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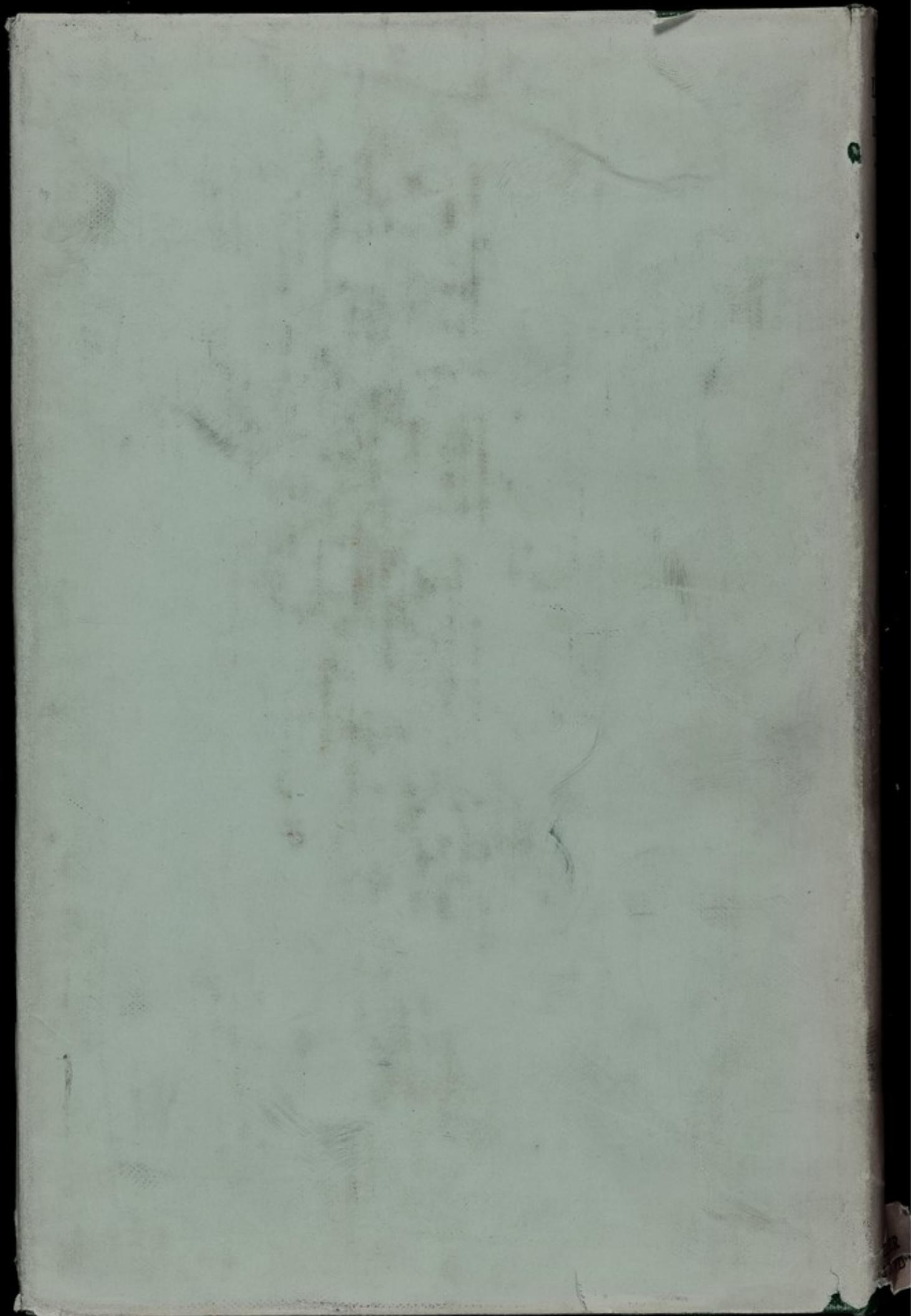
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LIVESTOCK IMPROVEMENT
IN RELATION TO HEREDITY AND ENVIRONMENT

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IN RELATION TO HEREDITY AND ENVIRONMENT

BY

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PREFACE

FORMAL genetics does not always provide a satisfactory or convenient approach to an understanding of the principles involved in questions of livestock improvement and selection. The breeder finds it too remote at many stages from practical applications and bearings; for the agricultural and veterinary student it usually follows too detached a route. The approach made here represents an attempt to outline the principles and to indicate how the genetic and environmental concepts are interwoven in the idea of stock improvement.

