

A SIMULATION OF WRIGHT'S SHIFTING-BALANCE PROCESS: MIGRATION AND THE THREE PHASES

FRANCISCO B.-G. MOORE¹ AND STEPHEN J. TONSOR²

¹*Kellogg Biological Station, Hickory Corners, Michigan 49060 and
Department of Zoology, Michigan State University,
East Lansing, Michigan 48825*

²*Kellogg Biological Station, Hickory Corners, Michigan 49060 and
Department of Botany and Plant Pathology, Michigan State University,
East Lansing, Michigan 48825*

Abstract.—Wright partitioned the shifting-balance process into three phases. Phase one is the shift of a deme within a population to the domain of a higher adaptive peak from that of the historical peak. Phase two is mass selection within a deme towards that higher peak. Phase three is the conversion of additional demes to the higher peak. The migration rate between demes is critical for the existence of phases one and three. Phase one requires small effective population sizes, hence low migration rates. Phase three is optimal under high migration rates that spread the most-fit genotype from deme to deme. Thus, a population-wide peak shift requires intermediate levels of migration. By altering the rates of phases one and three, migration affects the predominant direction of mass selection within a population. This study examines the degree to which migration, through its effects on phases one and three, determines the probability of a simulated population arriving at its genotypic optimum after 12,000 generations. These simulations reveal that there is a range of migration rates for which an entire population might be expected to shift to a higher peak. Below $m = 0.001$ peak shifts occur frequently (phases I and II) but are not successfully exported out of subpopulations (phase III), and above 0.01 peak shifts within demes (phase I and II), required to initiate phase III, become increasingly uncommon. Because it is unlikely that real populations will have uniform migration rates from generation to generation, the probable effects of varying migration rates on broadening the range of conditions producing peak shifts are discussed.

Key words.—Epistasis, interdemic selection, migration, population structure, shifting balance.

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Sewall Wright's shifting-balance process (SBP) is a mechanism by which complex genetic traits can evolve despite the pressure of individual selection to maintain a historical genetic arrangement (Wright 1982). A critical concept in the SBP is that of the adaptive topography. In such a topography, mean population fitness depends on allele frequencies at multiple loci. Wright was interested in topographies with multiple mean fitness optima (peaks) with intervening mean fitness minima (troughs). For this reason, gene-gene interactions are of central importance to the SBP (Wright 1977, 1978, 1982). Although multiple peaks may arise because of underdominance or multiallelic overdominance at a single locus, Wright saw adaptive topographies as arising primarily from interlocus interactions.

Wright viewed epistasis as pervasive. Kacser and Burns (1981) explicated a mechanism by which epistasis would be as pervasive as dominance for genes whose products function in metabolic chains or networks. Jinks (1983) suggested that epistasis may explain all or most cases of overdominance reported from combining ability

experiments. Even for genes with purely additive effects on the phenotype, when the fitness function is nonlinear, phenotypically additive genes will exhibit epistasis for fitness. For example, with optimizing selection, an allele with a positive genotypic value can have positive or negative fitness effects, depending on the sum of genotypic values for all loci affecting the trait. Because of Wright's interest in epistasis, because it would appear to be the most general class of gene interaction, and because there is mounting evidence for its importance as a mode of gene action, we focus on epistasis as a component of the SBP.

When epistatic interactions exist, they can constrain the ability of a large population to evolve in the direction of the most-fit genotypes. These constraints are the fabled fitness valleys of the multilocus, multi-peaked adaptive topography of the type Wright envisioned.

Underlying a multi-peaked adaptive topography is a multilocus genotypic fitness surface in which the relative fitness of any allele depends on the genotype in which it is manifested (see

Provine 1986, pp. 307–317 for a discussion of the confusion surrounding Wright's original fitness surfaces). The allele frequencies within a (random-mating) deme determine the predominant genotypes within which an allele is manifested. The direction and magnitude of selection acting on epistatically interacting loci is thus determined by the deme's allele frequencies. Likewise, the mean fitness of a deme depends on the frequency of interacting alleles, and this can result in multiple fitness optima in a Wrightian adaptive topography.

In an infinitely large population, evolution by natural selection will bring the population to the local fitness optimum, leaving the remaining fitness surface unexplored. In spatially structured populations with small deme sizes, random genetic drift can result in an exploration of the entire surface. Migration among demes limits the extent of stochastic divergence in allele frequency among demes and limits the ability of the population as a whole to move among peaks. To understand the evolutionary process in structured populations, Wright therefore believed that one needed to understand the interactions of random genetic drift, the epistatic fitness effects at drifting loci, and the homogenizing effects of migration among demes.

Wright (1977, p. 455) partitioned the shifting-balance process (SBP) into three phases (Wade and Goodnight 1991). Phase I is the stochastic drift of allele frequencies within demes, which can shift a deme into the attractive domain of an alternative peak. Phase II is the shift of allele frequencies towards the optimum of the "new" peak through individual selection within the shifted deme. Phase III is the conversion of surrounding demes to a higher peak through immigration from a previously peak-shifted deme (i.e., interdemec selection).

Phase I is most effective with low migration among demes and small effective population size. Phase III occurs most readily with high rates of migration among demes. Only with some intermediate level of migration can both phases I and III occur (Wade and Goodnight 1991). However, the range of migration rates between 0.0 and 1.0 that allow the SBP remains almost entirely unknown. Wade and Goodnight (1991) found that mean fitness increased at levels of migration below 0.05. However, the genetic causes of changes in mean fitness have not been established. It has been by no means clear that for any given epistatic system there is any constant migration rate

that will allow all three phases of the SBP to occur (Hartl and Clark 1989, pp. 323–324). The purpose of this study was to explore the interaction of migration and the three phases in determining the domain of migration rates for which the SBP is likely. We focus here on the role of migration as a factor governing the time to and frequency of populationwide peak shifts.

