GENETIC SLIPPAGE IN RESPONSE TO SELECTION FOR MULTIPLE OBJECTIVES

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It seems clear that selection for manifold objectives is the universal rule in both wild and domesticated populations. Deliberate selection can supplement but never supplant natural selection; hence it can do no more, no less than change the requirements for reproduction by the individual. The essential difference then, between deliberate and natural selection lies in the number of generations during which the population has been subjected to a given complex of selection pressures. Even this difference may become indistinct after a population has been under a similar pattern of continuous deliberate plus natural selection for many generations, particularly when one considers that the spectrum of emphases in wholly natural selection must shift with fluctuations or trends in the environment.

An approach to phenotypic equilibrium, or at least grudging apparent response in wild populations under continuous natural selection is more or less taken for granted. Plant and animal breeders, by contrast, would like their supplementary deliberate selection to yield rapid improvement in domesticated species. What is more, we have sometimes attempted to predict the rate of improvement ($\Delta\bar{P}$) to be expected from (1) estimates of genetic variability for individual characters (H_i), and (2) the phenotypic superiority in each trait of the individuals that are allowed to reproduce ($\bar{s}_i$). This situation may be merely one more example of the need for overhauling an incomplete set of assumptions when their predictive accuracy fails, and for continuing evolutionary progress in the mental adaptation of one deme of *Homo sapiens*, perhaps aided by inter-deme migration, introgression, and co-adaptation!

If and when one finds that in a given population, phenotypic response to continued selection has become negligible relative to expectations based upon the selection differentials and heritabilities for certain characters, it seems logical to assume that:

(1) Something is amiss in the estimates of heritability or their interpretation, or that
(2) relationships among the multiple objectives of selection are the culprits, or both.

Our purpose here is to consider some of the evidence concerning refractory response to continued selection in domesticated animals and the ways in which the inevitable selection for multiple objectives may be responsible.

Evidence from Selection Experiments with Domesticated Animals

Need for Controls

Any precise check on the correspondence of actual and expected response to selection (that is, $\Delta\bar{P} = \bar{s}_i H_i \pm ?$) depends upon separation of genetic and environmental trends. This requires some type of control population which remains genetically constant during whatever intervals of time are required to measure effects of environmental change. At least these requirements hold unless one adopt the simplifying empirical assumption that the absolute trend over long periods of time must be positive to constitute evidence of response to selection. The weaknesses of such an assumption are that (1) it ignores the possibility that genetic response may be necessary merely to maintain a given level of performance, and (2) it permits either over-optimistic or over-pessimistic conclusions to be drawn because of environmental changes, particularly during the relatively short segments of time in which results from a given selection experiment ordinarily are obtained. Unfortunately, the problem of genetically constant controls in animals is not as simple as storing seed for several years, and the use of such controls to measure environmental mental change in selection experiments with domesticated animals is just beginning (Goodwin *et al.*, 1955). Meanwhile we must make as much sense as we can from results obtained without such controls.

Interpretation of Published Results

Published reports of sluggish response to selection in animals are rare indeed, possibly due to editorial frowning or author reluctance concerning publication of negative results! At least there are many reports showing that much improvement, presumed to be at least partly genetic, has been produced in such traits as egg production in chickens, milk production in dairy cattle, and growth rate in swine and in meat chickens (see Lush, 1951; and others). Goodale's (1938) selection for large body size in mice certainly produced major change over a long period.

In some of the more carefully planned experiments selection was applied in opposite directions in two strains derived from a common stock. MacArthur's (1949) experiment with body size in mice and the later one at Edinburgh (Falconer, 1953; Falconer and King, 1953) were by far the most extensive and complete, but the Illinois experiment with growth rate of swine (Krider *et al.*, 1946) and

the Alabama experiment with feed utilization of swine (Dickerson and Grimes, 1947) also are of interest. In each case selection was able to separate genetically distinct strains, but it is noteworthy that response to selection was greater for:

(1) The trait (body size in mice) which presumably had no previous history of continuous selection in one direction;

(2) the early generations of the experiment; and,

(3) when the direction of selection was reversed from that which characterized the previous history of the population.

In these experiments selection for a single trait was intended, but correlated changes in a number of other characters were obtained. At this point it should be emphasized that a "simple" experiment with deliberate selection for a single character is likely to be too simple to provide results of maximum usefulness for understanding the nature of selection response in either domesticated or wild populations. This holds because so many different characters are given consideration in disbursing the privilege of reproduction, and because of the inevitable pleiotropic associations among characters.

In other selection experiments with domesticated animals results can be judged only by the absolute time trends in performance. Probably the least optimistic published report of selection response comes from the mildly inbred lines of swine maintained by experiment stations cooperating in the Regional Swine Breeding Laboratory (Dickerson *et al.*, 1954). In this case the average time trends involving some 49 lines over a period of ten years were essentially zero for litter size at weaning age and negative for individual body weight at 154 days of age, even after removing the downward bias from inbreeding deterioration. It is gladly noted that the Minnesota workers (Fine and Winters, 1952; and Rempel and Winters, 1952) believe that their experience indicates essential agreement of selection response with expectation. Probably only time and better information will provide the correct interpretation. The mild inbreeding and lack of knowledge concerning environmental trends were definite handicaps to precise evaluation of selection response in these swine experiments.