The stimulus to make this attempt springs from discussions with my former colleagues and senior students in Western Australia, and with a great number of stockbreeders in many countries. If the topics of environment are surveyed in this book in a predominantly ecological light, it is because my contacts with livestock industries have ranged widely; my associations with practical breeders and livestock have been even closer than those with geneticists dealing with laboratory or statistical material. For my part, I am deeply indebted to breeders for the facilities and help they have so freely given to enable me to realise that a vast laboratory, as yet little used, exists in the field and on the range. Moreover, my conviction grows that it is not only a task but also the duty of geneticists, along with breeders, to seek those common meeting grounds on which the wider problems of livestock improvement and policies may be examined in broad perspective. Of the many breeders who have helped me to reach this point of view, Messrs A. L. B. and E. H. B. Lefroy must be among the first to accept my grateful acknowledgment of their encouragement, enlarged by ever-ready and acute criticism. My thanks are also due to Dr H. P. Donald for his generous help with the general and detailed presentation, to Professor R. G. White

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<div style="text-align: right">J. E. N.</div>

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CHAPTER I

GENERAL ASPECTS

DOMESTICATION of livestock began so far back in history that its origins are to-day mainly of academic interest. Throughout its course, however, there must have been a continual urge towards the selection of animals just a little more suited to the requirements or ideals (whatever they might be) of man. The ways in which this urge was expressed and the methods by which " improvement " was achieved are of special interest, because man is still a long way from being able to mould his livestock with anything like the precision with which he casts and forms his machinery and his buildings, or even with the speed at which he selects and grows improved plants.

" Improvement " is, moreover, a relative term; neither man himself, nor his environment, has fixed demands. What is more useful or more desirable to one person may be much less so to another, what is successful in one locality may be unsuccessful or ludicrous in another. Yet we are justified in thinking in terms of " improvement " in so far as it is an idea common, and quite definite, in the minds of stockbreeders irrespective of its specific objective or general trend.

With domestication, care of stock began and the foundations of husbandry were laid. The Arab horse and many kinds of dogs have certainly had much attention given to them over long periods of time, no doubt largely because of their intimate associations with man. For all the domesticated animals the standards of care continually change according to the status of the animal and its products. For instance, the artificial environment which the pig has so largely achieved can confer on that animal a higher degree of husbandry, on the average and in many countries, than is given to cattle or sheep.

These considerations are deliberately mentioned now because in all discussions on livestock improvement and husbandry it is difficult to lay down hard and fast rules of method or of objective. A broad view is essential.

The methods of the early stock improvers are little known,

A

except in certain cases. Most probably they began with local types of animals which, because they could be recognised as local types, had presumably some special advantages or adaptations to their local environment, whether those were based on economic, geographical, or physiological grounds, or were only imaginary. The immediate possibilities of interchange and traffic in livestock were relatively restricted until comparatively recent times, though in their slow, mass migrations the human populations were no doubt accompanied by the early domesticated beasts. Examples of these transferences are still to be found among the more primitive communities of the present day, for example, in the West African " longhorned " cattle which bear distinct resemblances to the ancient Hamitic stocks emanating from a north-easterly direction. But the other side of the picture is found, in about the last hundred years, in the wholesale and exclusive occupation of Australia and New Zealand by derivatives of European types of domesticated animals. (Kelley, 1941.) [1]

The importance of these local types must be stressed; much valuable historical and scientific research remains to be done in discovering more information about their characteristics and the factors which influenced their segregation into distinguishable types. It is not of course suggested that they were so distinct that no overlapping, or gradation from one type to another, occurred—few of our present " breeds " would escape criticism on that score—but these ancestral characteristics and their habitat reactions are significant in relation to the chief considerations which give the background of improvement.

