SELECTION IN PLANT POPULATIONS OF EFFECTIVELY INFINITE SIZE. V. BIALLELIC MODELS OF TRIOECY

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Manuscript received May 5, 1982
Revised copy accepted November 20, 1982

ABSTRACT

A one-locus two-allele model of trioecy (presence of hermaphrodites, males and females in one population) is considered, in order to study the conditions for the persistence of this system. All possible assignments of the three sex types to the three genotypes are considered. This leads to three different modes of inheritance of trioecy, namely (a) females heterozygous, (b) males heterozygous and (c) hermaphrodites heterozygous, where in each mode each of the remaining two sex types is homozygous for one of the alleles. For mode (c) trioecy is always persistent, and the dependence of the sex ratio (for the three sex types) on the ovule and pollen fertilities and on the hermaphrodite selfing rate is specified. For the other two modes, (a) and (b), trioecy is not protected, *i.e.*, it may not persist for any fertilities, viabilities or selfing rates. Thus, in this situation it is important to study the conditions under which the "marginal" systems of sexuality of trioecy, *i.e.*, hermaphroditism, dioecy and gynodioecy in mode (a), and hermaphroditism, dioecy and androdioecy in mode (b), may become established. The results show that each marginal system may evolve from each other via trioecy. The evolution of dioecy is easier in mode (a) than in (b), so that female heterogamety would be expected to occur more often than male heterogamety in the present model. Under some conditions the breeding system obtained in equilibrium populations may depend on the initial genotype frequencies.——The necessity of considering modes of inheritance for sexual polymorphisms is demonstrated by comparing our results with those obtained from an evolutionary stable strategy (ESS) analysis of a purely phenotypic model.

THE seed plants may be regarded as fundamentally bisexual, in that individuals are often able to function both as male and as female. However, populations containing unisexual individuals are often found, and such unisexual individuals may comprise the whole population (e.g., BAWA and OPLER 1975), or they may occur together with bisexual individuals. Unisexual individuals may show rudimentary structures of the opposite sex or may be imperfectly differentiated and produce small or even considerable quantities of gametes of the opposite sex. Such unisexual individuals often show clear taxonomic relationships to bisexual individuals from allied populations, species or genera (WESTERGAARD 1958; LLOYD 1975). In spite of this fundamental bisexuality, the seed plants present a rich array of breeding systems involving unisexuality. In addition to dioecy, with separate male and female individuals, and subdioecy in which some unisexual individuals are imperfectly differentiated, there is gynodioecy (separate females and bisexuals), androdioecy (males and bisexuals), and trioecy (males, females and bisexuals). These breeding systems have apparently repeatedly evolved from bisexuality (BAWA 1980; ROSS 1982), and such evolution is the main theme of this paper.

Previous theoretical papers have been concerned with gynodioecy, which is fairly common, and androdioecy, which is quite rare (*e.g.*, ROSS and SHAW 1971; LLOYD 1974, 1975; ROSS and WEIR 1975; ROSS 1978; CHARLESWORTH and CHARLESWORTH 1978; GREGORIUS, ROSS and GILLET 1982, 1983), but there appears to be no previous theoretical study of trioecy. This breeding system also is apparently rare but has been studied in the ash, *Fraxinus excelsior* (DARWIN 1877; ROHMEDER 1952), and may also occur in a species of blueberry, *Vaccinium angustifolium* (AALDERS and HALL 1963; HALL, AALDERS and WOOD 1966). Other possible examples, such as *Fuchsia procumbens* (GODLEY 1955, 1963), may be also interpreted as subdioecy.

Although it is well known that sexual reproduction in plants may involve various breeding (more specifically, sexual) systems, most models in population genetics are based on monoecious or dioecious populations. For both of these systems of sexuality the effect of selection is confined to change in gene and genotype frequencies among individuals of one sexual type, together with the regulation of the sex ratio in dioecious populations. In such models the problem of the maintenance of the sexual types themselves does not arise, since monoecious populations consist only of a single sexual type, and dioecious populations cannot persist with only a single sexual type (male or female). However, the ratio between the pollen and ovule fertility may vary considerably among individual plants (*e.g.*, HOROVITZ and HARDING 1972), up to the extreme situation in which some plants produce only female gametes and others only male gametes. Hence, at least temporarily, a population might consist of a mixture of bisexual (monoecious, hermaphrodite, andromonoecious, gynomonoecious, etc.) plants and unisexual (male, female) plants. In principle, this situation may give rise to five different systems of sexuality at the population level: dioecy, pure bisexuality (monoecy or hermaphroditism), gynodioecy, androdioecy and trioecy. The last three of these systems differ basically from the first two in that they allow for directional selection against one or more sexual types. In initially gynodioecious populations the females might be lost, and males might be lost in initially androdioecious populations. Consequently, selection with respect to sexual types can change these two systems of sexuality into a hermaphrodite (monoecious) one. Similarly, selection in trioecious populations may result in bisexuality, dioecy, gynodioecy, or androdioecy. This emphasizes the significance of trioecy for the evolution of all the other systems of sexuality, in particular dioecy.

The aims of this paper are: (1) to find conditions that allow the maintenance of trioecy; (2) to find conditions in which trioecious populations lose their bisexuals, with resultant dioecy; their females, with resultant androdioecy; their males, with resultant gynodioecy; or both males and females, with resultant bisexuality; (3) to consider the effects of the mode of inheritance of the sex polymorphism on these questions; and (4) to understand why trioecy is apparently rare in nature. Does trioecy function only as a transient state leading from one system of sexuality, e.g., hermaphroditism, to another system such as dioecy? These questions are treated with the help of three one-locus two-allele models of trioecy, by investigating the stability properties of the four marginal (*i.e.*, one or two morph) systems of sexuality (bisexuality, dioecy, androdioecy and gynodioecy).

