Artificial Selection of Desired Characteristics in Insects

By Anita M. Collins[1]

Introduction

Artificial selection is the alteration over time of phenotypic characteristics of a population of organisms through the intervention of man. Several major texts deal generally with theoretical and actual application of the science of genetics to artificial selection (see Lush 1945, Mather 1949, Falconer 1960, Li 1968, and Crow and Kimura 1970). Articles on artificial selection for insects include many on *Drosophila* spp. (see Robertson and Reeve 1957, Clayton et al. 1957, Madalena and Robertson 1975, and Frankham 1977) and on *Tribolium* spp. (see Wilson et al. 1965, Enfield et al. 1969, and Berger and Freeman 1974). Reviews of the application of artificial selection to insect populations (Bell 1963, Mackauer 1972, and Hoy 1976) have all held that it has great potential. Artificial selection has been used successfully for some time on two important domesticated insects—the silkworm, *Bombyx* spp. (Aizawa et al. 1961, Yokoyama 1979), and the honey bee, *Apis mellifera* Linnaeus (Rothenbuhler 1958, 1979; Rothenbuhler et al. 1968; Kerr 1974; Cale and Rothenbuhler 1975; and Goncalves and Stort 1978). Attempts have also been made to improve various insect parasites for use in pest control (Wilkes 1947; DeBach 1958, 1964; Hoy 1979; and Roush 1979).

A selection program must begin with basic information about the organism and the traits to be selected. Some understanding of the creature's reproductive strategies is necessary, including such things as how many males mate with each female, whether a male can mate more than once, how many young are produced at one time, and what interrelationships exist among those offspring. Theories about artificial selection in animals deal mainly with mammalian-type systems—a single mating (one male × one female), few offspring at one time, diploid inheritance in both parents, etc. The theories must be modified, then, for insects like the social, multiple-mating, haplodiploid honey bee. In any case, one must have a clear idea of what characters are to be selected and exactly how they will be measured. Knowledge of how the trait is inherited—whether it is controlled by one, a few, or many genes, will profoundly affect how it will be selected. Estimates of a genetic parameter called heritability will predict whether the trait will respond to selection, by how much, and how fast. Given this basic biological information, one can choose a breeding plan and its selection criteria intelligently.

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Desired Characteristics

Measurement

Many characters have been modified by selection. Morphological traits such as body weight (Enfield 1972) and thorax or wing length (Robertson and Reeve 1952) may be measured easily. Time of pupation (Englert and Bell 1970), temperature adaptation (White et al. 1970), disease resistance (Aizawa et al. 1961), DDT[2] resistance (King 1954, Robertson 1957), and sex ratio (Simmonds 1947), all physiological traits, may require more complex assessment. Evaluating behavioral traits such as host preference (Allen 1954), pollen collection (Mackensen and Nye 1966), geotaxis (Erlenmeyer-Kimling et al. 1962), phototaxis (Choo 1975a), dispersal (Ogden 1970), walking (Choo 1975c), and mating behavior (Manning 1968, Eoff 1977) may also be rather complicated. The special aspects of behavior genetics have been considered by Hirsch (1967), Dobzhansky (1972), McClearn (1973), Ehrman and Parsons (1976), and Fuller and Thompson (1978); and Boller (1979) discusses the special application of behavior genetics to insect rearing.

Some traits may be measurable only on certain individuals of a population or at certain times. For example, some traits such as egg-laying capacity, may be sex limited, or they may simply be expressed differently in each sex (Enfield et al. 1975). Other traits may require the organism's death before measurements can be made; so evaluation must be based on its closest relatives. In these cases, tests are conducted with progeny or sibs—individuals from the same litter or egg hatch of the same parents—leaving some alive and sacrificing others for measurement purposes. A familiar example of this form of study exists in the dairy industry, where bulls are evaluated on the basis of their offspring from many dams and used for more intensive breeding only if they are selected as sires. In insects, which usually have distinct

[2]1,1,1-Trichloro-2,2-bis(*p*-chlorophenyl)ethane.

life stages or castes, a particular character may have to be measured during one stage (Tucker 1980). The stinging behavior in worker honey bees, for instance, is not expressed by queens and drones. And finally, many behaviors in social insects reflect the activity of a group rather than of an individual. Honey production is an activity carried out by an entire honey bee colony; so the colony becomes the experimental organism (Rothenbuhler 1960).