When Wright first proposed the SBP (1931), very little was understood about drift, interdemec selection, effective population sizes, or epistatic variation in natural populations. Since then, considerable progress has been made in understanding the potential role of drift in natural populations (Kerr and Wright 1954; Buri 1956; Epling et al. 1960; Bowden 1982), epistasis in determining fitness differences (Burton 1990; Wade 1985; and for a review see Barker 1979), and interdemec selection (McCauley and Wade 1980; Wade, 1977; Wade and McCauley 1980, 1984; Goodnight 1985). However, the only empirical test of the SBP as a whole was made by Wade and Goodnight (1991), which indicates that the population structure can influence fitness changes in complex traits in a way that broadly corresponds to the expectations of the shifting-balance theory.

The necessarily large scale of investigations like that of Wade and Goodnight (1991) slows progress towards an understanding of the role of the SBP in nature. Until more experimental results are available, and as a theoretical underpinning providing increasingly explicit expectations for future empirical studies, a more mechanistic understanding of the interaction of relevant factors is needed.

To gauge the relative importance of the shifting-balance process we need to know what conditions (if any) are conducive to the SBP and the ubiquity of those conditions. Because of the complexity of the SBP and the role of stochastic processes, a comprehensive mathematical description has been elusive. Barton and Rouhani (1993) provided the most comprehensive view to date, but because of their need for mathematical tractability, their treatments are limited to purely additive genes or to intralocus allelic interactions. In lieu of a mathematical model, we have used a computer simulation to explore the process. We use a simulation that specifies an individual's genotype, fitness, and dispersal behavior. By keeping track of individuals in this way, we have avoided simplifications that prevent insight into the roles of migration and epis-

tasis in the SBP. Our overall goal was to describe the relationship between the migration rate and the probability of a populationwide peak shift. We looked for the domain of migration rates in which peak shifts occur with any frequency. We asked if one can expect an optimum migration rate for the SBP under the conditions of any particular population. We also examined the effect of the migration rate on the propensity for peak shifts through a combination of phases I and II, and migration rate's effect on phase III. Finally, we examined the relationship between the migration rate and the extent of deme extinction/recolonization, and its effect on the propensity for peak shifts.

MATERIALS AND METHODS

The Components of the Simulation

We modeled a diploid, obligately sexual, semelparous species. Density-independent mortality (hard selection) took place in the juvenile phase prior to migration and mating. Selection was based on genotype-dependent survival probabilities. Migration was followed by random mating of adults

A critical aspect of the shifting-balance process (SBP) is the variation of deme (subpopulation) size. The variation in deme size (N) allows variation in the absolute number of individuals emigrating from demes (mN), without requiring differential per capita migration rates (m) between demes with different mean fitnesses. This can drive the third phase of the SBP (Crow et al. 1990). In addition, variation in deme size also creates variation in the rate of random genetic drift. This affects phase I as well as altering the relative contribution of immigrant genotypes to the genotype and allele frequencies in the mating pool.

In real populations, it is not unreasonable to assume that some type of resource limitation often sets an upper bound (K) on the number of individuals that can survive within a population, and excess reproductive capabilities will tend to force populations towards that K (Verhulst 1838). Because, in this case, all populations are expected to remain near their carrying capacity, variation in size among demes near K must be regenerated each generation by hard selection within demes. In these simulations, hard selection associated with the genotypic composition of the demes results in variation in mean fitness among demes.

A finite maximum deme size was imposed by

incorporating a carrying capacity ($K = 30$), and intrinsic growth capabilities into a logistic function ($N_{(t+1)} = N_{(t)} + rN_{(t)}(K - N_{(t)})/K$, $r = 1.1$). This function determined the maximum number of individuals that could be born into that deme during the next generation ($N_{(t+1)}$). For each offspring, random male and female parents were chosen from within the deme and a randomly drawn copy of the gene at each locus was pulled from each of the chosen parents to produce an offspring (i.e., assortment was fully independent). This procedure was repeated until the necessary ($N_{(t+1)}$) number of offspring were produced. Because all demes have the same r and K , during each generation all demes tend towards the same carrying capacity. This demographic model tends to reduce divergence in deme size based on genotype frequencies and therefore reduce the opportunity for interdemec selection to take place. This is a relatively unfavorable scenario for the SBP.

In the event that at least one individual of each sex was not present, the deme was allowed to go extinct. Recolonization of extinct populations occurred only when individuals of both sexes chanced to migrate into the extinct deme in the same generation.

We simulated a population that contained three different fitness phenotypes. This allowed variably sized demes whose average deme size was related to phenotype. Each phenotype had a predefined absolute juvenile survivorship. No mortality existed outside of the juvenile phase. Using two loci, each with two alleles, provided us with nine genotypes. The nine genotypes provided three phenotypes based on the model of epistatic interaction employed by Crow et al. (1990). The average *absolute* fitnesses were as follows: double homozygote wild type = 0.636, individuals that were heterozygous at one locus but homozygous wild type at the other locus = 0.620, and individuals that had at least one copy of the mutant genotype at each locus = 0.700.

In Crow et al.'s formula, the three phenotypes have fitnesses that would be described by the following equations:

$$W_1 = 1, W_2 = (1 - s), \text{ and} \\ W_3 = (1 + ks).$$

In these equations, s determines the strength of selection and k determines the relative heights of the multiple peaks. For these simulations, s was set to 0.025 and k was set at 4 yielding *relative* fitnesses of 0.909, 0.886, and 1.000 for the

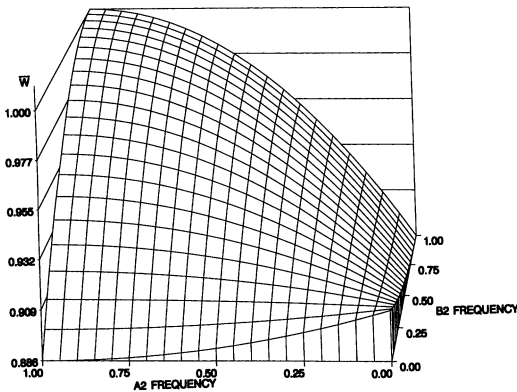


FIG. 1. Population fitness surface. This surface is created by plotting the expected mean population fitness (\bar{W}) against the frequency of the mutant alleles at two loci.

three phenotypes respectively. When random mating and infinite population sizes are assumed, this system produces the Wrightian adaptive topography shown in figure 1.