The experimental evidence suggests that both males and females differ from hermaphrodites at several gene loci in *V. angustifolium* (AALDERS and HALL 1963; HALL, AALDERS and WOOD 1966). In experimental trioecious populations of the combined monoecious (from northern Spain) and dioecious (from southern Spain) races of *Ecballium elaterium*, however, genetic control was through one gene with three alleles (GALÁN 1950; WESTERGAARD 1958). Consequently, the present models, although entirely feasible, are simpler than those found in nature. This raises the questions of why this should be so, and why should we study models of systems apparently not found in nature? The first question we are able to answer partially, since we found that trioecy could not be maintained in two of our three models. The second question also is partially answered by these results, since it is necessary to study both what is and what is not present in nature, in order to understand why one system is more successful than the other.

DESCRIPTION OF THE MODEL

The basic features of the model applied in this series are the following: population size is effectively infinite and reproduction occurs in separated generations; selfing among bisexuals is specified by the proportion of their ovules that are self-fertilized, and all of the nonself-fertilized ovules are assumed to be fertilized at random by pollen originating from the population pool of free pollen (*i.e.*, the totality of pollen grains not used in selfing).

The assumption of a one-locus two-allele control of trioecy implies that each of the three sexual types is represented by exactly one genotype. Theoretically, there are three different modes of assignment of sexual types to genotypes, namely

(a) bisexuals are homozygous for the one allele, males are homozygous for the other allele and females are heterozygous,

(b) bisexuals are homozygous for the one allele, females are homozygous for the other allele and males are heterozygous,

(c) males are homozygous for the one allele, females are homozygous for the other allele and bisexuals are heterozygous.

In preceding papers we addressed the problem of finding plausible models of gene action for different models of genetic control of systems of sexuality. The inherent principle is that all alleles could be considered to possess a bisexual potential, where the expression of the male, female or both potentials depends on particular incompatibility relationships realized at the diploid stage. This principle may *ad. lib.* also be applied to our three models.

Model (c) plays an exceptional role since, by definition, it guarantees persistence of trioecy for arbitrary pollen and ovule fertilities, as well as selfing rates and viabilities. This is easily recognized to be due to the fact that the bisexuals are heterozygous. Hence, trioecy in model (c) constitutes a structurally stable trimorphic system of sexuality.

If the bisexuals are homozygous, as in (a) and (b), the picture changes drastically. Model (a) comprises as marginal situations populations that consist only of bisexuals or of males and females. Under some conditions, a population may also be made up of bisexuals and females only. Thus, the marginal systems of sexuality implied by model (a) are bisexuality, dioecy and possibly gynodioecy. For model (b) the situation is similar, except that gynodioecy has to be replaced by androdioecy; with respect to dioecy (a) and (b) differ in that the former specifies the females and the latter specifies the males as the heterogametic sex. Therefore, in contrast to (c) these two models allow not only the study of conditions for the maintenance of trioecy, but also of whether and how one system of sexuality evolves from another within a single population. As is easily seen, this phenomenon is closely related to the conditions for stability of the marginal systems of sexuality in models (a) and (b). These questions may in turn be treated from the viewpoint of protectedness or nonprotectedness of certain alleles and genotypes. An allele is called *protected* if it cannot be lost from any state of the population where all possible genotypes are present with positive frequencies; moreover, it is required that the allele cannot stay for an indefinite number of generations at arbitrarily low frequencies. If all alleles are protected in this sense, then the allelic polymorphism is called protected (GREGORIUS 1982). For example, if the bisexual genotype is protected, then it cannot be lost in a trioecious population and, consequently, dioecy may not evolve from bisexuality. If, on the other hand, the hermaphrodites are not protected, a trioecious population could evolve toward dioecy.

To reduce the number of symbols in the following sections to a minimum, in all three models we use the convention that the average numbers of ovules and free pollen grains produced by the bisexuals are normalized to unity, and note that these fertilities include the effect of viability selection (GREGORIUS and ROSS 1981). Based on this convention, ϕ and μ denote the fertilities of the females and males, respectively, and σ denotes the average rate of self-fertilization of the bisexuals. Mating proceeds as follows. Let P_h, P_f and P_m be the proportions of hermaphrodites, females and males in the population. A proportion

$$\sigma P_h/(P_h + \phi \times P_f)$$

of the available ovules are self-fertilized. The remaining proportion of ovules

$$[(1 - \sigma)P_h + \phi \times P_f]/(P_h + \phi P_f)$$

is fertilized at random by the free pollen, of which proportion P_h is produced by the hermaphrodites and μP_m by the males.

All mathematical derivations concerning the analysis of protectedness or stability are deferred to an appendix.

RESULTS OF THE ANALYSIS

Probably the most remarkable result emanating from the APPENDIX is that for the models (a) and (b), in which hermaphrodites are homozygous, trioecy is not protected. This means that trioecy cannot become established from one of its marginal systems of sexuality (bisexuality, dioecy and gynodioecy or androdioecy) if the missing sexual types are introduced at low frequencies. Alternatively, this result means that there exist frequency regions for the three sexual types such that the population loses at least one of its sexual types when starting within these regions. This finding follows from the observation that it is impossible in these models to realize a situation in which all marginal systems of sexuality are simultaneously repulsive, *i.e.*, where each sexual type starting at low frequency subsequently increases. Therefore, it remains only to study the conditions under which some sexual types may persist and others may not. This will be done for each model separately.

Model (a): Here, the females are heterozygous, and they are protected if and only if $\phi > 2$, *i.e.*, if and only if females produce on the average more than twice as many ovules as hermaphrodites. This is identical with the condition for the maintenance of females among bisexuals only, *i.e.*, in the marginal gynodioecious system of sexuality containing no male plants (LEWIS 1941; and many later authors). If the males are introduced into this system, the question arises as to how fertile they should be to become established. Establishment and thus protectedness of the males is guaranteed for $\phi > 2$ if

$$\mu > \frac{\phi}{\phi - 2}\,(>0). \tag{1a}$$

Otherwise, if

$$\mu < \frac{\phi}{\phi - 2} \quad \text{and} \quad \phi > 2, \tag{1b}$$

then trioecy returns to gynodioecy if males are present at low frequency, *i.e.*, gynodioecy is locally stable. If $\phi \leq 2$, then females are not protected and, consequently, trioecy tends to pure bisexuality if males and females are rare, *i.e.*, monoecy is locally stable.