Results have been published from two strains of White Leghorn chickens under continuous selection for egg production, viability and other characters during 16 years at the University of California (Lerner and Hazel, 1947; and Dempster *et al.*, 1952) and at Cornell (Hutt and Cole, 1955). It is interesting to note that, in this isolated instance, Hutt appeared to be in complete agreement with Lerner and Dempster in the belief that no plateau had been reached in response to selection and that he was able to reach this conclusion without estimates of heritabilities or genetic correlations. This situation was obviously an example of an unstable equilibrium, so that it is not surprising now to read in a recently published synthetic book on mulish populations (Lerner, 1954) that Lerner is now temporizing with estimates of plateau in the range of 260 to 280 eggs. Three observations concerning the results from both experiments seem pertinent:

(1) The initial level of performance was low.

(2) Improvement was most rapid during the early years and has been slight during the last 8 to 10 years, even though it is too early for high betting odds that the slow-down is real.

(3) Respiratory diseases have sharply lowered performance in some recent years, which may not be entirely independent of genetic change produced by selection for egg production.

Finite Evolution in a Closed Flock

Flock History

The Kimber strain of Leghorns was established about 30 years ago with foundation stock from a number of the more successful breeders of that day. Intensive selection for a complex of economically important traits has been practiced throughout its history. These included fertility, hatchability, freedom from abnormalities, viability, sexual maturity, egg production, egg size, egg shape, shell thickness, texture and color, freedom from blood spots and, more recently, amount and viscosity of thick albumen. Mortality data since 1934 have included autopsy of all pedigreed females dying before the end of the pullet year of egg production, to determine the types of lesions present, with special attention to various types of neoplasms.

Absolute time-trends during the 23 year period 1931 through 1953 for a number of the more important traits will be compared with estimates of expected selection response. It certainly cannot be maintained that environment has remained constant during the period studied. Nutrition may have improved with knowledge in this field. Changes in floor space per bird, use of built-up litter and, in recent years, exposure of chicks to adult birds in adjacent pens, together with an ever-changing population of pathogens, and other factors, all may have produced fluctuations and trends in the environment. These same factors vary with time and location in the general population of chickens and must be recognized in any attempt to improve absolute levels of performance by selection.

Genetic Variability

Estimates of the proportion of phenotypic variation due to average gene effects, hereafter called *heritability*, are shown in Figure 1 for a number of the traits considered in selection. These estimates were based upon correlations obtained among paternal half-sibs, and hence should contain no contributions from dominance deviations or from epistasis involving dominance deviations, and less

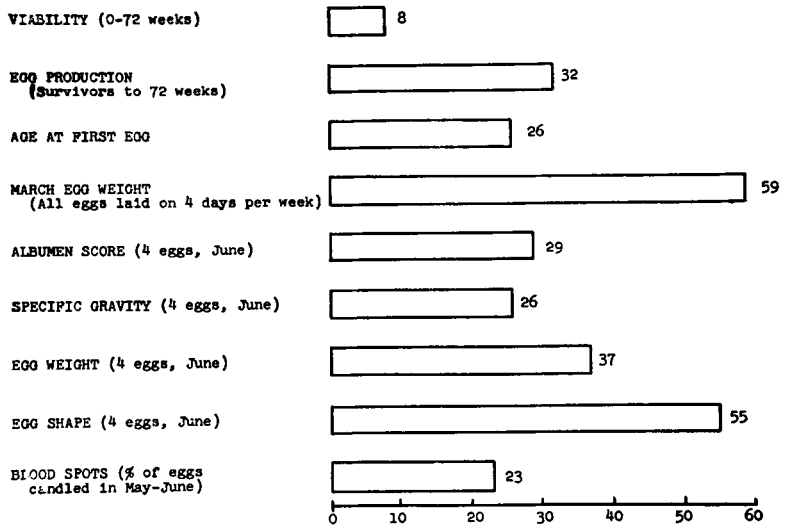

FIGURE 1. Approximate degree of heritability (in percent) of variation in individual phenotypes for some components of performance in the Kimber Leghorn flock (see text for details).

than one-fourth of any variance from average by average non-allelic interaction (Cockerham, 1954). The estimate of eight per cent for viability was made by Lush, Lamoreux and Hazel (1948), the one of 26 per cent for sexual maturity (age at first egg) was made by Hazel and Lamoreux (1947) and the figure of 23 per cent for incidence of eggs with blood spots detected by candling was taken from Farnsworth's (1955) exhaustive analysis. The remainder of the estimates were obtained from an intra-strain sample analysis of data for 3984 pullets hatched in 1951 from 299 dams, 52 sires and 6 strains. These estimates agree reasonably well with other published estimates (King and Henderson, 1954).

It is clear that after 30 years of selection there is no lack of variation due to average gene effects in the individual components of performance.

Selection Applied and Response Expected

Simple estimates of expected selection response may be obtained from selection differentials and heritability estimates, if one is willing to ignore temporarily genetic relationships among the several traits and to assume that the same population of environments occurs in successive years. This was done for selections of cockerel and pullet breeders from the populations hatched in 1951, 1952, and 1953. In Figure 2, the mean superiority of the full-sib families from which cockerel and pullet breeders were chosen is shown, relative to the whole population. The additional within-family superiority of pullet breeders is also shown. The solid bar is the expected annual phenotypic response. Since about one-third of all breeders were birds two or more years old, chosen on full-year records and progeny tests, the actual annual response expected may be somewhat different than that shown in Figure 2. However, these are intended to be only rough estimates of expected response. Major shortage of actual advance compared with these expectations provides evidence of negative relationships among the characters or some consequences of environmental changes.

