

## Age-Specific Selection\*

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**Abstract.** A model is presented for age-specific selection on the genotypes in a population. Each genotype is assigned a life table that specifies the viability and fecundity of its age classes. Breeding and reproduction occur at regular intervals, and generations overlap. Examples were generated on a digital computer. Gene frequencies and the distribution of individuals among the various age classes may oscillate until equilibrium is reached. Moreover, age structure and gene frequencies are intimately related; a change in either factor alone may bring about a change in the other. In an extension of the basic model, the fecundities of the genotypes were regulated by population density. Under the joint action of logistic control and age-specific selection, the growth curve of the population can, for some schedules of selection, show plateaus in an otherwise sigmoid increase. The relevance of the growth patterns obtained in different types of environments to current ideas of "r" and "K" selection is discussed.

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**Introduction.** Geneticists and ecologists have, until quite recently, tended to view the structure of populations in different ways. Gene frequencies and the forces which bring about changes in them are of primary concern to the geneticist, while the factors determining population size, density, and age structure are of particular importance to the ecologist. It is the purpose of this article to present two simple models for natural selection in which the viability and fecundity of each genotype may differ from one age to another. We shall show that gene frequencies, population size, and age structure are intimately related and together determine the behavior of a population under selection.

Gene frequencies change under natural selection because the various genotypes in a population leave different numbers of offspring. Each genotype is usually assigned a *selective value* that measures this success in transmitting genes to the next generation. Within each genotype, however, are individuals of different age, and the intensity of selection clearly depends on age.<sup>1,2</sup> This complication of selection that varies with age has been neglected in the models of population biology. The only exceptions we have found are the early works of Haldane<sup>3</sup> and of Norton,<sup>4</sup> whose intent was quite different from our own, and a very recent model by Istock.<sup>5</sup>

**A Simple Model.** Consider a population composed of the genotypes for two alleles at a single autosomal locus. The individuals of each genotype are divided into classes on the basis of age. Each genotype is assigned a schedule of births and deaths at each age. Reproduction occurs at regular intervals, and time is

measured in terms of these *breeding intervals*. The viabilities and fecundities are assumed to be alike in males and females. The population size is assumed to be large enough that the effects of sampling error may be ignored. Since organisms may live for a number of time intervals, the model is one of discrete breeding intervals and of overlapping generations. This model fits the breeding regime of many organisms, and by varying the length of the breeding intervals, it can be made to fit virtually all bisexual, diploid organisms. As the time intervals are made shorter, the model becomes in the limit one of continuous change where the viabilities and fecundities are continuous functions of time. As the time intervals are made longer, the model approaches one in which there is a single age class in each genotype and discrete generations.

The action of selection may be visualized as a simple matrix operation by following Leslie's<sup>6,7</sup> approach to population growth. For each genotype there is a "selection matrix" which contains the age-specific fecundities along the top row and the age-specific viabilities along the first subdiagonal. Multiplying this selection matrix by a column vector whose elements are the numbers of individuals in each age class for the genotype under consideration, we obtain a vector of individuals that will begin the next breeding interval. Let the viability of the genotype carrying alleles *I* and *J* in age class *L* be  $V_{IJL}$  and the corresponding fecundity,  $F_{IJL}$ . Let the number of individuals of this genotype of age *L* at the beginning of breeding interval *T* be  $N_{IJLT}$ . Denote the progeny of genotype *IJ* as  $PIJ_T$ . All individuals of age 1 or older at time  $T + 1$  must have advanced from the next lower age within the same genotype at the previous breeding interval, after the selection through mortality. Within each breeding interval we assume that mating is completely random. It is as if each adult sheds gametes according to its genotype and age-specific fecundity, and the new organisms are formed by random combination of pairs of gametes. The progeny generated in breeding interval *T* will be the individuals of age 0 at time  $T + 1$ . The progeny of a genotype are not necessarily of the same genotype; the alleles carried by a zygote depend on the genotypes of both parents. The progeny are reassorted to their proper genotypes according to the frequencies expected with Mendelian segregation under random mating. The model is diagrammed in Figure 1 for a genotype with four age classes. This process is repeated for each breeding inter-