It is very difficult for the males to become established if ϕ exceeds 2 only slightly. If, for example, $\phi = 2.1$, then the males must on the average produce more than 21 times as much pollen as the bisexuals. On the other hand, to arrive at moderate values for μ the required magnitudes for ϕ are not quite as extreme; nevertheless, protection of the males for $\mu = 1.5$ requires that ϕ should exceed 6. Figure 1 illustrates the region of (μ, ϕ) values for which males are protected.

In an analogous manner protectedness and nonprotectedness of hermaphrodites can be treated from the viewpoint of instability (repulsivity) and local stability of dioecy. Dioecy is locally stable, *i.e.*, trioecy returns to dioecy after the introduction of some bisexuals if

$$\sigma < \frac{1}{2}\phi(1 - 1/\mu), \tag{2a}$$

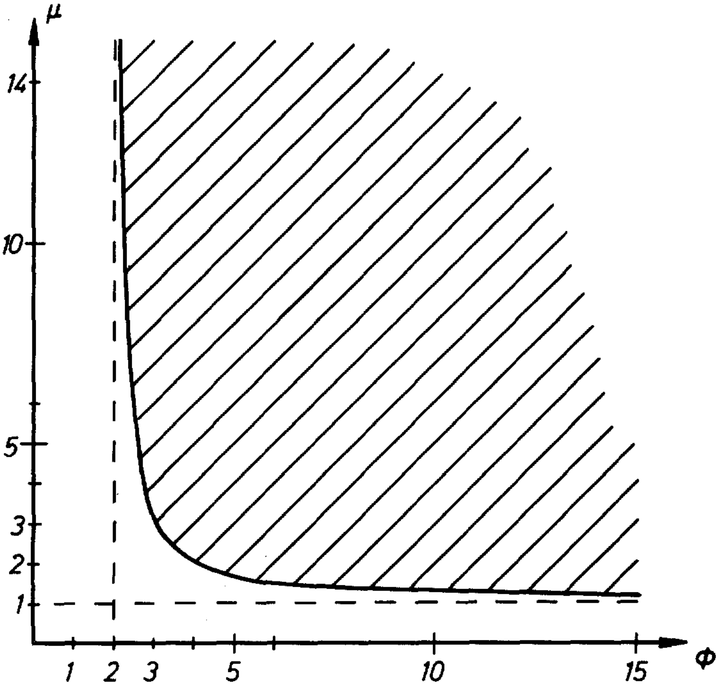

FIGURE 1.—The hatched region gives the male (μ) and female (ϕ) fertilities for which males are protected in model (a).

and otherwise, if

$$\sigma > \frac{1}{2}\,\phi(1 - 1/\mu), \tag{2b}$$

then the bisexuals are protected, and thus trioecy moves away from its dioecious marginal system of sexuality. Consequently, provided $\mu > 1$, dioecy is locally stable if the selfing rate of the bisexuals is not too large. In particular, the conditions (1b) and (2a) may be realized simultaneously, such that gynodioecy as well as dioecy are locally stable. Similarly, if $\phi \leq 2$ and (2a) holds, bisexuality and dioecy are both locally stable. Hence, if one of these two situations occurs in a trioecious population, it depends on the initial frequencies of the three sexual types whether the population tends to the one or the other marginal system of sexuality.

Among the remaining cases one is of particular interest, since it refers to a fundamental aspect of evolution in higher plants, namely, what are the conditions for the evolution of dioecy from hermaphroditism or monoecy? Clearly, such evolution requires that males and females be protected. According to the afore-mentioned considerations this is guaranteed if $\phi > 2$ and (1a) is met. Combining both inequalities into one yields after a little rearrangement, $\frac{1}{2}\,\phi(\mu - 1) > \mu$. Hence, since $\mu \geq \sigma \times \mu$, (1a) implies (2a), i.e., local stability of dioecy. Therefore, Figure 1 also specifies the range of male and female fertilities for which dioecy evolves from hermaphroditism or monoecy via trioecy. Strictly speaking, we have only proven that $\mu < \frac{1}{2}\,\phi(\mu - 1)$ implies protectedness of males and females as well as convergence to dioecy if bisexuals are rare. However, in numerous computer runs we confirmed the conjecture that there exists no intermediate frequency barrier for bisexuals that prevents convergence to dioecy. Moreover, it is worth mentioning that the selfing rate of the bisexuals has no decisive influence on the evolution of dioecy in the present model.

Model (b): Compared with the previous model, the role of males and females is now interchanged. The heterozygous males are protected if and only if

$$\sigma < 1 - 2/\mu$$

which requires that $\mu > 2$. Analogously to model (a), this is also the condition for the maintenance of males among bisexuals only, which is known from earlier studies of androdioecy (LLOYD 1975; ROSS and WEIR 1976; CHARLESWORTH and CHARLESWORTH 1978). The following considerations proceed along the same lines used in the treatment of model (a).

Females are protected if males are, i.e., $\sigma < 1 - 2/\mu$, which is equivalent to $\mu(1 - \sigma) > 2$ and, in addition, if

$$\phi > \frac{\mu(1 - \sigma^2)}{\mu(1 - \sigma) - 2} \; (>0). \tag{3a}$$

On the other hand, if

$$\mu(1 - \sigma) > 2 \quad \text{and} \quad \phi < \frac{\mu(1 - \sigma^2)}{\mu(1 - \sigma) - 2}, \tag{3b}$$

then androdioecy is locally stable. If $\mu(1 - \sigma) \leq 2$, then bisexuality is locally stable. Since $\mu(1 - \sigma^2)/[\mu(1 - \sigma) - 2]$ is an increasing function of σ, protectedness of males and females becomes more difficult the larger the selfing rates of the bisexuals. This is illustrated in Figure 2 where the (ϕ, μ) regions of protectedness for males and females are given for several rates of self-fertilization.

Only if the bisexuals do not self-fertilize are the conditions of protectedness for males and females the same as in model (a) with, of course, ϕ and μ interchanged.

