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Modern Problems of Population Genetics in Animal Husbandry

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Summary. Knowledge in animal husbandry derives from a complex of disciplines, and in this review the theory of one of these (population genetics) is discussed with regard to animal improvement, but with consideration of its implications in the other disciplines together with contributions from these to animal improvement programmes.

The conventional programme for genetic improvement is outlined, but with particular emphasis placed on the lack of knowledge as to just what constitutes an adequate foundation population and what procedures will provide maximum total response to selection. An adequate foundation population is one containing as wide a sample as possible of the genetic variability existing in the species, and it is argued that genes of low initial frequency may comprise a significant proportion of the genetic variability available to selection. Further, a significant proportion of this variability may result from the segregation of a relatively small number of genes of large effect. The need for detailed information on the nature of gene action determining quantitative variation is emphasised.

Maximisation of foundation population size is of prime importance, while the effective population size in subsequent generations of selection will largely determine total response to selection. Because of the restricted size of breeding programmes, selection responses will generally cease at less than the possible limit, so that methods of breaking through such apparent limits are discussed.

In practical breeding programmes, a number of characters are generally under selection, and improvement then depends on genetic correlations among these characters. But to predict changes under selection, or to interpret those that have occurred, the basic causes of genetic correlations must be understood. Such understanding is further complicated by the possibility of change in magnitude or even direction of a genetic correlation during selection.

Contributions from anatomy, physiology and animal behaviour are discussed in terms of information relevant to the definition of breeding objectives, optimum husbandry techniques, and limits to intensification in animal management. Artificial insemination has revolutionised dairy cattle breeding, and the development of techniques for oestrus synchronisation make more practical its use in other species. The implications of super-ovulation and egg transfer and modification of sex ratio on breeding programmes are considered, and the review concludes with a plea for information on the economics of breeding programmes.

Animal husbandry is most simply taken to mean the feeding, breeding, and management of domestic animals. As such, it is not a single entity, but a complex of disciplines (*e. g.* nutrition, physiology, behaviour, genetics), interacting with and dependent upon agricultural technology, agricultural economics, agricultural engineering, product technology, and human cultural and social phenomena. However, within this framework, two basic types of animal husbandry need to be distinguished:

(1) Where production is based on the grazing animal, with or without sown or improved pastures and fodder crops,

(2) Where production is based on pen-fed and intensively housed animals, such as in poultry and pig production, and in some areas, dairy and beef cattle production.

In the developed countries, intensification of agriculture has resulted in a general and continuing trend from extensive to intensive animal husbandry, best exemplified by the poultry industry which has been completely remodelled within the last 20 years (WILSON, 1966). SYKES (1963) has predicted that this must happen with other classes of livestock throughout the world. That it will with poultry seems undeniable, but for larger livestock, other factors seem likely to remain sufficiently important to preserve extensive husbandry. Extensive grazing will remain as a major form of land use in areas unsuitable for crop production. In areas marginally suited for crop production, ecological stability may depend in integration of cropping and grazing. The implications of this intensification from the viewpoint of animal breeding have been examined in detail by LERNER and DONALD (1966), who point out that "the word revolution is not too strong for the consequences of artificial insemination in dairy cattle breeding or of big scale operations in the poultry industry". Although this trend to intensification is inevitable and necessary in view of world food needs, opposition has been widespread (*e. g.* HARRISON, 1964, but see ROBERTSON, 1964) and although based largely on emotion and anthropomorphic reasoning, has resulted at least in the United Kingdom in legislation to safeguard the welfare of livestock kept under systems of intensive husbandry.

The application and importance of animal husbandry is obvious in view of the world food shortage and the acute need for increased production of animal protein (BYERLY, 1966; KOLARI, 1966; LERNER and DONALD, 1966). Increases in production may be achieved through two avenues, either by selective breeding to increase the inherent genetic potential of individual animals or by improvement in nutrition and management, which may depend on a genetic element in patterns of behaviour, nutritional requirements or physiological adaptation.

In this review, an attempt will be made to relate one of the basic disciplines (genetics, and in particular, population genetics) to animal husbandry. Major emphasis will be placed on the theory of population genetics relative to animal improvement, but the implications of population genetics in other aspects of animal husbandry will be considered. At this point, it would be well to mention that more immediate and spectacular increases in production can generally be achieved through improved management than through animal breeding. This has been best demonstrated in dairy cattle, for example in the New Zealand "Production Improvement Project" (New Zealand Dairy Board, 1955). Consulting officers were each allocated some 30 low-producing farms that had been selected on the basis of the willingness of their owners to co-operate. The consulting officers were able to study farm operations, enabling them to identify factors responsible for limiting production, and advise accordingly. As a result, the average butterfat production per farm increased by 40% and average production per cow by 15% over six years. In the same period, the maximum genetic improvement per cow that could be expected would probably be not more than 5%. Also in dairy cattle, there is tremendous variation between herds in production, but Robertson and Rendel (1954) found in England that no more than 10% of this variation in average milk yield was genetic, although the proportion was somewhat higher for fat percentage. Thus for milk yield, about 90% of the variation between herd averages was environmental (management, feeding, *etc.*). Similar results have been obtained in later studies (see Brumby, 1961).

However, as Robertson (1957a) has emphasised "the basic material for genetic improvement is present in our dairy breeds, and the problem of getting national improvement by breeding may, in fact, turn out to be simpler than getting it by improved management". This argument surely applies also to other livestock species. But a word of warning. I do not mean to imply that we must concentrate solely on animal breeding to increase productivity. All disciplines of animal husbandry must contribute and, in many cases, improvement in management (the animal environment) and improvement in the genotype must go together.

Within the limits of this review, it is not possible to consider in detail all the problems and implications of population genetics. The literature covered is selective and must reflect my own interests. I have endeavoured to refer to those papers and reviews that give more detailed or more expansive consideration to particular aspects, but in addition, the following reviews and papers should be consulted for further information (Great Britain: Ministry of Agriculture, Fisheries and Food, 1963; Rae, 1964; Bowman, 1966; Fredeen, 1966; Robinson, 1966).

The Conventional Programme for Genetic Improvement

The optimum strategy for genetic improvement should allow for maximum response per unit of time (generally, per year) and maximum total response. In order to obtain these objectives, the animal breeder has two major points of choice available, — *viz.* choice of the foundation population and choice of the breeding programme. Until quite recently, emphasis has been placed almost entirely on the latter, with the optimum programme defined as the one giving maximum genetic improvement per year. McBride (1965) has summarised this conventional approach as follows:

(1) Choose an adequate foundation population;
(2) Decide which characters are to be selected;
(3) Find adequate methods of measuring these characters;
(4) Determine the necessary heritabilities and correlations between characters;
(5) Construct a selection index;
(6) Determine which aid to selection should be used (ancestors, sibs, progeny, or lifetime averages);
(7) Calculate the optimum population structure by maximising the formula—

$$\frac{i_{MM} + i_{MF} + i_{FM} + i_{FF}}{l_{MM} + l_{MF} + l_{FM} + l_{FF}}$$

where i_{MM} = selection differential of males to breed males,
i_{MF} = selection differential of males to breed females,
i_{FM} = selection differential of females to breed males,
i_{FF} = selection differential of females to breed females,
l_{MM} = generation interval of males to breed males,
l_{MF} = generation interval of males to breed females,
l_{FM} = generation interval of females to breed males,
l_{FF} = generation interval of females to breed females;

(8) Modify this structure to fit the husbandry practices peculiar to the species;
(9) Close the herd or flock;
(10) Minimise inbreeding during selection, otherwise mate selected animals at random.