The first consideration is that the constructive breeder, or improver, is concerned with building upon the foundations already existing; his function is largely that of securing, in a few animals, those combinations of existing characteristics or qualities which, already present, seem to him to be undesirably dispersed over too many individuals. To this end the breeder sets up his " ideal type "—his conception of the maximum, or optimum, recombination of characters—and proceeds, according to some plan, to attempt to approach that ideal. By some sort of selection he endeavours to " improve "

[1] *See* References, p. 191.

his stock towards a standard which in his opinion represents an advance, at least over the average of the kind he knows or to which he has access. The standards, of necessity, have varied, and will continue to vary, according to the breeder's knowledge of stock and to the nature of the demands, utilitarian or aesthetic or both (or neither !), made upon his animals. There is always some purpose in or stimulus to his selection, whether it is based on performance alone (milk yield, draft, maturity, wool characters, etc.) or on adaptation to environmental conditions. In the latter, even temperament may be involved, as for example in the question of suitability to certain forms of management, close grazing or confinement requiring a different standard in this respect compared with extensive ranging.

On this question of selection, we have an idea of how some of the early livestock improvers worked, either directly from their records or by implication from their actions. Bakewell, the most famous of English improvers, collected his " likes " from many sources—but within one general type—and followed a plan of " like to like " mating before making his great contribution to the practice of livestock improvement by developing and using what is now known as the " progeny test " (Chapter XIII). Ellman of Glynde searched carefully for the reasons for his Southdown type before embarking on his plan for improvement of the local kinds of sheep and gave a lead to the modern studies of market requirements ; his table of the butcher's prices for different cuts of mutton might be used as a classical text for every young breeder. (Watson and Hobbs, 1937.)

But both these men, and their successors, recognised clearly the second consideration : that however good the potentialities may be for improved production, they cannot be detected reasonably unless they are given adequate opportunity for expression. Without the appropriate environment permitting expression, selection is limited and may be unavailing.

This association of stock improvement and husbandry, of selection and environmental control, has several aspects.

(a) In the first place it gives an explanation of why marked progress in some directions has been accelerated in comparatively recent years. The great revolution in British agricultural

methods which took place with the adoption of root crops and new rotations, occurred less than two hundred years ago. The turnip was one of the great factors in the development of British stock in that it provided a new technique in winter feeding, which meant a better sustained nutritional level for the stock throughout the year. This in turn enabled animal growth to proceed relatively unchecked, compared with the results of the severe fluctuations in nutritional environment previously obtaining. Because of this, new ideals of maturity of meat characters and of milk yield in cattle could be set before the animal breeder. Bakewell's genius was applied to the new possibilities under the new opportunities thus created, and the "Dishley" Leicester became established, replacing the old longwool type of Leicester; although his improved Longhorn cattle did not in themselves contribute much to the spread of cattle improvement, Bakewell's imitators laid the foundations of the modern Shorthorn and, later, the Aberdeen-Angus and other breeds.

During this early era of stock improvement, and stretching well into the first half of the nineteenth century, other developments were taking place which tended to assist the progress of breeding and husbandry. Social services were changing; with increased transport facilities and with the growth of newspapers, opportunities increased for contact and the interchange of ideas. Agricultural societies were formed, and whatever the present-day critics of shows may say, the early exhibitions of stock served a most useful purpose in stimulating interest in livestock improvement. Later in the nineteenth century, the introduction of the Babcock test permitted accurate recording of butter-fat production and so affected the development of dairy cattle.

(b) Also, *pari passu* these developments in the older countries, new lands were being opened to agricultural and pastoral occupation. Into them, *e.g.* Australia, livestock were being imported and two trends initiated: the adaptation of the imported types towards the new environment, and the attempt to establish or imitate the old, original conditions of husbandry in the new. A further stimulus towards change was being added and further possibilities discovered in the expanding stock populations.