These simulations followed single metapopulations (hereafter referred to as populations) that were composed of multiple subpopulations (hereafter termed demes). The migration rates (m) between demes were the per capita probabilities of leaving the parent deme during the dispersal phase. The probability of a given individual migrating to a new deme a given distance away was described by the gamma function,

$$\text{Prob}(X) = (m)^X(1 - m),$$

where X is the number of demes away the migrant would be traveling. Individuals were allowed to migrate up to five demes away from their parent deme. Any individual migrating X demes away was placed in a randomly chosen deme at that distance.

Genetic variation was introduced via mutation. A fixed mutation rate of 5×10^{-6} mutations per copy, per generation, per capita introduced mutants at each locus. This mutation rate was held constant throughout all simulations. For the original simulations, only forward mutations were allowed. Subsequent simulations with both forward and back mutations were then run over the range of migration rates in which populationwide peak shifts were likely to occur ($m = 0.001, 0.0025, \dots, 0.1$).

The initial conditions of the simulated population are as follows: A 10 by 10 matrix of demes was arranged in a torus to reduce edge effects.

Each deme originally consisted of 15 individuals each of whose gender was randomly chosen. Every individual in the initial population was genotypically identical. Hence, all demes were fixed at the local optimum corresponding to the lower peak in figure 1. The intent of these simulations was to determine the effect of migration on the movement of demes and eventually populations to the higher peak.

Separate runs were conducted for 13 migration rates from $m = 0.0$ to $m = 0.5$. Thirty trials were run at each migration rate. In addition to the 13 different migration rates, 40 trials were run in a large ($K = 3000$) panmictic population. This allowed the comparison of different levels of population structure to a totally unstructured population of equivalent size. Each simulation was run for 12,000 generations. Data from the 6000th and 12,000th generation were used in the analysis of these simulations.

Analysis of Simulations

The SBP is concerned primarily with events that can alter a population's genotypic composition and therefore its mean fitness. Because the population as a whole is the focal point of investigation, our results consist largely of frequencies taken across a population, or of the percentage of trials for which the population falls into a given class. The propensity of a given deme to shift to a higher mean fitness peak is a measure of the combined efficacy of phases I and II of the SBP. We were interested in the propensity for phases I and II to lead to peak shifts. We therefore determined the percentage of trials at a given migration rate in which the population had at least one deme shift.

The recruitment scheme used in these simulations tended to produce recruits near carrying capacity. Yet when the per capita migration rate is fixed for all genotypes differences in deme size are a necessary driving force behind the third phase. To determine the size difference between demes with different genotypic compositions we placed demes into three different categories based on mean fitness. "High-peak" demes were defined as demes that were fixed for the highest fitness genotype. "Low-peak" demes were defined as demes that have an expected mean juvenile fitness above 0.900 but below 1.000. "Trough" demes were defined as all demes with expected juvenile fitness below 0.900. An ANOVA was performed to test for differences in mean deme size between these deme types.

We were interested in exactly what range of migration rates allowed interdemec selection to convert the entire population to the domain of the higher peak. Therefore, for trials that had at least one deme shift, we calculated the percentage that ended in the fixation of the higher fitness genotype throughout the population (i.e., the tendency for phase 3 to occur once phases 1 and 2 have occurred) for each migration rate.

One expected characteristic of the shifting-balance process is that the global frequency of the highest fitness genotype will depend on the rate of migration between demes. Therefore, the frequency of the highest fitness genotype was determined for each run. From this the mean frequency of the highest fitness genotype was calculated for each migration rate.

The percentage of all trials that led to the fixation of the highest fitness genotype throughout the population is a direct measure of the efficacy of the SBP as a whole. Here the emphasis is on a complete transition from fixation of one genotype to the fixation of another genotype. We therefore calculated the percentage of all 30 populations (i.e., trials) at each migration rate that shifted entirely to the higher adaptive peak.

These simulations allowed the extinction and recolonization of demes. Differential extinction of demes based on genotype, and the differential export of individuals based on deme size are two potentially important sources of interdemec selection that can drive the third phase of the SBP. The mean percent of the original demes remaining at the end of a simulation was compared for simulations that had at least one deme shift versus simulations in which no deme shifts took place. The comparison was made for each migration rate. This provided a comparison of the predominance of extinction over recolonization between populations in which the SBP had been initiated and those in which it had not.

Confidence Limits for the Data

For each migration rate (treatment), we performed 30 trials, each consisting of one population of 100 demes. Because computational constraints restricted the number of trials to 30 per treatment, bootstrapped 95% confidence intervals were estimated by multiple resampling of the available trials. These confidence intervals were computed by bootstrapping 2000 random samples from the 30 trials and excluding the highest and lowest 2.5% of the bootstraps. This provides an unbiased estimate of the mean at the

TABLE 1. The mean number of individuals in demes of different mean fitness. High peak demes are fixed for the highest fitness genotype, low peak demes have mean fitness less than the high peak demes but equal to or greater than the original population mean fitness, and trough demes have lower mean fitness than the original population.

Deme type	Mean deme sizes		
	Mean	<i>N</i>	SD
High peak	26.9528	2973	1.4730
Low peak	24.3537	17,737	2.6201
Trough	23.4408	152	2.6085

cost of biasing the error estimates (Weir 1990). The confidence intervals were universally larger than 95% confidence intervals arrived at using parametric assumptions.

RESULTS

The results of the 6000th generation are qualitatively similar to those from the 12,000th generation. The results of simulations that include back mutation are indistinguishable from those with only forward mutations. Therefore, results from only the 12,000 generation of trials that did not include back mutation are presented.

Results of the Panmixia Model

In 40 trials, no individuals with the highest fitness genotype were recorded from runs based on a large population with random mating.

Peak Shift Propensity

Figure 2 is a plot of the propensity of demes to shift as a function of migration rate. Demic peak shift propensity is herein defined by the percentage of trials in which at least one deme shifts to the higher fitness peak. In the simulations we ran, migration rates above $m = 0.05$ showed no peak shifts. For all treatments below $m = 0.0075$, zero peak shift propensity lies outside the 95% confidence intervals.