Thus, by following through points (2) to (10), one may define a breeding programme to maximise improvement per year, and one may, with reasonable accuracy in the early generations, predict the rate of this improvement. But in the development of this theory, very little attention has been given to just what constitutes an adequate foundation population, or to obtaining the maximum total response to selection.

The Foundation Population

Choice of an adequate foundation population means that it should contain as wide a sample as possible of the genetic variability existing in the species, but at the same time, considering its adaptation to the environmental conditions under which selection is to be carried out, and its initial performance. In plant breeding, great emphasis has been placed on wide collection and testing of material of possible value in initiating breeding programmes, and this practice has recently received attention from animal breeders (Lush, 1961; Nordskog, 1961; Phillips, 1961; Scossiroli, 1965) concerned with the conservation of strains and breeds which are not currently used in breeding programmes, but which in the future may provide useful genetic material.

In the past, however, animal breeders generally have been content to utilise whatever strains or breeds happened to be available. Poultry breeders have sometimes chosen the best of available strains as a foundation population (McBride, 1965) but this is not necessarily the population which will give maximum response per year and maximum total response. Further, James (1966) in a theoretical examination, has tentatively concluded that selection from several populations is likely to provide a foundation stock genetically superior to one selected from within the one population thought to be of highest average breeding value.

The operational problem in choosing the members of a foundation population is one of sampling the available genetic variability. Thus the larger the foundation population, the more successful this is likely to be (Robertson, 1960). But the size of the population will be limited by practical and economic considerations. Sampling from several populations should not only give a genetically superior foundation stock, but one containing a wider sample of the genetic variability. I am here defining "foundation population" as the individuals actually used to initiate a selection programme, while "base population" will be used to refer to the particular population (or populations) from which these foundation individuals were taken.

The importance of sampling is demonstrated by selection experiments where replicate lines are derived from the one base population, as in recent experiments of one of my colleagues (L. P. Jones). Using ten full-sib families from the one base population of *Drosophila melanogaster*, replicate selection lines were initiated, where the foundation population of each line comprised one male and one female taken at random from each family. Responses to selection for increased abdominal chaetae number differed markedly between replicate lines over seven generations.

However, differences between replicate lines in rate of response and total response may also be due to inbreeding, resulting both from the limited size of the population and the increased inbreeding resulting from selection itself (Morley, 1954; James and McBride, 1958; Robertson, 1961a; McBride and Robertson, 1963). The differences between replicates in Jones' experiment cannot be attributed to inbreeding reducing response in some lines, as rates of response were greatest in lines with highest inbreeding. McBride (1965) has shown the effect of foundation population sampling on total responses obtained in the lines of McBride and Robertson (1963). The additional response obtained after crossing related lines from a single sample of the base population was considerably less than that obtained after crossing lines from different samples of the base population.

These differences between replicate lines in rates of response and total response will be largely due to desirable genes of low frequency in the base population. Such a gene then may be assumed to be present, if at all, in only one parent of one full-sib family. Their progeny then have a 50% probability of being heterozygous, so that the gene frequency in a pair of random individuals of this family will be 0, 25%, or 50%, and the gene will be lost in 25% of such sampled pairs. This effect can be seen in the replicate lines of McBride and Robertson (1963) and Jones (unpublished), where some initial families made quite different contributions to the genotypes of replicate lines in later generations. However, Robertson (1966) has pointed out "that if a selection response was mostly due to the fixation of genes at low frequencies in the initial (*i.e.* base) population, then the subjection of the population to a size bottleneck, of, say, one pair of parents, followed by several generations of random mating to re-establish linkage equilibrium, should drastically affect selection limits", and has given data on lines of *Drosophila melanogaster* selected for number of sternopleural bristles (derived from the same base population as that used by McBride and Robertson, 1963). In one set of lines, the foundation for each line comprised 25 pairs, and the selection intensity in each generation was 10 pairs out of 25 pairs. The second set of lines each derived from a single pair followed by six generations of random mating, when selection commenced at the same intensity as in the first set. The rate of response and the total response were lower in the second set, again demonstrating the effect of restriction of variability in the foundation population. But the total response was only about 30% less in this second set than in the first. Robertson has interpreted this as suggesting that desirable genes of low frequency in the base population are not particularly important in these selection responses.

However, even in the first set with an initial sample of 50 individuals, many genes of low frequency in the base population will not be represented. That these could contribute significantly to the total possible response is shown by the fact that the observed total response in the first set is less than 50% of that possible in selection from this population. Of course, here one cannot separate the effects of initial sampling from the effects of inbreeding during selection. But as Robertson (1966) points out, in populations of fairly small size "the limits to selection are artefacts of the intensity of selection and the population size rather than basic properties of the initial population" (*i.e.* base population). Here we must distinguish the base population (as the large random breeding population from which selection lines are derived) from the sample used as founders of a particular selection line. Compare then two selection lines initiated as different size foundation populations, but with the same selection intensity and number of parents in subsequent generations. Once the foundation sample is taken, genetic variability is restricted. For a large foundation population, the probability of including rare genes is high. But some, at least, of these will be lost through genetic drift in early generations before selection operates to increase their frequencies. At the other extreme where the foundation sample is very small, most rare genes will not be included, but the effect of drift will be much reduced because those genes that are included will be at appreciable frequencies. In either case, many genes of low frequency in the foundation population will not contribute to selection responses, and observed limits to selection will be less than the possible limit. We would argue then that genes of low frequency in the base population may comprise a significant proportion of the genetic variability available to selection. The extreme examples of such rare genes will be those with a severely deleterious effect on fitness, and which may often have a large effect on the quantitative character (JONES, 1967).

Short Term Selection Responses

The procedures involved in the choice of a breeding programme designed to maximise response per unit time are well-known and fully documented (LERNER, 1950, 1958). The theory, based on the concept of heritability (LUSH, 1940), provides a statistical description of population variability, and thus allows prediction of the expected response of the population to selection. This prediction is strictly valid only for a single generation, because the components of the phenotypic variance will themselves be expected to change with selection. These changes are not drastic, so that the theory does give a reasonable description of the short-term effects of selection, although just how long this "short-term" is will depend on the particular character under selection and the particular population. Experiments with laboratory animals (CLAYTON, MORRIS and ROBERTSON, 1957; CHUNG and CHAPMAN, 1958; MARTIN and BELL, 1960; ROBERTS, 1965) have generally shown fair agreement between predicted selection response and the observed short-term response averaged over replicate populations. But individual lines often differed markedly — an effect due either to initial sampling of the foundation population or to genetic sampling over the generations of selection. CLAYTON *et al.* (1957) found that genetic sampling could account for divergences among their lines selected downwards, but not those among the up-lines. The greater variation among the up-lines could result from sampling of the foundation population, if more genes causing increased expression of the character were at low frequencies in the base population.

