

CONSERVATION BIOLOGY

An Evolutionary–Ecological Perspective

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EVOLUTIONARY CHANGE IN SMALL POPULATIONS

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The arguments in favor of conservation have usually been based on ecological, economic or even ethical grounds. There are, however, important genetic considerations. Any strategy for the conservation of a particular species should, in part, be determined by knowledge (or inference) about the genetic structure of that species. The most stringent requirements arise when we consider the future needs of plant and animal breeders. If we are to feed the human species and its domesticates, it is necessary that a diversity of species be maintained—each in sufficient numbers to assure that genetic variability is adequate for continuing selection. It is not easy to predict man's future needs in this area. There are many plants which have not been evaluated as sources of oil, food and fiber, and the possibility of using single cell cultures, including the tissue culture of animal cells, has only barely been examined. Nevertheless, seed banks have been established (Harlan, 1975) and there is limited storage for the semen of some domesticated animals, but these efforts are just a beginning. We have already lost potentially valuable commercial strains of plant and animal species; the wild relatives of cultivars, which are a source of disease resistance and other useful genetic variation, are in peril.

Important as these issues are, I do not wish to dwell on them, but rather to concentrate on the effect of small population size on evolutionary change and survival. The case for preservation of genetic resources has been presented in detail before (Frankel, 1974).

We have already seen (Chapter 6) that endangered species can be maintained in parks and wildlife sanctuaries in limited numbers, and that restriction of population size has in itself a number of genetic consequences. Perhaps the most important of these, certainly in the short-term, is inbreeding depression, which for many species places an immedi-

ate lower bound on the population size which is compatible with survival. However, even in a population which is large enough to escape serious inbreeding, there may be a gradual loss of genetic variability which limits future evolutionary change. I suggest in this chapter that in random mating populations, such as are found in most mammals and birds, inbreeding considerations alone require that population numbers should be not less than fifty individuals. In the long-term, genetic variability will be maintained only if population sizes are an order of magnitude higher. The latter argument is based on the assumption that: (1) continued, and often rapid, evolutionary change is necessary for survival and (2) response to natural selection is limited by small population size.

Before developing this argument in detail, we should ask if evolutionary change is what we want. Do we wish to conserve the elephant, or ensure the survival of its elephant-like descendants? This is an important issue. If we are concerned with preserving the precise phenotype of a species, rather than a phylogenetic line in which we allow continued evolutionary change, our strategies will be very different. In captive propagated populations, it is possible to maximize evolutionary change, and in some circumstances to almost halt it entirely.

In the following discussion, I will be concerned largely with random mating populations, and with phyletic evolution entirely. Speciation is discussed in Chapter 9.

ADAPTATION

Adaptation and Extinction

The historical record shows many examples of episodic extinction and rapid evolutionary change, the most recent of which began in the late Pleistocene with the disappearance of many species of large mammals. There is a controversy over the cause of the Pleistocene extinctions; some attribute them to climatic change, others to the rise of the ecological dominance of man (Chapter 16). There is no doubt, however, about the cause of the current crisis. In addition to direct competition and predation by man, there has been a massive shuffling of the world's biota. In Australia, for example, introduced placental mammals, ornamental plants and pasture species are in direct competition with the native flora and fauna. On top of all this, we have the well documented large-scale habitat destruction (see other chapters).

In response to all of this ecological disruption, we expect, and have already seen, a great burst of evolutionary change. In a matter of years, we have observed the emergence of industrial melanism, insects which are resistant to insecticides, rabbits immune to myxomatosis and grasses which can grow on the tailings of lead and copper mines. Some species will adapt readily to their new environments; others, for reasons which are largely unknown, will not and face extinction. The immediate cause of

extinction may be a capricious event, such as fire or an epidemic, but a species which is vulnerable to these chance events is likely to be so because it has, in the past, adapted less well than its competitors to a changing environment. Ultimately, a population disappears if it cannot keep up with its physical or biotic environment. Adaptation is a crucial concept in any understanding of population survival.