Mode of inheritance

Once a technique for measuring a particular trait has been devised, understanding how the trait is inherited may be useful. The two major categories of traits are discrete, or qualitative, and continuous, or quantitative. With discrete traits, such as number of hairs and eye and body color, there may be one or only a few major genes controlling its expression. In these instances, relatively simple relationships exist among the several states of the trait (for example, brown eye color—the wild type—is dominant over the mutant scarlet). The dominant brown phenotype will be expressed if there are one or two brown alleles present. The recessive scarlet phenotype is expressed only when the organism is homozygous, carrying two scarlet alleles. There are also cases when incomplete dominance occurs, and crosses between discrete phenotypes will yield an intermediate phenotypic expression. An inheritance pattern of the discrete type may vastly simplify the selection procedure, perhaps even enabling complete fixation of one expression in one generation. Falconer (1960) discusses implications of simple modes of inheritance; more detailed discussions of the genetic analysis of discrete traits are in general genetics texts such as Strickberger (1968) or Merrell (1975).

Most characters that interest insect breeders will be quantitative traits. For characters like DDT resistance (Pielou and Glasser 1952), body weight (Bartlett et al. 1966), and mating behavior (Manning and Hirsch 1971, Kraemer and Kessler 1975), many genes are influencing the phenotypic expression of the trait, and clear-cut dominance relationships and modes of inheritance are not seen. Because quantitative traits are more complex and more common than qualitative traits, my discussion of artificial selection deals mainly with quantitatively inherited characters.

Effect of environment

The phenotype, or observable properties, of an organism is what is being measured. The phenotype is the result of interactions between the genotype, or genetic makeup, of the organism, and the environment that it lives in. For selection to occur, the phenotype must have some variation that can be attributed to the genotype. If all variation of the phenotype is caused by environmental conditions, then selection cannot be successful. Therefore, studies need to be conducted with a controlled environment that will reduce environmental variation during measurement of a phenotype. Measurements may have to be made in precisely controlled environmental chambers with the insects at a constant temperature and humidity, on the same food source, measured at the same age, and so forth. The more closely all environmental conditions that might affect the character can be controlled, the more accurate will be the assessment of the genotypic variation present in the population. The effects of environment on heritability and selection response are discussed by Falconer (1952) and Rendel and Binet (1974).

The type of character being measured will also influence the amount of environmental variation affecting the expression. Morphological and physiological traits are less open to environmental influence during development and expression than are behavioral traits.

Measured phenotypic variance, V_P, can be divided into several components. The first is the genetic variance, V_G, which itself can be divided into additive genetic variance, V_A, dominance deviation, V_D, and interaction deviation, V_I. All other variation is environmental, V_E, and is considered beyond experimental control. So

$$V_P = V_A + V_D + V_I + V_E.$$

Of the three types of genetic variance, V_D and V_I are generally considered to be less important than V_A. V_D arises from the property of dominance among the alleles making up a genotype; and V_I, usually rather small, is generally treated as a negligible complication. The breeding value of the organism, V_A, can be measured relatively easily in several ways and expressed as a ratio of additive genetic variance to total phenotypic variance. This ratio is the estimated heritability. The assumption made here, that environmental deviations and genotypic values are independent of each other, is not entirely true. Kulinčević and Rothenbuhler (1975), for example, found that susceptibility to disease varied with the virulence of the pathogen. One way this complication can be overcome is by specifying that the genotype be measured under specific conditions. Another assumption that is not always justifiable is that a specific environmental difference has the same effect on different genotypes (Bray et al. 1962, McNary and Bell 1962, Jinks and Connolly 1975). But comparing genotypes under favorable and unfavorable conditions may show that a genotype that does best under one set of conditions may not have the greatest yield or fitness under another. This variance of interaction between genotype and environment, usually regarded as part of the environmental variation, should not be overlooked in measurement of a characteristic, par-

ticularly when the same species is studied in different habitats (Druger 1962, Nye and Mackensen 1970).

Heritability

One of the most important properties of a quantitative trait is its heritability, h^2, the ratio of additive genetic variance to the total or phenotypic variance;

$$h^2 = V_A/V_P,$$

that is, the proportion of total variance attributable to additive effects, which are the average effects of all genes affecting a character. The size of h^2 indicates how alike related organisms are. The most important function of h^2 in the genetic study of quantitative traits is that it can predict how reliable the phenotypic value is as a guide to the organism's actual breeding value. So heritability is a measurement of the proportion of the phenotypic variation that is attributable to genetic causes amenable to selection.

