CHAPTER 12

Selection

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I. INTRODUCTION

Honey-bee breeding is a small subset of the much larger enterprise of farm-animal breeding and, to some extent, of plant breeding. The comparative enormity and profitability of, for example, the cattle, swine, and poultry industries are the economic underpinnings of population-genetic and stock improvement theory. A fuller review of this theory, which sets the foundations of honey-bee breeding, can be found in Lush (1945), Mather (1949), Li (1955), Lerner (1958), Falconer (1960), and much of this volume. Lerner and Donald (1966) provide a less mathematical approach to the subject that considers the interplay between the technology and the economics of breeding, which should be of interest to both geneticists and practical bee breeders.

Most breeding programs are designed so that the "best" parents are selected and used to produce the next generation. In general terms, the "best" parents should produce the "best" offspring and the average quality of the stock is improved. Such guidelines are deceptively simple, especially with honey bees.

This chapter suggests ways to define and measure honey-bee characteristics so that the "best" parents for honey-bee stock improvement programs can be selected. Home computers make possible the application of fundamental selection theory to the selection programs of small family-owned bee-breeding enterprises. Since these form the majority of bee-breeding enterprises, this chapter speaks primarily to the needs of smaller programs.

II. BEE IMPROVEMENT TOOLS

Humans have been involved in bee husbandry since prehistory (Crane, 1983). However, the breeding of bees and hence their genetic improvement awaited the developments of movable-frame beekeeping equipment (Langstroth, 1853) and methods to produce large numbers of queen bees (Doolittle, 1888). The addition of instrumental insemination techniques for honey bees (Watson, 1927; Nolan, 1932) and their later improvement (Laidlaw, 1944; Mackensen, 1947, 1948; Mackensen and Roberts, 1948; Harbo, Chapter 15) have brought the mating of bees under complete control and "opened a wide door to both bee breeding and genetics" (Cale and Rothenbuhler, 1975).

Throughout the world, apiculturalists have looked through this door and agreed that it is not only desirable but, in some cases, necessary that the discoveries of the past 150 years be used to improve honey-bee stocks or to maintain already improved stocks. However, major differences of opinion exist concerning the definition of improved stock.

III. DEFINING IMPROVEMENT

A. Commercial Interests

World-wide, apiculture is extremely diverse. As an agricultural enterprise it involves corporations that handle many thousands of colonies with modern mechanical technology, small single-family businesses, still smaller side-line businesses used to supplement incomes from other sources, and rural development programs designed to increase income of individuals and groups in developing nations.

These commercial enterprises realize profits mostly from the sale of honey and wax to the general public and of queen bees, colonies, and package bees to other beekeepers. In some parts of the world, colonies of bees are rented for pollination services. Additionally, royal jelly, propolis, and pollen are sold, usually in small quantities. World-wide, some commercial beekeepers make most of their living producing and selling such products.

This wide variety of commercial interests leads to many differing views of what constitutes stock improvement. Improved honey production, handling qualities of bees, colony population growth, wax production, and efficient pollination of specific crops may or may not be desired depending upon the specific origin of a beekeeper's profit. Generally, improved stocks which show increased production in a broad sense with reduced management costs are desired.

B. Recreational Interests

Many beekeepers in much of the world keep bees for recreation. In some areas recreational or hobby beekeepers far outnumber commercial beekeepers. In these areas the commercial beekeepers often earn much of their living by supplying queens, bees, materials, and advice to the hobbyists. Although recreational beekeepers usually value the harvest of at least some honey, characteristics other than productivity often lead their lists of desirable improvements. Some urban hobbyists require especially gentle bees. Others, particularly in Europe, want bees that are typical of the subspecies that evolved in their areas. Still others desire bees having a specific morphological characteristic such as a black or yellow body color.