An outstanding, but perhaps not unexpected, result of these developments has been the establishment of local centres of breeding or selection which serve as the springs from which the streams of stock improvement spread. In so far as the total environment in a locality is, or can be developed to be, suitable for the expression of characteristics or qualities of some economic significance, that locality is likely to become the home of some more or less distinctive type, which in its turn tends to be used by a process of " grading " (see Chapter XI) in the improvement of either adjacent stocks or stocks kept under similar, or approximately similar, conditions. Again, in the case of types or breeds transplanted into new environments, it appears that success, in the sense that the original type is reproduced or held, depends to a large extent upon how closely the original environment can be recapitulated in the new. These aspects are clearly illustrated in, *e.g.*, the local centres of Merino stud breeding which have, at different times and with distinct types, become established in the Riverina (New South Wales), Tasmania, South Australia, etc., and also in the experience that the offspring of imported stock frequently tend to assume somewhat aberrant forms when compared with the standard set in their ancestral habitat.

(*c*) Unfortunately, the fact that certain stimuli of husbandry have been quite spectacularly applied to effect degrees of improvement of form, production, and performance, has led to two different reactions on the part of some breeders. That good husbandry has appeared essential to improved production has led one group to believe that high feeding and management can override completely what is inherited, and another group to despair of real inherent improvement without the application of distinctly artificial husbandry. Neither view is correct ; the former may be grossly uneconomic, the latter is without foundation ; a sounder approach is a midway one. If account is taken of those historical, geographical, and economic, as well as the biological, considerations of animal improvement discussed above, it will be recognised that control of environment and of type selection must be closely associated and that progress lies in the careful adjustment of the two within the limits imposed by each.

Many of the environmental factors are beyond control by

the breeder and yet individually, or in conjunction, may exert quite important effects upon his stock and the question of their improvement. A few examples may suffice : Topography and geographical location influence not only agricultural systems but also livestock populations, *e.g.* the suitability of the water buffalo to swamp or irrigated areas, of the Merino or the mountain breeds of sheep to exposed, extensive ranges, of wool-producing sheep to some, but only some, unimproved and unimprovable " back " countries, of the mule or the pony to different sets of difficult transport conditions. Climatic conditions have pronounced effects directly as well as indirectly, *e.g.* temperature and humidity on respiratory rate and general metabolism to the exclusion of temperate zone breeds of cattle from certain tropical areas (Manresa *et al.*, 1940). Economic factors may establish the profit of an enterprise in otherwise unsuitable localities : city dairy herds in many countries, hot-house lamb production in North America (and political " considerations " may give advantage to otherwise quite unsound systems and procedures !).

Yet certain animals have become freed in recent times of many of the restrictions of environment in that techniques of husbandry have been developed to bring them under highly artificial conditions. For instance, the pig and the fowl (quite apart from the rabbit and other smaller animals) are now kept in very close conditions of domestication, so that control of environment has reached a high level, while in certain cases the use of air-conditioned barns for milch cattle is justifiable when the economic site of the herd permits. But two important and closely related aspects of these artificial situations must be mentioned ; the more certain factors are controlled, the more significant do variations in other factors become (*e.g.* Dunlop and Williams, 1939), and the greater the attention that must be directed towards genetic as distinct from environmental improvement.

(*d*) The early stages of environmental amelioration usually allow marked steps forward in stock improvement, just as production, say of meat or milk, rapidly responds to a change from low to high nutritional level, but as the general level of husbandry rises, the differences become less marked. The course of improvement tends on the average to assume a

slower tempo as it proceeds unless some new, and distinctly advantageous, method of management, of feeding, or of selection and breeding is introduced, from which point a fresh stage of improvement is initiated. To put this another way : in any population there is a tendency, on the average, to establish a limit of productivity for a certain set of environmental conditions, which include economic as well as husbandry and nutritional factors. For example, a dual-purpose performance for meat and milk which admittedly does not express the fullest capabilities for either form of production, may be *practicable* under certain agricultural conditions. Within each environmental level, however, there are individual variations in performance which must be attributed to inherent differences in response, and where environment has become relatively stabilised, these genetic differences become important. But when environmental stimuli are also being improved, the difficulties of dissociating in practice what is genetic and what is environmental are great.

