $m \geq 1$, the relation is concave and favors dioecy. The β curve is the female fitness relation [$\beta = 0.8(1 - r)$]. The broken line gives the equilibrium r —only those m with α and $\beta > 1/2$ favor hermaphroditism. The 0.8 in both the male and female relation refers to the fertility-independent cost. See text for further discussion.

through male function increases through the input of resources. Again, the hermaphrodite should pay some cost for building female structures, which a pure male ($r = 1$) does not. A model that incorporates this, and allows many shapes for the male gain relation is $\alpha = cr^m$ (in which $c \leq 1$). Fig. 1 shows this function for various m (and $c = b = 0.8$).

Now, the equilibrium allocation maximizes

$$\alpha \cdot \beta \text{ or maximizes } cr^m b(1 - r). \quad [1]$$

This implies that [setting $\partial(\alpha \cdot \beta) / \partial r = 0$]: $r = \frac{m}{1 + m}$. [2]

Likewise, SH is stable provided:

$$c \left(\frac{m}{1 + m} \right)^m > 1/2 \quad [3]$$

and

$$b / (1 + m) > 1/2. \quad [4]$$

If $b = c = 1$ (no fixed cost), these conditions reduce to $m < 1$. This means that the reproductive success through male function must be negatively accelerated (or convex)—that the increase in reproductive success for male function must be greater for the first resources put into it than for further resources (see Fig. 1). If there are fixed costs, it is necessary that the male gain curve be even more convex (as shown in Fig. 1; note where both α and $\beta > 1/2$). Assuming that fixed costs are symmetric ($b = c$), Fig. 2 shows the values for b and m that favor SH. To summarize the results: (i) Dioecy is favored by a concave male gain curve, or by high fixed costs for male or female function (see also ref. 11); SH is favored by a limited ability to gain reproductive success through male function (a convex male gain curve). It is clear that the chances for an individual to reproduce through male function thus play a key role in the evolution of SH. (ii) Interestingly, the allocation of resources to male versus

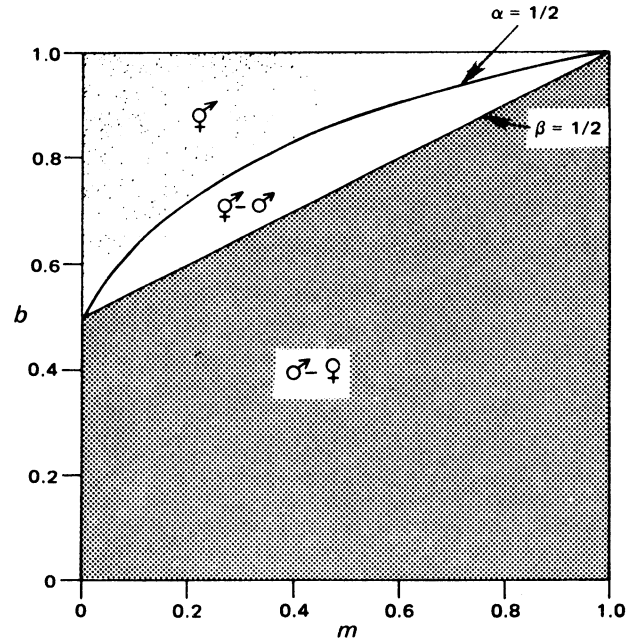


FIG. 2. When be a hermaphrodite? The male fitness relation is $\alpha = br^m$, the female $\beta = (1 - r)b$. Hermaphroditism is favored when both α and β are $> 1/2$. This is shown for various m and b . Also shown is the region that favors dioecy (and a mixed population δ and ϕ).

female function (r) is not affected by fixed costs, even though such costs are important in the stability of hermaphroditism.

There are at least two situations that may cause the female gain curve to be nonlinear, even if sperm does not limit the production of offspring. If offspring compete among themselves (e.g., limited propagule dispersal as in some plants), the female gain relation may be convex. This further favors SH, and selects for a more equitable allocation of resources to male versus female function. The curve may become concave if offspring survival is tied to their effective dispersal, and if dispersal depends upon attracting some biotic agent (e.g., seed dispersal by animals). As pointed out to me by K. S. Bawa (personal communication), such a situation would favor dioecy.

What limits male reproductive success?