Dioecy is locally stable if

$$\sigma < \phi - 1, \tag{4a}$$

and if

$$\sigma > \phi - 1, \tag{4b}$$

which requires $\phi < 2$, then the bisexuals are protected. Consequently, it is also possible for the present model that a trioecious population tends to two different marginal systems of sexuality (dioecy and androdioecy, or dioecy and bisexuality), when starting with different initial frequencies for its three sexual types (see also Figure 2(a) of ZIEHE and GREGORIUS 1982).

On the other hand, if males and females are protected according to (3a), then a simple rearrangement of this inequality yields $\phi - 1 > \sigma + [2\phi/\mu(1 - \sigma)]$, which shows that (3a) implies (4a). Hence, (3a) and its graphical illustration in Figure

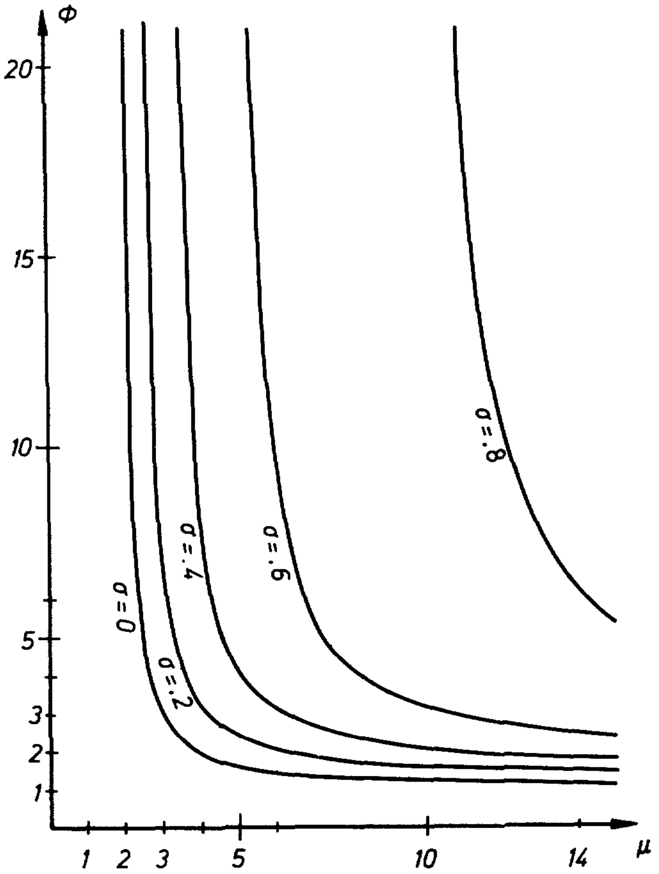

FIGURE 2.—For each given selfing rate (σ) the region to the right of and above the pertaining curve specifies the female (ϕ) and male (μ) fertilities for which females and males are protected in model (b).

2 specifies also the range of male and female fertilities and selfing rates for which dioecy may evolve from bisexuality via trioecy. The statements concerning convergence to dioecy in the previous model apply analogously to the present one.

When both models of inheritance of trioecy [refer to Figures 1 and 2 or inequalities (1a) and (3a)] are compared it becomes evident that the conditions for the evolution of dioecy are less stringent if the females are heterozygous (or equivalently the males are homozygous) provided males and females are viewed relative to the pollen and ovule fertilities, respectively, of the bisexuals. This is due to the fact that the selfing rates enter into the conditions of protectedness of males and females if the males are heterozygous.

Model (c): Since this mode of inheritance assumes that the bisexuals are heterozygous, trioecy persists at any event. However, the fertilities and the selfing rate determine the sex ratios that are eventually realized among the zygotes. It is proven in the APPENDIX that hermaphrodites exceed a frequency of 0.5 immediately after the first generation, and consequently, they are always more frequent than the males and females together. The frequency proportion between the two unisexual types changes gradually over the generations and, ultimately, settles down at the following ordering relationships:

males are more frequent than females if $\mu(1 - \sigma) > \phi$;
females are more frequent than males if $\mu(1 - \sigma) < \phi$;
males and females are equally frequent if $\mu(1 - \sigma) = \phi$.

As we see, the sex ratio of the unisexuals does not only depend on their fertilities, but it is also affected by the selfing rate of the bisexuals. More specifically, selfing favors the females since under the present normalization males must be $(1 - \sigma)^{-1}$ times as fertile as females to guarantee a 1:1 sex ratio.

DISCUSSION

In the preceding two papers about gynodioecy and androdioecy (GREGORIUS, ROSS and GILLET 1982, 1983) we emphasized the necessity of considering several possible modes of inheritance of sexual polymorphisms when trying to explain their evolution and maintenance. We showed that different reasonable models of genetic control for these sexual dimorphisms lead to markedly different conditions for the maintenance of unisexual types. Such differences are, therefore, unlikely to be discovered with the help of solely phenotypic models. At the extreme it is even possible to construct genetical models that alone imply stability of andro- and gynodioecy irrespective of the selective forces or selfing rates involved. This situation is trivially realized for any biallelic model in which all hermaphrodites are heterozygous, and, as we have seen with respect to the present model (c), the same principle applies to trioecy. Such a situation is hard to realize for any phenotypic model. Since dioecy also is essentially subject to a biallelic control mechanism we have to accept at least theoretically that other systems of sexuality such as gynodioecy, androdioecy and trioecy may have a similar status with respect to their evolutionary stability as dioecy. This of course raises the question as to why systems of sexuality other than monoecy or hermaphroditism and dioecy seem to occur infrequently in nature. We do not intend to answer this question, but we suspect that a satisfactory answer cannot be found without having regard to the problem of the likelihood for the emergence and evolution of particular systems of gene action.