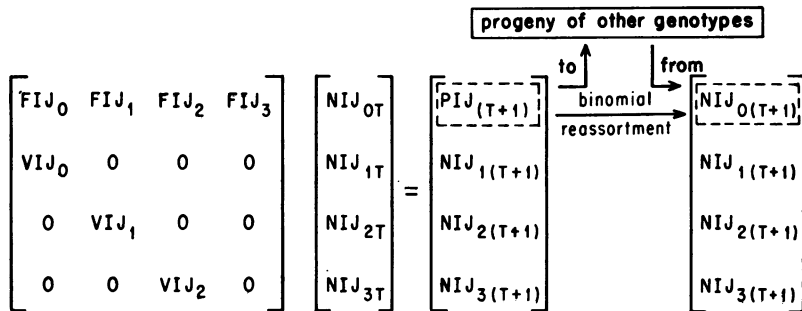


FIG. 1.—The basic model for age-specific selection. See text for explanation of symbols.

val. Since in the simple model the fitness components are constant and not functions of population number, the population must grow indefinitely large or diminish to extinction according to the fecundities and viabilities. This first model is thus one of exponential growth.

**An Illustration of the Basic Model.** We have investigated the behavior of populations fitting this model on a digital computer. An example is presented in Figure 2, showing the behavior of a population over 25 breeding intervals. The viabilities are alike for all genotypes and decrease by half with each age; hence

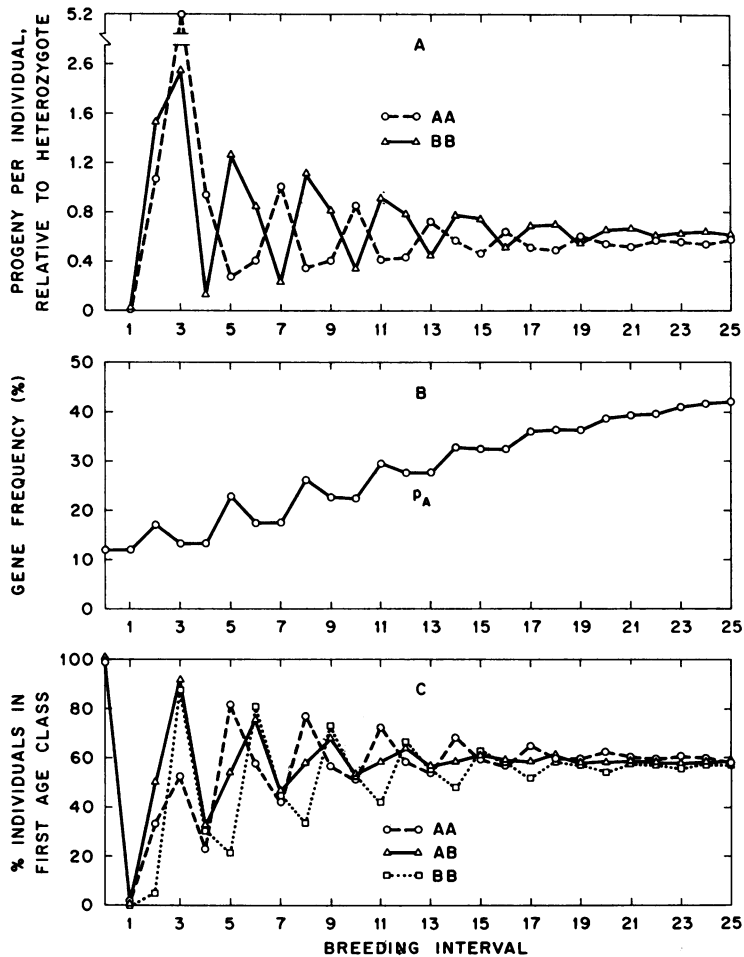


FIG. 2.—An example of age-specific selection under exponential population growth.

*Panel A:* Numbers of progeny per individual for the two homozygotes, relative to the heterozygote.