Under Bateman's principle, SH will be favored by a combination of low fixed costs and limited opportunities for an individual to reproduce through male function. Several factors may limit male reproductive success: (i) Adult immobility and copulation may combine to limit the availability of partners, so that only a few are available in each breeding period. (ii) Small group size [such as found in some parasitic molluscs (7)] also limits the eggs to be fertilized. (iii) The ability of an individual plant to get its pollen to conspecific stigmas may be limited if the pollen is carried by insects. The individual may saturate its pollen vectors, so that fitness gains for the first pollen produced are greater than those for further pollen produced. It may also be that only a few individuals mate with each other (most pollen gets taken off by the next plant), implicating small group size. (iv) The male gain relation is also affected by how a sperm recipient uses its partner's gametes. The recipient's reproductive interests are not expected to coincide with those of its mate, resulting in a conflict. This will be developed further in the next section.

Altenberg (12) noted that SH shows a large tendency (in animals) to be associated with immobility in the adult stage combined with internal fertilization and copulation. Immobility

combined with the external fertilization (or internal fertilization without copulation) tends toward dioecy. As an example, echinoderms (13) and pelecypods (14) typically release gametes into the environment, and the vast majority are dioecious (in spite of their relative immobility). Furthermore, scattered examples of SH in these groups tend to be associated with the brooding of offspring. Gastropods typically copulate (15), as do flatworms (Platyhelminthes), barnacles, earthworms, and leeches—SH is the most common form of reproduction in these groups. There are, however, some interesting exceptions to this copulation rule. Nematodes copulate and seem no more immobile than flatworms, yet almost all are dioecious. Sponges do not copulate, yet SH is very common. I suggest that low adult mobility and internal fertilization (with copulation) might well limit reproductive success through sperm. In an external fertilizer, reproductive success through male function would be much closer to being proportional to the amount of sperm shed into the environment. This would cause the male gain curve (Fig. 1) to be almost linear; this, combined with any fixed costs, would select for dioecy. External fertilization may have one other effect. It may be difficult for a hermaphrodite individual to keep its sperm from fertilizing its own eggs, if both are released free into the environment. If high inbreeding depression would result from such a union, dioecy may be the means by which an individual avoids the problem (16). The almost linearity of the male gain relation puts the situation near the hermaphrodite-dioecy boundary. Factors such as the avoidance of selfing or fixed costs may thus easily determine the selective outcome. Why so many sponges are hermaphroditic may also be explicable because they possess a unique system of sperm transfer (17). Specialized cells pick up sperm (which come into the recipient's body) and transport it to the eggs. This system could well limit male reproductive success, depending upon how the transport system saturates in its ability to carry. These are gross patterns and are not meant to be a critical test of the hypothesis. However, they are suggestive. A detailed literature review may allow identification of factors in various groups that play a role in the limitation (or enhancement) of male reproductive success.

Male-female conflict in hermaphroditic animals

This section (and the next) discusses aspects of reproduction in hermaphroditic organisms, particularly from the viewpoint of male reproductive success. Animals differ from plants in that cross or reciprocal copulation is absent from plants, but present in many animals. The animal discussion will focus on cross-copulation. Here I deal more with the implications of SH for reproductive behavior (and male versus female resource allocation), than with the factors favoring SH in the first place (even though such a dichotomy is probably not completely possible).

Many hermaphroditic animals [particularly gastropods (15) and flatworms (18)] have structures for the digestion of sperm (and other products) received in cross-copulation. Bateman's principle suggests that individuals copulate not so much to gain sperm to fertilize eggs as to give sperm away (to gain access to another's eggs). Fitness through male function depends upon the ability to have one's sperm used as gametes (instead of perhaps food, although some sort of mixed strategy may be advantageous if the food is translated into fertilized eggs for the food provider). There must often exist a conflict of interest between mating partners—as a recipient each should be inclined to accept sperm (not necessarily for fertilization of its own eggs) in order to give its sperm away. As a donor, one should be selected to induce one's partner to use the new sperm in fertilization. We know very little about sperm displacement (and

competition) in hermaphrodites (18), but work on insects suggests that the most recent copulation fertilizes most of the eggs (19). If this is true for hermaphrodites, and if individuals copulate often (to attempt access to another's eggs, to get food, or both), then conflict of interest in use of sperm has played an important role in SH. I suggest that the complex internal structure of the genital system of flatworms and some molluscs, the evolution of hemocoelic (sperm injected into the body cavity) insemination (some leeches and flatworms), and some complicated precopulatory displays (conceivably an assessment of the likelihood that sperm will be used as gametes by the potential partner—snails, slugs, flatworms) are explicable when one realizes that the interests of the partners are often in conflict (2). The complex internal structure may have evolved as a system to control the movement of materials (see below) received in cross-copulation. Hemocoelic insemination may have begun as a method by which an individual bypasses this control system, to gain even greater access to eggs.