C. Geographical Range

Beyond this, the range of commercial and hobby beekeeping with *Apis mellifera* extends throughout the world from the tropics to above the arctic circle. This range includes the Old World with its wide variety of ecogeographical subspecies and, through human introduction, the New World areas of the Americas, Australia, and New Zealand, and to some extent the home ranges of *A. cerana, A. dorsata,* and *A. florea.*

This geographical disparity leads to still more variation in bee stock breeding goals. Beekeepers in temperate zones consider overwintering abilities and properly timed spring build-up patterns important. Beekeepers in tropical areas consider colony maintenance through rainy seasons or long droughts and rapid build-up when nectar flows begin important. These examples could head very long lists of stock quality needs, and hence breeding goals arising from the geographical range of beekeeping.

D. Species Diversity

The eastern honey bee, *A. cerana,* is a hive bee and is commercially exploited with much the same bee-husbandry techniques used with *A. mellifera.* Movable frame hives, queen-rearing, and even instrumental insemination (Woyke, 1975) are usable techniques with this species.

Currently, the use of *A. cerana* is restricted to its naturally occurring range (Ruttner, Chapter 12). This is because *A. mellifera* is considered a better honey producer. However, as the pests and parasites of the genus become spread throughout the world there may be specific uses for pollination or hobby beekeeping in other parts of the world where *A. cerana* is not currently found.

Much of the discussion concerning the effects of the commercial and recreational interests and geographic range on *A. mellifera* breeding goals also applies to *A. cerana*. Additional concerns, such as the improvement of pollination effectiveness on crops originating in Europe or Africa, may be breeding goals unique to *A. cerana*.

Additionally, *A. dorsata* and *A. florea* are not "kept" but feral. Colonies are commercially exploited through intensive organized honey hunting. The migratory and absconding nature of these species is a major obstacle to their commercial management. However, a beginning has been made at managed "migrations" of *A. florea* (Dutton and Simpson, 1977). Further management developments may stimulate attempts to breed more commercially desirable stocks of these species.

E. Many Stocks

Thus, what constitutes improvement in bee stock is dependent on a number of considerations. The tremendous variation in the world of beekeeping, including beekeeping interests, existing stocks of bees, local climates and floral resources, complicates the definition of bee stock improvement. Clearly, several answers and stocks are required (Rinderer, 1977), each suited to the needs and desires of specific groups of beekeepers.

IV. BREEDING FOR CONFORMATION

A. Ecogeographical Subspecies

Conformation breeding is the breeding of stock to fit a defined "ideal" phenotype for a breed. Because humans have only recently been able to breed bees, there are no recognized breeds defined by conformation standards as there are in other domestic animals. Indeed, professional beebreeder associations do not even have mechanisms to set standards and recognize breeds. The ecogeographical subspecies of bees (Ruttner, Chapter 2) replace breeds in the minds of some apiculturalists. Subspecies descriptions, especially those detailing morphological averages, are often misunderstood to be equal to breeder association conformation standards which define the ideal breed "type" and thereby establish the selection criteria for stock breeders.

Breeding bees toward a "type" set by the average of an ecogeographical subspecies is founded on the idea that the "best" bees for an area are those that evolved in that area. A related concept is that since such bees have become "best" for an area through the evolutionary processes of natural selection, selection to improve the stock is unnecessary. The role of artificial selection is to select against "foreign" genes introduced by the importation of bees representing other subspecies.

Certainly, such thoughts are not completely wrong. The evolutionary formation of subspecies is clearly a response to climatic and ecological differences. Ecogeographical subspecies represent the "best" bee for the naturally occurring ecology of an area.

However, neither are such thoughts completely correct. The "best" produced by natural selection is most certainly the best inclusive reproductive fitness suited to an area. It is doubtful that such inclusive fitness includes traits which best coincide with the economic interests of beekeepers, especially in areas extensively changed by modern agriculture.

It is even more doubtful that the economic value of bees can be improved or maintained by breeding programs based on morphology alone. The success of bees, both in nature and as agricultural animals, is too closely tied to behavior. Only when morphology is shown to be highly correlated genetically to desired economically related behavior will it serve as a useful measure in selection. Of course, some apiculturalists value morphological characteristics for their aesthetic qualities. Because of this, even breeding programs strongly aimed at producing stock having superior performance sometimes include a few morphological traits in their selection criteria.