Variation among replicates will be a function of the nature of genetic variation in the base population, the size of the foundation population, the number of parents used each generation, and the selection intensity. If the genes controlling the character are at more or less intermediate frequencies in the base population, replicate variation will increase as the foundation population size decreases. If desirable genes at low frequency contribute significantly to thegenetic variation in the base population, maximum variation between replicates will be expected for intermediate foundation population size. For very small foundation populations, the chance of including rare genes is low for all lines, while for very large foundation populations, most rare genes will be included in all lines. At intermediate foundation population sizes, some rare genes will be included in some lines, leading to increased variation among replicates. But, for those desirable genes included in the foundation populations, their initial frequency is likely to be less at the larger population sizes, so that selection intensity becomes important. Thus, for a given number of parents selected each generation, the number of individuals scored increases as the selection intensity increases. The probability of selecting rare desirable genes then should increase also, reducing variability among replicates.

Therefore, when the initial sampling is considered together with the effective population size (N) and selection differential ($\bar{i}$), variation among replicates will increase as $N\bar{i}$ decreases. Many replicates therefore will be needed at low values of $N\bar{i}$ (ROBERTSON, 1960). In contrast, at larger population sizes, the increased probability of a rare recombination event may lead to some increase in variability among replicates. It is important that the basis of replicate variability be understood as an animal breeding programme is essentially equivalent to a single replicate line in these laboratory experiments.

The expected response to selection is given by the expression:

$$\Delta G = \bar{i}\, h^2\, \sigma_p$$

where $\bar{i}$ is the standardised selection differential (in standard deviation units), h^2 is the heritability, and σ_p is the phenotypic standard deviation. Thus, for a given character in a particular population, more intense selection is expected to increase the response per generation. This expectation was experimentally verified by CLAYTON *et al.* (1957), but they found that the realised heritability (FALCONER, 1953) decreased as selection intensity decreased. As the numbers of parents each generation were the same in all lines, smaller selection intensities meant fewer individuals scored, so that the lower realised heritabilities might simply reflect restriction of genetic variability at the inital population. This suggestion is supported by recent results in our laboratory (FRANKHAM, JONES and BARKER, unpublished). We found no consistent effect of selection intensity (10, 20 and 40%) on realised heritabilities, for lines with the same number of parents used each generation, but using this same number as the foundation population for each line. In these experiments, the effect of population size on responses was studied also, using 10, 20 and 40 pairs of parents each generation. In general, at each selection intensity, response increased as population size increased, with average realised heritabilities over the first twelve generations of 14.6%, 16.2% and 18.3%.

One other comparison in relation to population size is of particular interest in this experiment. For a given total size of population (*i.e.* number of individuals measured each generation), DEMPSTER (1955) suggested that the optimum selection intensity for maximising total response to selection would be 50%. Three comparisons within particular total sizes can be made in this experiment, *viz.*

200 pairs measured — 40 pairs parents, 20% selection intensity,
20 pairs parents, 10% selection intensity.
100 pairs measured — 40 pairs parents, 40% selection intensity,
20 pairs parents, 20% selection intensity,
10 pairs parents, 10% selection intensity.
50 pairs measured — 20 pairs parents, 40% selection intensity,
10 pairs parents, 20% selection intensity.

Within each of these three, realised heritability increased as selection intensity decreased. Thus, even in the short-term considered (12 generations), there is the suggestion that maximising the intensity of selection may not allow optimum long-term utilisation of genetic variability. This effect would be at least partly attributable to genetic sampling during selection, due to the smaller numbers of parents used each generation in lines with higher selection intensity. Thus the rate of inbreeding is increased, with a greater decrease in genetic variability and reduced response per unit of selection applied.

But selection itself has an inbreeding effect, proportional to the heritability and the squared selection differential (ROBERTSON, 1961a). Thus maximising response per generation will maximise the rate of inbreeding. There are then two effects in opposition, but what will be the result of their interaction on selection responses? Clearly, this will depend on the effect of inbreeding on the character under selection. For one showing significant inbreeding depression, consider selection in two populations each with the same number of parents each generation, but at different selection intensities. The higher selection intensity will give greater initial response, but the associated higher rate of inbreeding would be expected to lead to more rapid decline in response. Responses then may show a crossover pattern, with the lower selection intensity giving less initial response per generation but greater total response than the higher intensity.

Even for a character that exhibits little or no inbreeding depression, a similar crossover pattern of responses might result, due to the effect of inbreeding on fitness, leading to a lower limit for the higher selection intensity. Unfortunately, there is little experimental evidence on these effects, and no clear indication of the importance of selection intensity in relation to inbreeding. In an experiment previously referred to, JONES (unpublished) selected for abdominal bristle number in *Drosophila melanogaster* at intensities of 10, 20 and 50% but with the same number of parents each generation, and found a tendency for increased inbreeding as selection intensity increased, but this was masked by variation among replicates. As these lines were under selection for only seven generations, they gave no indication of long-term trends, and there was no suggestion of a crossover pattern of responses. Within selection intensities, however, there was a clear relationship between increase in inbreeding and response; in lines responding fastest, the increase in inbreeding was greatest. The basis of this can be seen by utilising the "spread of genes" technique developed by JAMES and MCBRIDE (1958) and further discussed by JAMES (1962a) and MCBRIDE (1965). In this technique, the proportions of genes contributed by each of the matings in a particular generation are followed through each of the succeeding generations. They have shown that the selection process continues to operate on a given generation for up to four generations; that is, the descendants of a mating in the given generation may be eliminated up to four generations later. Referring to the initial generation, responses will depend on the sample of genes included in the initial families. Selection will act to increase the frequencies of desirable genes, increasing the contributions of those initial families that carried such desirable genes, and consequently increasing inbreeding.

If desirable genes were distributed evenly over all initial families, and were all of similar phenotypic effect, the contributions of initial families to later generations would be equal (apart from chance effects) and inbreeding would be minimised.

The differences between replicates with strong positive association between rate of response and rate of inbreeding therefore suggest that desirable genes of low frequency in the base population are important, and that desirable genes show a wide range of phenotypic effect, and do not conform to the classical polygene concept.

Similarly in the experiments of FRANKHAM, JONES and BARKER (unpublished), different selection intensities may be compared at each of the three population sizes used, *viz.* 10, 20 and 40 pairs of parents each generation. These lines were not pedigreed, so inbreeding cannot be calculated, but within population sizes, higher selection intensities gave greater response per generation and greater total response over 50 generations of selection. However, as not all lines had ceased responding to selection, the possibility of a crossover response pattern cannot be eliminated.

In these experiments the character under selection (abdominal bristle number) does not exhibit inbreeding depression (KIDWELL and KIDWELL, 1966), and the imposed artificial selection was not strongly opposed by natural selection, in that on the average, they did not rapidly regress on relaxation of selection. Therefore no generalisation on the importance of selection intensity in relation to inbreeding can be made from these experiments, and it is important that further work should be done with characters exhibiting inbreeding depression and more closely related to fitness.

Nevertheless, MCBRIDE (1965) has pointed out some practical implications of the inbreeding effects of selection. He has shown that there is generally a regularity in the changes in proportions of genes from matings in a given generation over the succeeding generations. In each generation then, there are many matings whose descendants will not contribute to future generations, so that pedigree information may be used "to reduce the size of a generation by culling descendants of ancestors which will probably be eliminated. The ultimate level of inbreeding will not be affected and a better use may be made of breeding facilities". Also, "the presence of regular changes in these proportions of genes is an excellent diagnostic of additive gene action, and thus the absence of such changes can be used to diagnose plateau situations".