Prerequisites for Phase III

In these simulations, the size of a deme depended significantly ($P < 0.0001$) on the expected mean juvenile survivorship of the population (table 1). Fitness-dependent mean deme size differences occurred despite a recruitment scheme that tended to produce recruits at carrying capacity.

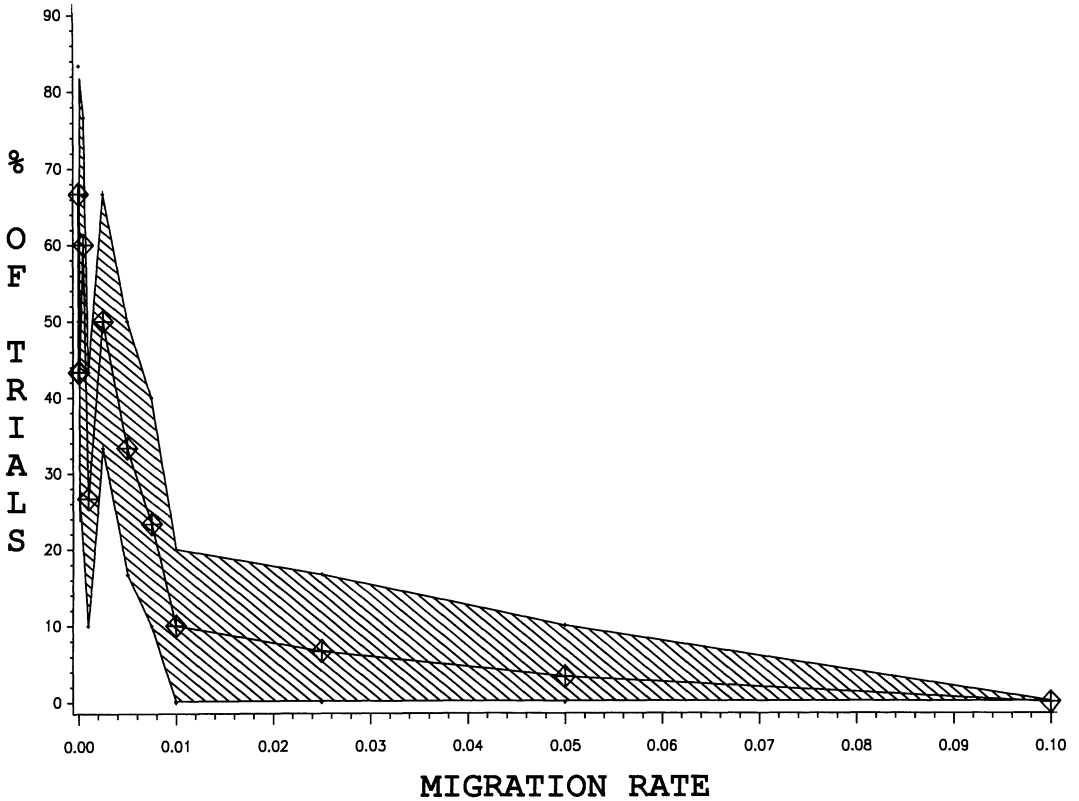


FIG. 2. The percentage of trials in which at least one deme shifted versus the migration rate. Shaded areas are 95% confidence intervals.

Phase III Propensity

Figure 3 depicts the percent of trials with a deme shift present that led to the fixation of the higher fitness genotype throughout the population (i.e., the tendency for phase 3 to occur once phases 1 and 2 have occurred). When m was less than or equal to 0.001, phase three never occurred. The tendency for fixation to occur climbs rapidly from 0.0% to 100% between $m = 0.001$ and 0.0075. Above this point, populationwide fixation of genotypes once the first deme has shifted is 100% until the migration rates increase to the point where no deme shifts occur ($m = 0.05$).

Shifting-Balance Process (SBP) as a Whole

The frequency of the highest fitness genotype in these simulations was dependent on the migration rate (fig. 4). The maximum frequency of the highest fitness genotype was 0.35 when m was equal to 0.0025. When m exceeded 0.10 there

was a 0.00 frequency of the highest fitness genotype. The frequency of the highest fitness genotype also dropped below 0.10 when the migration rate dropped below 0.0005.

The percentage of trials that lead to the fixation of the highest fitness genotype (fig. 5) throughout the population is maximized at 30.0% fixation of the higher fitness genotype when $m = 0.005$. No whole-population peak shifts were seen below $m = 0.001$ or above $m = 0.1$.

Population Size

Figure 6 demonstrates that deme extinctions are related to migration rate. Deme extinction rates for trials that have had at least one deme peak shift and trials that have had no peak shifts are similar. However, populations in which demes have shifted have fewer extinctions throughout the range of migration rates.

DISCUSSION

A fundamental outcome of the shifting-balance process (SBP) is that when gene interactions