Many apiculturalists wish to preserve local ecogeographical subspecies. In Europe, this desire sometimes is used to support arguments for the exclusive use of "conformation" breed stocks in a subspecies area. The goal of preservation is certainly desirable. However, it must be remembered that the complete description of a subspecies includes the variation of both morphological and nonmorphological characters as well as the average value of characters. The inclusion of bees as protected wild animals in larger nature preserves coupled with the exclusion of beekeeping in such areas would better serve the goals of preservation.

B. Commercial Stocks

In a very few instances, long-term selection by commercial bee breeders has produced surprisingly uniform stock which under the rules of large-animal breeder associations might qualify as a breed. The conformation standards of these stocks have been established by single beekeepers through years of practical beekeeping. Usually, such stocks have combinations of three to five strikingly improved characteristics. In other respects they seem similar to stocks of bees from which they were derived. Breeding goals with such stocks generally involve maintenance of stock quality rather than further significant improvement.

V. BREEDING FOR IMPROVEMENT

The majority of bee-breeding programs involve selection for specific stock-improvement goals. All such programs have resource limitations, and decisions in several areas must be made in order to optimize program success.

A. Genetic Theory

The foundations of selection rest in the mathematical disciplines of quantitative and population genetics. The basic starting point to the understanding of selection is the concept that phenotype (the characteristics of an animal which can be observed) results from the influences of the animal's genetics, the environment in which the animal is found and the interaction between these two factors. This concept can be extended to populations of animals. The variation of phenotypes in a population of animals can be attributed to the variation resulting from the genetics of the population, the variation resulting from the environment of the population and the interactions between these two sources of variation. The variation in phenotypes resulting from genetics can be further subdivided into different types of genetic events. Variance due to additive genetic events is especially important. Additive variance is the chief genetic cause of resemblance between relatives and therefore the chief determinant of how easily a population can be improved by selection (for further discussion see Collins, Chapter 11). One mathematical relationship for populations which has special interest, because it predicts response to selection, is

$$R = h^2S \tag{1}$$

where R is the predicted improvement or response resulting from selection, h^2 is the heritability of the characteristic under selection in the population, and S is the selection differential. Further, R is the difference between the average phenotypic value (the direct measures) of the parental population and the average value of the offspring of the selected parents, while h^2 is an estimate of the genetic variation in the population which is susceptible to change through genetic selection. As a proportion it ranges from 0 to 1. It serves as a guide to determine the reliability of phenotypic measures as measures of breeding value. The selection differential S is measured in standard deviation units as the difference between the average of the population of potential parents and the average of the selected parents. Since S is expressed in standard deviation units, so is R.

B. Measurement

Regardless of all else, the accurate measurement of characteristics is essential to a selection program's success. Only through accurate measurement can the relative breeding value (Collins, Chapter 11) of potential parents be determined.

Accurate measurement reduces the phenotypic variance. Since h^2 is the ratio of additive genetic variance (V_a) to phenotypic variance (V_p);

$$h^2 = \frac{V_a}{V_p} \tag{2}$$

reductions in V_p have the desirable effect of increasing h^2.

The most important way to increase accuracy is to make measurements on bees which are in a common environment and have had similar management histories. The group of colonies should have had an equal start at some point in their recent histories. Ideally, they then would be measured when apiary or other testing conditions permit a full expression of the colonies' capabilities. For example, honey production measures should be made during nectar-flow conditions which are typical of conditions in which the improved stock is expected to perform.

Second, more precise measures or repeated measures as a method to gain precision may improve accuracy. Whether or not they do can be determined for specific selection programs by comparing the ranking of breeding values obtained from more and less precise methods. Measurement and associated record keeping are expensive, yet they are essential to all breeding programs. Thus, the costs of measurement are important. Small increases in accuracy gained from costly measurement systems are likely valueless. The costs would reduce the number of colonies that can be evaluated. This may force a breeder to decrease the selection differential (Collins, Chapter 11) in an attempt to avoid the problems attending inbreeding (Woyke, Chapter 4; Laidlaw and Page, Chapter 13). Thus, the predicted response to selection may be reduced by using costly and precise measurements which do not greatly improve comparisons of breeding values.