It is clear that selection applied was sufficient to cause major genetic changes if average environment had remained constant and if characters had been independent. Over a ten year period the accumulated advances expected would have been 53 per cent in viability, 5 weeks earlier sexual maturity, 129 more eggs per pullet surviving to 72 weeks of age and an increase of 7.4 grams in egg weight (over 3 ounces per dozen). The expectation for viability is obviously impossible, because it would exceed the maximum.

Actual Time-Trends

Viability

Viability and egg production of each pullet hatched from 1931 through 1941 was measured to 365 days after her first egg, provided this period ended before October 1 of her second year; thereafter, viability was measured to a standard age of 72 weeks. Within each of the periods the trend in viability was clearly downhill. Viability was better for 1932 pullets (88 per cent) than in any year since.

Egg Production of Survivors

During the period 1931-1941 there was a slight upward trend, although egg production was as high in 1931 as in any later year (231 eggs in both 1931 and 1941); thereafter, the trend was downward. Notice that years of poor viability also tended to be

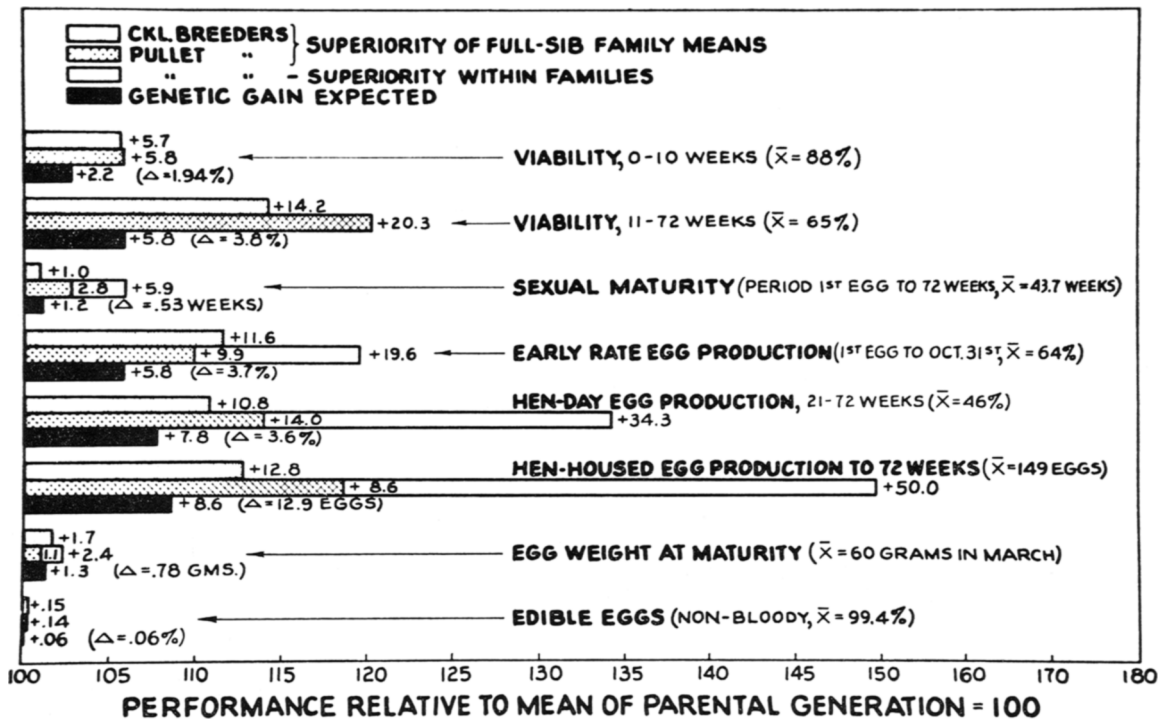

FIGURE 2. Annual selection differentials and rough estimates of expected gains under simplest assumptions (see text). Δ indicates absolute gain expected, $\bar{x}$ the mean of the unselected population from which breeders were chosen.

years of later sexual maturity and lower egg production, with notable exceptions.

Sexual Maturity

(Length of period, first egg to 72 weeks)

Until 1951 there appeared to be a fairly steady trend toward earlier age at first egg, amounting to about two weeks gain in 20 years. This is about one-fifth of the expected gain, assuming that selection throughout the period was similar to that applied in the 1951-1953 sample period. This gain was wiped out, at least temporarily, by mounting incidence of respiratory disease in 1951-1953.

Egg Size

The measure of egg size was mean weight of all eggs laid by a bird on days when birds were trap nested during March, when most birds were 12 or 13 months old. Egg size increased approximately one ounce per dozen during the period 1931-1941. It has remained close to 25 ounces per dozen ever since 1939, although selection indicated an expected advance of over four ounces per dozen.

Blood Spots

All eggs trap nested during May and June (sometimes longer) of each bird's second year were candled to detect blood spots. During the first two years for which records were summarized, incidence of bloody eggs averaged about three per cent. Intensive family and individual selection was applied, and the incidence since has not exceeded one per cent, being under one half of one per cent for the last five years. Because of the recent low incidence, further expected advance is trifling, about 0.6 per cent in ten years.

Other Factors

The other components of performance which certainly have been given attention in selection are fertility, hatchability, and abnormal chicks (crooked toes, bad navels, etc.); shape, texture, thickness and color of shell; and during recent years, thick albumen quality. Time did not permit inclusion of results for all traits in this presentation. They are mentioned however, to underscore the fact that selection in domestic animals is truly directed toward multiple and inter-related objectives.