On this question much further investigation of the inherited and its modifications is required so that practical stockbreeding schemes can be soundly determined. Otherwise it is possible that claims may be made for genetic betterment when their real basis is in better management ; the contrary is not nearly so likely to be claimed or admitted.[1]

(*e*) When so-called primitive types of agriculture and their associated stock were first encountered by people accustomed to a form of productivity which appeared distinctly advantageous, a natural assumption was that the first step towards improvement lay with the introduction of improved types, the objects being either replacement of the primitive or grading by crossbreeding. Also with the occupation of new areas, the claims of importation were obvious. Colonial empires

[1] This particular aspect of the main problem is frequently overlooked by breeders and scientists ; perhaps especially by those breeders who accuse the geneticist of making little practical contribution to breeding. The very progress that has been made by practice and science towards greater control of environment, though adopted in practice in varying degrees, has tended to restrict the opportunities for spectacular achievement and to reduce the number of " soft spots " in the line of attack. Actually, it adds strength to the argument for closer mutual association and co-operation.

provide many examples of these ideas. Yet experience has shown that once the balance or association of environment and hereditary constitution, with its limitations, is recognised, a new conception of what is necessary has had to be made. This is founded on the observation that individuals frequently exist that are capable of high performance even under the low, " primitive " level of husbandry, which, with their existing adaptation to it, can provide a more efficient basis for selection and improvement (for example, the Sahiwal and other cattle breeds in India and the Afrikaner cattle in South Africa). Further, under such circumstances there is often a social or human adaptation to the conditions which resists adjustment to higher demands of stock husbandry.

These considerations have been introduced at some length because they are involved in the complex background of stock improvement. Their impacts are different in degree and direction according to locality and the broad economic and social contexts of the livestock industries. Because an individual breeder may not be, or believes he is not, concerned with some of them is no reason why he should not bear them in mind, and even if the breeder neglects them that is no reason why the scientist should be excused from regarding them or should evade their implications.

CHAPTER II

PARTICULAR PROBLEMS

THE glorious uncertainty of breeding appeals only to the few ; the great majority are inclined to prefer a reasonable expectation of what the progeny of any mating are likely to be. The breeder is interested in the animals which deviate from expectation in the plus or minus directions of performance and productivity. Constructive breeding policies should aim either at plus combinations or else at reducing the frequency with which undesirable deviations occur.

There are several ways of raising the milk production of a country. The yield of every cow may be increased—most likely by improved nutrition and management ; the average production can be raised also by increasing either the yields of the group of best producers, or the proportion of high-producing cows in the population. Some of these steps would accomplish a greater total milk production with actually a decreased cow population. Or, if it were possible to select those kinds of cows which were more efficient in converting available foodstuffs into milk, a higher total production could be obtained by keeping more cows without further call upon the food supply. Practical policies usually include some combination of two or more of these ways ; and the problem is similar in the individual herds.

All of these ways presuppose the existence of some quantum of genetic differentiation just as much as they presuppose a general degree of freedom from disease and ill health. Even the first-mentioned assumes an inherent capacity for response to raised nutritional conditions, while the others depend upon the recognition of individual variation, or deviation from the average of the population. In one form or another these variations of character or response are the raw material with which the breeder works ; he is therefore ultimately interested in their causation and his chances, or even certainty, of controlling them. Unless the variations are due to chance, the success of breeding plans must depend upon the possibility of

increasing the precision of breeding methods, that is, upon the scientific control of the causes of deviations from the expected.

This greater precision can be achieved in many ways, and since some objective in breeding—an " ideal type "—has to be laid down as the first step, it is opportune to mention at this stage the scientific tests or measurements that can be introduced to aid in defining what is a desirable animal. The incursion of precise methods differs of necessity in the various kinds of animals, according to the form of performance or productivity demanded, or to the combinations of attributes required, for no one animal is expected to give a simplex yield of any one thing. For example, a certain sort of fat lamb may be the objective ; its prime represents the attainment of certain proportions of fat, lean, offal, and bone within a reasonable time and with a certain economy of nutritional supply, but towards its production a series of other qualities are necessary in its dam, such as an economical growth to her maturity of first pregnancy, a pelvic formation amenable to easy parturition, a milk yield sufficient to nourish her offspring adequately, a temperament suited to the exhibition of maternal care, especially to the new-born lamb, a level of fecundity which can be exploited to produce a satisfactory " drop " of lambs, and a " constitution " such as to give a sequence of successful pregnancies long enough to ensure a low capital depreciation per lamb weaned. Again, the function of a mare of draft type is to perform a certain amount of tractive work throughout a number of years as well as to raise offspring of the same sort. The situation becomes more complex in the so-called dual- or triple-purpose animals, but even in the simplest cases the existence of as yet unmeasurable qualities leaves room for the exercise of breeding skill or art as well as the introduction of scientific tests or records.