It may even be that aspects of the neurohormonal control of egg maturation and deposition have evolved in relation to this male-female conflict. If *A* and *B* copulate, and each will copulate again soon, selection favors introducing (with sperm) chemicals that turn on egg maturation and deposition (because this individual may only fertilize eggs until its partner's next copulation). Likewise, counter selection would favor the recipient's attempting to stop this influence. The idea that an individual would be selected to induce its partner to lay eggs at a rate faster than the partner would be selected to should hold even in dioecious species (with periodic mating). Insects may provide some examples—secretions (given in copulation from specialized glands) have been shown in several species to increase or turn on the production and laying of eggs (20). This has been interpreted as simply a male giving the female a cue that she now has sperm. Where the female mates once for life this may well be so. However, with periodic mating, the potential is present for the chemical being more than just a cue. As one final example of male-female conflict, one might be inclined to attempt to put one's partner in a situation which prolongs the interval until its next copulation. If one copulates mostly to give sperm away, then destroying the partner's ejaculatory organ may be such a strategy.

In order to understand how gains in fitness change with resources put into male function, we need to know how one individual may alter the use of its sperm by another. We also need to know what natural selection favors in terms of sperm use by a recipient. For example, is it possible that individuals may use a precopulatory display to assess something about the genes of a potential partner?—to use sperm from "superior" (in some way) individuals? Let us define "female choice" to be the nonrandom use of sperm from different partners, based on some character displayed by a partner. Fisher (21, 22) proposed a theory of female choice in dioecious organisms based on the following idea. Suppose that females choose mates (in a polygynous species in which males contribute only sperm) on the basis of some character *Y* that increases the female's immediate reproductive success. If the female choice genes are common throughout the population (which is why Fisher made them depend upon some immediate benefit to the female), then selection will favor genes exaggerating the character of choice, *Y*. This is because females produce sons with more *Y* and these sons are chosen. This is a positive feedback; the female choice itself being the selective force. The same principle may also operate with hermaphrodites. Because the variance in reproductive success through male function is probably considerably higher than the variance through female function (the averages must be the same), any character that individuals use to choose

sperm donors may become exaggerated through time. This is because large gains in fitness are possible through enhanced male function. One wonders if the love-darts (calcium darts shot into the partner's body prior to copulation) of some snails (23) are the result of such a process, which perhaps began with female choice on the basis of either a gift of calcium (an aid in shell-making) or demonstration by the partner of increased ability to metabolize and use calcium.

Male-female conflict in higher plants

It is a common assumption that plant-pollinator relations have evolved with the major selective force being seed set; that plants are in general limited in their abilities to get pollen to fertilize their ovules (24, 25). While there is certainly evidence that in some situations seed set is limited by pollen (25-28), the assumption may not be generally true. The evidence cited for it may often be reinterpreted with Bateman's assumption. For example, Cruden (24) has shown that the ratio of pollen grains to ovules is smallest in selfed species (those with cleistogamous flowers) and becomes larger as one moves through partially selfed to outcrossed species. He interprets the results in terms of the efficiency of the pollination system *to get pollen for the fertilization of ovules* (i.e., pollen limits seed set). However, the same pattern is explicable under the sex-ratio idea of "local mate competition" (29) applied to resource allocation in hermaphrodites. The direction of change in the pollen-to-ovule ratio is as predicted by the local mate competition model, which makes no assumptions (except under complete self fertilization) about pollen limiting seed set. Even where seed set is limited by an individual's ability to get pollen, it is incorrect to view pollen production as if pollen existed simply to allow plants to produce fertilized seeds. Because any zygote gets half its genes from each gamete type, pollen and seeds must be considered equivalent means by which a hermaphrodite individual may achieve reproductive success. It is for this reason that the allocation of resources to male versus female function maximizes the $\alpha \cdot \beta$ product.

If it is assumed that pollen does not in general limit seed set, then the relations between plant and pollinators have evolved mostly with the selective force being male reproductive success; fitness gains through the giving off of pollen. The question becomes the means by which an individual can get its pollen to conspecific stigmas, in competition with other pollen. This is not to say that natural selection will not favor increasing the efficiency of pollen reception. Resources freed by such efficiency can be expended in other ways that increase the individual's fitness. Likewise, efficient reception of pollen may allow an individual to exclude certain types of pollen (from another species) and to control competition among the pollen it does receive. Willson (30) has independently suggested that pollen will often not limit seed set and has listed several ways in which plants may increase their reproductive success through getting their pollen to conspecific stigmas. She used the assumption in a hypothetical scheme for the evolution of dioecy, through increased male reproductive success (sexual specialization). The same forces may well have played an important role in monoecy [also noted by Willson (30)], in which the individual flower, not the individual plant, is specialized for reception and dispersal of pollen. Monoecy also allows the two types of flowers to be placed on different parts of the plant, which would be advantageous if dispersal of pollen was enhanced (over reception) by a flower's position.