Factors Limiting Response to Selection

It is quite clear the average response to selection is much less than expectations based simply upon intra-environmental heritability estimates and selection differentials for each character (that is, $\Delta\bar{P}_i < \bar{s}_i H_i$) in populations which have been selected for a similar complex of phenotyic traits during many generations, and particularly so when environmental influences fluctuate widely between generations. Ultimate response to deliberate plus natural selection for total performance in domesticated species bears closer resemblance to the gains from continuous natural selection for reproduction

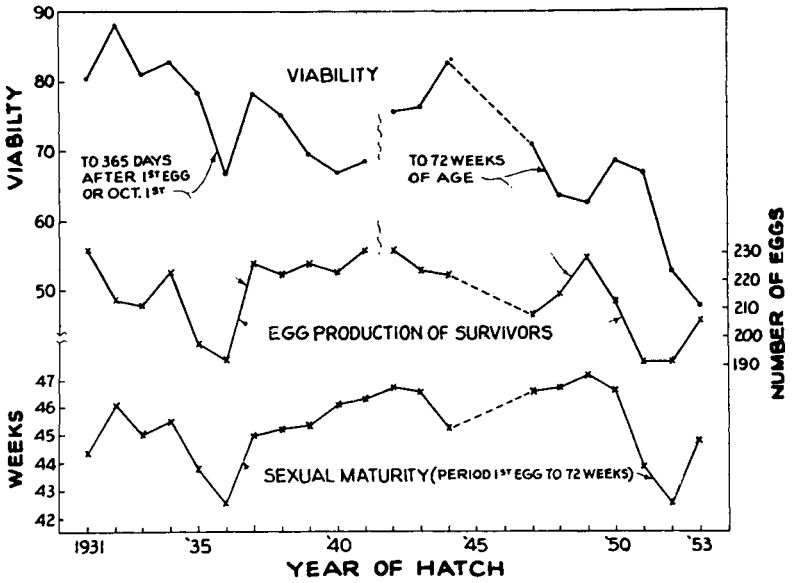

FIGURE 3. Actual time-trends in viability and the sexual maturity and total egg production of survivors (see text for details).

fitness in wild populations than it does to the response obtained in early generations of selection experiments with metric characters which have no prior history of continuous selection in one direction.

The probable causes of the apparent slippage between generations in the response to selection may be classified as follows:

(1) Inter-environmental, in successive periods of time or in different locations at the same time.

(a) Adverse time-trend in the environment.

(b) Genetic-environmental interaction, or imperfect positive correlation (that is, $r_{ij} < 1 - > 0 - > -1$) between phenotypic expressions of the same genotype in different environments.

(2) Intra-environmental.

(a) Lower heritability for total performance (or effective reproductive fitness) than for its components, as a consequence of dominant favorable but recessive unfavorable pleiotropic effects of genes on the components of performance or of other negative relationships among the components.

(b) Reverse mutations.

(c) Inbreeding or random loss of useful genes.

Inter-Environmental Slippage

There is certainly no doubt that environmental influences vary enormously with time at a given location and with location at a given time. The history of total mortality and of certain types of lesions found in the pedigreed Kimber flock at autopsy of all females which died by 72 weeks of age is shown in Figure 5, for the 20 year period 1934-1953. It illustrates how periodic introduction of new diseases or modified forms of old ones may very well more than cancel gains in genetic resistance to past causes of death. For example, the incidence of deaths showing neoplastic lesions has gone through three cycles of five to eight years each since 1934. In the first, leucosis mortality, mainly neural, rose from two to twelve per cent and then subsided; in the next, leucosis was more largely visceral, rising rapidly to 22 per cent and then gradually falling to three per cent over a five year period. In the most recent eight year cycle leucosis, still chiefly visceral, rose gradually to eleven per cent in 1949 and has declined steadily since to less than one per cent in 1954. However, since 1947 the incidence of dead birds showing various types of respiratory lesions has mounted steadily, reaching peaks of 23 and 29 per cent, respectively, in the 1952 and 1953 pullets. During these two years pullets were brooded for several weeks with adult birds in an adjacent pen. This was done in the vain hope of increasing the incidence of leucosis, but it may have contributed exposure to respiratory diseases. In 1954, incidence

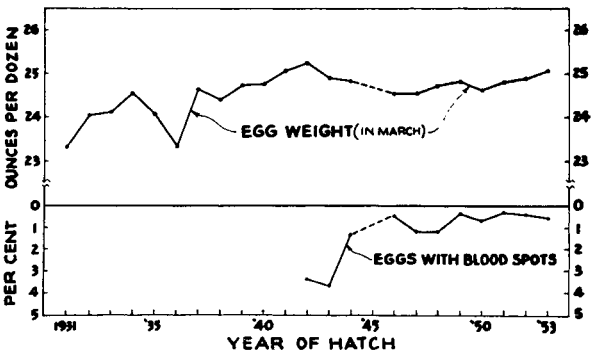

FIGURE 4. Actual time-trends in egg size and in incidence of eggs with blood spots.