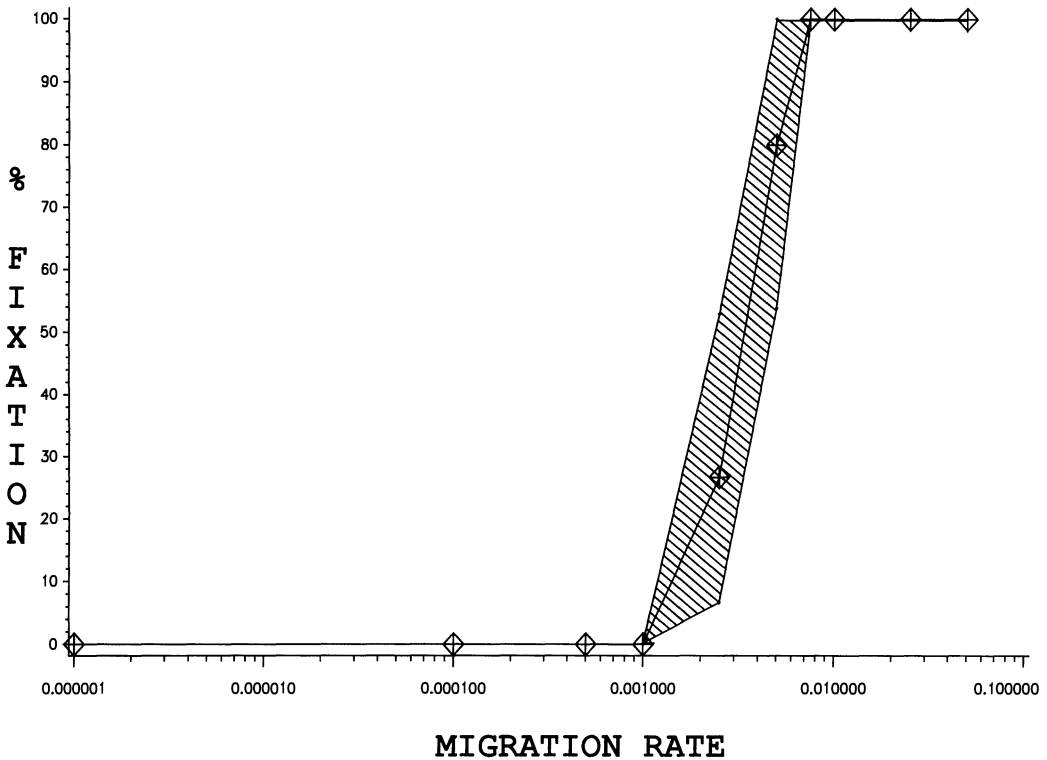


FIG. 3. The percentage of those populations with a deme shift that experienced a fixation of the highest fitness genotype throughout the entire population versus migration rate. Shaded areas are 95% confidence intervals.

affect fitness, population substructuring can increase the mean absolute fitness of a population. This occurs through the interaction of drift, selection, and migration. This study indicates that the migration rates between demes are important in determining genotype frequencies at fitness-related loci when epistasis is involved.

These simulations demonstrate that there is a nonzero optimum migration rate for the SBP. Although the optimum migration rate for the fixation of the highest fitness genotype is low ($m = 0.005$), extremely low rates of migration actually decrease the frequency of the highest fitness genotype. Below $m = 0.0001$, population-wide fixation of the highest fitness genotype declines to zero. An actual range of migration rates exists in which the shifting-balance process is relatively likely to change the genotype frequencies in the direction of increased absolute fitness. In the case of the system examined in these simulations, this range of migration rates does not extend to zero.

The shifting-balance process as envisioned by Wright is the result of three phases occurring

simultaneously within a deme-structured population. Migration rate influences all three of these phases. Because migration rate has opposing effects on drift and selective diffusion, there is a lower limit on the "benefit" of lowered migration rate on population fitness.

Several analytical investigations of the first two phases of the shifting-balance theory have been made (Lande 1985; Barton and Rouhani 1987; Rouhani and Barton 1987a,b; Charlesworth and Rouhani 1988). Recently Barton and Rouhani (1993) have also investigated the three phases combined. All of these studies have centered on a quantitative (i.e., continuously distributed) polygenic trait with optimizing selection. Our simulation did not use many loci each having equal (and additive) effects on the trait of interest, instead we used two loci to completely determine phenotype and fitness, and selection is necessarily directional.

In the case of a polygenic trait under stabilizing selection, we have a fitness difference between two phenotypic peaks of size H with all variation in the phenotype produced by the additive effects

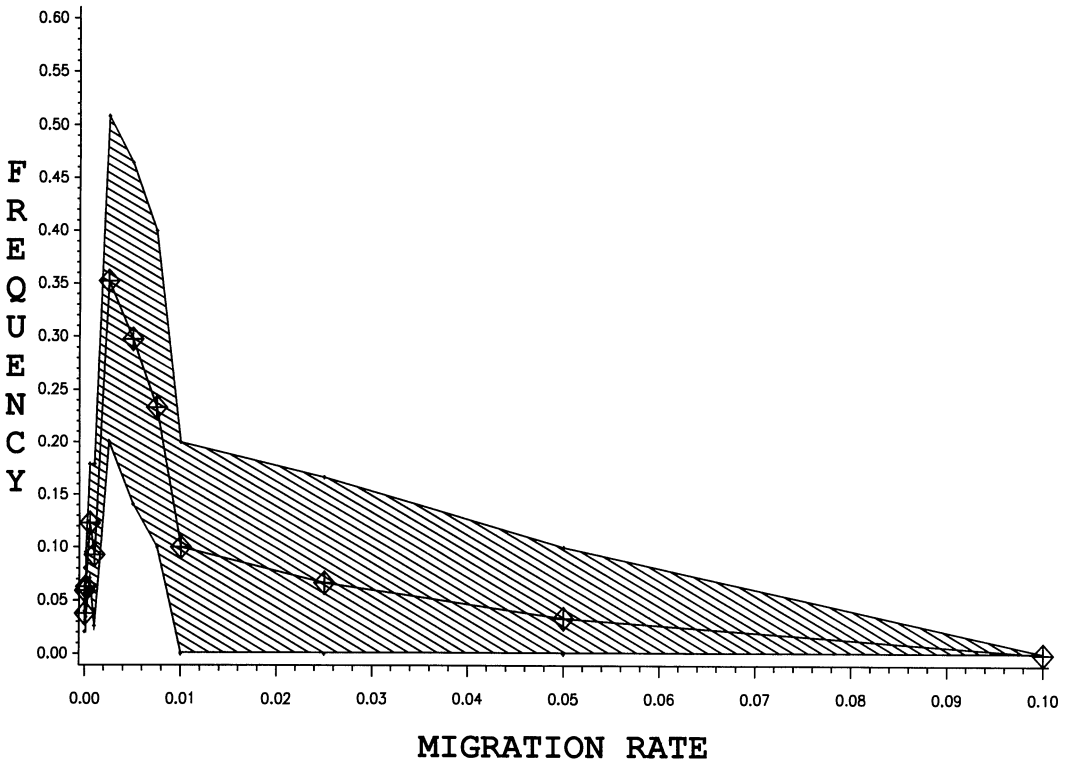


FIG. 4. Frequency of the highest fitness genotype versus migration rate. Shaded areas are 95% confidence intervals.

of many loci. As mentioned in the introduction, this sets up epistatic interaction among the “additive” loci when the population is near the optimum phenotype. The magnitude of the interaction between any two loci is extremely small and all such interactions are equal. This provides quite weak epistasis for fitness between loci and an astronomical number of approximately optimal combinations of allele frequencies for each of the phenotypic peaks. In the second case, with two loci determining phenotype and fitness, the same difference in fitness (H) between two optima is created by a two-locus, two-allele interaction. In this case, epistasis for fitness is quite strong, and there may be only one set of allelic frequencies that can produce the optimum mean fitness.

