

FREQUENCY-DEPENDENT SELECTION UNDER MIXED SELFING AND RANDOM MATING

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1. INTRODUCTION

In population genetic theory, the solutions of a model often represent the conditions in terms of the various parameters of selection, migration, mating system, etc., that allow stable polymorphisms under a specific genetic system. Certain elements of a predictive theory may then utilise this knowledge of the possible outcomes (Lewontin, 1967). Further, a comparative analysis of different models might provide certain ways to "explain" experimental observations. In so far the theory has guided empirical explanations, we may argue for the potential use of such theoretical efforts in evolutionary biology. In this note we shall illustrate this briefly, using a simple deterministic model involving frequency-dependent selection at a diallelic locus segregating in a large mixed selfing and random mating population. Frequency-dependency favouring the rarer genotype (apostatic selection) in one or more fitness components (viability, mating propensity, fecundity, etc.) has drawn wide attention in recent years (Spiess, 1968, for review), essentially as an attractive alternative to the overdominance model for stable polymorphisms, and as a model of genetic feedback mechanism regulating population changes.

In our work on the genetics of inbreeding plant populations (Allard, Jain and Workman, 1968), true or marginal overdominance was emphasised in terms of the "explanations" for an observed excess of heterozygosis as well as in the simulation of models under a variety of selection specifications (Workman and Jain, 1966; Jain and Workman, 1967; Jain and Marshall, 1968). For multilocus models, the existence of multiple peaks was discussed as being a significant property of the polymorphic, interacting gene systems (Jain, 1968). In this note, frequency-dependent selection is shown to yield far more favourable conditions for stable polymorphisms than hitherto reported for these other models.

2. RESULTS AND DISCUSSION

Hayman (1953) developed solutions of a model involving the relative selection values of the three genotypic classes A_1A_1 , A_1A_2 , A_2A_2 given by $x : 1 : y$ respectively in zygotic selection just prior to the census stage. Inbreeding due to varying proportions of selfing (s) and outcrossing ($t = 1 - s$) in conflict with heterozygote advantage ($x, y < 1$) results in the limits on (x, y) as shown in fig. 1 where regions A, B represent the values of (x, y) leading to the fixation of alleles A_1 and A_2 respectively, and regions C, D with stable nontrivial equilibria. In regions C and D the population has fewer or more heterozygotes respectively than expected on the basis of Hardy-Weinberg theorem. Two points to note are: (i) with increasing s ,

the amount of heterozygote advantage required increases, and (ii) the homozygote fitnesses need to be nearly equal for the cases of low amounts of overdominance. Thus, regions C, D are much smaller for heavy inbreeding.

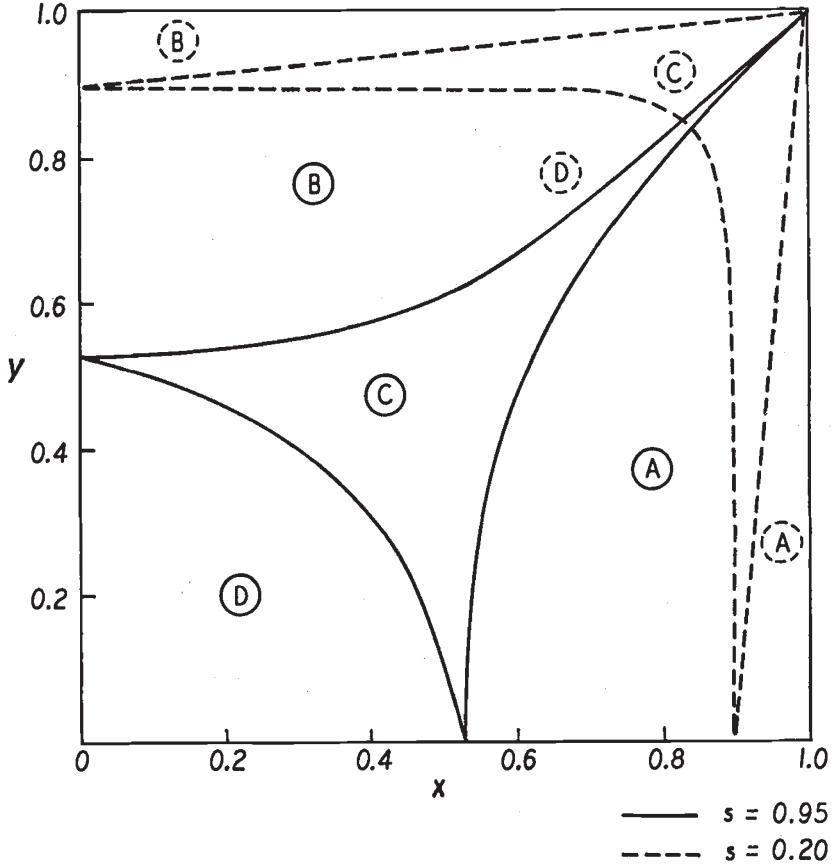


FIG. 1.—Phase diagrams for Hayman's model with $s = 0.20$ and 0.95 , $x, y < 1$ (overdominance).