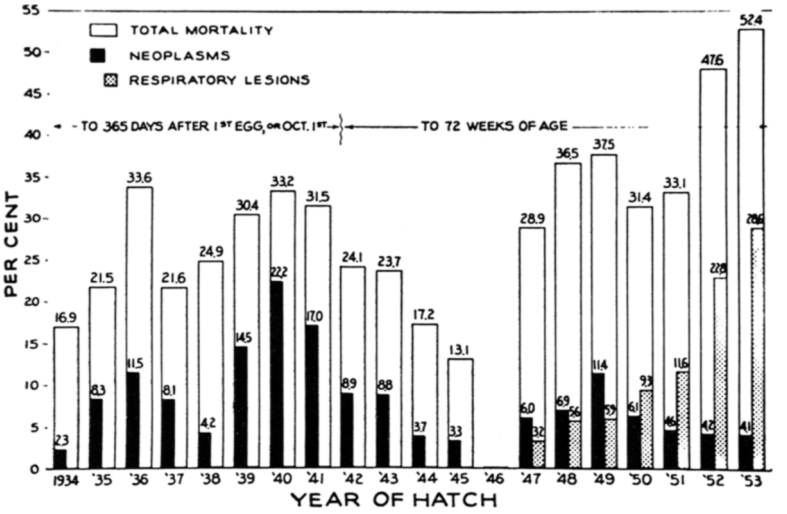

FIGURE 5. History of total mortality and of the incidence of neoplasms and respiratory lesions.

of deaths of pullets with respiratory lesions has fallen below ten per cent, presumably because of the introduction of immunization for a form of bronchitis with live virus innoculation.

Adverse "Treadmill" Environment

Perhaps host-pathogen relationships provide one of the more plausible illustrations of possible consistently adverse cyclic environmental changes. When a pathogen of increased virulence evolves, mortality rises in the host population. This causes natural, and possibly deliberate, selection for resistance in the host population. Isolation and death of affected individuals also may act as selection for avirulence of the pathogen. The net effect would be a genetic change in the host population without appreciable gain in total performance or fitness.

This may happen repeatedly with various pathogens or parasites. It might well be termed a "treadmill" environment, because it would require constant selection effort and genetic change in the host population merely to maintain performance. It may be argued with some justification that development of techniques for immunizing individuals for various diseases should tend to eliminate this wasted selection effort, permitting its use for improvement of characters other than resistance to disease. However, if live virulent pathogens are used to obtain immunity, the net effect may be to maintain an ever increasing array of virulent pathogens in the host population, instead of letting natural selection bring them under control. Use of avirulent pathogens to secure immunity may be the more obvious answer. Other factors such as increased population density or crowding also may be involved.

There is great need for genetically constant control populations to measure actual time-trends in environmental influences. Only with such data can estimates be made of the amount of natural and deliberate selection that is required to enable populations to keep pace with their environments. The experience of small-grain breeders with ever changing races of rust, smut and other diseases probably is of significance to those working with animal populations as well.

Genetic-environment Interaction

Evidence concerning the differential effects of changing environment on the phenotypic expression of a series of genotypes in animals is rather conflicting and fragmentary. Such interactions in animals have been demonstrated with differences in genetic resistance to disease under varying exposure (Hutt *et al.*, 1945; King *et al.*, 1952), and with genetic differences in nutritional requirements (Lamoreux and Hutt, 1939 and 1948), but often have been sought in vain.

Genetic-environmental interaction may range from none if correlation is perfect, ($r_{ij} = 1$) between duplicate genotypes in different environments, to intermediate or random when $r_{ij} = 0$ or even negative (when $r_{ij} \rightarrow -1$). If $r_{ij} = 1$, genotypes would be ranked exactly the same in the different environments, except for the uncontrolled random environmental variability within each level. In this situation there would be no loss of progress, unless an adverse environmental trend existed. However, if $r < 1$, there will be loss of genetic progress. Relative to genetic advance when $r_{ij} = 1$, efficiency will fall to 0 as $r_{ij} \rightarrow 0$ if the number of environments is infinite.

The situation when $r_{ij} = 0$ is equivalent to the one described above under adverse "treadmill" environment. A still worse possibility would be negative correlation between duplicate genotypes in different environments (that is, $r_{ij} < 0$). For

example, suppose increased genetic resistance to one disease tended to reduce its resistance to another. This would produce host-pathogen cycles with a vengeance! If there were only N diseases, an average $r_{ij} = \frac{-1}{(N-1)}$ would make average improvement in resistance *nil*. Fortunately, there is some slight indication that r_{ij} may be mildly positive within the *same* yearly environment (Lush, Lamoreux and Hazel, 1948; Robertson and Lerner, 1949). We can only hope that this holds between *different* environments.

Flux in Gene Frequencies and Average Heterozygote Advantage

If mean environment and the consequent requirements for reproductive fitness remained constant from generation to generation, gene frequencies eventually might be expected to reach a rather stable equilibrium in any given population. However with continual environmental flux, the combination of gene effects which produces maximum total performance changes between successive environments. If one accept the reasonable model of a finite number of genes or segregating hereditary units each with pleiotropic effects on different components of fitness, together with a more nearly infinite number of gene combinations, then it follows that the selective advantage of a given gene will vary from one environment to the next. Genes whose effects are rather consistently favorable or uniformly unfavorable in the whole range of environments will move toward fixation or elimination, leaving genetic variability in the population almost completely dependent upon genes having favorable effects in some environments and unfavorable effects in others. In particular, genes whose unfavorable effects tend to be recessive and whose favorable effects show some degree of dominance will tend to be held at relatively high frequencies, as postulated by Hull (1945).