1. Field Measurements

The nature of beekeeping often requires the field measurement of characteristics. Doubtless, field conditions increase environmental variation. Unless attention is given to reducing this variation, measurements may be sufficiently inaccurate that selection yields little or no improvement because of the relationships shown in Eqs. (1) and (2). In effect, the h^2 can be substantially reduced.

Uniform management of colonies is one important approach to reduce environmental variation in field tests. Using queens of equal ages introduced to equal-sized populations of bees, and equal amounts of equipment, diet supplements, drug treatments, etc., are useful. Depending on what is being measured, the time of day and weather conditions might also be important.

Often, commercial breeding programs require several apiary locations because large numbers of colonies will be tested. Different apiaries, even when they are near, will often have average scores that are quite different. There is no way to completely control such between-apiary variance, but its effects on the accuracy of measurement can be reduced. We can assume that the entire difference between the average scores between apiaries is due to location differences. Probably this is not entirely true since it ignores the likely interactions between the bee stock and the variety of local conditions which differ between apiary locations. Nonetheless, if we make this assumption and through using certain statistical tests discussed in most statistics books [see Snedecor and Cochran (1967)] find that the individual colony scores in each apiary are normally distributed, then the process of comparing colonies in different apiaries becomes relatively straightforward. First, each apiary is described in terms of its own mean and standard deviation. Second, the individual responses can then be transformed into standard deviation units and compared, in order to select parents. An individual's position in a population is called its z score and is calculated as

$$z = \frac{X - M}{s} \tag{3}$$

where X is the colony's score, M is the apiary's average score, and s is the standard deviation of the apiary's scores. The effects of Eq. (3) are shown in Fig. 1. A score which equals the apiary average becomes zero, and most scores range from -3 to $+3$. These scores can be compared between apiaries and thus permit the identification of the best parents in a breeding program regardless of the main effects arising from apiary location.

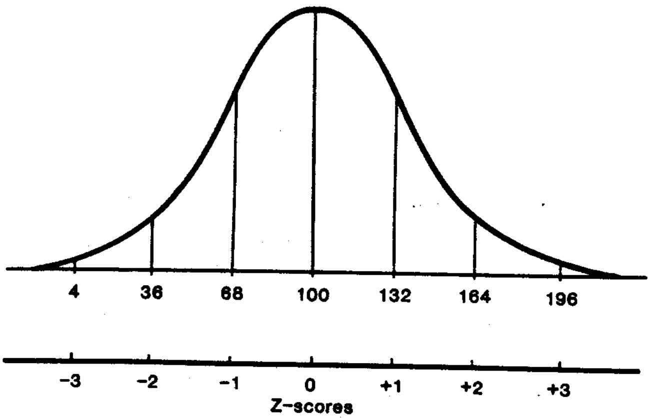

Fig. 1. Illustration of the conversion of a normal distribution of phenotypic scores to *z* scores, using a normal distribution of honey production values in kilograms.

2. *Correlated Measurements*

The difficulties of accurately measuring honey-bee characteristics in the field cannot be underestimated. Honey-production measures require nectar-flows; pollination-activity measurements depend strongly on the attractiveness of competing floral sources (Martin and McGregor, 1973); disease-resistance measures depend on the occurrence of epizootics or costly testing. Climate, weather, drifting, unequal colony strengths, and unequal past histories of colonies all make field measurements of colonies less accurate. Also, the direct field observation of characteristics can be costly. If, for example, honey production is measured throughout a year, the cost is measured as only one generation of selection in a year and a lack of accuracy caused by a complete season of environmental variation. A correlated measure might be more accurate or at least be less costly.

