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Why be an hermaphrodite?

MANY animals and most higher plants are hermaphrodites. The basic argument of this paper is that the sex habit of a species is determined by selection acting on the number of offspring produced by individuals of different types. The argument differs radically from most earlier explanations of the evolution of hermaphroditism (reviewed by Ghiselin)^{1,2}, although it is formally similar to a recent explanation³ of sequential hermaphroditism, in which individuals function first as one sex and then the other.

Our fundamental assumptions are as follows. (1) Genes in a zygote can act as switches, directing development into one or other type (male, female, hermaphrodite), or, in hermaphrodites, can alter the relative allocation of resources to male and female functions. (The theory does not apply if sexual type is determined by cytoplasmic factors, as is sometimes the case for male sterility in plants.) (2) The total production of male plus female gametes by an individual is constrained to lie within a “fitness set”, which cannot be altered by genetic change. It will be shown how the form of the fitness set determines the sex habit.

Consider, for concreteness, a plant species, and let m , f , and h be the numbers of male, female and hermaphrodite individuals

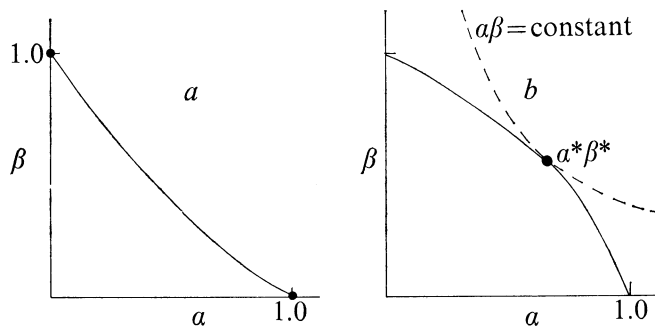


Fig. 1 *a*, A “fitness set” for the allocation of sex function. α is the pollen produced by a hermaphrodite, as a fraction of the total produced by a male individual. β is the corresponding parameter for a female. All possible values are assumed to be to the interior of the curve. With a concave curve, the hermaphrodite population is not an ESS, but a dioecious population is. *b*, Optimal resource allocation for an hermaphrodite. With a convex tradeoff curve, the hermaphrodite is an ESS. The ESS resource allocation ($\alpha^*\beta^*$) is the point on the curve which maximises the product $\alpha\beta$.

respectively in a population (counted at conception). For simplicity all individuals are assumed to have the same survival rate to adulthood. A male can produce N pollen grains, a female can produce n seeds, and an hermaphrodite αN pollen grains and βn seeds. The fitness set can then be represented as a graph of α against β , as in Figs 1 and 2.

Suppose the population produces R offspring. Assuming self-incompatibility, and using “fitness” to mean the expected number of offspring produced by an individual,

$$\text{fitness of a male} = R/(m + ah),$$

$$\text{fitness of a female} = R/(f + \beta h),$$

$$\text{fitness of a hermaphrodite} = R[\alpha/(m + ah) + \beta/(f + \beta h)].$$

If the situation is to be evolutionarily stable, two conditions must be satisfied: (1) the fitnesses of any types actually present in the population must be equal, and (2) the values of α and β in hermaphrodites, if present, must be an “evolutionarily stable strategy,” or ESS⁴; that is, the actual phenotype, ($\alpha^*\beta^*$), of the hermaphrodites present in the population must be as fit as or fitter than any mutant phenotype ($\alpha\beta$) lying in the fitness set.

Case 1. $h = 0$. Population dioecious. By condition (1), $R/m = R/f$, or $m = f$. This is the familiar conclusion that the primary sex ratio is 1:1 when the costs of male and female offspring are equal⁵.

A dioecious population can be invaded by an hermaphrodite mutant if $\alpha/m + \beta/f > 1/m$; that is, if $\alpha + \beta > 1$. It follows

that a dioecious population is stable only if the fitness set is concave (Fig. 1*a*). If it is convex (Fig. 1*b*), then only the hermaphrodite population is stable.

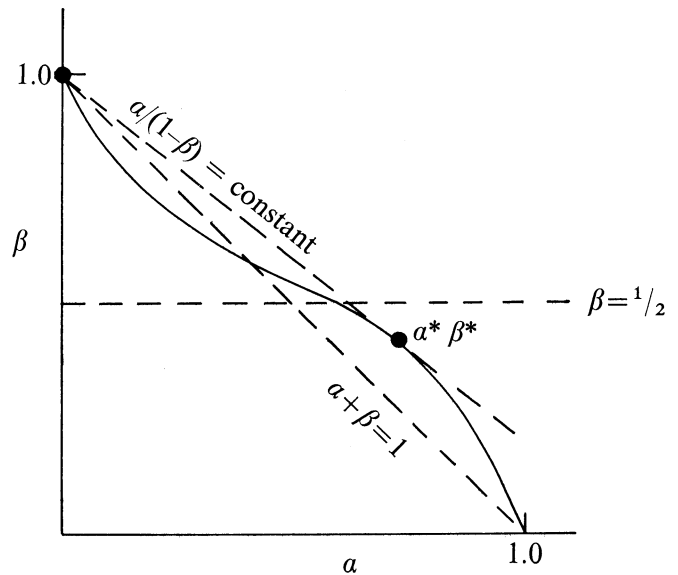


Fig. 2 An ESS which is a mixture of sexual types. If the curve is convex-concave, it may be possible for a pure sex (in this case a female) to invade. The resulting mixture is stable if (i) $\alpha^* + \beta^* > 1$, (ii) $\beta^* < 0.5$, (iii) $\alpha^*\beta^*$ is the point which maximises $\alpha/(1-\beta)$. This curve illustrates gynodioecy.