The situation is exactly reversed in our biallelic models (a) and (b) of trioecy in which all bisexuals are homozygous for the same allele. In this case trioecy cannot persist indefinitely for constant viabilities, fertilities and selfing rate. In other words, trioecy is only a transient system of sexuality that always approaches one of its marginal systems, namely, bisexuality, dioecy and gynodioecy or androdioecy; which of these is eventually realized depends on the relative male and female fertilities and the selfing rate of the bisexuals, but it may also depend on the initial frequencies of the three sexual types. Therefore, the trioecious models (a) and (b) are particularly useful for studying possible conditions for the evolution of one system of sexuality, notably dioecy, from another such system, notably hermaphroditism or monoecy, within a single population. As it is shown dioecy evolves from hermaphroditism or monoecy only if new mutant males and females are protected. Since the first mutational event usually creates a heterozygote, this implies that as the first step gynodioecy becomes established in model (a) and androdioecy in model (b). Consequently, if the dioecious population has evolved according to model (a), then the females are the heterogametic sex, and if it has evolved according to model (b), the males form the heterogametic sex.

The conditions for the evolution of dioecy are by no means symmetric for these two models, as might have been expected at first sight. Whereas the selfing rate of the hermaphrodites does not appear at all in these conditions for model (a), it plays a crucial role for model (b). This result for model (a) contrasts with the results from some earlier models of gynodioecy (e.g., ROSS and WEIR 1975; LLOYD 1975). High rates of self-fertilization require unrealistically large male or female fertilities to allow evolution of dioecy via androdioecy, *i.e.*, in model (b) (consult Figure 2). Moreover, the effects of male and female fertility on the evolution of dioecy are inversely related in the two models: If in model (b) dioecy evolves for $\phi = x$ and $\mu = y$ and for a given selfing rate, then evolution of dioecy is also guaranteed in model (a) for arbitrary selfing rates if x and y are interchanged, *i.e.*, $\phi = y$ and $\mu = x$. Recall that the male and female fertilities μ and ϕ are comparable to each other since they are multiples of the pollen and ovule fertilities, respectively, of the hermaphrodites.

This asymmetrical relationship between the two models with respect to the role played by the unisexuals continues within each of the models: Suppose that in model (a) the conditions for the evolution of dioecy are met for a situation in which the males are relatively more fertile than the females, *i.e.*, $\phi = x$ and $\mu = y$ with $x < y$; then dioecy evolves also if these fertilities are interchanged between the two sexes, *i.e.*, if $\phi = y$ and $\mu = x$. However, this conclusion does not always hold in the reverse direction; if evolution of dioecy occurs for $\phi = x$, $\mu = y$ and $x > y$, it might not be guaranteed for $\phi = y$ and $\mu = x$. The opposite is true for model (b): evolution of dioecy for $\phi = x$, $\mu = y$ with $x > y$ and a given selfing rate implies evolution of dioecy for the same selfing rate if $\phi = y$ and $\mu = x$; the reverse direction does not always hold. Therefore, loosely speaking, the chances for dioecy to evolve via gynodioecy are more numerous if the females are relatively more fertile than the males, whereas this is the other way around for the path via androdioecy.

To substantiate our criticism of purely phenotypic models we contrast our results to those of CHARNOV, MARYNARD SMITH and BULL (1976). These authors considered exactly the same model as we did with the exception that they made no assumptions concerning the mode of genetic control of sexuality and excluded self-fertilization. All of their conclusions are based only on certain relationships between ϕ and μ and must, therefore, be expected to also apply to any assumption specifying possible modes of genetic control for the three sexual types, including our three models. The analysis used in the above-cited paper is built upon a comparison of the fitness values of the three sexual types. These fitness values correspond to the "realized fitnesses" derived in a more general context in part I of the present series (GREGORIUS and ROSS 1981). Translated into the notation used here, the authors state "that a dioecious population is stable only if $1/\phi + 1/\mu < 1$." Since in our model (c) dioecy is unstable by definition for all selection values, this statement is of course not

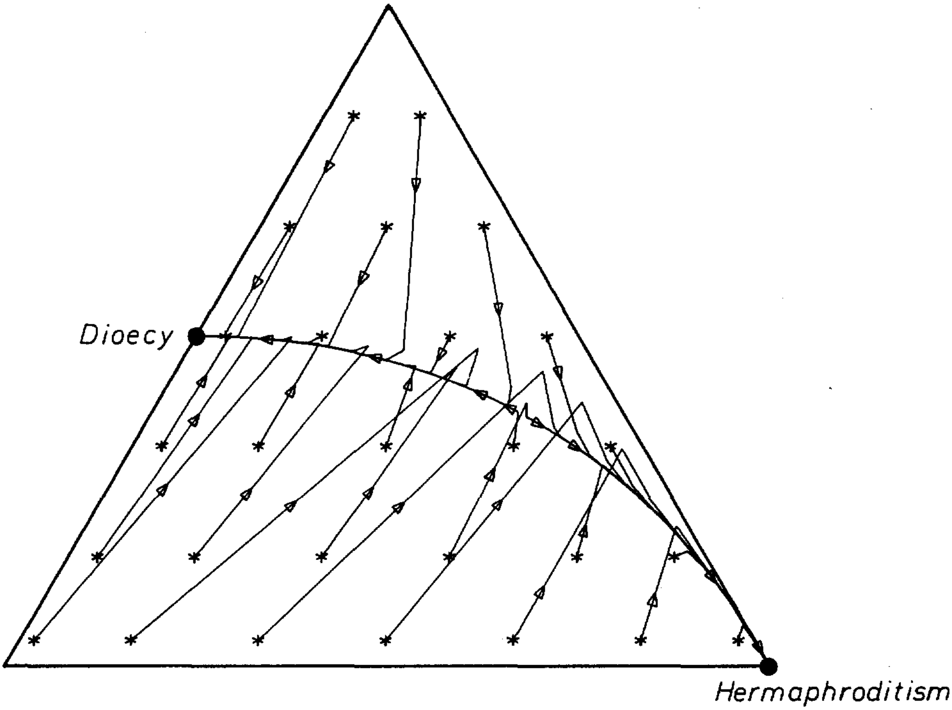

FIGURE 3.—The change of frequencies in sexual types over generations for model (a) in a de Finetti-diagram. Evolution toward dioecy or bisexuality depends on initial frequencies.