Various tests of performance will be discussed later (Ch. XIII) ; for the present, only the advantage of using such records in defining type is emphasised. Among such records, techniques for which exist, are milk yield, butter-fat, persistence of lactation, age, fertility, pulling tests, block tests for meat animals, fleece weight and yield, litter growth and survival, etc.

Whatever may be the composition of the " ideal type ",

the breeder's concern is with the form of character combinations involved and with keeping it in subsequent generations. In both these the difficulty of distinguishing between modifications due to environment and variations due to inheritance is again manifest, so that the precision with which type can be recognised, depending on the precision of measurement, is not greatly enhanced unless the records of tests permit analysis and elimination of environmental effects. That is, ultimately, the use of performance records must be corrected or qualified to allow for the parts of the deviations due to non-genetic influences.

This complication is inherent in a great number of practical breeding problems, especially those related to the more complex physiological characters of productive capacity (such as milk yield, meat, fleece weight and kind), in the sense that some shades of their expression are attributable to quantitative reactions of external factors of temperature, humidity, nutrition, and management, etc. As results, confusions of thought and inadequacies of selection techniques were incorporated in breeding policies when the whole characterisation of an animal was regarded ; and also the discovery of more precise rules of inheritance was delayed until observation was concentrated on simple characters, relatively unaffected by environment. The confusions were increased when apparently gross variations occurred such as the emergence of a black sheep in a white flock, wherein a major colour change was so spectacular that it distracted attention from the more important phenomenon that the animal was still a sheep, with all its other characters coming within the range of variation in the population of which its flock mates were a sample.

CHAPTER III

HOW INHERITANCE WORKS

THE scientific study of inheritance is of relatively recent development but has contributed reasonably simple explanations of the major underlying phenomena. No full discussion of these is presented here, the intention is rather to treat those concepts which in their broad essentials offer a working basis for understanding the methods applied in animal improvement, and their limitations. For this purpose only a few examples will be considered.

As a first approach it is useful to note an apparent paradox. With due allowance for the fact that all animals reproduce their kind, a spectacular if minor difference in characterisation frequently tends to be overemphasised. For example, the occurrence of a red calf from black Aberdeen-Angus parents is striking ; though now it is recognised as due to one of the simplest genetical situations, it formerly gave rise to much speculation. The important fact is that except in its colour such a red Aberdeen-Angus is still of Aberdeen-Angus type ; in its conformation, its hornlessness, its aptitude for beef development, and so on, it resembles its parents much more closely than in the colour of its coat. Further, it can pass on its general characterisation (it is still a bovine) just as its parents have done to it. Regarding it as a whole, it has certainly inherited a complex of characters, in relation to which its coat colour is insignificant. Yet in the study of such simple differences in characters the modern knowledge of genetics was largely developed, finds many of its classical examples, and encounters some of its major difficulties in being considered somewhat unreal and inappreciable by the practical stockbreeder. (The practical implications of the cases where simple characters, such as coat colour, hornlessness, etc., are so-called breed characters will be discussed more fully later.) On the other hand, there are fairly simple genetic situations in which a gross change in characterisation may result, such as in the " bulldog " calf ; but their occurrence

is relatively infrequent in a population of animals, so that the practical breeders tend to discount them unless a particular herd, or part of the population, is severely affected.

Those inherited units, or factors, which instigate or influence the developmental processes leading to particular characterisations, are now called *genes*. The facts and problems of inheritance depend upon the ways in which genes are passed on from one generation to another, and upon how genes act and interact. Great numbers of genes are concerned in inheritance in any particular animal, but a direct understanding of the ways in which the hereditary mechanism operates can be obtained by neglecting all the other genes and characters which are alike, and paying attention only to those that are dissimilar. In the cattle coat colour example mentioned above the inheritance of red *v.* black can be considered quite apart from the characters which are " cow " ; then red and black form a pair of contrasting colour expressions whose inheritance can be followed independently of any other set of characters.