Despite these differences, the general conclusions are that peak shifts can occur and that the probability of a peak shift depends on the level of structuring in the population. This agrees with work on quantitative polygenic traits in continuous (Rouhani and Barton 1987a; Barton and Rouhani 1993), and discreet (Lande 1985; Bar-

ton and Rouhani 1987; Charlesworth and Rouhani 1988; Rouhani and Barton 1987a,b) populations. Barton and Rouhani (1993) analyzed all three phases of the SBP for both optimizing selection on an additive polygenic trait and selection against heterozygotes within a locus. They concluded from this that the SBP is likely to produce similar results without regard for the type of genetic system that produces an adaptive landscape. Our results support this conclusion by demonstrating that interlocus interactions between a discrete number of loci act similarly to their two models.

Phase III of the shifting-balance process has been far less analyzed than the processes underlying phases I and II. Crow et al. (1990) have demonstrated that under a relatively wide set of circumstances, phase III would be expected to proceed readily despite the barriers presented by hybrid breakdown. Their model starts with two demes at two different peaks and examines the effect of migration between the demes on the propensity of the low-peak deme to shift. They conclude that very little migration is necessary

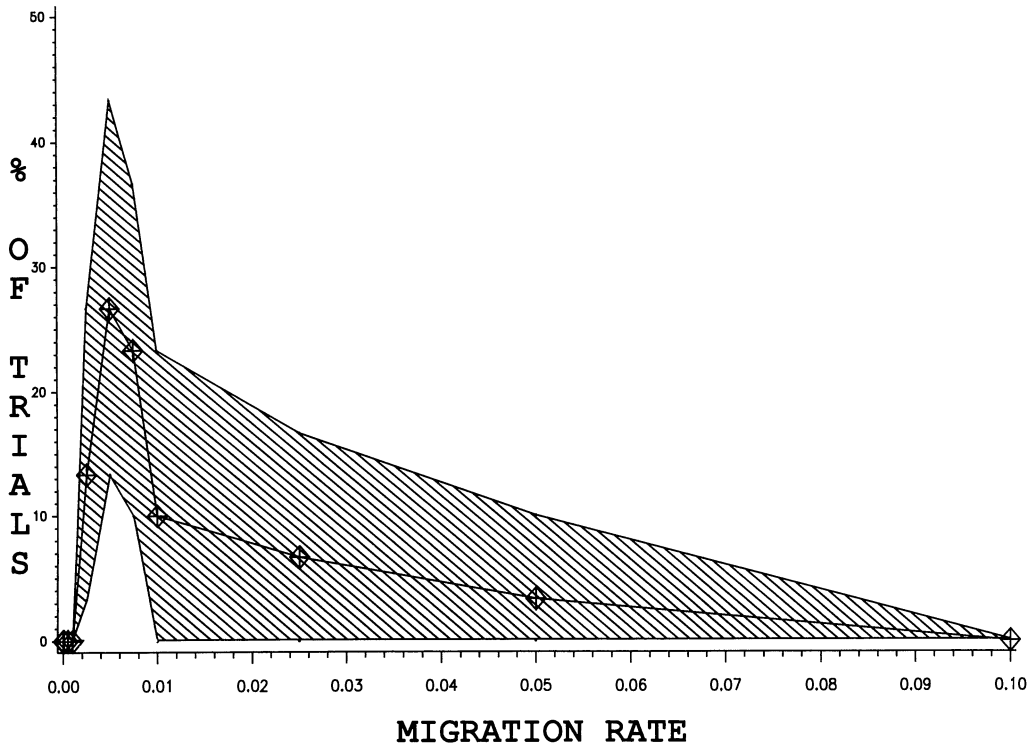


FIG. 5. The percentage of trials in which the highest fitness genotype was fixed throughout the population versus migration rate. Shaded areas are 95% confidence intervals.

to affect the phase III shift. They state that “whatever weaknesses it (SBP) may have are not in the third phase.” It should be noted that the strong influence of migration should prevent a deme from shifting to a higher peak when surrounding demes are all on the lower peak. The same sensitivity to migration that makes phase III pervasive over a wide range of migration rates restricts phase I to very low migration rates.

Although our model was restricted to the two-locus case, the genetic system used in our simulation was modeled after Crow et al. (1990). As in Crow et al. (1990), our study showed a wide range of migration values over which phase III was effective. All migration rates above 0.001 allowed phase III to occur. This means that in our simulations, phase III was frequently successful when m was two orders of magnitude less than s . This occurred despite the following ways in which our simulations differed from Crow et al.’s: (1) the number of demes involved, (2) the initial genotype frequencies, (3) the nature of differences in migrant numbers between demes, and (4) the inclusion of phases I and II.

Barton (1992) has recently presented an alternative interpretation of Crow et al.’s (1990) simulations. Barton points out that differential migration rates between two demes alone can allow the higher migration rate deme to overwhelm the lower migration rate deme’s genotype. Given sufficient differences in per capita migration rate, migration and not selective advantage will allow one deme to dominate. However, for two reasons our simulations favor Crow et al.’s interpretation that selection is an important factor. First, we generated all of our variation in genotype frequency and deme size while in the presence of migration. This implies that migration is not successfully swamping out all the effects of selection and drift. Second, because our model included no difference in per capita migration rate between demes, any deme with a novel genotype must have been exporting many fewer individuals than the combined total of all surrounding demes. In this case, only the relatively greater resistance of the higher fitness demes to invasion can explain the success of the third phase.