*Panel B:* Frequency of allele A.

*Panel C:* The age structure as reflected in the percentage of individuals in the first age class.

Selection parameters for this example: (1) Identical viabilities for the genotypes over the five age classes:  $V_{AA} = V_{AB} = V_{BB} = 0.5, 0.5, 0.5, 0.5, 0.0$ ; (2) Fecundity schedules:  $AA = BB = 0, 0, 4, 2, 1$ , and  $AB = 0, 1, 5, 2, 1$ ; (3) Initial number of individuals, all in the first age class:  $N_{AA} = N_{AB} = 2, N_{BB} = 21$ .

the survivorship curve is diagonal. The heterozygote has a fecundity advantage. The initial frequency of allele *A* is 0.12, and the population was begun with all individuals in the first age class. Geneticists usually define selective value as the number of progeny per individual, and so we have plotted this "apparent selective value" in *panel A*. Since only fecundity differed among the genotypes, the number of progeny is in this case an accurate index of selective value; if deaths had occurred at different rates among the genotypes, births alone would not be sufficient to measure selective value.<sup>8</sup> The number of progeny is given relative to that of the heterozygotes. The apparent selective values fluctuated widely for about 15 breeding intervals before stability was reached. In the example both homozygotes had the same viability and fecundity at each age, so the difference in the number of offspring is clearly related to the changing age structure. The frequency of allele *A* (*panel B*) showed an increase toward an equilibrium at 0.5, with an erratic fluctuation which damped slowly. The over-all course of gene frequency is almost linear and clearly departs from the almost-sigmoid curves obtained with age-free models. As an index of age structure, we have plotted (*panel C*) the percentage of individuals in the first age class. Since this age group receives individuals by birth from the other age classes, it is a sensitive measure of changes in the age structure. The age structure fluctuated widely for about 15 breeding intervals, and then displayed a damped approach to stability.

In examples (not shown) where the age distribution has reached equilibrium and the gene frequency is then changed, large disturbances in the age structure occur as the gene frequency returns to equilibrium. The two most important components of our models, the age structures and the life history schedules of selection for the genotypes, interact to determine the approach of the population to its equilibrium structure. The sorts of changes observed under this model of constant selection might well lead an observer to invoke variation in the environment or disturbances within the genome to account for fluctuations in gene frequency or age structure. Yet these phenomena are natural consequences of a more realistic model, and give us some feeling for the sort of changes that may occur in nature. A change in the age structure alone is sufficient to produce changes in gene frequency, and conversely, a change in gene frequency alone is sufficient to produce large disturbances in age structure.

**A Logistic Growth Model.** The model presented earlier has one major drawback when applied to most populations; it is a model for exponential growth. To remove this unreal assumption, a second model was devised incorporating one kind of logistic control in which reproduction is decreased as the numbers of any genotype approach the carrying capacity of the environment. Assume that each individual in the population utilizes the same quantity of environmental resources, but that each genotype may have a different carrying capacity, *KIJ*. Then, the progeny generated by the *M* age classes of the *NIJ* individuals is given by

$$PIJ_{(T+1)} = \sum_{L=1}^M NIJ_{LT} \cdot FIJ_L \left[ \frac{KIJ - NTOTAL}{KIJ} \right].$$

These progeny are reassorted to the different genotypes with the binomial Mendelian operator used in the exponential model. The bracketed feedback term in the above expression is limited to an arbitrary minimum value of 0.01 to prevent the generation of negative progeny if  $KIJ$  is less than  $NTOTAL$ , the total number of individuals in the population, and also to permit some reproduction at equilibrium.

The standard logistic model assumes equivalence of all individuals in the population. However, this assumption is not valid if the population is composed of genotypes with different viabilities and fecundities or of individuals of different ages. This complication has been considered by Anderson<sup>9</sup> for a population with discrete, nonoverlapping generations, where all members of the population at any time are in the same age class. We have generalized and extended this type of analysis in the present paper by the age-specific scaling of viability and reproduction for each genotype under a model with overlapping generations.