Getting one's pollen to conspecific stigmas is not equivalent to male fitness, because fertilization followed by seed production is still to come. The pollen recipient may discriminate for or against certain types of pollen. This choice of pollen is well

documented in higher plants, at the level of the stigma or style and (if fertilization occurs) seed development (31-34). This again provides the basis for male-female conflict (which pollen is used? which ovules mature?). I suggest that two facets of angiosperm evolution are most easily explicable in terms of this conflict. These are hybridization and double fertilization.

Plants face one situation probably absent in most animals. A male *Drosophila* who displays interest in copulation to a female who turns out to be the wrong species will almost always be rejected. He is not selected to pursue the attempted copulation, because he likely has other mating options. However, a pollen grain (a male), once on a stigma, has no other options for reproduction. Selection would thus favor the pollen growing, even if the resulting hybrids would be of low vigor. However, the recipient individual would be selected to stop the foreign pollen (except in special situations), particularly if the resulting hybrids would be inviable. Imprecise pollen distribution combined with this male-female conflict may have played a large role in plant evolution. A large percentage of higher plant species are polyploids, and most of these are allopolyploids—derived from a doubling of chromosome numbers after interspecific (or varietal) hybridization (35, 36). While botanists have long recognized that mating behavior by animals limits interspecific crosses and have also stated that pollen dispersal mistakes favor such crosses, I have found no statement that the crucial difference is the "no option" situation with regards to male reproductive success (35-37).

Suppose that a pollen grain is able to effect fertilization. In angiosperms that will mean double fertilization (38-40). The pollen nucleus divides by mitosis into identical copies; one fertilizes the egg, the other fuses with various numbers of haploid nuclei (usually two, both identical copies of the egg nucleus) to form the endosperm nucleus. The endosperm is a tissue that provides nutrition for *its* developing zygote (but it may or may not be the food reserves in the mature seed) (38-40). The nutrients for the endosperm come from the tissues of the maternal plant. The adaptive significance of double fertilization has remained a puzzle, although statements about the advantages of heterozygosity of endosperm and/or the need for endosperm to be an "aggressive" tissue (competing in some way for nutrients with the surrounding tissue) are common in the literature (38-40). I can suggest two possibilities, both involved with a conflict situation. (i) The developing zygotes are at best full sibs. The endosperm is in most cases genetically identical (except for a double dose of female-derived genes) to its zygote. Thus, there may well be competition among various endosperms for resources (to be given to its zygote) (41). The second fertilization clearly raises the relatedness of the endosperm to its own zygote, *relative* to the endosperm and any other zygote (except where pollen grains are themselves full sibs). In species in which the female-derived nuclei (destined to be endosperm) are not identical to the egg nucleus, this effect is most marked. Thus, this makes it more likely that the endosperm will compete for food for its zygote. This argument derives from the theory of kin selection and treats the endosperm as an individual killing itself to aid a relative (42, 43). (ii) There is one other possibility. If abortion of fertilized ovules is common in higher plants, then many pollen grains that fertilize never realize reproductive success. There is thus a conflict between pollen and the maternal plant: it may be advantageous for the mother to sacrifice some fertilized ovules (perhaps on the basis of some assessment of their father's genes). It may even be advantageous for ovules to allow themselves to be killed, because they are sibs to other ovules. However, it is clearly disadvantageous for the pollen nucleus to allow itself to be killed. It may well be that double fertilization is a pollen's way of competing for resources (i.e.,

becoming part of the food-garnering structure: endosperm) in a situation in which conflict often exists between its interests and those of its mate. If double fertilization is indeed one resolution of a conflict situation, then perhaps its absence in gymnosperms can be interpreted as the alternative resolution. Clearly, it is advantageous for the maternal plant to avoid either of the two conflicts discussed above. Perhaps in the gymnosperms the conflict has been resolved in the favor of the maternal plant.

If ovules are cheap, relative to the final input of resources into seeds, a likely strategy would be for a plant to produce many of them (along with more flowers that increase male function), collect the genomes from various fathers, and then abort most. In this way, the evolution of floral structures is guided by male reproductive success and female choice.

Conclusions

Bateman's principle provides a key to understanding many facets of reproduction in hermaphroditic organisms. If sperm does not limit egg production, then conflict exists between individuals as to sperm use. The ability to reproduce through male function (thus, the resolution of this conflict) plays an important role in selection for (or against) hermaphroditism. While the principle is probably not necessary for male-female conflict, it certainly makes the conflict more extreme. This paper adds to earlier (9, 10, 16, 44, 45) suggestions on the adaptive significance of various forms of hermaphroditism.

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