The problems attending the measurement of honey production and its cost in generation time have stimulated the development of several measures correlated with honey production. Hoarding behavior (Milne, 1980a), worker-bee longevity (Milne, 1980b), pupal weight (Milne, 1980c), pollen-basket measurements (Milne and Pries, 1984), and a single day's honey production (Szabo, 1982), have all been identified as correlates of overall honey production.

Many other important characteristics of honey bees can be evaluated through correlated measurements. Tests of honey-bee colony defense (Collins, 1979) and response to various diseases (Rinderer *et al.*, 1975; Rinderer and Elliott, 1977; Milne, 1983) have all been developed. Indeed, almost every scientific experiment studying bees uses a measurement system which might be developed into a useful correlated measure of an important bee characteristic.

The development of useful correlated measures or indirect measurement (Falconer, 1960), including laboratory testing (Milne, 1985; Rinderer, 1977), is an important current interest of honey-bee geneticists. There are no widely accepted guidelines for the development of correlated measures for selection programs. Generally, large-animal and poultry breeders have much closer control of environmental sources of variance and can better rely on direct measures of the characters that interest them. Also, they are usually concerned with physiological characters such as weight gain or butterfat production, rather than the results of complex behavioral processes such as honey production or colony defense. Nonetheless, statistics and quantitative genetics contain all the theory necessary to establish guidelines for the development of useful correlated measures.

First, relatively simple studies are required to determine if candidate measurement systems produce results which are correlated with the results of measurements of the actual trait to be improved. Such studies, if properly designed, also will provide estimates of phenotypic means and variation.

The evaluation of such tests involves considering the correlation value, which can range from 0 to 1, the statistical significance of the correlation, the number of colonies used to produce the correlation, extreme data pairs, and the relative costs of the two evaluation systems. At this point, correlative measurement systems which produce low correlations (perhaps 0.2) or prove more costly than direct measurement might be discarded. Statistical significance can only properly be interpreted when the numbers of colonies measured are considered. A correlation of 0.764 from measurements on 10 colonies would be considered highly significant statistically, as would a correlation of 0.081 from measurements on 1000 colonies (Snedecor and Cochran, 1967). However, since the goal is to create ways to accurately measure the breeding value of parents, the first correlation would be considered highly *important* but the second would be considered trivial. Extreme pairs of data from only one or two colonies may create significant and apparently important correlations. The likely sources of single colonies producing scores sufficiently extreme and strong to substantially alter correlation are chance, genetic dominance, or extreme environmental events. Additive genetic variance, the substance of breeding value, is a function of the population generally, and the scores of a single colony should not strongly change an important correlation.

Second, the value of the correlated measure to a selection program must be demonstrated. Experiments can be designed using selected matings which will permit the calculation of h^2 and genetic correlations as well as providing additional information on phenotypic correlations. Such experiments are generally costly with bees, and this expense justifies the use of simple correlation studies.

The results of heritability and correlation studies provide the basis for evaluating the value of correlated measurement systems. Equation (1) is the foundation of this evaluation. Response of desired characteristics (R_d) to selection based on correlated measures is

$$R_d = h_c^2 S r_g \cdot \tfrac{2}{3} \tag{4}$$

where r_g is the genetic correlation between the two measurement systems, h_c^2 is the heritability of the correlated measure, and the $\frac{2}{3}$ is the result of drones being one generation behind queens in a population (Moran, 1984).

Since the response of desired characteristics based on direct measures [Eq. (1)] can also be predicted, the ratio of

$$R_d/R \tag{5}$$

compares the relative value of the two measurement systems. However, this assumes that the two measurement systems permit the same sized groups of parent and progeny populations to be measured and that the costs of both measurement techniques are identical. Neither assumption is likely to be valid, and the apparent simplicity of Eq. (5) must be expanded to include the costs of measurement and their real effect on possible changes in the selection differential (S) as it is limited by other selection program constraints. Thus, the ratio of economic responses ER_d/ER is

$$ER_d/ER = [(h_c^2 S_c r_g/M_c)/(h^2 S/M_d)] \tag{6}$$

where M_c and M_d are the total estimated monetary costs of measurement for each program, respectively. In the estimates of M_c or M_d, users of Eq. (6) should account for increased costs incurred by operating more colonies required to improve S or S_c. The numerical value calculated for Eq. (6) is then a comparison of the amounts of population improvement in standard deviation units expected per unit of money spent in stock evaluation.