Major Genes and Quantitative Characters

Evidence presented earlier suggested that the genes controlling a quantitative character may show a wide range of phenotypic effects, and not conform to the classical polygene concept. Certainly polygenes of small effect may contribute to the variation, but a significant proportion of this variation may result from the segregation of a relatively small number of genes of large effect. The effects of autosomal genes of large effect on responses due to artificial selection have been considered by Latter (1965 a, b, 1966). Such genes have been demonstrated by Thoday, Gibson and Spickett (1964) and Spickett and Thoday (1966) in *Drosophila*, and Wehrhahn and Allard (1965) in wheat. These findings provide the first step in penetrating "through our statistical parameters to a knowledge of the individual genes controlling the variability" (Robertson, 1966).

In livestock, contributions to an understanding of the genetic basis of quantitative variation may come from another direction resulting from the analysis of known major genes and their association with quantitative economic characters. Major emphasis has been placed on the blood group loci and the many biochemical systems discovered in recent years (Ogden, 1961; Robertson, 1961b; Briles, 1964; Gilmour, 1965; Lush, 1966), while in poultry, plumage and comb type genes also have been investigated (Potemkowska, 1965; Crober and Hawes, 1966).

In terms of livestock improvement, such genes could prove useful, either where there is a significant average difference in some economic character between animals carrying a particular gene and those without it, or where heterozygotes at the marked locus are superior in some economic character to homozygotes. These aspects have been considered in the above reviews. For the first, some significant associations have been found but their value for livestock improvement would be small. For the second, superiority of heterozygotes for certain blood group systems in poultry has been found for some productive characters in some studies. But no clear pattern of relationships has emerged.

Total Selection Responses

In the ideal situation for evaluating alternative possible breeding programmes, the breeder would wish to predict not only initial responses per generation or per year, but the total improvement expected and the number of generations necessary to obtain it. It is in this latter that existing theory is inadequate.

On the simplest additive theory, selection is expected to increase the frequency of desirable genes until they reach fixation. The population then may be said to have reached the 'possible limit' (Robertson, 1960), additive genetic variance and the heritability will be zero, and the population will not respond to reverse selection. The assumptions implicit in these expectations are:

(1) Large population size,

(2) No overdominance or epistatic gene action,

(3) No negative genetic correlation between the character under selection and reproductive fitness,

(4) Absence of linkage (assuming population size is not infinite).

Robertson (1960) developed a theory of selection limits based on fixation and the effects of population size. Here the limits are a function of the effective population size and the selection intensity. The limitations of this model were discussed by Robertson and are demonstrated by the results of McBride (1965) and our own experiments. But the importance of population size is clear in the latter – the larger the population size, the greater the total response.

However, in many selection experiments, although the populations reached a point of cessation of response, additive genetic variance remained in the populations at this limit (or selection plateau). Lerner (1954) first emphasised this property of a population "to equilibrate its genetic composition and to resist sudden changes", and argued that this genetic homeostasis is "based on natural selection favouring intermediate rather than extreme phenotypes", the suggested mechanism being "the superiority with respect to fitness of the heterozygous over the homozygous genotypes". These observed selection limits result from the failure of assumptions (2) to (4) above, in that selection may favour heterozygotes at some loci, or there may be negative genetic correlations. These latter may be either initially present or result from the changes under selection, and could be either between the components of a phenotype treated as a single character, or between fitness and the character under selection (*i.e.* opposing natural selection). If linkage between genes affecting different components, or between fitness genes and + genes (considered by Mather and Harrison, 1949) were the basis of the correlation, the limit would be expected to be only temporary, the probability of recombination increasing with greater number of generations or larger population size, provided of course that the genes are not already fixed. Similarly, linkage between + and – genes (Mather, 1941) could lead to a temporary limit below the possible limit.

No adequate theoretical treatment of the effects of linkage on selection response has been achieved, although Griffing (1960), Nei (1963), and Felsenstein (1965) have made some approach to the problem. Some progress, however, has been made using Monte Carlo methods with digital computers (Fraser, 1957; Martin and Cockerham, 1960; Gill, 1965; Latter, 1965b, 1966; Bellmann and Ahrens, 1966), which have shown that rates of response may be reduced when genes are closely linked. Hill and Robertson (1966) also using simulation techniques have considered the effects of linkage on selection limits, as an extension of Robertson's (1960) theory. For a two locus model, linkage was of importance when both loci had roughly equal effects on the character under selection, the greatest reduction in total response occurring when the desirable genes at both loci had low initial frequency and large effect. From their results, Hill and Robertson conclude that it seems "rather unlikely that any general theory could be constructed to be useful in the more complex situations which must exist in practice". Experimentally, Rasmuson (1955) found that application of a temperature shock to increase recombination resulted in some increase in rates of response for increased sternopleural bristle number in *Drosophila*, although total responses were similar to those in untreated lines. Further, suppression of recombination on the second and third chromosomes did reduce (although only to a small extent) responses to selection for sternopleural bristles (Robertson, 1966).

JAMES (1962b), in an extension of the work of ROBERTSON (1956) and LATTER (1960) has attempted to take account of opposing natural selection by considering the limit as an equilibrium between directional and centripetal selection. On this model, the expected limit is less than that predicted by ROBERTSON (1960), the difference increasing with increasing effective population size, increasing heritability of the character under selection, and increasing intensity of natural selection. Again, the limitations of the model are discussed by JAMES, particularly the absence of data on the intensity of centripetal selection, and the confounding of centripetal selection with the effects of inbreeding on fitness. Both ROBERTSON and JAMES emphasised that their models could not predict exactly what would happen in reality, but that they may stimulate critical experimentation, and help in the interpretation of those experiments.

Although experimental evidence on the nature of selection limits is accumulating, it has been clear for some time (DICKERSON, 1955) that selection limits are being approached in certain livestock, notably poultry. If for no other reason than the restricted size of most breeding programmes, these limits will be less than the possible limit, so that attention has focussed on methods of breaking through such apparent limits. Further, as the approach to a limit is likely to be asymptotic, the rate of genetic improvement may become uneconomically slow long before the limit is reached.

ROBERTS (1966a, b) has reported on limits to selection for body-weight in the mouse. In a line selected for increased weight, additive genetic variance apparently had been exhausted at the limit. But in the line selected for decreased weight, loci affecting body weight were still segregating at the limit and opposing natural selection appeared to be responsible. In *Drosophila* (REEVE and ROBERTSON, 1953; ROBERTSON, 1955) selection for small body size resulted in apparent exhaustion of additive genetic variance, while little or no reduction occurred under selection for large size. In selection for abdominal bristle number in *Drosophila*, CLAYTON and ROBERTSON (1957) found additive genetic variance remained at the limits of response to selection in either direction. Thus, as emphasised by ROBERTS (1966b), understanding of the genetic nature of selection limits can best be achieved by detailed investigation of specific cases, preferably utilising a range of characters in a variety of organisms.

The difficulty of overcoming natural selection against extreme phenotypes has not been solved. Certain measures to reduce the effect, *viz.* avoidance of inbreeding and selection at less than maximum possible intensity, were suggested by LERNER (1954). DEMPSTER (1955) and ROBERTSON (1960) showed that the optimum intensity of selection (that giving highest limits) was 50%, but ROBERTSON suggested that the curve of the relationship of selection limit against proportion selected may be very flat, particularly when the number of individuals measured each generation is large. Our results referred to earlier, support this suggestion. Thus there is yet another advantage in maximising population size; the larger the population, the less the opposition between maximum initial response and maximum total response.