Adaptation and Natural Selection

Adaptation, the acquisition or modification of traits which 'fit' the organism more perfectly to its environment, is a process known only by inference. The products of adaptation (for example, the structure of teeth for grazing or browsing, protective coloration and mimicry, migratory and territorial behavior, pollination and seed dispersal mechanisms) are recognized from the relationship between structure and function. Rarely, however, do we understand adaptation in terms of changes in gene frequency, since in general we are a long way from translating physiology and behavior into instantaneous birth and death rates for known genotypes.

Notwithstanding our ignorance, it is likely that the most important adaptive traits are continuously varying (quantitative) characteristics. Since adaptation is the result of natural selection (although not all natural selection is adaptive) we can draw on considerable experience with selection in laboratory and domesticated animals to make some inferences about population size and evolutionary change.

We can distinguish between three modes of selection for quantitative traits. These are: (a) stabilizing selection, or selection against extreme values; (b) directional selection, in which one extreme is at an advantage; and (c) disruptive selection, or selection for extreme values, and against intermediates.

There is no doubt that stabilizing selection is the predominant mode of selection in natural populations. For many traits the greatest fitness, as measured by survival or number of offspring, has been found to be very near the mean for the population. Examples are shell size in snails (Weldon, 1901), size of duck eggs (Rendel, 1943), clutch size in swifts (Lack, 1954) and adult height and birth weight in man (Cavalli-Sforza and Bodmer, 1971). Conversely, directional selection, while common in animal or plant breeding, is probably rare in nature. It is thought that the best adapted individuals "exhibit a harmonious combination of all characters" (Lerner, 1954), so that extreme individuals, which may be "fit" for one trait, will be unbalanced with respect to others. Consequently, fitness often declines under directional selection for a single trait.

The third mode, disruptive selection, is not well understood; its importance in natural populations is controversial. It is, perhaps, operative in patchy environments and may play a role in speciation.

Natural selection, then, appears to be a complex process in which a slowly changing species accompanies a slowly moving niche, "always slightly behind, slightly ill-adapted, eventually becoming extinct as it fails to keep up with the changing environment because it runs out of genetic variation on which natural selection can operate," (Lewontin, 1978). For any trait changing under selection, the rate of response is a function of the selection intensity and the heritability of the trait. Both of these quantities are affected by genetic drift. It is well known that populations which have been through a bottleneck or which have been maintained at a small population size do not show as great a response to artificial selection as do large populations.

GENETIC DRIFT AND EFFECTIVE POPULATION SIZE

In a finite population, the array of genotypes in any generation is formed by sampling gametes from the previous generation; virtually all of the genetic effects which arise in small populations are an unrepresentative consequence of sampling, a process known as genetic drift. In small populations, gene frequencies change from generation to generation, even in the absence of selection, mutation or migration. These random changes lead to a gradual increase in homozygosity, and, if they go unchecked, will ultimately lead to fixation at all loci and hence a complete loss of genetic variability. At the level of the phenotype, we can commonly observe three effects of genetic drift: (a) inbreeding depression, due either to loss of heterozygosity or to fixation of deleterious genes; (b) random change in the phenotype, especially changes in the means of quantitative characters; and (c) a decrease in genetic variance (and hence a lowering in heritability).

For a given population size, the rate of genetic drift varies depending on the mating structure and the distribution of offspring number (Chapter 12), so the theoretical consequences of drift are usually calculated for an idealized population in which each individual contributes gametes equally to a pool from which the next generation is formed.

Any population of N individuals will have a sampling variance in gene frequency which is equivalent to the sampling variance of an ideal population of N_e individuals. N_e is then the effective population size (more strictly called the variance effective number) of the population whose census number is N . This is an important concept. In much of the following discussion concerning inbreeding depression or loss of genetic variance the population size will be the effective rather than the census number.

Kimura and Crow (1963) present a comprehensive account of this the-

ory, but we can illustrate the relationship between actual and effective population number with a few important examples.

1. *The effect of variance in progeny number.* Let the variance in progeny number be σ^2 , and the census number N . Then

$$N_e = \frac{4N}{2 + \sigma^2}, \text{ approximately.}$$

Suppose, for example, that the mean family size is two, and the variance is four. Then $N_e = 2/3 N$. On the other hand if every mating pair contributes exactly two offspring to the next generation, that is, there is no variation in family size, then $N_e = 2N$. Effective number is decreased by increased variation in progeny number and, conversely, N_e is maximized when all families contribute equally to the next generation. Crow and Morton (1955) calculated from observed distributions of progeny number in a variety of species that the effective size ranged from 0.6 to 0.85 of the census number.