Next, consider the following model of frequency-dependent selection with two components of relative fitnesses:

Genotype	A_1A_1	A_1A_2	A_2A_2
Relative frequency of zygotes in n th generation	$f_1^{(n)}$	$f_2^{(n)}$	$f_3^{(n)}$
Frequency-dependent fitnesses	$1 - t_1 f_1^{(n)}$	$1 - t_2 f_2^{(n)}$	$1 - t_3 f_3^{(n)}$
Frequency independent fitnesses	x	1	y

Then, the recursion relations following Hayman's scheme are given by $f_1^{(n+1)} \propto x(1 - t_1 f_1^{(n)}) \{s(f_1^{(n)} + \frac{1}{4} f_2^{(n)}) + t(f_1^{(n)} + \frac{1}{2} f_2^{(n)})^2\}$, etc., and denoting $p = f_1 + \frac{1}{2} f_2 = 1 - q$, and $F = \frac{1 - f_2}{2pq}$, two simultaneous nonlinear equations in p

and $F, \Delta p = \Delta F = 0$, are obtained. By methods of computer simulation, these are solved iteratively for finding equilibria (defined at $f_i < 10^{-5}$, or for regions of fixation, $p > 0.99995$ or < 0.00005 taken as $p = 1, 0$ respectively). Clarke and O'Donald (1964) gave exact solutions for the case $s = 0$ and $t_1 = t_2 = t_3$, to show that there may be up to three equilibria, not more than two of which are stable. Stability was tested either by using various initial frequencies or by small perturbations in equilibrium frequencies. The equilibria were determined for x and y varied with 0.1 increments in order to plot the regions A-D for the cases (a) $t_1 = t_2 = t_3 = 0.3$ and (b) $t_1 = 0.2, t_2 = t_3 = 0.3$ (asymmetrical).

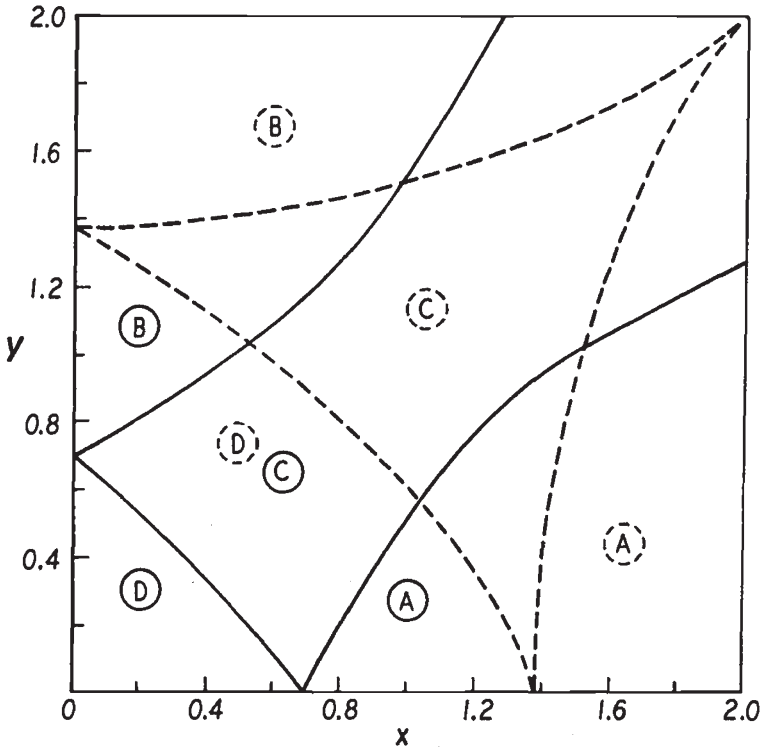


FIG. 2.—Phase diagrams for frequency-dependency model (a) with $s = 0.20$ and 0.95 , $0 \leq x, y \leq 2$. Note that for $s = 0.95$, region C of stable equilibria remains large for underdominance ($x, y > 1$).