LERNER (1958) has suggested cyclic or intermittent selection as an alternative to selection at low intensity. One of my colleagues (K. A. RATHIE) has recently done some experiments on this, with cyclic selection treatments (selected generations: relaxed generations) of 1:1, 1:3, 3:1 and 6:2. Over the period considered (up to 24 generations of selection), cyclic selection had no apparent advantage; progress in n selected generations under cyclic selection being much the same as in the same number of generations of continuous selection. Of course, this does not preclude the possibility of an advantage to cyclic selection in terms of limits, and it should be noted that the fitness of the cyclic lines did not decline significantly. Cyclic selection offers another apparent advantage in providing additional opportunity for recombination in the relaxed generations. Two treatments were used in the relaxed generations, one with the same number of parents as in the selected generations, and one with a large number of parents (80 pairs). For 1:1 cyclic selection, the latter effectively doubles cross-over frequency. No differences in the responses obtained were observed between these treatments. This is perhaps not surprising in view of the results of HILL and ROBERTSON (1966) that doubling the cross-over frequency produces at most an increase of 6% in the total response, and further, in terms of rate of response, that linkage has little effect in the first N/2 generations.

However, given that selection limits have been or will be reached in livestock populations, the problem involves increasing the rate of progress as the population approaches the asymptote, or renewing progress at the limit. LERNER (1958) has classified possible procedures into two general categories:

(1) Utilising the genotypic variability which is present, but which is not expressed under the particular conditions of the selection programme,

(2) The production of new variation either through immigration or by mutagenic agents.

Methods proposed for the utilisation of existing variation have their basis in the work of WADDINGTON (1953, 1956), who showed that a phenotypically invariant character could be made to exhibit variation by a suitable environmental treatment. Selection on this variability built up a genotype which eventually produced the character in the absence of treatment. In this case, the environmental treatment produced the desired character. At the limit stage in an animal breeding programme, it might be difficult to envisage such a suitable environmental treatment.

But the essence of the problem is to bring to phenotypic expression genetic variability that was previously unexpressed, allowing the identification of desirable genotypes. Thus abnormal environments or stress treatments may be employed either to disrupt normal development of the character or to standardise the environment, as in the study of ABPLANALP (1962). As animals under extensive grazing management are generally exposed to nutritional stress for at least part of the year, selection under such a stress artificially imposed may operate on useful additional genetic variability

A similar approach to the modification of invariant characters utilises instead of an environmental treatment a major gene that affects the character and induces variability. Studies of DUN and FRASER (1959) on vibrissae number in the mouse and RENDEL (1959a) on scutellar bristle number in *Drosophila* have shown that significant responses may be achieved.

These studies on invariant characters can be taken one step further. Normally selection programmes are devised to utilise characters exhibiting phenotypic variability and additive genetic variance. In the light of these experiments, animal breeders need not be so inhibited and might well consider reconstruction of their economic livestock species. For example, experiments to disrupt canalization of various wool production characters in Merino sheep are being considered (S.S.Y. YOUNG, pers. comm.)

The possible value of production of new variation by mutagenic agents is currently uncertain. The technique seems to be widely favoured in plant breeding (Food and Agriculture Organisation of the United Nations/International Atomic Energy Agency, 1965), but conflicting results have been obtained in animals. Using X-irradiation to increase mutation rates, SCOSSIROLI (1954) and SCOSSIROLI and SCOSSIROLI (1959) made further progress selecting for sternopleural bristle number in a *Drosophila* population that had been plateaued for many generations. However, CLAYTON and ROBERTSON (1964) selecting for the same character in *Drosophila*, did not obtain marked increases in response under irradiation. Work on *Drosophila* in our laboratory is also conflicting (JONES, 1967; BARBARA J. HOLLINGDALE, unpublished) although it seems that significant responses under irradiation can be obtained but only when genes of large effect are involved. In the only experiment reported for domestic animals, ABPLANALP, LOWRY, LERNER and DEMPSTER (1964) found no difference in response between irradiated and control lines of poultry.

The production of new variation through immigration would seem the simplest approach for animal breeding programmes. Here the populations under selection are generally closed and often of relatively small size, so that rates of inbreeding may be high. A consistent policy of introduction of animals of high breeding value will reduce inbreeding and maintain genetic variability, allowing greater total progress. Where restriction of population size has lead to chance loss of desirable alleles and decrease in fitness, crossing of two populations that are at or near selection limits and then selecting from among the cross progeny should allow further progress (FALCONER and KING, 1953). In this case, LUSH (1948) and LERNER (1950) suggested that a few generations of random mating without selection should follow the crossing to allow recombination between the genotypes of the two populations. But McBRIDE (1965) has pointed out that any advantage to be gained must be weighed against the loss of time involved, and gives evidence that lines relaxed after crossing and then selected take some time to equal the merit of lines selected immediately after crossing. But the situation is far from clear and needs further investigation, as pointed out by HILL and ROBERTSON (1966) from their finding that linkage disequilibrium (due to an excess of repulsion gametes) is likely in populations derived from crosses between selected lines or between selected lines and unselected populations.

One result from ROBERTSON's (1960) selection limit theory is important here. He has shown that if two lines of equal size (N) are crossed, and selection continued at the same intensity in the cross population (of size 2N), the expected limit is the same as if selection at this intensity in a population of size 2N had been used all the time. In populations of the large economic livestock, however, breeding operations are spread over some number of discrete units (herds, flocks), often of small size. To the extent that these remain closed, the size of individual units is important, but there is generally a high migration rate among the units within a breed (WIENER, 1955; BARKER and ALLINGHAM, 1959) so that the effective size of the breed population is more relevant than that of individual units. This migration, however, is directional as numerous studies of breeds of the various species have demonstrated that they all show an hierarchical structure, with the genetic makeup and progress of the breed dictated by the relatively small number of major breeders' units (ROBERTSON and ASKER, 1951; SHORT and CARTER, 1955; STEWART, 1955; WIENER, 1953; DAVEY and BARKER, 1963; McPHEE, 1965). As these major breeders' units are often closed, the potential total improvement of the breed is, at least in part, limited by their size. In fact, units lower in the structure whose stock trace back to a number of major breeders' units, should have a greater potential for improvement than the major breeders themselves.

Here we are considering improvement within a breed, but it is unfortunate that emphasis in large animal breeding has been placed on the concepts of "pure" breed and breed improvement. The desirability of maximising genetic variation in the foundation population has already been pointed out, and the variation would undoubtedly be increased in a population comprising a mixture of breeds. In poultry breeding, the breed concept has practically disappeared, with new strains being developed largely from crossbred foundations.

Heterosis and Crossbreeding

So far, we have considered improvement of economic characters through selection, but many of the characters of importance in livestock production are not amenable to this approach because of their very low heritability. Most characters of this type are either closely associated with, or are components of reproductive fitness so that additive genetic variance has been exhausted (or nearly so) by natural selection, although significant non-additive variation may remain. Thus, expected responses to artificial selection will be small, and in populations of limited size, observed responses will be further reduced by inbreeding depression. Conversely, however, such characters generally exhibit heterosis in crosses so that, as suggested by McBRIDE (1965) "it would be desirable to select for low heritability traits between strains and breeds on their ability to produce superior commercial crosses. This would then allow selection within strains to be directed towards the improvement of high heritability characters". Determination of the optimum approach again is limited by lack of knowledge of the gene action involved. Is there any point in selecting from among the crossbred population? Is there likely to be significant unexpressed genetic variability, in which case selection under stress treatments (environmental or genetic) as discussed for plateaued populations, could provide useful improvement? Another approach would be to use programmes such as reciprocal recurrent selection to increase the performance of crossbreds from particular strains. This procedure is theoretically attractive (CRESS, 1966), but available experimental evidence is conflicting (BELL, MOORE and WARREN, 1955; KOJIMA and KELLEHER, 1963; RICHARDSON and KOJIMA, 1965). In poultry breeding particularly, reciprocal recurrent selection may be useful once additive variance within lines has been exhausted, but only provided that the lines still contain utilisable non-additive genetic variance. The practical utility of the method then may be limited by the genetic composition of foundation stocks. It may also be limited by the effort involved in testing the crosses on an adequate scale, and the associated problem of maintaining the two lines at a size sufficient to minimise increase in inbreeding.