2. *Unequal numbers of the two sexes.* Whenever the numbers of each sex contributing to the next generation are not equal,

$$N_e = 1 / \left(\frac{1}{4N_m} + \frac{1}{4N_f} \right), \quad (1)$$

where N_m and N_f are the number of males and females respectively. This is particularly important in species which maintain stable harems (for example, elephant, seals, zebras, vicunas, and some bats). A breeding population in which there are 90 effective females but only 10 effective males has a total effective size of 36, not 100.

3. *Fluctuation in population size.* If population size varies from generation to generation, the effective number is the harmonic mean:

$$\frac{1}{N_e} = \frac{1}{t} \left(\frac{1}{N_1} + \frac{1}{N_2} + \dots + \frac{1}{N_t} \right), \quad (2)$$

where N_t is the effective size at the t^{th} generation. Suppose, for example, that a population which normally maintains an effective size of 1000 drops for one generation to 50. Then, over a ten generation interval,

$$N_e = 10 / \left(\frac{1}{50} + \frac{9}{1000} \right) = 345. \quad (3)$$

A rare crash in size, as frequently occurs through drought or disease, clearly has an important effect on effective number.

This treatment of effective size assumes that each individual mates essentially at random with the other members of the group. Such an assumption may be appropriate for some highly vagile animal species, but

is inadequate for many plants and many nonflying animals. In these latter species, inbreeding is very common; often a population is sharply subdivided into many smaller interbreeding groups. When the degree of relationship between mates is a function of geographical separation, a netical analysis of population structure is much more complicated.

SHORT-TERM EFFECTS: INBREEDING DEPRESSION

This subject is covered in some detail in Chapters 9 and 12, and will only be briefly discussed here. Empirically, it is clear that species differ markedly in their resistance to inbreeding depression. There are numerous plants which reproduce naturally by self-fertilization. Of all terrestrial animal species, mammals and birds are probably the most sensitive, perhaps because of their low inherent reproductive rates. In the latter species inbreeding depression is the most important consequence of reduced population size.

The degree of inbreeding in a population is measured by the inbreeding coefficient, f ; if the effective size is N_e , f increases by $1/2N_e$ per generation. In small populations, therefore, inbreeding depression accumulates gradually over many generations. A single instance of close inbreeding through, for example, the founding of a population with a small number of individuals, does not necessarily mean that the descendants will be highly inbred. Immigration of unrelated individuals into an inbred population reduces the level of inbreeding dramatically.

Inbreeding has deleterious effects on survival and reproduction, and affects such characters as growth rate and adult size. For many traits inbreeding depression, as a proportion of the mean, is of the order of one third of the inbreeding coefficient, and perhaps twice as great for fecundity. Overall, the effect of inbreeding on fitness is probably much greater than this. Latter and Robertson (1962) estimated that the effect in *Drosophila* of inbreeding on a competitive index (which for this purpose we will equate to fitness) was $e^{-2.7f}$. That is, for a small f , the reduction in fitness is 2.7 times the inbreeding coefficient. Sved and Ayala (1970) showed that homozygosity in *Drosophila pseudoobscura* for one of the autosomes representing about one fifth of the genome, reduced fitness by about 20 percent. Despite these deleterious effects, a small amount of inbreeding can be tolerated. Animal breeders accept inbreeding coefficients as high as a one percent increase per generation (that is, $N_e = 50$) in domestic animals without great concern. Natural selection will, of course, tend to counter the immediate deleterious effects of genetic drift. There will be a minimum population size, depending on the species, at which the population will be able to cope with the inbreeding effects, albeit with some cost in survival and reproductive rate. In the absence of regular introduction of unrelated stock, I suggest an effective size of at least 50 for large mammals.

Finally, it is important to emphasize that inbreeding accumulates at a rate which is directly related to the generation interval. A population of 50 randomly breeding elephants will take several hundred years to reach a ten percent level of inbreeding; mice will attain this figure in less than ten years.