Third, model selection programs comparing direct and correlated measures or different correlated measures would provide final demonstrations of a correlated measure's efficiency, and additional estimates of h^2, plus genetic and phenotype correlations.

There are several ways that a correlated measure can be better or worse than a direct measure. Environmental variance can be reduced substantially and h^2 will become substantially higher, such that $h_c^2 r_g$ is greater than the h^2 of the direct measurement system. However, $h_c^2 r_g$ might be less than h^2 but the actual mechanics of measurement might be sufficiently simple and relatively inexpensive that S_c can be dramatically improved over S. Alternately, correlated measures might substantially improve R based on a strongly increased h^2 but cost so much that the numbers of progeny and S must be reduced to unacceptable levels.

C. Selection of Stock for Several Characters

Generally, bee breeders would like to improve stock for more than one characteristic simultaneously. This is understandable since the economic value of a stock depends on several characteristics.

1. *Tandem Selection*

One approach to improving several characteristics in a stock is using sequential or tandem selection. One character after another receives the breeder's attention. The usefulness of this approach depends on the genetics of the characteristic. Quantitative characteristics genetically regulated by several loci and multiple alleles are poor candidates for tandem selection. When selection is relaxed for such characteristics, the average population response tends to return toward original levels. If the improved characteristic was based on selection for additive effects and the average population response does not tend to return toward the original levels, then the additive effects which are useful for the improvement of other characteristics have probably been lost.

There is one valuable use for tandem selection in well-planned honey-bee selection programs. Very frequently a breeder desires specific morphological characteristics in the stock. Often, such characteristics depend upon relatively simple genetic events (Tucker, Chapter 3), and a careful assembly of base stocks prior to embarking on a selection program will produce a parental population very nearly uniform for the desired morphological features and still containing ample additive genetic variance to support the improvement of desired quantitative characteristics.

2. *Independent Culling Selection*

A second approach to simultaneously improving several characteristics is to evaluate each characteristic separately, determine S for each characteristic, and only accept parents for the next generation which meet the culling standards for all characteristics. This approach to bee stock improvement certainly would work but does present difficulties. The number of characters which can be placed under selection becomes very restricted (Table 1). It quickly becomes apparent that independent culling selection can only be

TABLE 1. Relation Between the Number of Selected Characteristics and the Number of Progeny Which Must be Produced Each Generation[a]

Number of characters	Probability of a single colony being selected	Number of colonies required each generation
1	0.2	500
2	0.04	2,500
3	0.008	12,500
4	0.0016	62,500
5	0.00032	312,500
6	0.000064	1,562,500

[a] These relationships assume that the working breeding population is 100 colonies and that the top 20% of the population meets the culling level for each characteristic.

done for a few characters, and then only by quite large corporations or cooperatives.

3. *Selection Index Breeding*

Selection index breeding assumes that the breeding value of potential parents can be expressed in a single number (I). Such a number, or selection index score, would be a compound value derived from the colony's individual phenotypic scores, the h^2 of the characteristics, the genetic correlations between these characteristics, and the relative economic value of the characteristics as judged by the bee breeder.

In a selection program, the I for each potential parent of the next generation is calculated and those having the highest ones are used as parents. Hazel and Lush (1942) and Hazel (1943) have compared selection index breeding to other methods of selection for multiple characteristics and demonstrated that it provides the most rapid method of improving the economic value of a stock.

As an illustration of the mechanics of building a simple selection index, consider two characteristics, honey production and colony defensive behavior. Honey production values can be converted to z scores as explained earlier and illustrated in Fig. 1. In the same way, quantitative measure of colony defensive behavior can also be converted to z scores at the apiary level and combined.