Simultaneous Selection for Two or More Characters

Although the discussion of selection responses above was concerned with single character selection, in practical breeding programmes a number of characters are normally under selection. Following the analysis of HAZEL and LUSH (1942) for *n* equally important, uncorrelated characters, YOUNG (1961) and FINNEY (1962) have considered the relative merits of tandem selection, independent culling levels and index selection for genetically correlated characters that may vary in relative economic importance. Index selection was shown never to be inferior to selection by independent culling levels, which in turn was never inferior to tandem selection. Experimental comparison of these methods (RASMUSON, 1964; SEN and ROBERTSON, 1964) does not provide a critical evaluation of the theory, except that index selection and independent culling were superior to tandem selection. Derivation of an index or of culling levels both depend on estimated genetic parameters of the population, so that the derived values will be valid for short-term selection only. Nevertheless, selection indexes have been frequently derived and extensively used in commercial poultry breeding (DICKERSON, 1962). On the other hand, independent culling levels, which are often operationally more convenient and may be economically superior, particularly when only two characters are under selection, have not been used much (but see YOUNG and TURNER, 1965).

But both methods are subject to the same problems, particularly negative genetic correlations between any two of the characters under selection. DICKERSON (1955) has discussed in detail the problems due to correlations among the variety of characters considered in selecting poultry for egg production. To the extent that a negative correlation is due to linkage, it should be broken by recombination during continued selection (MATHER and HARRISON, 1949). But where a high negative correlation is due largely to pleiotropy, very little progress can be expected. Unfortunately, there is no way of knowing prior to selection the relative contributions of linkage and pleiotropy to any observed correlation, nor the nature of action of pleiotropic genes. Thus, where increased expression of both of two negatively correlated characters is desired, theoretical predictions of the outcome of selection may be quite erroneous.

However, the magnitude and even direction of a genetic correlation may change during selection. LUSH (1948) suggested that simultaneous selection for two characters would cause a decrease in the genetic correlation, and that they would finally become negatively correlated. Genes with a favourable effect on both characters, or genes with a favourable effect on one character but no effect on the other, would be raised to high frequencies and contribute little to the additive genetic covariance. But genes with a favourable effect on one character and an unfavourable effect on the other would be brought to intermediate frequencies under continued selection, thus generating a negative genetic correlation. Another model has been developed by RENDEL (1963), where correlation results from the two characters sharing resources for development. If the distribution of resources to the two characters is under genetic control and variable, then it may change under selection, and depending on the initial level of resources, may result in a change in the sign of the correlation. On the other hand, continued selection could lead to the generation of correlations through production of closely linked gene complexes.

BOHREN, HILL and ROBERTSON (1966) have considered the theory of correlated responses in one character, when selection is applied to some other character. They conclude that "if the patterns of correlated responses in any situation are to be fully understood, it will be necessary to analyse the basic causes of the genetic correlations between characters. Our results point clearly to the need for the development of new experimental techniques for this purpose". This comment should be extended to include possible changes in the genetic correlation as a result of selection.

Although some aspects of the theory of genetic correlations (particularly in terms of pleiotropy) have been discussed by LE ROY (1963) and BOHREN, HILL and ROBERTSON (1966), no theory has been developed (nor does it seem likely to be) that would allow prediction of changes in the genetic correlation. Further, little experimental evidence is available. In support of LUSH's prediction, FRIARS, BOHREN and MCKEAN (1962) reported decreases in the genetic correlations between characters under simultaneous selection in poultry, while FESTING and NORDSKOG (1967) observed significant decreases in the genetic correlation between egg weight and body weight in poultry, when either character was under selection. One of my colleagues (A. K. SHERIDAN) is selecting for two bristle characters in *Drosophila* that show a genetic correlation of about +0.4 in the base population. Selection for the two characters is being done in all four combinations of up and down selection, but 20 generations of selection have not resulted in any consistent pattern of changes in the genetic correlation.

The possibility of change in genetic correlation is of importance in breeding programmes in other connections. Thus I have referred under selection limits to negative genetic correlations, either initially present or resulting from changes under selection, between fitness and the character under selection or between the components of a phenotype treated as a single character. In selection for increased shank length in poultry (LERNER and DEMPSTER, 1951) a negative correlation between shank length and fitness developed during selection, leading to cessation of response. In any selection programme in a closed unit of limited size, fitness must be expected to decline because of inbreeding, but in this population, despite continued inbreeding, fitness considerably improved on suspension of selection (LERNER, 1958).

It is well recognised that the characters under selection in animal breeding programmes, such as milk yield, growth rates, numbers of eggs produced, are highly complex characters that could be treated as the end-product of interaction among inter-related components. Selection for the productive character itself implies that the appropriate underlying system of developmental, anatomical, and physiological components will be selected. But there are, no doubt, many combinations of the components which would lead to a more productive animal, so that selection for the productive character itself might not result in the best possible combination, particularly if there are negative genetic correlations among the components (COCKREM, 1962). It is at this point, as emphasised and extensively discussed by ROBERTSON (1963) that our knowledge is completely inadequate. Although the main outlines of the endocrinological, biochemical and physiological processes affecting, say, milk production are fairly well known, practically nothing is known of the variation between animals in these processes. In fact, as ROBERTSON points out, "the genetically important steps in the complex of physiological and biochemical processes might be only a small fraction of the *necessary* biochemical steps".

Thus we return again to the need for information on the genetic basis of quantitative variation. Much of the earlier discussion has indicated the difficulty of dealing in terms of the classical polygene theory of average effects of genes and statistical concepts. This theory involves one main premise — that quantitative differences, in so far as they are inherited, depend on the segregation of genes at many loci, that the effects of these genes are additive, but that they are of small effect and not individually distinguishable. Non-additive interactions between genes, either intra-locus (dominance) or between loci (epistasis) are known to exist, but are included in theory only in so far as a proportion of their effects can be treated as additive, the remainder being ascribed to dominance or epistatic deviations from the additive model. Although linkage between genes was not considered in the basic theory, recent theoretical work that considers its possible importance has been referred to earlier. However, understanding of the effects and importance of dominance and epistasis, of the effects of linkage, and the basis of genetic correlations depend on knowledge of gene action. Future progress in the understanding of quantitative genetic variation therefore depends on analysis at the level of the gene, on knowledge of the effects of the genes through the proteins they control, and on understanding of the developmental and physiological pathways involved.