LONG-TERM EFFECTS

Even in populations which are unaffected by inbreeding depression, sampling effects cause fluctuations in gene frequency which have important consequences for the future evolution of the species. Some genes will be lost by chance, especially those which are initially rare in the population, and alleles which are maintained by selection at some intermediate frequency will drift away from their equilibrium value. The theory of selection in finite populations is very complicated; the outcome depends very much on assumptions about the mode of natural selection.

At the phenotypic level, we observe changes in the frequency of simply inherited characteristics, and for quantitative traits, drift in the mean and, most often, a reduction in genetic variance. These last two effects will be discussed in detail, but it is the loss of genetic variation which, I believe, is of critical importance.

Random Changes in the Phenotype

Aside from the general effects in inbreeding depression, changes in phenotype are obvious in inbred lines of laboratory animals. Wright (1977a), for example, recounts his early experience with inbred lines of guinea pigs, each of which could be recognized as a result of changes in morphology, physiology, color pattern and temperament. In his general view of the evolutionary process, Wright attaches great importance to changes in the mean of small populations, for it is only through genetic drift that new adaptive combinations of traits are created. Hence, Wright suggests, the splitting of species into isolated subpopulations promotes evolutionary change. This view has wide but by no means universal acceptance. Fisher, for example, always argued that evolutionary change is maximized in large populations.

Since for most quantitative traits natural selection tends to favor an intermediate value, any change in an already well adapted organism will be deleterious and will be opposed by selection. On theoretical grounds, the drift in populations of reasonable size (for example, 500) is not great and should be countered by natural selection with little selective death. In fact, the observation that a trait changes in mean value in small popu-

lations probably indicates that it is not adaptively important in that environment.

Depletion of Genetic Variance

Phenotypic variance can be partitioned into three components: environmental variance, genotypic variance and a genotype-environment interaction variance. The last term is often overlooked. It arises when the best genotype in one environment is not necessarily the best in another. The genotypic variance can be further partitioned into additive, dominance and epistatic terms. Of these, it is through additive variance (sometimes called the genetic, or genic variance) that a population responds immediately to natural selection. The ratio of the additive to phenotypic variance is called heritability; if the heritability of a trait is zero, there can be little, if any, adaptive change.

Our understanding of the forces underlying the maintenance of genetic variance for quantitative traits is quite superficial. We do know however, that variation is ubiquitous, and that most traits respond readily to selection. The ultimate source of genetic variability is, of course, mutation, but the probability that a new mutation will reach a reasonable frequency depends on the mutation rate, the population size and the current mode of selection for the trait. Under directional selection, any mutation which favors the change but is not deleterious in other respects will tend to increase in frequency. Stabilizing selection, however, allows only genes with a small effect to accumulate (Fisher, 1958).

Let us ignore for the present the effects of natural selection and consider only the rates of gain and loss by mutation and drift. In very small populations, the loss of variability by sampling will be greater than the gain by mutation, and there will be a net loss of variation. Conversely, in very large populations, mutation will dominate the process, and we expect a steady gain. For each trait there will be a population size at which the rates of gain and loss are equal, and there will be no net change in the existing level of variability.

If there is no dominance or epistatic variance, additive variance is lost at the same rate as heterozygosity, that is, at a rate of $1/2N_e$ per generation. This value is probably reasonably accurate for most traits. The rate of gain by mutation is less easily determined. We have some meager information on the rate of production of new variation for bristle characters in homozygous lines of *Drosophila*. These data, reviewed by Lande (1976), suggest that this rate is of the order of one thousandth of the environmental variance. For a number of bristles, therefore, we expect an approximate equilibrium between gain and loss when $1/2N_e = 10^{-3}$, that is, $N_e = 500$. Selection and linkage complicate this simple picture enormously, but I will attempt to show that even strong selection does not result in dramatic reductions of additive variance.