A most interesting feature of this genetic-environmental model is that the degree of dominance may be low within any single environment but high for the average over a series of different environments. This leads to a concept of fluctuating rather than of stable equilibrium gene frequencies. Within the restricted population of environments of a single year or generation for a given population, selection may be effective in producing genetic response quite in line with the intra-environmental heritability of total performance. The slippage between generations may occur simply because much of the genetic response under one environment is irrelevant in the environments into which the population subsequently moves.

It should be noted that a deliberate abrupt change in the definition of total performance upon which selection of breeders is based is essentially the same phenomenon as an abrupt change in environment. Either way one exposes a new set of average gene effects to selection, and progress is to be expected toward a new equilibrium provided the altered environment or altered requirements for reproduction persist in a consistent manner over many generations.

There are several approaches by which the validity of this genetic-environmental model might be tested. One is use of genetically constant populations to measure environmental change between years or generations. Barring deterioration effects, this may be done in plants simply by storing seed, but is a more intricate problem in animals (Goodwin *et al.*, 1955). This approach, however, will only

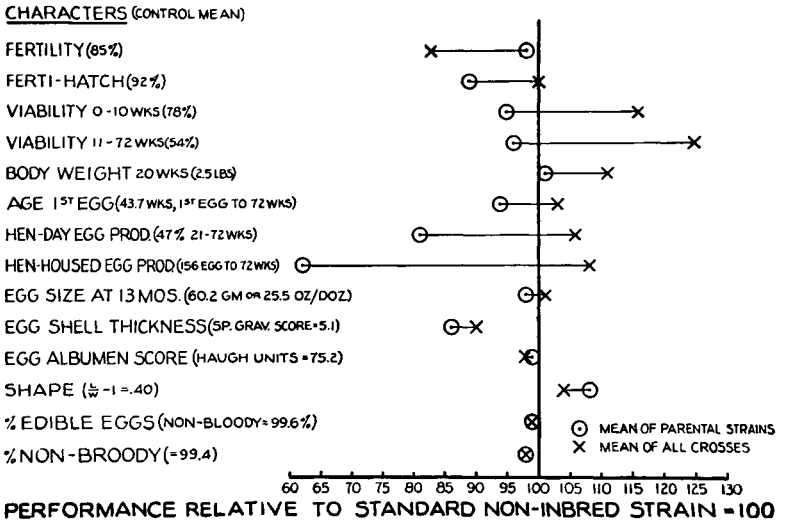

FIGURE 6. Mean performance of nine egg strains of chickens (0) and of their 72 crosses (X) relative to a standard non-inbred strain for components of performance.

aid in detecting that portion of the genetic response which *is* realized under subsequently altered environments, by contrasting means for the selected with the control populations in successive generations.

Another approach is comparison of heritability estimates derived from the inter-environmental phenotypic regression of progeny on parent with the intra-environmental estimates based upon phenotypic correlation among paternal half-sibs. This comparison would be obscured by upward bias in offspring-parent regression due to heritable variation in maternal effects and to positive correlation of environmental effects on the dam with the direct maternal influence on her young. It is most likely to prove useful in species or characters having negligible direct maternal effects and would be more meaningful when applied to total performance than to its individual components. If genetic environmental interaction is important, lower estimates of heritability and either smaller positive or larger negative genetic correlations between components of total performance should be obtained from the inter-environmental parent-offspring regression than from the intra-environmental half-sib correlation.

Selection experiments under different controlled environments provide a still more critical test, particularly if accompanied by a genetically constant control population to measure the uncontrolled changes in environment.

Intra-Environmental Slippage

By intra-environmental slippage is meant the negative discrepancy between actual response and that expected from selection differentials and heritabilities for individual components of total performance, assuming no mean change in environment (that is, $\Delta\bar{P}_i < \bar{s}_i\ \bar{H}_i$). By definition such slippage must be some consequence of (1) relationships among the components of reproductive fitness or (2) negative genetic regression, from prevailingly deleterious reverse mutations or from random loss of useful genes. The more obvious relationships between components which suggest themselves are:

(1) Negative genetic correlations, or at least smaller positive or more negative genetic than phenotypic correlations among components. The net effect would be lower heritability (H) and greater degree of dominance (k) for total performance compared with the weighted mean for its components (that is,

$$H_t < \frac{\Sigma w_i H_i}{\Sigma w_i} \text{ and } k_t > \frac{\Sigma w_i k_i}{\Sigma w_i}).$$

(2) Multiplicative gene effects, and multiplicative combination of components to produce total performance, curiously would tend to mask the effects of dominance and of negative genetic correlation among components within panmictic populations or in crosses between populations at widely different phenotypic levels of performance, but *not* when populations at *similar* levels are crossed (*e.g.* in crossing breeds, strains or inbred lines).

Evidence for intra-environmental slippage in selection for total performance in swine and its genetic interpretation has been considered earlier (Dickerson, 1949, 1951, 1952, 1954). Similar evidence for corn has been considered by Hull (1945) and for corn and soybeans by Leng *et al.* (1949).

Genetic Correlations Smaller or More Negative Than the Corresponding Phenotypic Correlations Among Components of Performance

It has been shown elsewhere (Dickerson *et al*, 1954) that, for the artificially simple case of selection for n equally variable and heritable components with the same genetic (r_{Gij}) and phenotypic (r_{ij}) correlation between any pair, the ratio of heritability of total performance to that observed for each component separately will be

$$\frac{H_t}{H_i} = \frac{1+(n-1)r_{Gij}}{1+(n-1)r_{ij}}$$

Clearly, response to intra-environmental selection would $\rightarrow 0$ as $r_{Gij} \rightarrow \frac{-1}{(n-1)}$, and would be reduced to the extent that $r_{Gij} < r_{ij}$.