The value of heritability ranges from 0 (no genotypic influence on the variation of the trait) to 1 (all variation of the trait is genetically produced). Traits that are closely connected to reproductive fitness generally have low heritabilities. For example, values for litter size, egg production, egg-laying rate, and ovary size range from 0.1 to 0.3. Another reason for a low heritability value is inefficient measurement. If the technique does not accurately measure the desired trait, environmental variance, V_E, may be increased considerably; the proportion resulting from additive genetic causes would be reduced; and heritability would be decreased. Higher h^2-values are expected in characters less important to reproductive fitness such as coat color, patterns of spotting (h^2=0.95 in mice; Strickberger 1968), and spot number (McWhirter 1969). These traits may be controlled by one or just a few genes. As an example of h^2-values, consider some traits of *Drosophila melanogaster* Meigen: abdominal bristle number, 0.5; body size, 0.4; ovary size, 0.3; and egg production, 0.2 (Falconer 1960).

Heritability is a property not only of a specific character but also of the population and of the environmental circumstances influencing measured individuals. Environmental variance depends on the conditions of culture or management of the organism—more variable conditions reduce the heritability, more uniform conditions increase it. Genetic components are influenced by gene frequencies in the population, and these may differ between populations because of their different histories. Small populations maintained for a long time become more genetically uniform than do large, randomly mating populations, and they show lower heritabilities.

The simplest way to evaluate heritability would be to measure a population of mixed genotypes and one of identical genotypes in several environments. The first population would provide an estimation of total phenotypic variance;

$$V_P = V_A + V_E.$$

The second would measure only environmental variance, because all genotypes would be identical. The difference between these two phenotypic variances would be the additive genetic value. Heritability could then be directly calculated from the ratio of additive genetic variance to total phenotypic variance.

The standard approaches to measuring heritability require comparing the merits of related individuals and estimating heritability from the covariance between them or from a regression or correlation coefficient. Estimates of heritability from covariance and correlation in domestic animals must consider a major environmental source of covariance, the maternal effects. But such influences as a common uterine and rearing environment for animals of the same litter or mother may not be particularly important in insects.

A straightforward method for estimating heritability is to use the regression of offspring on parent. The data, measurements of parents and the mean values of their offspring, are used to calculate a regression coefficient, b. If this is the regression of offspring on one parent, b_{op}, it is a valid measure of $\frac{1}{2}h^2$; if the regression is offspring on midparent (average of the two parents), b_{op}, it actually measures h^2. Examples of using this method for estimating heritability in insects are found in Enfield et al. (1966), Morris and Fulton (1970), and Wong and Boylan (1970).

Heritability is most often estimated by sib analysis. Each of several males (sires) is mated to several females (dams), and some offspring from each female are measured. The individuals measured form a population of half-sib and full-sib families. An analysis of variance is calculated to divide the phenotypic variance into components attributable to differences in sires, in dams mated to the same sires, and among offspring of the same female. The variance component from sires, dams, and the total must be calculated from the mean square values (table 1). The total variance, or phenotypic variance, is calculated because it is not necessarily equal to the observed variance as estimated from the total sum of squares, though the two seldom differ by much. With these values, estimates of heritability can be made from the sire component, the dam component, or a combination of the two (table 2).

Table 1.—Formulas for calculating components of phenotypic variance from analysis of variance mean squares (*MS*) for a population of sibs and half-sibs[1]

Source of variance	Variance	Calculation[2]
Between sires	σ^2_{sire}	$= MS_{sire} - MS_{dam}/dk$
Between dams	σ^2_{dam}	$= MS_{dam} - MS_{within}/k$
Within progenies	σ^2_{within}	$= MS_{within}$
Total population	σ^2_{total}	$= \sigma_{sire} + \sigma^2_{dam} + \sigma^2_{within}$

[1]See also Falconer (1960).

[2]d=number of dams; k=number of offspring per dam.