**An Illustration of the Logistic Model.** Most studies of population growth are made under the implicit assumption of no selection acting within the population. When this assumption is not valid, a large error can result, as indicated in Figure 3. The values plotted in this figure are for the logistic model when all three genotypes have identical diagonal survivorship curves, but one homozygote,  $AA$ , has an advantage in both fecundity and numbers at the start of the population growth. Counterbalancing these advantages, the  $AB$  and  $BB$  genotypes have successively higher values of  $K$  so that  $KAA < KAB < KBB$ . In *panel A*, the growth of the entire population ( $NTOTAL$ ) is initially quite rapid. If an

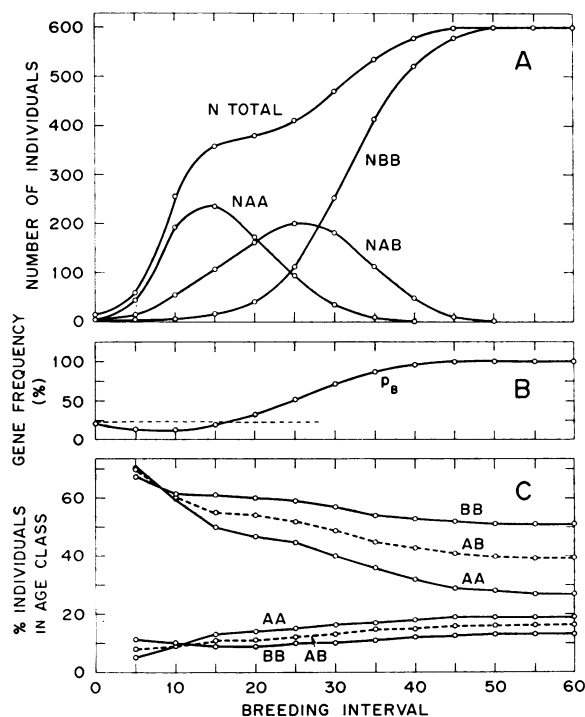


FIG. 3.—An example of age-specific selection under logistic population growth.

*Panel A:* Changes in total number of individuals and numbers of the genotypes.

*Panel B:* Change in the frequency of allele  $B$ ; the dashed line indicates the initial frequency.

*Panel C:* The age structure as reflected by the percentage of individuals in the first (*top*) and third (*bottom*) age classes.

Selection parameters for these curves are: (1) Identical viabilities for each genotype over the five age classes:  $VAA = VAB = VBB = 0.5, 0.5, 0.5, 0.5, 0.0$  (2) Fecundity schedules:  $AA = 0, 3, 5, 2, 1$ ;  $AB = BB = 0, 2, 5, 2, 1$ . (3) Carrying capacities:  $KAA = 500$ ;  $KAB = 750$ ;  $KBB = 1000$ . (4) Initial numbers of individuals, all in the first age class:  $NAA = 9$ ;  $NAB = 3$ ;  $NBB = 1$ .

investigator had no knowledge of the genetic structure, it might be concluded that by the 15th breeding interval the population was approaching an equilibrium population size of about 375 individuals. Subsequently, however, the population increases in size and reaches its true equilibrium level of about 600 individuals in the 50th breeding interval. Again, if observed in nature, it would probably be concluded that the "hump" in the growth curve was caused by an environmental change affecting the carrying capacity for the entire population. However, given a knowledge of the genetic structure of the population, it is apparent that the action of natural selection produces the hump. That is, the *AA* genotype is replaced by the heterozygote which, in turn, is replaced by the *BB* homozygote.

There are four major variables that determine the shape of a population growth curve under logistic control. In Figure 3, the rapid initial growth of the *AA* homozygote is a result of its combined advantages in initial numbers and high fecundity when *NTOTAL* is small. With the model for exponential growth presented earlier, the *AA* genotype would rapidly constitute the majority of the individuals and it would remain the most frequent genotype. Under logistic control however, as the population grows the relatively low *KAA* value chokes the growth of this homozygote while the total population size still permits the *AB* and *BB* genotypes, with their higher *K* values, to increase in number. In the present example, the logistic control acts exclusively on fecundity and, since all genotypes have the same viabilities, the shape of the growth curve is primarily determined by the fecundities, initial numbers, and values of *K*.