Negative genetic correlation among components is merely another way of saying heterogygote advantage or overdominance, as indicated earlier. Evidence of reality of negative genetic correlations among components is not plentiful as yet, but is accumulating. In chickens there is evidence of negative genetic correlation of egg production with body size (Gyles *et al.*, 1955) and with egg size (Shultz, 1953), of large egg size with reproductive fitness (Lerner and Gunns, 1952), and of egg production with the maternal effects on early growth and conformation (Dillard *et al.*, 1953).

Some additional evidence concerning genetic and phenotypic correlations among certain components of performance in the Kimber flock is shown in Table 1. Notice that both total egg production of survivors and winter egg production have rather large negative genetic correlations with egg weight in both March and June samples, and that the phenotypic correlation is zero or slightly positive, indicating a definite positive environmental correlation. Amount of firm albumen and specific gravity (indicator of shell thickness) also bear a negative genetic relationship to egg production but phenotypic and genetic correlations are similar in size. The several egg quality items appear to bear positive genetic relations to each other.

A complete picture of intra-environmental heritability of the index or total performance score actually used in selection is needed before any

TABLE 1. ESTIMATES OF GENETIC AND PHENOTYPIC CORRELATIONS AMONG SOME COMPONENTS OF PERFORMANCE IN A STRAIN OF WHITE LEGHORNS

	Source Variation*	Correlation with W.E.P.	M.E.W.	J.E.W.	ALB.	S.G.	SH
EGG PRODUCTION	G	.85	—.39	—.26	—.32	—.24	—.50
(Survivors, to 72 weeks)	P	.73	—.04	.12	—.28	—.28	—.10
WINTER EGG PRODUCTION (W.E.P.)	G		—.40	—.32	—.20	.09	—.73
(Oct.-Jan., inclusive)	P		—.01	.14	—.22	—.30	—.14
MARCH EGG WEIGHT (M.E.W.)	G			.96	.51	.44	—.09
(All eggs, 18 days)	P			.80	.09	.06	—.04
JUNE EGG WEIGHT (J.E.W.)	G				.34	.44	—.15
(4 eggs per hen)	P				.01	.01	—.06
ALBUMEN QUALITY (ALB.)	G					.14	.30
(4 eggs per hen in June)	P					.26	—.12
SPECIFIC GRAVITY (S.G.)	G						.51
(4 eggs per hen in June)	P						.03
SHAPE $\frac{(L\ )}{(W\ )} - 1$ (SH)							

*G = Genetic, based on sire component of variation.
P = Phenotypic, based on total variation within strain and year. Data from 3,984 hens hatched in 1951 from 299 dams, 52 sires and 6 strains.

estimate of the relative importance of inter- and intra-environmental slippage can be made.

In swine some evidence for a negative genetic relationship of suckling ability with efficiency of gain, and of carcass desirability with rapidity of growth has been reported (Dickerson 1947; Dickerson and Grimes, 1947). Cockerham (1952) found low heritability rather than negative genetic correlations between litter size weaned (viability) and growth rate, within inbred lines of swine. In cattle and sheep, heritability of the more important traits, other than those related to reproductive capacity, appears to be very high, leading to optimism concerning the probable response to selection. If the amount of selection for these economic traits can be increased greatly, compared with that applied during prior history of the population, optimism probably is justified. However, careful study of genetic correlations among traits and of inter-environmental heritability of the newly-defined net basis of selection may temper such optimism. Recent reports of negative relationships between scores of body conformation and milk production (Freeman and Dunbar, 1955) provide an example of a possibly unnecessary impediment in selecting for an economic character. Perhaps only a redefinition of desirable conformation is needed! However, earlier estimates of this relationship were less discouraging (Harvey and Lush, 1952; Touchberry, 1951).

Multiplicative Gene Action and Combination of Components of Total Performance

The fact that heterosis tends to be much greater for total performance than for its components has been noted in crosses of inbred lines of guinea pigs by Wright (1922) and of swine by Dickerson (1949, 1951). Similar results have been reported in poultry by Warren (1942), Dickerson *et al.*, (1950), King and Bruckner (1952), Glazener *et al.*, (1952) and others. This phenomenon may be ascribed to the fact that total performance tends to behave as a multiple of its components. For example, annual egg production per egg set to produce the laying pullet may be thought of as the product of fertility, hatchability, viability, sexual maturity, egg production, egg size, egg quality, etc. A small amount of heterosis in each component becomes relatively very large for the total product.

An interesting example is provided by the results shown in Figure 6 for nine strains of White Leghorns, some partially inbred, their 72 crosses and an outbred control strain, in 1953. Mean performance of parental strains and of all crosses is shown as percentage of the mean for the outbred control strain. All pullets were from the same five weekly hatches and were brooded, reared and housed together. Respiratory disease was severe for pullets hatched during this period. The features of interest here are:

(1) the number of components showing heterosis;

(2) the much greater heterosis (or inbreeding effect) for total product than for its components.

Fertility (and to a lesser degree, hatchability) is a function of parental phenotype and would be expected to exhibit heterosis only when strain-crosses are used as breeders.

Percentage superiority of crosses over the nine pure strains, giving equal weight to each percent of superiority in viability from zero to ten weeks, hen-housed egg production, egg size and shell thickness, was 229 percent. This ignores the gain in

hatchability and in viability from 11 to 20 weeks of age and the slight loss in albumen score. This example is extreme, probably because of the complex of respiratory disease which persisted through the pullet year. Supplementary data indicates a much smaller superiority of crosses over the control strain when respiratory infection is not serious, which is an illustration of the genetic-environmental interaction discussed earlier.