Table 2.—Formulas for calculating heritabilities from phenotypic variances determined from analysis-of-variance mean squares for a population of sibs and half-sibs (table 1)[1]

Heritability estimate	Calculation
h^2_{sire}	$4\sigma^2_{sire}/\sigma^2_{total}$
h^2_{dam}	$4\sigma^2_{dam}/\sigma^2_{total}$
$h^2_{combined}$	$2(\sigma^2_{sire} + \sigma^2_{dam})\sigma^2_{total}$

[1]See also Falconer (1960).

Heritability can be estimated from the offspring-parent relationship in a population with the structure set up for sib analysis. For many domestic animals, however, such a population structure has few male parents, so the simple regression of offspring on one or the other of the parents is unsuitable. But heritability can be estimated from the average regression of offspring on dams—regressions are calculated for each group of dams mated to the same sire, and they are pooled to give a weighted average.

These methods of estimating heritability have been developed for use with diploid organisms. If the particular insect being evaluated is not diploid in both sexes, somewhat different forms may be required. For example, Rinderer (1977) modified sib analysis for the honey bee, a haplodiploid colonial organism; he also delineated several problems of estimating heritability in a haplodiploid social organism.

Artificial Selection

Selection methods

Selection of males and females with the desired characters to parent the next generation can be done in several ways (see Wright 1921, Mather 1941, and Hazel and Lush 1942). Single individuals can be chosen on the basis of their own phenotype (for example, the expression of a particular mutation) to be mated with a specific other individual. This is individual selection. In a variation on individual selection called mass selection, large numbers of selected individuals are put together en masse for mating, a common occurrence in rearing large numbers of insects.

Family selection is the choice of individuals based on the mean phenotype of the family that they come from. This method requires selection of the entire family for use as parents and is preferable for characters having low heritability. But the method is limited because all members of the family will generally be reared in the same environment. One variation of family selection is sib selection, usually used for traits requiring the death of an organism, in which an individual's phenotypic value is based on measurements of its siblings. Another is progeny testing in which offspring are measured. If only the best individual from each family is chosen for mating, the method is referred to as within-family selection. This approach is desirable if a common environment, such as a shared uterus, has a major effect on the size of the environmental variance.

In all cases of selection by group, the calculations of h^2 and R (response to selection), differ from those used with individual selection (see Kojima and Kelleher 1963, Wilson et al. 1965, Berger and Freeman 1974, and Katz and Enfield 1977). For these calculations, an assumption is made that the generations are kept separate—individuals are selected from a base population, used to parent offspring (first selected generation), and only the offspring are chosen to parent the second selected generation. The generations would *not* be separate if selected individuals from the base population and the first generation were intermated to produce the second generation. For most insect-rearing procedures, generations will probably be discrete.

Response to selection

Selection will change the population mean of the selected character by an amount, R, the response to selection. A second parameter, selection differential, S, is the measure of average superiority of those individuals selected as parents over the total population. R and S (fig. 1) are related by the regression coefficient of the offspring on their parents, b_{op}. So

$$R/S = b_{op}, \text{ or } R = b_{op}S.$$

If there are no significant nongenetic causes of resem-

blance, such as maternal effects, and the selected phenotype is not correlated with general fertility and viability within the selected population, then R and S can be related directly to heritability. So

$$R=h^2S.$$

The relationship of R, S, and h^2 is most useful for prediction. Once parents have been selected for production of the next generation, S will be known. The value of b_{op}, the regression coefficient, can be calculated from the previous generation; or an estimate of heritability can be made from the parental population. Selection does change the population, and these two values, b_{op} and h^2, can change with the selection. Theoretically, then, the prediction is accurate only for a single generation. In practice, however, the predicted value of regression or heritability actually holds true over several generations (Falconer 1960).

There are two factors affecting the size of the selection differential, S. These are the proportion of the population selected to be parents and the phenotypic standard deviation of the trait being selected. If a small proportion of the population is selected for mating, that proportion will represent only the most extreme members of the population; their mean value, $\bar{X}p'_o$, will be very different (high value of S) from the mean of the total base population, $\bar{X}p'_o$ (fig. 1). But, if the proportion of parents is larger, many will have more intermediate values and the parental mean, $\bar{X}p'_o$, will be less different (low value of S) from the total mean, $\bar{X}p'_o$. The phenotypic standard deviation, or variation, affects the size of S, the difference between selected extremes and the base population. With large