The present level of genetic variation in a population will have been largely determined by the selection history—the time since the last bottleneck—and the effective size of the population. The effects of continued stabilizing selection are most difficult to assess, but there is little evidence that additive variance is affected markedly. In theory, stabilizing selection reduces all components of the phenotypic variance. Reduction in the genotypic component occurs through fixation of genes, the buildup of linkage disequilibrium (Bulmer, 1976) and, ultimately, developmental feedback systems that evolve to stabilize the phenotype (Waddington, 1957). These are, however, very slow processes. Kimura (1965), Latter (1970) and Lande (1976) have shown that considerable genetic variance can be maintained by mutation under stabilizing selection.

Directional selection also reduces additive variance, but again, slowly. Theoretically, genetic variance changes at a rate proportional to the third moment of gene effects, and if, as conventional wisdom suggests, quantitative traits are controlled by a large number of genes each with small effect, the third moment will be close to zero and genetic variance will change very slowly. In addition, there is the possibility that closely linked genes can act as a repository of variability. Under selection pressure this variation can be released slowly by recombination.

In general, experimental evidence supports the theoretical arguments. Reduction in variance through stabilizing selection is difficult to achieve, but positive results have been obtained (Rendel, 1960; Prout, 1962). These experiments, however, have been difficult to interpret, and it is not always clear whether it is the genetic or the environmental component of variance which has been changed. The consequences of directional selection are much clearer. There have been numerous experiments of this kind; one of the longest running is the Illinois corn experiment in which there has been continued response to selection for oil and protein content for 76 generations. Selection began in 1896 with a starting population of 163 open pollinated ears. Twelve to 24 parents were chosen by each generation. The response to selection for oil content is shown in Figure 1 and the pattern for protein was similar. Over the course of the experiment, a response of 20 standard deviations of additive variance for high oil and protein content has been achieved. Less spectacular results have been obtained for selection (in reasonably large populations) in diverse laboratory organisms such as *Drosophila*, *Tribolium* and the mouse. Examples may be found in Falconer (1960). These experiments demonstrate convincingly that additive genetic variance is not depleted rapidly by selection.

What, then, can we conclude about the effect of natural selection on genetic variance? Strong selection reduces additive variance, but weak directional or stabilizing selection probably has little effect. In some ex-

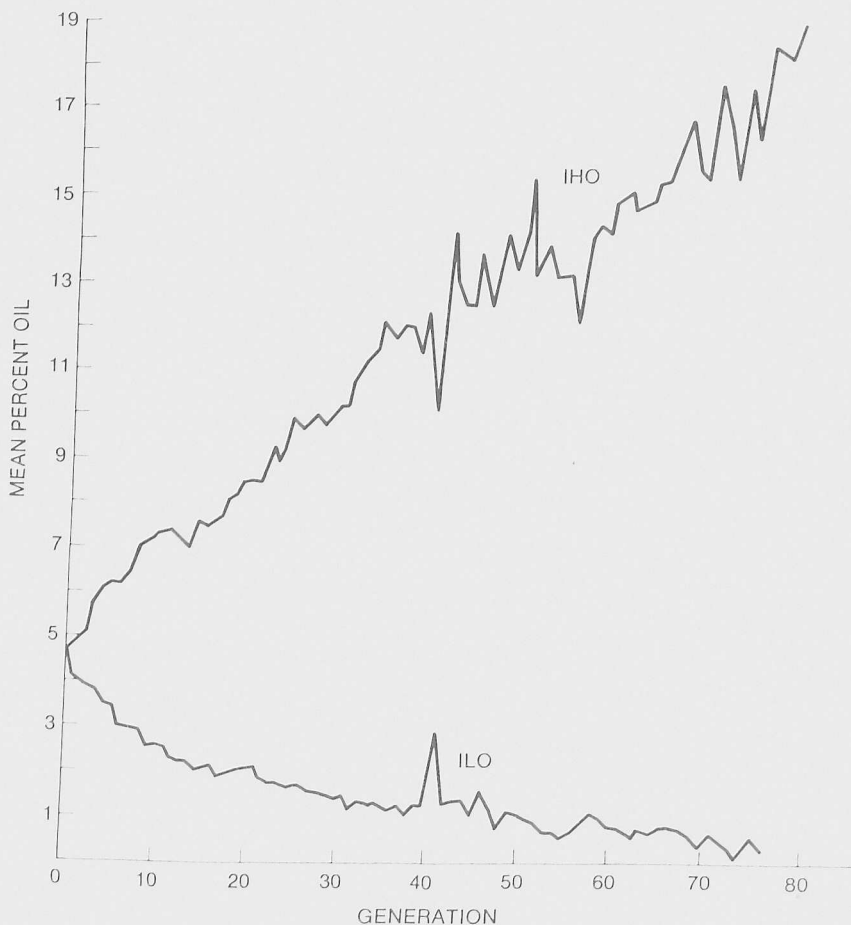


FIGURE 1. Mean percent of oil in ears of *Zea mays*—selected high (IHO) and low (ILO). (From Dudley, 1973)