The phase diagrams for the case (a) and two levels of inbreeding are given in fig. 2. The most significant result to note is the enlargement in regions C, D to include $x, y > 1$ (underdominance), with increasingly greater region under higher selfing levels. Comparing with Hayman's model (fig. 1), note that both restrictive conditions of the overdominance model are relaxed due to the frequency-dependent component becoming proportionately more important with higher inbreeding. Thus, the homozygote fitnesses (x, y) at any given stage could vary over a range of underdominance levels and need not be close to each other. As noted by Clark and O'Donald (1964) for $s = 0$, the marginal selective values at equilibria in region C may show underdominance. Further, it was noted for the asymmetrical case (b) with

$s = 0.20$ and 0.95 that the region C was slightly smaller and that the two stable equilibria obtained for $s = 0$ and 0.2 in the $(x, y > 1)$ range tend to converge toward a single stable point for increasingly higher selfing (e.g. $s = 0.95$) so that the multiple peaks under this model do not necessarily represent a wider region C (unlike epistatic, multilocus cases). In summary, it appears that apostatic selection offers a very potent model at least in theory favouring the maintenance of genetic variation in inbreeding populations.

It also follows from the shifts in phase boundaries that the estimation of constant selective values (x, y) using only a limited number of generations or from a single generation data with the assumption of equilibrium as done

TABLE 1

Relative selective values (x, y) of homozygotes with and without frequency-dependency

Percentage selfing	Equilibria under Clarke-O'Donald model (a)					Hayman's model *	
	Frequencies of			x	y	x	y
	A_1A_1	A_1A_2	A_2A_2				
0.20	0.0008	0.0286	0.9706	0.4	1.3	0.40	0.93
0.20	0.3236	0.3528	0.3236	1.4	1.4	1.41	1.41 (metastable)
0.95	0.4828	0.0344	0.4828	1.4	1.4	1.21	1.21 (metastable)
0.95	0.3812	0.0313	0.5875	1.4	1.5	} these equilibria are inadmissible	
0.95	0.1816	0.0208	0.7976	1.3	1.6		

* The estimates of (x, y) at equilibria are given by

$$x = \{2f_1(2f_2 - C)\} / \{f_2(4f_1 + C)\},$$

$$y = \{2f_2(2f_1 - C)\} / \{f_1(4f_2 + C)\},$$

where $C = f_2 - t(4f_1f_2 - f_2^2)$ (Hayman⁸).

in the past could be misleading if, in fact, frequency-dependency was involved. Table 1 lists a few examples of nontrivial equilibria and the sets of appropriate selective values under the two models with or without frequency-dependent selection. Clearly, the model should be identified through additional independent tests of the modes of selection before one could establish the overdominance or some other factor maintaining polymorphisms. Note that even the means of (x, y) estimated over a set of seasons on the basis of any single fitness component (say, seed number) rather than the overall survival rates might result in erroneous predictions. Moreover, it is now apparent that such estimates would not be sufficient to describe the extent and stability of polymorphisms. Multistage data over several successive generations are required to discern among these and other models of selection. Experiments are now underway to determine the role of frequency-dependency in barley populations along these lines. Several other models of frequency-dependency have also been simulated involving a matrix of frequency-dependent competition coefficients. The results to be presented in detail elsewhere provide evidence on the overwhelming theoretical role of frequency-dependency in inbreeding populations. Biological evidence would further provide significant information on the

dynamics of ecological interactions, co-adaptation and adjustments in the mating system. The properties of self-regulation and integration may become known to involve one or the other frequency-dependent factors under a very wide range of situations *e.g.* interspecies competition (Marshall and Jain, 1969), optimum hybridity (Harding *et al.*, 1966), self-incompatibility alleles (Sheppard, 1960), and pollination ecology (Faegeri and Pijl, 1966).

3. SUMMARY

1. A model of selection in a large, mixed selfing and random mating population was simulated using digital computer in order to study frequency-dependent selection involving advantage for the rarer genotype.

2. With increasingly higher levels of selfing, frequency-dependency could allow wider conditions on the frequency-independent component of fitnesses such as to maintain stable polymorphisms with underdominance. An asymmetrical model further showed that two different stable equilibria tend to converge with greater selfing.

3. The significance of such situations as a theoretical alternative to the postulated widespread role of overdominance in inbreeding populations was discussed particularly in terms of the problems of estimating selection parameters.

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