Anatomy and Physiology

The possibility of "reconstruction of the economic livestock species" was referred to earlier. Clearly, detailed anatomical and physiological information will be necessary to make this feasible. But at a simpler level, some reconstruction of the objectives of livestock improvement are already possible. For example in beef cattle breeding considerable emphasis has been placed on both live animal and carcase shape, with the objective of modifying the muscle-weight distribution and increasing the proportion of higher priced cuts (see review of BARTON, 1967). Detailed anatomical investigations (BUTTERFIELD, 1963) have shown no variation in this proportion for animals of widely varying shape, so that such selection is pointless. However, variation in muscle: bone ratio (or percentage muscle in a fat-free carcase) has been demonstrated (BERG and BUTTERFIELD, 1966). As one aim of beef cattle breeding is to increase the amount of muscle produced per animal, inclusion of this character should be of value, although the magnitude of its genetic variation is as yet unknown.

It has been suggested that too much emphasis in breeding programmes has been placed on production per animal, and that production per acre (or per hectare) or per man-hour of labour may be more relevant; that is, that efficiency of production has been neglected. As feed costs comprise the major item of expenditure under intensive or semi-intensive management systems, efficiency here refers to efficiency of food conversion, the ratio of product output to feed input. However, the correlations between efficiency and production are high (*e.g.* MASON, ROBERTSON and GJELSTAD, 1957, for milk yield; KOCH, SWIGER, CHAMBERS and GREGORY, 1963, for rate of gain in beef cattle; WILLIAMS, 1966, for wool growth in Merino sheep), as would be expected in any case in physiological terms (ROBERTSON, 1963). But these correlations are not unity, and some variation between animals in efficiency remains to be utilised. What is the physiological basis of this variation? Evidence on cattle and sheep would suggest that there are relatively little differences between animals in digestive efficiency (HANSSON, BRÄNNÄNG and CLAESSON, 1953; WALLACE, 1956; BLAXTER and WAINMAN, 1961), and that differences between animals are mainly in how they partition the absorbed nutrients. We have here the beginnings of a physiological analysis which, appropriately extended, will be of value in future breeding programmes. But total food intake will vary between animals, and contribute to variation in productivity. What is the relationship between intake and efficiency? Will the ranking of individuals on efficiency differ at different levels of intake? In poultry, SIEGEL and WISMAN (1966) found no difference in feed efficiency (gms gain in body weight per gms feed consumed from 1 to 4 weeks of age) between lines selected for increased and decreased 8 week body weight when on *ad libitum* feeding, but a higher efficiency for the high body weight line when feed consumption was comparable for both lines. Evidence from Merino sheep is conflicting — DUNLOP, DOLLING and CARPENTER (1966) found no evidence of a strain x nutritional level interaction, while WILLIAMS (1966) found such interactions to be significant for efficiency and rate of wool growth. To the extent that these interactions are significant, they could be of importance under intensive management systems such as high stocking rates where some animals may not obtain their potential food intake, and they would need to be taken into account in defining breeding objectives.

Similarly, information from other disciplines of animal husbandry, particularly behaviour, may well be relevant to the definition of breeding objectives, optimum husbandry techniques, and limits to intensification.

Animal Behaviour

Social behaviour in livestock populations has been studied most extensively in poultry. With the recognition of a social ranking in poultry populations (the peck order), it has been shown that this essentially determines priorities at feed and watering troughs, *etc.* (reviewed by GUHL, 1953; WOOD-GUSH, 1955). Thus under conditions of poor husbandry, the production of birds low in the peck order may be reduced through lowered feed intake. Various production characters have been shown to be related to position in the peck order, *viz.* sexual maturity (JAMES and FOENENDER, 1961), egg number (GUHL, 1953; MCBRIDE 1964a), egg weight and egg mass (MCBRIDE, 1964a). These relationships have been discussed by MCBRIDE (1962, 1964b), who suggests that the relationship does not depend on competition for food, but on general physiological changes resulting from the social stresses to which birds low in the peck order are exposed. In an integrated flock with a developed peck order, a low level of aggressiveness will be maintained, but as husbandry conditions decline or as the level of aggressiveness of the strain increases, so production will be adversely affected. In breeding programmes, it then may be desirable to select for low aggressiveness (shown to be possible by CRAIG, ORTMAN and GUHL, 1965), or to select for a peck order — productivity relationship such that the production of only the lowest individuals in the peck order is reduced (MCBRIDE, 1964b). The existence of social rankings in other economic species has been demonstrated (Cattle — BEILHARZ and MYLREA, 1963; MCPHEE, MCBRIDE and JAMES, 1964. Pigs — MCBRIDE, JAMES and WYETH, 1965). Although no relationships between social rank and production characters have yet been found in cattle (MCPHEE *et al.*, 1964; BEILHARZ, BUTCHER and FREEMAN, 1966), social rank has been found to influence growth of pigs (MCBRIDE, JAMES and HODGENS, 1964). Such relationships may well be of considerable importance under conditions of more intensive husbandry.

Variation in mating behaviour is also of importance in breeding populations. SIEGEL (1965) has demonstrated genetic variation for male mating ability in chickens, measured in the absence of competition. Although in selection for this trait, no correlated response in aggressiveness was observed, GUHL and WARREN (1946) have shown that socially dominant males leave more progeny in multiple male mating groups. Such an effect will contribute to increased variation in number of offspring per parent, thus reducing the effective population size. In sheep, LINDSAY (1966) has shown in multiple ram breeding flocks that infertile rams will not only contribute no progeny themselves, but may maintain the attention of ewes which consequently will not be served by other rams. Specific mating preferences among genotypes are well known in *Drosophila* and mice (BARKER, 1962; LEVINE and LASCHER, 1965), while some examples in wild birds are given by OWEN (1964). If such preferences between similar genotypes occur in livestock populations (one example in Merino sheep has been described by HAYMAN, 1964), they will result in increases in inbreeding.

Reproduction

The tremendous development of artificial insemination in dairy cattle over the past 20 odd years is well known. But A.I. in itself does not lead to any increase in the rate of genetic improvement, contrary to early predictions that it would do so by increasing the usage of the best bulls. Thus in early studies (in England — ROBERTSON and RENDEL, 1954; review of American studies — BAYLEY, 1964) little or no differences in average production were found between A.I. and natural service progeny groups. The initial problem was one of determining just which were the "best bulls", and the advantages of A.I. in increasing progeny group size and accuracy of the progeny test were shown by ROBERTSON and RENDEL (1950) and SPECHT and MCGILLIARD (1960). Maximisation of genetic improvement through A.I. then depends on optimisation of the bull testing and selection procedures (SEARLE, 1962; SKJERVOLD and LANGHOLZ, 1964; VAN VLECK, 1964). Although it is doubtful whether any A. I. organisations have succeeded in reaching their optimum operation, real improvement through A.I. is being achieved. In England and Wales in 1964—65 on within herd comparisons, A.I. bred Friesian heifers averaged 35 gallons per lactation more than natural service bred contemporaries. In Ayrshire, Guernsey and Jersey breeds, A.I. bred heifers had advantages of 20, 18, and 22 gallons respectively (L. K. O'CONNOR, pers. comm.). Similar superiority of A. I. progeny has been reported in Canada (MARTIN, RENNIE and BOWMAN, 1965) and in the U.S.A. (reviewed by BAYLEY, 1964).