periments, even with prolonged selection there has been as much additive variance in the selected population as there was in the original population. Therefore, we can tentatively conclude that the major determinant of the level of genetic variance in natural populations is the balance between genetic drift and mutation.

FOUNDER EFFECTS AND SELECTION RESPONSE

The previous section was concerned with the chronic effects of small population size. Here I want to examine the effects of bottlenecks (restriction in size followed by recovery) or of the founding of populations

from a small number of individuals. The experimental investigations of response to selection in small populations (Frankham et al., 1968; Hanrahan et al., 1973) show that response to selection is less in small than in large populations, but in general the effects are not great. Even in the most extreme situation, when a population has been founded from a single pair, three quarters of the additive variance remains, which means that, on the average, there is still an opportunity for an appreciable response.

Hammond (1973) collected some data which illustrate the effect of small founder populations very well. He established populations of *Drosophila* from one, 10 and 50 pairs, and then measured the response to selection for abdominal chaetae over 10 generations. These data (Table I) show that the realized heritability (a measure of the observed change) in populations established from 10 pairs differs very little from that in populations established from 50. As expected, populations founded from one pair, but not maintained at this level, showed three quarters of the maximum response.

Founder effects, although they may not greatly restrict immediate selection response, nevertheless introduce major changes in the gene pool so that the pattern of change may be very different from that in the population from which the gene pool was derived. An important theoretical contribution to the theory of bottlenecks is that of Nei et al. (1975). The founding of new populations from small numbers is of considerable evolutionary significance; the subject warrants much more theoretical and experimental attention.

TABLE I. The relationship between founder population size and subsequent selection response.

Founder size	Treatment*	Number of replicates	Realized heritability
1 pair	1-1	28	.051 \pm .018
	1-10	21	.157 \pm .007
	1-20	18	.152 \pm .007
10 pairs	10-10	24	.185 \pm .004
	10-20	21	.177 \pm .006
50 pairs	50-50	17	.202 \pm .006
	50-100	9	.205 \pm .006

*The treatments (for example, 1-10) indicate that the population size was reduced to a certain number of pairs (for example, 1) for a single generation, and was subsequently maintained at a higher number (for example, 10 pairs per generation).

(From Hammond, 1973)

MANAGEMENT OF ENDANGERED SPECIES

In the preceding discussion I considered the effect of small population size on evolutionary potential—assuming no human interference. I now wish to briefly consider the consequences of intervention. In some circumstances, particularly when a breeding population is maintained in a zoo or reserve, decisions which relate to breeding have evolutionary consequences. It must be remembered that programs that minimize inbreeding and genetic drift are not conducive to simultaneous evolutionary change. For example, one way to maintain effective population size is to ensure that each family contributes equally to the next generation by culling only within families. Another option, if management is sufficiently intense, is to employ mating schemes which lead to maximum avoidance of inbreeding. All such methods reduce the response to natural selection and postpone the elimination of especially abnormal genotypes. Given a choice, however, it is perhaps best to sacrifice evolutionary change at the present, if by so doing one is conserving genetic variation for future evolutionary change. This is especially true in captive breeding situations where the return of stock to the wild is anticipated. In such cases we wish to avoid domestication.

Though domestication may be no substitute for conservation—such a step is essentially irreversible—it is, I feel, inevitable, at least in the long run. I do not wish to enter this arena, other than to point out that many of the behavioral traits which accompany domestication appear to have a high heritability and can be selected for relatively easily (Fuller, 1969). Far too little is known about the changes which occur in the process of domestication; we need to identify the traits involved, understand their inheritance and perhaps catalog those species which are preadapted for commensalism with man. Hale (1969) gives an excellent review of the evolution of domestication.