true. But even if the formation of the hermaphrodite genotype is not forced by an initially dioecious population in the succeeding generations, as in the models (a) and (b), the condition $1/\phi + 1/\mu < 1$ is sufficient neither for local stability of dioecy nor for the evolution from monoecy to dioecy. This is easily verified with the help of the inequalities (2a) and (4a), or (1a) and (3a), respectively (with $\sigma = 0$). However, both inequalities (1a) and (3a) for the evolution of dioecy from monoecy imply $1/\phi + 1/\mu < 1$. Hence, it seems that either one of the genetical models (a) or (b) leads to more stringent conditions for the stability of dioecy than the purely phenotypic model. In view of the absence of assumptions about inheritance in the phenotypic model this is a logical contradiction, and the same reasoning applies analogously to some of the results contained in a later paper by CHARNOV (1979). These discrepancies seem to follow from the fact that *a phenotypic model does not allow in general for the treatment of the dynamic aspects of the model without specifying the inheritance of the traits considered.*

Another interesting situation is found in models (a) and (b), in which a major disturbance in genotype frequencies may lead to a different equilibrium type from that initially present. For example, equations (2a) and (2b) show that for model (a) with certain ϕ, μ and σ values both hermaphroditism and dioecy are locally stable equilibrium types. Thus, the introduction of a few mutants would not disturb either equilibrium type, but the coming together of two previously distinct populations could result in the evolution of either hermaphroditism or dioecy, depending entirely on the proportions of the various genotypes in the initial mixed population. Thus, the evolution of dioecy or of hermaphroditism could be entirely independent of the selection values (ϕ, μ and σ), and depend only on the initial genotype frequencies. Figure 3 gives population trajectories in a de-Finetti diagram for $\phi = 1.5$, $\mu = 3.5$ and $\sigma = 0.5$ and for a range of initial genotype frequencies. For example, the initial genotype frequency set $P_h = 0.8$, $P_f = P_m = 0.1$ leads to hermaphroditism in equilibrium populations, whereas $P_h = 0.2$, $P_f = P_m = 0.4$ leads to dioecy.

Another topic of interest is that the evolution of dioecy is apparently easier to achieve under the models when females are heterogametic than when males are. This situation is of course contrary to what is found in nature, where male heterogamety is the more frequent (WESTERGAARD 1958), and it suggests that it may be desirable to use the methods given here in studies of other genetic models.

This work was supported by a Heisenberg fellowship (H.R. G.) and a grant from the Deutsche Forschungsgemeinschaft (M. D. R.).

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APPENDIX

Case (a)

Begin with a genotypic polymorphic structure $G = (P_h, P_f, P_m)$. P_h, P_f, P_m denote the frequencies of the hermaphrodites, females and males, respectively. In the present model, the females are assumed to be heterozygous, and the hermaphrodites and males are each represented by one of the homozygous genotypes. The transition equations read:

$$P'_h = \frac{\sigma P_h}{\bar{\phi}} + \frac{(1-\sigma)P_h + \frac{1}{2}\phi P_f}{\bar{\phi}} \times \frac{P_h}{\bar{\mu}}$$

$$P'_f = \frac{\frac{1}{2}\phi P_f}{\bar{\phi}} + \frac{(1-\sigma)P_h}{\bar{\phi}} \times \frac{\mu P_m}{\bar{\mu}}$$

$$P'_m = \frac{\frac{1}{2}\phi P_f}{\bar{\phi}} \times \frac{\mu P_m}{\bar{\mu}},$$

where $\bar{\phi} = P_h + \phi P_f$, $\bar{\mu} = P_h + \mu P_m$.

As follows from GREGORIUS (1982), the allele of the males is protected if $\phi > 2$ and not protected if $\phi < 2$. It can be easily seen that the female genotype is protected if and only if the allele of the males and, equivalently, the allelic polymorphism is protected. Since it is not possible for the frequency of a genotype to become zero in a finite number of generations, a homozygote genotype can be lost only by convergence of the genotypic structure to an equilibrium point on the boundary where this genotype has frequency zero.

On the boundary $P_h = 0$, the transition equations for P_f, P_m read $P'_f \equiv \frac{1}{2} \equiv P'_m$, and hence $\hat{G}_d := (0, \frac{1}{2}, \frac{1}{2})$ is globally attractive along the boundary. Letting G denote genotypic polymorphic structures,

$$\frac{P'_h}{P_h} \xrightarrow[G \to \hat{G}_d]{} \frac{1}{\mu} + \frac{2\sigma}{\phi} =: L_d.$$

If $L_d < 1$, then $\hat{G}_d$ is attractive, and the hermaphrodite is not protected. If $L_d > 1$, then $\hat{G}_d$ is repulsive and the hermaphrodite is protected, since $\hat{G}_d$ is the only equilibrium point on this boundary.

On the boundary $P_m = 0$, the fixation point $P_h = 1$ is always an equilibrium point, and it is globally attractive along this boundary if $\phi \leq 2$. If $\phi > 2$, then there exists an additional equilibrium point $\hat{G}_b$ defined by

$$\hat{P}_f := \frac{\frac{1}{2}\phi - 1}{\phi - 1} > 0 \text{ and } \hat{P}_h := 1 - \hat{P}_f,$$

which is attractive for all points on the boundary except the fixation point $P_h = 1$. (If $\phi = 2$, then $\hat{G}_b$ is the point $P_h = 1$.) Assuming $\phi \geq 2$ and letting G denote genotypic polymorphic structures,

$$\frac{P'_m}{P_m} \xrightarrow[G \to \hat{G}_b]{} \mu \times \frac{\phi - 2}{\phi} =: L_b.$$

If $L_b < 1$, then $\hat{G}_b$ is attractive and the male genotype is not protected. If $L_b > 1$, then $\hat{G}_b$ is repulsive.

Protectedness of the allelic polymorphism implies $\phi \geq 2$. But if $\phi = 2$, then $\hat{G}_b$ is the fixation point $P_h = 1$ and $L_b = 0 < 1$, and hence the fixation point is attractive. Therefore, the allelic polymorphism is protected if and only if $\phi > 2$.