Given adequate testing of males and selection on estimated breeding value, the genetic advantages of A.I. are derived from the possible increase in the selection differential from male selection. Decreasing the number of males thus used per generation might be thought to increase rates of inbreeding, but this does not seem likely (EDWARDS, 1959) because of the small effective number of males per generation in livestock breeds under natural service (LUSH, 1946). However, the use of A.I. within small individual closed herds or flocks may be disadvantageous for this reason, as shown by DUNLOP and YOUNG (1961) for Merino flocks in Australia. In sheep and beef cattle under extensive management, A.I. generally has not been considered feasible. But with the development of the intravaginal sponge technique for oestrus synchronisation under such conditions (ROBINSON, 1965; ROBINSON and LAMOND, 1966; ROBINSON, 1967), a mating programme could be compressed into a practicable short period of time. Similarly in pigs, oestrus synchronisation has been achieved with the use of a feed additive (POLGE, 1966).

In females, increased selection differentials may be obtained using super-ovulation and egg transfer techniques. Thus numerous offspring may be produced from a selected female during one breeding season by repeated transfer of her eggs to suitable recipients. With the recent development of a non-surgical method for egg transfer (ROWSON and MOOR, 1966), this procedure becomes more practical. Further, as fertilised sheep eggs may be stored in the uterus of a rabbit for up to five days, long distance migration of superior genotypes is simplified (ADAMS, ROWSON, HUNTER and BISHOP, 1961) and "may become in the future a method of choice for improving native breeding stock in developing countries" (Great Britain, Agricultural Research Council, 1966). PLATT (1966) suggests a possible extension of this technique where the nuclei of fertilised zygotes each would be replaced by the nucleus from a body cell of a superior individual to produce a number of animals all identical twins of the original adult.

Artificial modification of the sex ratio would be advantageous in most, if not all, livestock species. In mammals, this modification has been based on attempts to separate X- and Y-spermatozoa (reviewed by SCHILLING, 1966), but to date variable success has been reported. In poultry with the male homogametic, this approach is not possible, but marked changes in sex ratio have been reported by PARŠUTIN, ŽMURIN and RUMJANCEVA (1966) following supplementation of the diet of hens with amino acids, or injection of amino acid into the whites of eggs prior to incubation. The potential advantage of sex ratio modification is generally considered as an increase in the probability of a given sex in the offspring of a particular mating. Thus where selected (or contract) matings are utilised by dairy cattle A.I. organisations to provide young bulls for progeny testing, increasing the probability of male offspring obviously would be advantageous, and would allow some increase in the selection differential of females to breed males. However, in terms of rates of genetic improvement, the consequences and possible advantages of sex ratio modification do not seem to have been evaluated. Thus in dairy cattle, it might be presumed that increasing the proportion of females at birth would be advantageous, the excess females replacing male calves that would be sold for meat production. This may mean increased economic return to the breeder, but what of genetic improvement? Assuming a stable age structure in the herd, the number of heifers required for replacements is fixed, and the advantage in producing extra female calves lies in the increased possible selection intensity among females. This will be achieved only if all heifers were production tested on their first lactation, or if there were available some means for early selection of heifers before the commencement of their first lactation. In poultry, on the other hand, the economic advantages are more obvious, extra females providing increased return to the breeder from their sale to commercial producers. As the testing capacity of the breeder may be assumed to be fixed, any increase in rates of genetic improvement from increasing the proportion of females will depend on the relative effects of numbers of families tested and average family size (ROBERTSON, 1957b; RENDEL, 1959b; SMITH, 1960). Given then that artificial control of the sex ratio will become possible, we would wish to know beforehand the optimum sex ratio in each species — that is, optimum in terms of maximising genetic improvement and maximising economic returns.

I would like to conclude this review with a reference to the economics of breeding operations. I summarised earlier the conventional approach to the derivation of a breeding programme, as outlined by MCBRIDE (1965). In addition, one normally recommends that the operational viewpoint be taken; that the improvement achieved must be sufficient to more than compensate for the costs involved. But these costs are generally unknown and unanalysed. Some attempts have been made to assess the relative economic value of various selection characters in livestock (DUNLOP and YOUNG, 1960; MOAV and MOAV, 1966; SOLLER, BAR-ANAN and PASTERNAK, 1966), but little is known of the overall costs and returns of breeding programmes. One would assume that these have been considered by the commercial poultry breeding organisations, at least for internal information, and SKALLER (1964) has outlined the factors determining the economics of poultry breeding programmes. Results of such investigations would be of value not only to individual breeders, but to Governments and those concerned in the formulation of national policies and international aid programmes.

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Zusammenfassung

Grundlage der Entwicklung der Tierzüchtung sind die Erkenntnisse einer Reihe von Wissensgebieten. In der vorliegenden Übersicht wird über eine dieser Disziplinen, die Populationsgenetik, berichtet, und zwar speziell über die Theorie der Verbesserung von Leistungseigenschaften unter Einbeziehung anderer Disziplinen und ihrer Beiträge zum Tierzüchtungsprogramm.

Es wird das konventionelle Programm für eine genetische Leistungssteigerung skizziert, aber mit besonderem Nachdruck darauf hingewiesen, daß keine genaue Kenntnis darüber besteht, was als angemessene Ausgangspopulation anzusehen ist und welche Maßnahmen den größten Selektionserfolg sichern. Eine angemessene Ausgangspopulation sollte die in der Spezies vorhandene genetische Variabilität im größtmöglichen Umfange enthalten, und es wird die Ansicht vertreten, daß Gene, die in der Ausgangspopulation mit geringer Frequenz vorhanden sind, doch einen signifikanten Anteil der einer Selektion zugänglichen genetischen Variablität ausmachen. Ein weiterer signifikanter Anteil dieser Variabilität

dürfte aus der Spaltung einer relativ geringen Anzahl von Majorgenen herrühren. Die Notwendigkeit eingehender Unterrichtung über die Art der Genwirkung, welche die quantitative Variabilität bestimmt, wird betont.

Es ist von primärer Wichtigkeit, die Ausgangspopulation so groß wie möglich vorzusehen, der Selektionserfolg in den folgenden Generationen wird wesentlich durch die vorhandene Populationsgröße bestimmt. Infolge der beschränkten Größe der Züchtungsprogramme erreicht die Selektion in der Regel nicht das Mögliche; Methoden zur Durchbrechung solcher Grenzen werden besprochen.

In praktischen Züchtungsprogrammen wird im allgemeinen auf eine Reihe von Eigenschaften selektiert, die Leistungssteigerung hängt dann von den genetischen Korrelationen zwischen diesen Eigenschaften ab. Um aber durch Selektion zu bewirkende Veränderungen abschätzen oder aufgetretene erklären zu können, ist es notwendig, die Ursachen der genetischen Korrelation zu erkennen. Das wird durch die Möglichkeit von Stärke- oder sogar Richtungsänderungen der Korrelationen während der Selektion erschwert.

Es wird schließlich über die Beiträge anderer Disziplinen, wie Anatomie, Physiologie, Verhaltensforschung, zur Festlegung der Zuchtziele, zu den besten Zuchttechniken und bezüglich der Grenzen einer Intensivierung der Tierhaltung berichtet. Die künstliche Besamung hat eine Revolution in der Rinderzüchtung bewirkt und durch die Entwicklung von Techniken zur Synchronisation des Geschlechtszyklus wird ihre Anwendung auch bei anderen Arten möglich. Es werden die Auswirkungen von Super-Ovulation und Ei-Übertragung sowie der Veränderungen des Geschlechtsverhältnisses behandelt. Die Übersicht schließt mit dem Ersuchen, daß auch über Fragen der Ökonomik von Züchtungsprogrammen informiert werden sollte.

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