The Crow et al. (1990) model of selective dif-

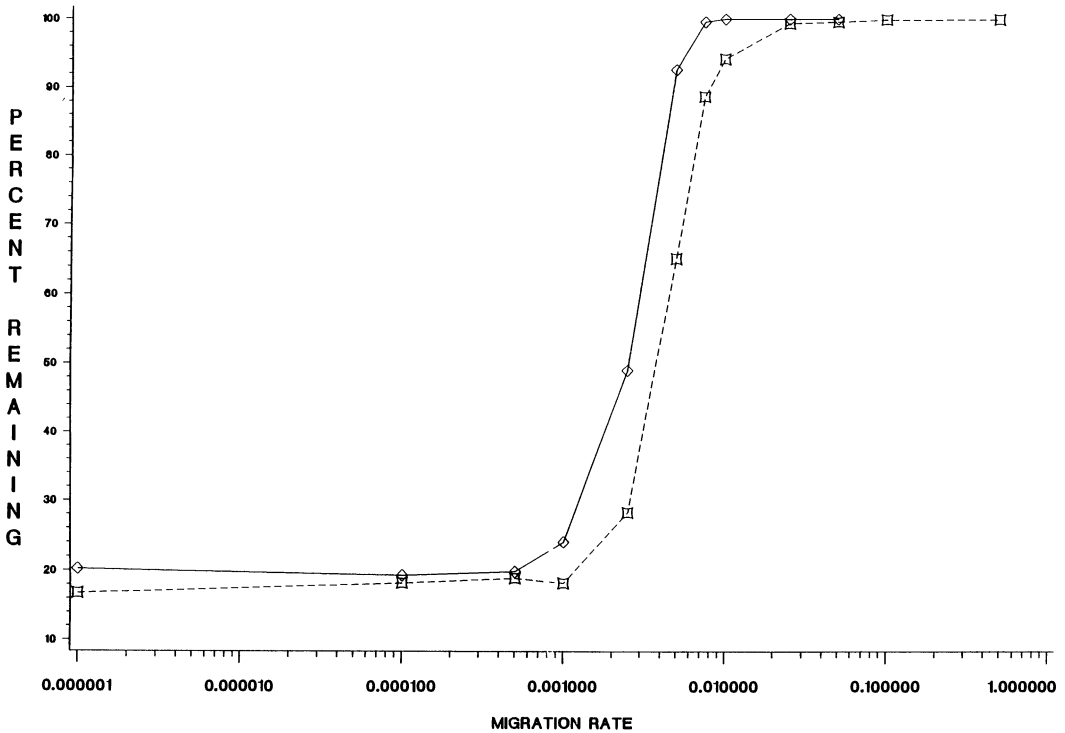


FIG. 6. Percentage of demes remaining after 12,000 generations versus migration rate for populations that have (diamonds) and have not (squares) had at least one deme that shifted peaks.

fusion between demes relies only on difference in migration rates between demes. Our model allows differential extinction and recolonization of demes as well. The ability of remaining demes to recolonize extinct demes should be more sensitive to migration rate than is the extinction rate of extant demes. This results from the probability of a colonization's dependence on two colonists (i.e., a function of m^2) of opposite sex arriving simultaneously. This will lead to the increasing loss of demes to extinction and a disproportionate decrease in the replacement of these demes by recolonization as m decreases. This pattern was born out in these simulations (see fig. 6). A decrease in the number of extant demes at low m will decrease the probability of a peak shift occurring at low migration rates. In addition, as demes go extinct they create holes that are barriers to the exchange of individuals between the remaining demes under isolation by distance or stepping-stone migration. For this reason, extremely low migration rates probably cause an escalating decrease in the efficacy of the shifting balance as a population persists for long periods without a peak shift.

The mean deme size for low peak demes was less than the mean size for high-peak demes. The extinction rate within populations that had high-peak demes was therefore less than the extinction rate for populations that had no high-peak demes. This allows differential extinction and colonization to become a potential force in the shifting balance process. The biggest differences in the extinction rate for shifted versus nonshifted demes seem to occur when m is less than 0.025 (see fig. 6). If different assumptions were made about recolonization, for example, if sets of migrants from a single deme colonized vacant sites, the role of differential recolonization as a cause of interdemic selection could be greatly enhanced. It must be emphasized that the effect of colonization and extinction on the differentiation or homogenization of demes may be quite specific to a given model of propagule movement and composition (Wade and McCauley 1988).

Periodic fluctuations in migration rate may increase the propensity for fixation of peak shifts throughout a population by decoupling phase III from phases I and II (e.g., Wright 1977, 473). Figure 6 demonstrates that there is a threshold

below which little or no effective export of high fitness genotypes might be expected. However, it is below this level of migration that one expects to have the highest frequency of demes that will shift. Occasional increases in migration rate could therefore rapidly spread peak shifts that are most likely to have occurred during low migration rate.

Biased migration, fluctuating migration rate, and an increase in the number of demes can all increase the likelihood of the SBP occurring. The model of migration that we have used has been based on equal per capita rates of migration for all demes. The range of migration rates conducive to the shifting-balance process should be expanded if migration rate fluctuates, is genotype-sensitive (e.g., m increases as deme productivity increases), triggered by extinction, or targeted towards demes with low population density.

The period of stasis between populationwide peak shifts may be affected by the number of demes available. Wright envisioned the SBP as being most likely to occur over tens of thousands of demes (M. J. Wade pers. comm. 1991). We have included only 100 demes in our simulations. Increasing the number of demes increases the probability of having at least one peak shift occur. This will increase the frequency of populationwide peak shifts at relatively high migration rates.

The generality of any model is limited by assumptions made in the name of tractability. Most of the assumptions made in this analysis were unfavorable for the SBP. Our results can therefore be expanded in that the efficacy of the SBP should be greater under less restrictive assumptions. We discussed above how some more favorable assumptions than those we made would improve the efficacy of the SBP relative to these results. It is more difficult to generalize across different adaptive landscapes (i.e., different genetic models). At present, it is impossible to investigate the entire range of possible types of gene interactions. This problem will not be overcome until we have a detailed understanding of what types of epistasis are common in the empirical world. Until such information is available, the generality of all models of the SBP will be restricted.