If the genotypic polymorphism is protected, then $\phi > 2$ and $L_d, L_b \geq 1$. It can be easily shown that, due to the interdependence of the expressions for L_d and L_b, $L_d, L_b \geq 1$ is equivalent to $L = L_b = 1$. If $L_d = 1$, then $L_b = (\phi - 2)/(\phi - 2\sigma)$, so that $L_d = L_b = 1$ implies $\sigma = 1$. But then the transition equation for P_f reads $P'_f = P_f \times \frac{1}{2}\phi/\bar{\phi}$ and it holds that $P'_f = P_f$, i.e., $\frac{1}{2}\phi = \bar{\phi}$, on the straight line connecting $\hat{G}_d$ and $\hat{G}_b$. Setting $P'_f = P_f$ and rearranging, the equation of this line is $P_f = \frac{1}{2} - (1/\phi) \times P_h$. To see that all points on this line are fixed points, consider the transition equation for P_h which, after insertion of $\bar{\phi} = \frac{1}{2}\phi$, $\sigma = 1$, and the expression for P_f,' now reads

$$P'_h = P_h \times \left[\frac{2}{\phi} + \left(\frac{1}{2} - \frac{1}{\phi}P_h\right) \times \frac{1}{\bar{\mu}}\right].$$

$$\begin{aligned} \text{But } \bar{\mu} &= P_h + \mu\left(1 - \left(\frac{1}{2} - \frac{1}{\phi}P_h\right) - P_h\right) \\ &= \mu\left(\frac{1}{2} - \frac{1}{\phi}P_h\right) + P_h - \mu\left(1 - \frac{2}{\phi}\right)P_h \\ &= \mu\left(\frac{1}{2} - \frac{1}{\phi}P_h\right) + P_h - \mu\left(\frac{1}{\mu}\right)P_h \\ &= \mu\left(\frac{1}{2} - \frac{1}{\phi}P_h\right) \end{aligned}$$

and thus

$$P'_h = P_h \times \left(\frac{2}{\phi} + \frac{1}{\mu}\right) = P_h \times L_d = P_h.$$

Hence, in the vicinity of the fixed points $\hat{G}_d$ and $\hat{G}_b$, at least all points on the line $\frac{1}{2}\phi = \bar{\phi}$ do not fulfill the requirement of protectedness which states that the population trajectory should be properly repelled. Consequently, it is not possible to have both homozygotes protected simultaneously, and it follows that the genotypic polymorphism is never protected.

Case (b)

We begin with a genotypic polymorphic structure $G = (P_h, P_m, P_f)$ where P_h, P_m, P_f again denote the frequencies of the hermaphrodites, males, and females, respectively. In this model, the males are heterozygous and the hermaphrodites and females are each represented by one of the homozygous genotypes. The transition equations read:

$$P'_h = \frac{\sigma P_h}{\bar{\phi}} + \frac{(1-\sigma)P_h}{\bar{\phi}} \times \frac{P_h + \frac{1}{2}\mu P_m}{\bar{\mu}}$$

$$P'_m = \frac{(1-\sigma)P_h}{\bar{\phi}} \times \frac{\frac{1}{2}\mu P_m}{\bar{\mu}} + \frac{\phi P_f}{\bar{\phi}} \times \frac{P_h + \frac{1}{2}\mu P_m}{\bar{\mu}}$$

$$P'_f = \frac{\phi P_f}{\bar{\phi}} \times \frac{\frac{1}{2}\mu P_m}{\bar{\mu}},$$

where $\bar{\phi} = P_h + \phi P_f$, $\bar{\mu} = P_h + \mu P_m$.

It follows from GREGORIUS (1982) that the allele of the females is protected if $(1 - \sigma)\mu > 2$ and not protected if $(1 - \sigma)\mu < 2$. It is obvious that the protectedness of the allele of the females and, equivalently, the allelic polymorphism is equivalent to the protectedness of the male genotype. As in case (a), a homozygote genotype can be lost only by convergence of the structure to an equilibrium point located on the boundary where this genotype has frequency zero.

On the boundary $P_h = 0$, $\hat{G}_d := (0, \frac{1}{2}, \frac{1}{2})$ is a unique globally attractive equilibrium point. Letting G denote genotypic polymorphic structures,

$$\frac{P'_h}{P_h} \xrightarrow[G \rightarrow \hat{G}_d]{} \frac{1+\sigma}{\phi} =: L_d.$$

If $L_d < 1$, then $\hat{G}_d$ is attractive, and the hermaphrodite is not protected. If $L_d > 1$, then $\hat{G}_d$ is repulsive, and the hermaphrodite is protected.

On the boundary $P_f = 0$, the fixation point $P_h = 1$ is always an equilibrium point, and it is globally attractive along this boundary if $(1 - \sigma)\ \mu \leq 2$. If $(1 - \sigma)\ \mu > 2$, then there exists an additional equilibrium point $\hat{G}_b$ defined by

$$\hat{P}_m := \frac{\frac{1}{2}(1-\sigma)\mu - 1}{\mu - 1} > 0 \text{ and } \hat{P}_h := 1 - \hat{P}_m,$$

which is attractive for all points on the boundary except the fixation point $P_h = 1$. (If $(1 - \sigma)\ \mu = 2$, then $\hat{G}_b$ is the fixation point.) Assuming $(1 - \sigma)\ \mu \geq 2$ (and thus $\sigma < 1$) and letting G denote genotypic polymorphic structures,

$$\frac{P'_f}{P_f} \xrightarrow[G \rightarrow \hat{G}_b]{} \frac{\phi}{1+\sigma} \times \frac{(1-\sigma)\mu - 2}{(1-\sigma)\mu} =: L_b.$$

It holds that $L_b = 1/L_d \times [(1 - \sigma)\mu - 2]/[(1 - \sigma)\mu]$. If $L_b < 1$, then $\hat{G}_b$ is attractive and the female genotype is not protected. If $L_b > 1$, then $\hat{G}_b$ is repulsive.