Each colony then has two z scores, one for each characteristic. The z-score conversions bring the two measures into the same scale of standard deviation units. This allows the two scores to be weighted for economic value, h^2, and genetic correlations without concern about adjusting for unequal scales of measurement.

A selection index (I) score including economic value may be expressed as

$$I = z_{hp}V + z_d \tag{7}$$

where z_{hp} is the colony's honey production breeding value, z_d is the colony's defense behavior breeding value, and V is the relative economic value of honey production compared to defensive behavior. Equation (7) assumes that the economic value of increasing the defensive behavior by one standard deviation is the standard of comparison and has a value of 1. V, the relative economic value of increasing honey production by one standard deviation, is then set by the breeder according to his breeding goals. If honey production improvement is considered half as important as defensive behavior improvement then V would be set at 0.5; if twice as important, then V would be set at 2. Equation (7) is the simplest form of a selection index.

Since heritabilities are involved in estimating responses to selection [Eq. (1)], they must be incorporated into the selection index in a way that does not dilute the relative economic value assigned to the two characteristics. The equation

$$I = z_{hp}V(h^2_{hp}/h^2_d) + z_d \tag{8}$$

adjusts I to accommodate the differential h^2 values of the two characters while maintaining the economic evaluations of the breeder. This formula will favor improvement of the characteristic having the higher h^2. When building a base stock prior to selection, a breeder would probably wish to include a large number of superior colonies for the character with the lower heritability.

The genetic correlation (r_g) between two characteristics is generally the correlation of breeding values. It estimates the proportion of the total additive genetic variance for both characteristics which affect both characters. It can be accommodated into the selection index as

$$I = z_{hp}V(h^2_{hp}/h^2_d) + z_d(1 - r_g) \tag{9}$$

Where r_g is positive or near zero, selection for both characteristics will predictably improve both. Where r_g is strongly negative, selection has much less chance of simultaneously improving both characteristics. In the example of honey production and defensive behavior, no estimate of r_g exists. However, hoarding behavior, which is a measure related to honey production, is positively correlated to one aspect of defensive behavior and negatively correlated to two other aspects (Collins *et al.*, 1984; Collins, Chapter 11, Table V). Nonetheless, simultaneous selection using a selection index can improve honey production and reduce defensive behavior (unpublished Honey-Bee Breeding, Genetics, and Physiology Laboratory data).

The selection index [Eq. (9)] presented here is limited to two characteristics. More elaborate selection indexes can be developed (Hazel, 1943; Lush, 1948; Falconer, 1960), which use multiple regressions and covariance components to construct the index. Where all the required genetic parameters are known for more than two characteristics, a selection index can be developed from multiple analyses of covariance. When necessary, bee breeders can probably find help in developing formulas specific to their own needs from animal breeders at universities near them.

When genetic parameters are not known, or only some are known, a selection index is still useful. As a minimum, estimates of breeding value based on phenotypic scores can be coupled with the relative economic value of each trait [Eq. (7)]. Such a procedure would be an improvement over independent culling levels, tandem selection, or off-hand field evaluations.

D. Special Constraints

The propagation of bee stock in a selection program provides a challenge to bee breeders. The ease of producing many daughter queens from one or a few colonies tempts a breeder to use too few parents. Certainly, a strong S will predictably improve stock more rapidly. However, one which is too strong will eliminate valuable additive genetic variance from the potential breeders of the next generation. Also, bees suffer more from inbreeding depression than other animals (Woyke, Chapter 4), and special care is required to maintain general genetic heterozygosity while changing the gene frequencies for the trait under selection. Laidlaw and Page (Chapter 13) and Moritz (1984) provide guidance concerning the minimum numbers of parents required to satisfactorily maintain general stock quality.

Certainly no long-term breeding program should use fewer colonies. Probably, most breeding programs employing selection would benefit from using more than the minimum numbers. Economics will dictate the specific numbers desirable for specific programs.

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