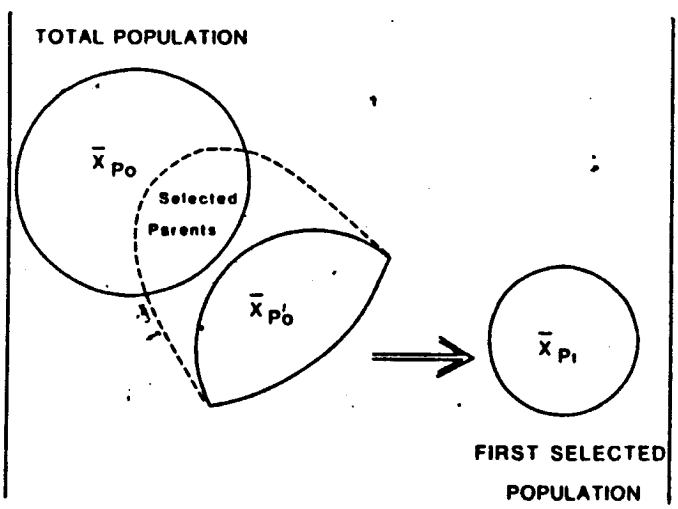

Figure 1.—Diagrammatic representation of response to selection, R, and selection differential, S. $R=\bar{X}p_1-\bar{X}p_o$, and $S=\bar{X}p'_o-\bar{X}p_o$.

variation, the extremes will be quite different from the average values for the trait, hence a high value of S. With little variation, the differences can be slight. The estimate of S for different traits and different populations is expressed in terms of σ_p (square root of V_p) to determine the quantity i, intensity of selection. So

$$S/\sigma p=i, \text{ or } R=i\sigma_p h^2.$$

Manipulation of heritability, intensity of selection, or phenotypic variation can improve the rate of response, R. To increase heritability, one must decrease the environmental variance by manipulating rearing and measurement conditions. Decreasing proportion of individuals selected, and so increasing the intensity of selection, will have a similar effect. Of course, this decrease is limited by the size of the population being used for selection, which will be somewhere between the maximum number of organisms that can be reared and measured at any one time and those required to maintain a biologically functioning population. The selection intensity practiced per unit of time can also be increased by decreasing the generation interval or by maximizing the number of offspring produced in each generation. For honey bees, this increase might be several hundred colonies per year, while for *Drosophila* the number of measured units (flies) may be several orders of magnitude greater. Phenotypic variation is much less amenable than heritability or intensity of selection to manipulation because it is limited to what is biologically available. To manage phenotypic variation, a breeder should insure that the base population has maximal variation included in its members, or he should use crossbreeding during the selection program.

While artificial selection is being done, natural selection will also be affecting the population. Mainly, it will alter the fertility of the selected parents and the viability of the offspring (Wilkes 1947, Hiraizumi 1961, Kress et al. 1971). Using weighted values from the parents based on the different numbers of offspring that each group contributes to the succeeding generation, one can recalculate the selection differential. This quantity is the effective selection differential rather than the expected selection differential. If there is a large difference between these two calculated values of S, then this population is undergoing a great deal of natural selection.

There will be some variability in the population mean from generation to generation (fig. 2), mainly because of how the environment affects the expression and measurement of the phenotype. So, to be most precise, estimates of R need to be made over several generations. Such estimates are made by fitting a regression line to a series of generation means (Robertson and Reeve 1952, Englert and Bell 1970). The slope of this regression line then represents the best measure of the average response per