Protectedness of the allelic polymorphism implies $(1 - \sigma)\mu \geq 2$. But in the case $(1 - \sigma)\mu = 2$, $\hat{G}_b$ is the fixation point $P_h = 1$ and $L_b = 0 < 1$, and hence the fixation point is attractive. Therefore, the allelic polymorphism is protected if and only if $(1 - \sigma)\mu > 2$.

If the genotypic polymorphism is protected, then $(1 - \sigma)\mu > 2$ and $L_d, L_b \geq 1$. It can be easily shown that, due to the interdependence of the expressions for L_d and L_b, $L_d \times L_b < 1$. Therefore, the condition $L_d, L_b \geq 1$ can never be fulfilled and, hence, the genotypic polymorphism is not protected.

Case (c)

Once again we begin with a genotypic polymorphic structure $G = (P_f, P_h, P_m)$, where P_f, P_h, P_m are defined as in the previous cases. Here, the hermaphrodites are heterozygous, whereas the females and males are each represented by one of the homozygous genotypes.

The transition equations read:

$$P'_f = \frac{\frac{1}{4}\,\sigma\,P_h}{\bar{\phi}} + \frac{\phi P_f + \frac{1}{2}\,(1-\sigma)P_h}{\bar{\phi}} \times \frac{\frac{1}{2}\,P_h}{\bar{\mu}}$$

$$P'_h = \frac{\frac{1}{2}\,P_h}{\phi} + \frac{\phi P_f}{\phi} \times \frac{\mu P_m + \frac{1}{2}\,P_h}{\mu}$$

$$P'_m = \frac{\frac{1}{4}\,\sigma P_h}{\bar{\phi}} + \frac{\frac{1}{2}\,(1-\sigma)P_h}{\bar{\phi}} \times \frac{\mu P_m + \frac{1}{2}\,P_h}{\bar{\mu}}$$

where $\bar{\phi} = \phi P_f + P_h$, $\bar{\mu} = P_h + \mu P_m$.

It follows that

$$P'_h - \tfrac{1}{2} = \frac{\phi P_f}{\bar{\phi}} \times \frac{\mu P_m + \frac{1}{2}\,P_h}{\bar{\mu}} - \tfrac{1}{2} \times \frac{\phi P_f}{\bar{\phi}}$$

$$= \frac{\phi P_f}{\bar{\phi}} \times \frac{\frac{1}{2}\,\mu P_m}{\bar{\mu}} > 0,$$

so that after the first generation $P_h > \frac{1}{2}$. This implies the protectedness of the genotypic polymorphism for all sets of parameters ϕ, $\mu > 0$ and $0 \leq \sigma \leq 1$.

The existence of invariant regions in the set of all genotypic structures can be shown by means of the relationship

$$\frac{P'_f}{P'_m} = \frac{\frac{1}{4}\,\sigma\bar{\mu} + \frac{1}{2}\,(\phi P_f + \frac{1}{2}\,(1-\sigma)P_h)}{\frac{1}{4}\,\sigma\,\bar{\mu} + \frac{1}{2}\,(1-\sigma) \times (\mu P_m + \frac{1}{2}\,P_h)}$$

$$= \frac{\frac{1}{4}\,\sigma\mu P_m + \frac{1}{2}\,(\phi P_f + \frac{1}{2}\,P_h)}{-\frac{1}{4}\,\sigma\mu P_m + \frac{1}{2}\,(\mu P_m + \frac{1}{2}\,P_h)}$$

$$= \frac{\bar{\mu} + 2\phi P_f - (1-\sigma)\mu P_m}{\bar{\mu} + (1-\sigma)\mu P_m}.$$

It follows that $P'_f/P'_m < 1$ if and only if

$$2\phi P_f - (1-\sigma)\mu P_m - (1-\sigma)\mu P_m = 2[\phi P_f - (1-\sigma)\mu P_m] < 0,$$

which in turn results in: $[P_f/P_m < 1]$ is invariant if $\phi < (1-\sigma)\mu$, $[P_f/P_m > 1]$ is invariant if $\phi > (1-\sigma)\mu$, and if $\phi = (1-\sigma)\mu$, then $[P_f/P_m < 1]$, $[P_f/P_m = 1]$, and $[P_f/P_m > 1]$ are invariant.

The following equation yields statements concerning the attractiveness of these regions.

$$\frac{P'_f}{P'_m} - \frac{P_f}{P_m} = \frac{P_m[\bar{\mu} + 2\phi P_f - (1-\sigma)\mu P_m] - P_f[\bar{\mu} + (1-\sigma)\mu P_m]}{P_m[\bar{\mu} + (1-\sigma)\mu P_m]}.$$

Denoting the numerator by Δ, then

$$\Delta = \bar{\mu}(P_m - P_f) + P_m[2\phi P_f - (1-\sigma)\mu(P_f + P_m)].$$

(1) Let $\phi < (1-\sigma)\mu$ and $P_f \geq P_m$. Then

$$\Delta \leq \bar{\mu}(P_m - P_f) + (1-\sigma)\mu P_m(P_f - P_m)$$

$$= (P_m - P_f)(\bar{\mu} - (1-\sigma)\mu P_m).$$

Since $\bar{\mu} - (1-\sigma)\mu P_m > 0$, it follows that $\Delta < 0$ and thus

$$\frac{P'_f}{P'_m} < \frac{P_f}{P_m}.$$

(2) For $\phi > (1-\sigma)\mu$ and $P_f \leq P_m$ it follows analogously that $\Delta > 0$ and hence $P'_f/P'_m > P_f/P_m$.

(3) If $\phi = (1-\sigma)\mu$, then $\Delta = (P_m = P_f)(\bar{\mu} - (1-\sigma)\mu P_m)$. Hence, $P_f/P_m < 1$, $P_f/P_m > 1$ imply $P'_f/P'_m > P_f/P_m$ and $P'_f/P'_m < P_f/P_m$, respectively. Consequently,

(1′) if $\phi < (1-\sigma)\mu$, then $P_f < P_m$ ultimately holds,
(2′) if $\phi > (1-\sigma)\mu$, then $P_f > P_m$ ultimately holds,
(3′) if $\phi = (1-\sigma)\mu$, then $P_f = P_m$ ultimately holds.