The equilibrium number, about 600 individuals of genotype *BB*, differs from *KBB* (1000 individuals) because reproduction and viability are independent in this model. That is, only reproduction is controlled by the  $[(KIJ-NTOTAL)/KIJ]$  term. Death rates are considered to be independent of population size and related only to the viabilities specified at the beginning of a run.

*Panel B* of Figure 3 presents the change in the frequency of the *B* allele under this logistic selection. The initial advantage of the *AA* homozygote is reflected in a decrease in the frequency of the *B* allele for the first 15 breeding intervals. Subsequently, the *B* allele increases in frequency until apparent fixation in the 50th breeding interval.

After an initial oscillation similar to that discussed in connection with the exponential model, the age distribution of individuals in each genotype approaches stability (*panel C*). The frequencies of the individuals undergoing selection in each age class and genotype are in the expected orders. That is, a genotype being adversely affected by natural selection is expected to have a lower frequency of young individuals and a higher frequency of old individuals than a genotype with a selective advantage. All three genotypes have approximately the same proportion of individuals in the second age class. The age distributions presented for the *AA* and *AB* genotypes become progressively less meaningful as the *A* allele is eliminated from the population. The point in carrying out this calculation to the 60th breeding interval is to demonstrate that the elimination proceeds without a gross disruption of the age distribution of the eliminated genotypes.

Of considerable interest in population biology is the nature of  $r$  and  $K$  selection.  $r$  selection acts in a relatively unrestricted environment by favoring those phenotypes with high fecundity and prereproductive viability. In contrast,  $K$  selection acts in limited environments to favor phenotypes that can tolerate high population densities without severe loss of their reproductive potential. The  $AA$  homozygote in the example shown in Figure 3 displays a rapid initial increase in numbers. But, as population size increases, the fecundity advantage of this genotype is lost, and it is rapidly eliminated by the  $BB$  homozygote, which has an advantage under  $K$  selection. However, if in the example shown in Figure 3 the environment cycles with a periodicity of no more than 15 breeding intervals and each genotype is reduced in size in proportion to its numbers at the end of each cycle, the genotypes with an advantage under  $K$  selection will become less and less frequent until they are eliminated from the population. Clearly, different population structures may be produced by extreme  $r$  or extreme  $K$  selection. However, every genotype has both  $r$  and  $K$  characteristics to varying degrees, and the interaction of the two kinds of selection determines the population structure during the approach to equilibrium.

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<sup>1</sup> Dobzhansky, Th., R. C. Lewontin, and O. Pavlovsky, *Heredity*, 19, 597.

<sup>2</sup> Ohba, S., *Heredity*, 22, 169 (1967).

<sup>3</sup> Haldane, J. B. S., *Proc. Cambridge Phil. Soc.*, 23, 607 (1927).

<sup>4</sup> Norton, H. T. J., *Proc. London Math. Soc.*, 28, 1 (1928).

<sup>5</sup> Istock, C. A., *Behav. Sci.*, 15, 101 (1970). His model differs from ours in that it does not consider distinct genotypes or the approach to equilibrium, but looks at the consequences of age-specific selection on the population as a whole.

In addition, Drs. B. Charlesworth and J. T. Geisel have informed us that they are also studying the problem of age-specific selection, although from a somewhat different viewpoint.

<sup>6</sup> Leslie, P. H., *Biometrika*, 33, 183 (1945).

<sup>7</sup> Leslie, P. H., *Biometrika*, 35, 213 (1948).

<sup>8</sup> We have incorporated methods of calculating reproductive values, intrinsic rates of increase, and generation times for the individual genotypes in our computer program. Unfortunately, there are difficulties in defining these quantities for populations whose age structures are not stable. We defer consideration of these matters.

<sup>9</sup> Anderson, W., manuscript in preparation.