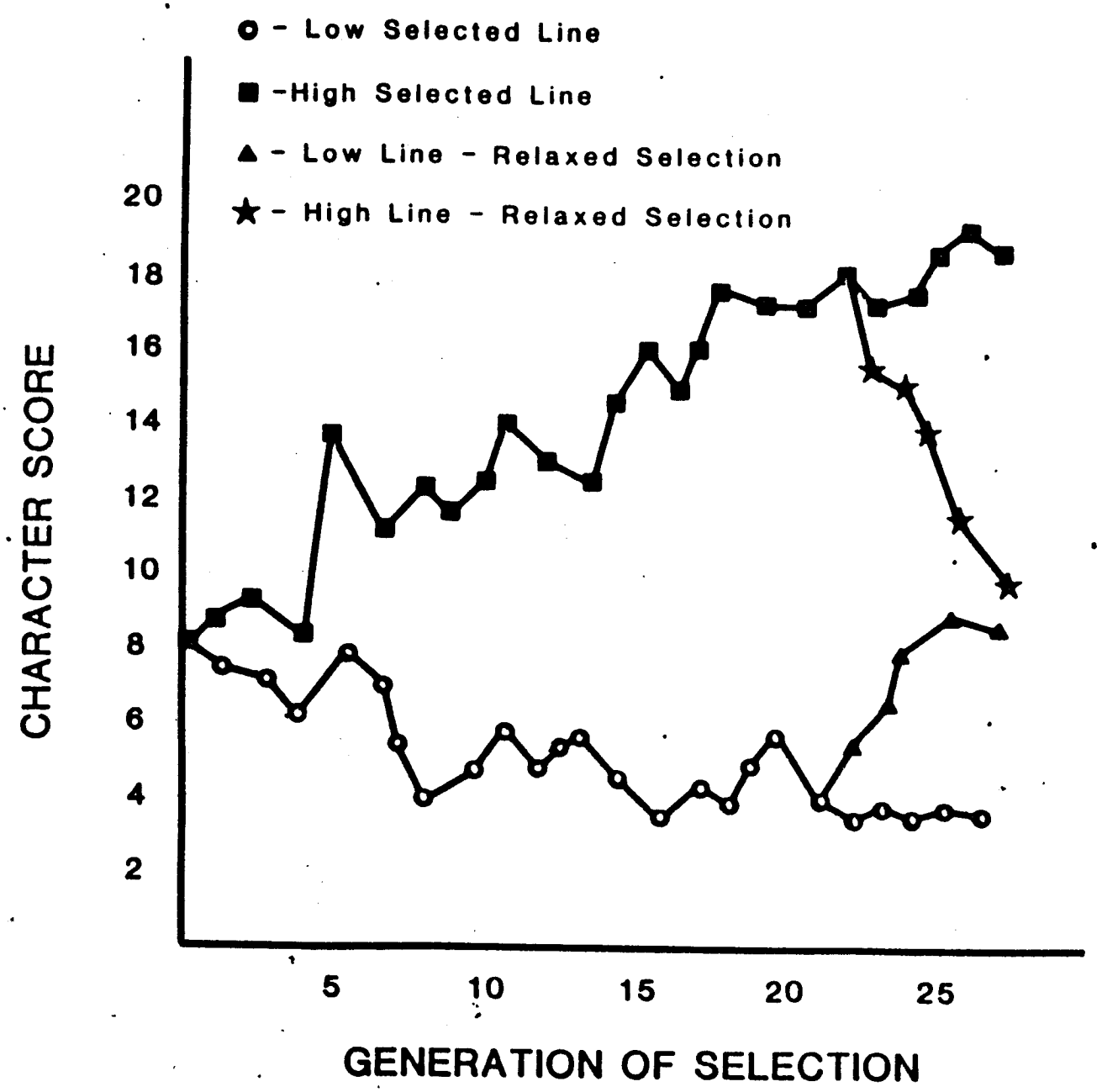

Figure 2.—Results in a hypothetical bidirectional selection program.

generation. If selection is bidirectional—for example, if one is selecting for high body weight in one population and low body weight in another—calculation of the response will be better than a comparison between a selected population and an unselected control; bidirectional selection gives a greater divergence of the two populations being compared.

Heritability can also be estimated as

$$h^2 = R/S.$$

If the value for S used in this calculation is the effective, or weighted, selection differential, it will eliminate the effects of natural selection and estimate heritability only on the basis of artificial selection. This realized heritability may not be the best estimate of the actual value of h^2, but it is the most useful figure for comparing the effectiveness of different selection procedures, especially when different intensities or methods of selection are in use. Realized heritability is usually calculated as the slope of a regression line fitted to a plot of the generation means, R, by the cumulative value of the selection differential, S (Meyer and Enfield 1973, Choo 1975a).

Other considerations in selection

In the same way that generations differ, responses to selection may differ between different lines or populations undergoing selection (Defries and Touchberry 1961) Genetic parameters such as heritability and the regression of offspring on parents may also differ. If the selection is bidirectional, the response may be asymmetric (Englert and Bell 1970). That is, selection may proceed more rapidly in one direction than in the other (fig. 2). Falconer (1960) gives several possible causes for this variation in response.