A combination of partial dominance and multiplicative gene action could help explain (1) an apparent lack of dominance for phenotypic variation within populations and (2) consistent indication of dominance from results of crossing strains, breeds or inbred lines, when both are measured on the observed arithmetical scale. Within a given inbreeding population multiplicative gene action *without dominance* would place the heterozygote below this mean of the homozygotes (for example, $AABB = 1.2 \times 1.2 = 1.44$, $AaBb = 1.1 \times 1.1 = 1.21$ and $aabb = 1.0 \times 1.0 = 1.0$); this would mean apparent negative dominance for the observed phenotypic values. Whatever degree of dominance exists for multiplicative gene action will be underestimated from intra-population analysis of observed phenotypic values for total performance as well as for its components (for example, $AABB = 1.2 \times 1.2 = 1.44$, $AaBb = 1.105 \times 1.105 = 1.22$, $aabb = 1.0 \times 1.0 = 1.0$ equals no dominance on observed scale but slight dominance of the favorable multiplicative effect). However, when populations are crossed which differ in gene frequencies at many loci but have similar phenotypic levels of performance, multiplicative combination of gene effects would act to magnify rather than mask the effects of dominance (for example, $AAbb \times aaBB = AaBb$ with performances $1.2 \times 1.0 = 1.2$, $1.0 \times 1.2 = 1.2$ and $1.105 \times 1.105 = 1.22$, respectively). These consequences of multiplicative gene action could be important if average degree of dominance is slight; they need to be investigated more theoretically and through analysis of log-transformed data. Neal (1935) and Hull (1952) have interpreted linearity in corn yield between F_1, F_2 and P_1 as evidence of strictly additive gene action, but the fit needs to be tested further in animal data.

Genetic Regression

Deleterious reverse mutation and random loss of genes through inbreeding are both possible sources of genetic loss which would occur even though the environment remained unchanged between generations. The fact that selection in either natural or domesticated populations is directed toward the whole complex of multiple objectives which constitute total performance or reproductive fitness means that the selective advantage of individual genes will be very slight, particularly when the selective advantage of a gene varies between environments. Under these circumstances even mild inbreeding surely, and reverse mutation possibly, will be a significant source of genetic regression which will cancel a part of the genetic response to selection.

Selection for Balance

To the extent that intra-environmental selection favors balanced or intermediate levels of gene effect on the different precursors of a given component of performance, less of its genetic variability will be due to average gene effects. Most of the deviations from average gene effects are not included in calculating expected response to selection based upon individual or progeny performance within a population.

When the desired balance is one between separate components of performance, precious selection pressure may be squandered by selecting individuals closely for uniformity or conformity to some intermediate optimum value for a trait such as egg size or shape, since segregation and recombination will regenerate most of the range again in each generation. The alternative of selection only in one direction for each trait but varying attention given each trait according to the deviation of the population mean from the desired opimum allows selection to make use of more of the genetic variability present.

Summary and Conclusions

Time-trends in performance of a closed population of chickens were compared with the response expected from known intra-year selection differentials and heritabilities for separate components of performance when a steady environment and independence of components are assumed. Evidence concerning environmental changes, results from crossing strains, and estimates of genetic and phenotypic correlation among components also were considered.

The results suggest that continuous deliberate and natural selection for total performance operating in a domesticated population may be considered as the counterpart of natural selection for reproductive fitness in wild populations. In either case, an approach to fluctuating plateau is likely although intra-environmental variability due to average gene effects and the selection applied remain as large as ever for separate components of performance.

Such *apparent* refractory response to selection is attributed partly to inter-environmental slippage arising from an adverse environmental trend or a succession of different environments, under which genetic-environmental interaction allows genetic response to selection within an environment but makes this response partially or completely irrelevant under subsequent environments. This leads (1) to average superiority of heterozygotes in total performance or reproductive fitness over a series of environments, but to a much lesser degree of dominance for the *net* effects of genes within the narrower range of environments of a single genera-

tion, and (2) to fluctuating rather than to stable equilibrium gene frequencies, because of irregular reversals of selection response at individual loci as the population moves from one population of environments to another. A major and sustained change in the pattern of selection applied is the equivalent of a similar major change in environment; either is likely to permit progress for a time toward a new plateau.

Intra-environmental slippage in selective response also is to be expected as a result of (1) smaller or more negative genetic than phenotypic correlations among components leading to lower heritability for total performance than for its components, as a consequence of prior selection, pleiotropy and dominance, and (2) genetic regression, from random loss of useful genes and from reverse mutation. Deviations from average gene effects due to interaction of non-alleles are largely excluded from estimates of heritability and thus from the estimates of expected response to selection. Multiplicative gene action is indicated by the multiplicative combination of heterosis effects on components of performance in crosses between strains, breeds or inbred lines; this would tend to mask dominance in phenotypic variability within populations but magnify it in crosses between populations.

The problem of exploiting genetic variability in populations of cross breeding plants and animals which have become refractory to continued intra-environmental selection for individual and progeny total performance cannot be evaded. Methods of selecting directly for performance in crosses should reduce intra-environmental slippage but will minimize inter-environmental slippage only to the extent that crosses can be tested under diverse environments within each generation or cycle of selection.

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