Case 2. $m = f = 0, h = 1$. Population hermaphroditic. If ($\alpha^*\beta^*$) is the phenotype of typical members of the population, and ($\alpha\beta$) of a rare mutant, then ($\alpha^*\beta^*$) is an ESS if the fitness of ($\alpha\beta$) is less than or equal to that of ($\alpha^*\beta^*$) for all points on the boundary of the fitness set. For stability against small perturbations, this requires that $(\alpha/\alpha^* + \beta/\beta^*)$ be at a local maximum when $\alpha = \alpha^*, \beta = \beta^*$. This is equivalent to the requirement that the product $\alpha^* \cdot \beta^*$ be a maximum (Figure 1*b*).

This is analogous to MacArthur’s⁶ conclusion that selection will maximise the product of the number of males and females in a dioecious species. If the fitness set is bounded by the line $\alpha + \beta = 1$, as will be approximately true if pollen and seed production are limited by the same resources, then the ESS is for an hermaphrodite to divide its resources equally between pollen and seeds⁷.

Case 3. $h \neq 0, f \neq 0, m = 0$. Population gynodioecious. The criterion $\alpha^*\beta^*$ maximal provides a local stability criterion for a hermaphrodite population. But can a population with $h = 1$ be invaded by males or females? It can be invaded by females if $R/\beta^* > 2R$, or $\beta^* < 0.5$. Provided, however, that $\alpha + \beta > 1$ for some part of the fitness set, hermaphrodites will not be completely eliminated.

Figure 2 shows a fitness set for which the ESS is gynodioecy. Let ($\alpha^*\beta^*$) be the stable phenotype of the hermaphrodites. Then the stable sex ratio, obtained by equating the fitness of females and hermaphrodites, is given by $f = h(1 - 2\beta^*)$ ⁸. This implies an excess of hermaphrodites, as is in fact observed in natural populations⁹. It also implies that as the frequency of females increases, the resource allocation by the hermaphrodite shifts towards male function. This shift has also been observed¹⁰. The fitness of a rare mutant with a different resource allocation, ($\alpha\beta$), is given by

$$V = R[\alpha/(m + \alpha^*h) + \beta/(f + \beta^*h)] \\ = R[\alpha/\alpha^* + \beta/(1 - \beta^*)]/h$$

The condition for ($\alpha^*\beta^*$) to be an ESS is that V should be at a

local maximum; which is equivalent to the requirement that $\alpha/(1-\beta)$ should be at a maximum when $\alpha = \alpha^*$, $\beta = \beta^*$. The ESS can therefore be found by drawing a tangent as in Fig. 2.

The conditions for androdioecy, $h \neq 0$, $f = 0$, $m \neq 0$, are similar. All three types can coexist only in the artificial and unlikely case, $\alpha + \beta = 1$ exactly.

The conclusions can be summarised by saying that we would expect to find monoecy or hermaphroditism in species for which the fitness set is convex, dioecy if it is concave, and androdioecy or gynodioecy if it is concave-convex.

Are there any general reasons why fitness sets should be convex? We can offer three suggestions. (1) Low mobility: in animals, Ghiselin^{1,2} has noted that hermaphroditism tends to occur in species with low adult mobility. Low mobility will tend to be associated with a convex fitness set because in such species there will be little sexual dimorphism (except perhaps dwarf males) since males will not involve special locomotory or aggressive structures for seeking out and holding females. This means that a single individual can effectively serve both functions. Furthermore, low mobility limits male reproductive success—the number of eggs that a male can competitively fertilise (or an hermaphrodite acting as a male) should rise at less than a linear rate with resource input into male function. Note that this model assigns a different role to low mobility than the classical “low density model” as developed by Ghiselin^{1,2}. Even if all the eggs produced in the population are fertilised, the convex fitness set implies hermaphroditism.

(2) Low resource overlap: in plants pollen production occurs earlier in the season, for each species, than seed maturation. The two processes therefore depend, in part, on different resources, and one would therefore expect a hermaphrodite to do better than a linear combination of male and female. In animals, brooding will imply a convex set because female expenditure will occur later than male expenditure. Ghiselin¹ has pointed out that hermaphroditism in animals tends to occur in immobile species in which individuals brood the young.

(3) Cost sharing: in insect-pollinated plants, some energy must be expended by all types on producing organs of attraction which may serve both male (pollen) and female (ovule) function. If a plant's reproductive success tends more to be limited by its ability to attract pollinators than its direct input of resources into gametes, the fitness set will tend to be convex. The conclusion depends on assumptions, which merit further investigation, on how a plant allocates resources between organs of attraction and more directly reproductive structures. It does,

however, suggest that dioecy should be rarer in insect-pollinated than in wind- and water-pollinated species.

We do not claim that the selective forces associated with resource allocation are the only ones relevant to the evolution of hermaphroditism. In plants, dioecy may evolve as a mechanism to prevent self-fertilisation¹¹. When associated with self-fertility, hermaphroditism may be an adaptation to situations (for example, parasitic and sessile animals; annual, monocarpic and colonising plants^{1,2}) in which opportunities for cross-fertilisation are rare^{1,2}. We have also ignored possible effects on resource allocation of factors such as sperm storage (which is common in invertebrates^{1,2}) and pollen or sperm competition. Models considering these factors are now being developed and will be published elsewhere. The relative importance of these various selective forces can be determined only by comparative studies of the distribution of the sex habit, which we are undertaking.

The model outlined in this paper, and its biological interpretation, was developed independently in Utah and at Sussex.

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