Finally there is the question of whether to maintain a single large population or to split the species into a number of smaller breeding units. Such decisions will be primarily made on political or ecological grounds, but the latter course seems to have distinct genetical advantages. If a species is maintained in a number of small populations, not only is the danger of accidental extinction (for example, by disease) reduced, but an opportunity for local adaptation exists which may increase the chance of ultimate survival. Genetic drift can be countered by allowing occasional migration. In the absence of selection we know that the subpopulations would have the properties of a single intermating group if only one or two migrants were exchanged each generation. There is little information on the joint effects of selection and migration in small subdivided populations, but some theorizing by Avery (1978) suggests that migration rates of the order of one per generation increase the overall genetic variability,

both for heterotic loci and for loci selected in opposite directions in the subpopulations.

CONCLUSIONS

We know very little about the selective forces involved in the maintenance of polymorphisms for single genes or adapted gene complexes, and I have not considered the effects of genetic drift at this level. I have instead treated the problem of the conservation of genetic variability from the point of view of a quantitative geneticist, whose observations are the means, variances and covariances of continuously varying traits rather than gene frequencies, mean heterozygosity or the proportion of polymorphic loci. Based on our current knowledge of quantitative traits, I have suggested that the evolutionary potential of populations maintained in reasonably effective numbers (that is, in terms of hundreds and not tens of individuals) is not seriously impaired. I think that most quantitative geneticists working with animal populations would come to the same conclusion.

The subject of the quantitative geneticist has been the laboratory bred organism or the domesticated species, rather than the natural population. Nevertheless, most important adaptive changes which occur in evolution are changes in continuously variable traits, and there is every reason to believe that the single gene theory is inadequate for our understanding of the dynamics of such changes. Extrapolation from laboratory to natural populations is greatly complicated by the differences in complexity of the two kinds of environments. The reduction in size or disappearance of one species has repercussions on others (Chapter 2). I think it is fair to say that we have an incomplete understanding of these interspecific interactions. Another unknown is the importance of density dependent selection. A trait which is favored at high density may be disadvantageous at low density, and hence a reduction in number would add to the genetic load. Any change in the ecosystem, therefore, has the potential to alter the patterns of adaptation, and a species may face a serious crisis if it has to make too many changes at once. Negative genetic correlations make the situation worse, for if we try to select for two antagonistic traits simultaneously, we can expect little change in either.

I have already suggested that in the short-term the effective population size should not be less than 50. I tentatively propose that in the long-term the minimum effective size should be 500. Below this latter value, it is likely that genetic variance for complex traits is lost at a significantly faster rate than it is renewed by mutation. In reaching this conclusion I

have adopted the view that it is important to maintain a pool of variation upon which future selection may operate. The number I have chosen is based on extremely meager evidence, and I stress that much more research is needed before we can answer such questions with confidence. There is no doubt that a species which maintains an effective size ten times this value would be in less danger of genetic deterioration.

Some species can recover from very small populations. The elephant seal has suffered extreme reductions in size and has apparently lost a great deal of its heterozygosity (Bonnell and Selander, 1974). Nevertheless, its ability to respond to selection is unknown. Other species may be in danger at a much greater effective size. In populations with a density dependent birth rate, there may be a critical size (well above 500) below which the population is doomed to extinction on purely ecological grounds.

Although I have argued that reduction in size does not seriously limit selection response, this does not mean that a population will be able to adapt to new conditions. The increase in genetic load due to a change in the ecosystem may be so great that the necessary genetic change, no matter whether the population size is 10 or 10 million, is beyond the reproductive capacity of the species.

Finally, it should be pointed out that these conclusions are concerned with evolutionary changes in identifiable, random-mating subpopulations, and hence are biased towards highly vagile animal species. From the point of view of conserving the genetic variation of the species, one elephant may be as good as another. This is certainly not true of most plants where microdifferentiation and ecotypic variation need to be taken into account. If you have seen one redwood you have not seen them all.

SUGGESTED READINGS

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- Also, the September, 1978 issue of *Scientific American* is devoted entirely to evolution. The article by Lewontin on adaptation is particularly relevant.