Despite these restrictions we have demonstrated that phases one, two, and three can occur together under one genetic model with very unfavorable population dynamic models. Because we used a genetic model similar to Crow et al.,

we can also predict that increasing the number of loci involved or decreasing the relative difference in peak heights (k) will increase the critical migration rate necessary for phase three (Crow et al. 1990), although we cannot predict the effect of these factors on phases I and II.

Dominance and the strength of selection should also affect the critical migration rate (Phillips 1993; Crow et al. 1990). In general, our model (dominant genotype favored) allows phase three to occur at lower critical migration rates than the reverse model (recessive genotype favored) (Phillips 1993). The effect of changes in dominance on phase one, however, may allow a greater effect of drift caused by the ability of the recessive alleles to persist in low-peak demes while being protected from selection in heterozygotes. This should increase the range of migration rates that allow peak shifts to occur, such that there may be an offsetting effect of dominance on phases one and three. The effect of changing selection strength on critical migration rates is dependent on the model of dominance used and the recombination rate (Crow et al. 1990).

In conclusion, a simulation relying on a strictly mechanistic model of two epistatic loci in a structured population of finite size demonstrates the efficacy of the shifting balance process. These simulations demonstrate that there is a fundamental conflict between the demands on population structure for success of the first verses the third phase of Wright's theory. The conflicting requirements of these two phases leave a window of migration rates that allows peak shifts to occur and subsequently spread in these simulations. Efficacy of the shifting-balance process can therefore be bounded by maximum and minimum migration rates.

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LITERATURE CITED

- Barker, J. S. F. 1979. Inter locus interactions: a review of experimental evidence. *Theoretical Population Biology* 16:323-346.
- Barton, N. H. 1992. On the spread of new gene combinations in the third phase of Wright's shifting-balance. *Evolution* 46:551-557.
- Barton, N. H., and S. Rouhani. 1987. The frequency of shifts between alternative equilibria. *Journal of Theoretical Biology* 125:397-418.
- . 1993. Adaptation and the "shifting balance." *Genetical Research* 61(1):57-74.
- Bowden, B. S. 1982. Temporal dynamics of microgeographic structure of genetic variation in *Microtus californicus*. *Journal of Mammalogy* 63:625-638.
- Buri, P. 1956. Gene frequency in small populations of mutant *Drosophila*. *Evolution* 10:367-402.
- Burton, R. S. 1990. Hybrid breakdown in physiological response: a mechanistic approach. *Evolution* 44:1806-1813.
- Charlesworth, B., and S. Rouhani. 1988. The probability of peak shifts in a founder population. II. An additive polygenic trait. *Evolution* 42:1129-1145.
- Crow, J. F., W. R. Engels, and C. Denniston. 1990. Phase three of Wright's shifting-balance theory. *Evolution* 44:233-247.
- Epling, C., H. Lewis, and F. M. Ball. 1960. The breeding group and seed storage: a study in population dynamics. *Evolution* 14:283-255.
- Falconer, D. S. 1981. An introduction to quantitative genetics. Longman Group, London.
- Goodnight, C. J. 1985. The influence of environmental variation on group and individual selection in a cress. *Evolution* 39:545-558.
- Hartl, D. L., and A. G. Clark. 1989. Principles of population genetics. Sinauer, Sunderland, Mass.
- Jinks, J. L. 1983. Biometrical genetics of heterosis. Pp. 1-46 in R. Frankel, ed. *Heterosis*. Springer, Berlin.
- Kacser, H., and J. A. Burns. 1981. The molecular basis of dominance. *Genetics* 97:639-666.
- Kerr, W. E., and S. Wright. 1954. Experimental studies in very small populations of *Drosophila melanogaster*: I. Forked. *Evolution* 8:172-177.
- Lande, R. 1985. Expected time for random genetic drift of a population between stable phenotypic states. *Proceedings of the National Academy of Sciences, USA* 82:7641-7645.
- McCauley, D. E., and M. J. Wade. 1980. Group selection: the genetic and demographic basis for phenotypic differentiation of small populations of *Tribolium castaneum*. *Evolution* 34:813-821.
- Phillips, P. C. 1993. Peak shifts and polymorphism during phase three of Wright's shifting-balance process. *Evolution* 47:1733-1743.
- Provine, W. B. 1986. Sewall Wright and evolutionary biology. University of Chicago Press, Chicago.
- Rouhani, S., and N. Barton. 1987a. Speciation and the "shifting balance" in a continuous population. *Theoretical Population Biology* 31:465-492.
- . 1987b. The probability of peak shifts in a founder population. *Journal of Theoretical Biology* 126:51-62.
- Verhulst, P. F. 1938. Notice sur la loi que la population suit dans son accroissement. *Correspondence Mathématique et Physique* 10:113-121. Reprinted in E. J. Kormandy, ed. 1965. *Readings in ecology*. Prentice-Hall, Englewood Cliffs, N.J.
- Wade, M. J. 1977. An experimental study of group selection. *Evolution* 31:134-153.
- . 1985. The effects of genotypic interactions on evolution in structured populations. *Proceedings of the XV International Congress of Genetics* 15: 283-290. Oxford & IBH, New Delhi.
- Wade, M. J., and C. J. Goodnight. 1991. Wright's shifting balance theory: an experimental study. *Science* 253:1015-1018.
- Wade, M. J., and D. E. McCauley. 1980. Group selection and genotypic differentiation of small populations. *Evolution* 34:799-812.
- . 1984. Group selection: the interaction of local deme size and migration in the differentiation of small populations. *Evolution* 38:1047-1058.
- . 1988. Extinction and colonization: their effects on the genetic differentiation of local populations. *Evolution* 42:995-1005.
- Weir, B. 1990. Genetic data analysis. Sinauer, Sunderland, Mass.
- Wright, S. 1931. Evolution in Mendelian populations. *Genetics* 16:97-159.
- . 1977. *Evolution and the genetics of populations*, vol. 3. University of Chicago Press, Chicago.
- . 1978. The relation of livestock breeding to theories of evolution. *Journal of Animal Science* 46:1192-1200.
- . 1982. Character change, speciation, and the higher taxa. *Evolution* 36:427-443.

Corresponding Editor: B. Walsh