The genetic structure of populations undergoing selection will change through generations. One of the effects of this change is that the size of the response does not remain at its initial level but becomes smaller with succeeding generations until the population reaches a plateau for the phenotype, the selection limit. In figure 2, for example, the low-selected population has reached a plateau at generation 20 because the desired alleles have been fixed (Bell et al. 1955, Brown and Bell 1961, McEnroe 1967). If further progress is desired, the population must be given greater variation through the introduction of other alleles. These new alleles can be introduced by crossing highly selected lines, by introducing environmental stress, by changing the selection criteria, by using radiation (Bartlett et al. 1966), or by outcrossing the selected population.

At the same time that selection for a desired trait is being carried out, there may be unintentional selection of correlated traits (Robertson and Reeve 1957, Hiraizumi 1961, Wong and Boylan 1970, Kress et al. 1971, Choo 1975b). Among the several causes for unintentional selection is pleiotropy—one gene influences more than one characteristic. Or several genes may be closely linked on the chromosome, and selection for one gene will inadvertently carry along its linked associates. Conversely, beneficial combinations of several genes may have evolved together and be closely linked; though, if these linkages are broken up during selection procedures, the product might be less desirable or even harmful, phenotypes. Finally, traits may be correlated in some way because of common parts in those traits. For example, honey bees have a 0.5 correlation between the rate of hoarding sugar syrup in the comb and their response to alarm pheromones. So high hoarders are usually fast responders. This correlation may exist because response to a chemical stimulus (sugar or alarm pheromone) is necessary for both types of behavior (A. M. Collins and H. A. Sylvester, unpublished data).

A major consequence of continued selection, particularly in small populations, is inbreeding depression, a reduction in the reproductive capacity and physiological efficiency of the organisms undergoing selection. Hybrid vigor (heterosis) occurs when the fitness lost during inbreeding is restored after two inbred lines are crossed (Cale and Gowen 1956, Enfield et al. 1966). One selection method uses both inbreeding depression and hybrid vigor by inbreeding many lines selectively for several generations then crossing them to restore their fitness. Generally, this technique is effective only in closely related populations such as those reared in laboratories. Since widely different wild populations fail to show heterosis when crossed, each may be adapted to its own environment, and progeny produced by crossing them are adapted to neither (Falconer 1960).

In some organisms, breeding can have dramatic effects. In honey bees, for example, the system for sex determination is tied to homozygosity of a specific locus. Homozygous and, in the case of haploids, hemizygous bees are male. Heterozygous bees are female. Continued inbreeding rapidly increases homozygosity. Within a few generations, the probability that many of the diploid bees will also be homozygous and develop as males becomes quite high. As diploid males are generally destroyed by the workers, the colony rapidly deteriorates. If such a situation arises in organisms undergoing selection, the rate of inbreeding during selection must be kept low.

When lines are crossed to make use of hybrid vigor, some crosses will produce progeny that are more fit than those produced by others. This variation is due to the combining ability of each line. If the ability of a particular line to combine with several other lines is measured and a mean calculated, the result is the general combining ability. Specific combining ability is the measurement of increased vigor between two lines. One can choose the expression of combining ability by using a program called reciprocal recurrent selection (Kincaid and Touchberry 1970, McNew and Bell 1970). In this plan, the selection of parents in the lines is based on the performance of their progeny from crosses with another line. The best combining parents are then mated within their respective lines.

The selection index

In practice, the least effective way to select for several characters is to use tandem selection—to select for one trait at a time. Instead, an independent culling level can be established for each trait being selected, and all animals below this level for any trait are culled. This technique requires many more animals than are needed for tandem selection to have enough selected to carry on a viable population. And selection may be slowed if culling levels must be reduced to leave a viable breeding population. So the best way to select for several characteristics is to use a selection index, which combines all the phenotypic measurements into a single value. Each trait may be weighted according to its relative economic value, heritability, and correlation with other traits in the index. The result is one number that determines the culling level (Hazel 1943, Falconer 1957, Tallis 1962, Okada and Hardin 1970, and Yamada et al. 1975). Hoy (1979) gives an excellent flow chart showing the decisionmaking and experimental steps in developing such a program. Before attempting to develop an artificial selection program for a particular organism, one should review the literature on related organisms to discover if there may be special problems because of their specific biology.

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