The mechanism of gene transmission can be broadly summarised as follows :

It is regulated by the behaviour of the *chromosomes* during the processes of cell division and multiplication that are fundamental to growth and reproduction. Each body cell (*somatic,* as opposed to *germ,* cell) of each species of animal includes in its nucleus a double set of chromosomes in pairs, each chromosome with its complement of genes. The following can be taken, subject to further investigation, as typical chromosome numbers : horse, cattle, goat, 60 ; sheep, 54 ; pig, cat, 38 ; ass, 64 ; dog, 78 ; rabbit, 44 ; duck, 48-76. A typical number can be termed 2n. During ordinary cell division the 2n chromosomes each divide so that every daughter cell receives 2n chromosomes with their complement of genes and the chromosome number and gene complex is preserved.

In the formation of the germ cells, however, the process of cell division takes a different course, and at a certain stage a special " reduction division " occurs, before which the chromosomes pair off and then separate so that one member of each pair passes to each of the daughter cells. As a result, the final free germ cell, or *gamete,* whether male sperm or female

ovum, receives only one half the chromosome content of its parental cells, *i.e.* n chromosomes. The development of the fresh individual begins with the fertilisation of an ovum (egg) by a sperm; the n chromosomes of the male gamete are added to the n of the female gamete to re-establish in the fertilised ovum, or *zygote*, the typical 2n chromosome number, and hence the gene complex, of the parental species. It is entirely a matter of chance which member of a chromosome pair may pass to any gamete.

Just as the chromosomes are paired, so also are the genes. The corresponding or contrasting characters are described as *allelomorphic*. Thus, in cattle coat colour we can speak of black as allelomorphic to, or the allele of red, and describe their appropriate genes as those for black and red. A familiar, but by no means universal, phenomenon is that one allele is *dominant* to the other member of the pair; in this case black is known to be dominant to red and symbols may be used to represent the genes as *B* and *b* respectively. On these lines and neglecting altogether all other genes or characters, an animal possesses in its somatic cells two genes; its genetic formula can be one, and only one, of the following : *BB*, *Bb*, *bb*. In the first two cases it is black in character, *B* being dominant to *b*, and in the third, red; that is, in such a case of simple dominance and inheritance dependent on a single gene pair, animals may express the same character, qualitatively, though they may have different genetic formulae. For convenience and clarity it can be said that the two kinds of black are of the same *phenotype* (appearance) though of different *genotype* (genetic constitution in respect of these particular genes).

The importance of this distinction is revealed when the behaviour of the different types in inheritance is considered. In the red animal (*bb*), the gametes can obviously each receive only *b*; mating red with red can result only in *b*×*b* to give *bb* zygotes, that is, red offspring, known as *homozygous* recessives. In the homozygous dominant black (*BB*) the situation is the same, its gametes are all *B*, and mated to homozygous black this type will produce only *BB*. In other words, both homozygous types, *BB* and *bb*, breed pure for their respective colour characters.

The other black phenotype (*Bb*) behaves differently and must have a different origin. If a homozygous black were mated to a red, a *B* gamete would unite with a *b* to give a *Bb* zygote, *i.e.* a *heterozygous*, or impure, black, and clearly this is the only type which could emerge from such a mating, *B* (black) being dominant to *b* (red). That is, the first cross generation, termed F$_1$, of such a mating would all be heterozygous blacks.

A knowledge of the behaviour of this type on subsequent breeding, and the frequency of occurrence of heterozygous individuals in a population, provides explanation for many of the simpler, and formerly obscure, problems in animal breeding and selection, especially when qualitative character differences such as this colour pair are involved. The gametes of *Bb* individuals may be either *B* or *b*; breeding heterozygous individuals *inter se* provides opportunity for either paternal *B* or *b* to fertilise maternal *B* or *b*, hence the possibilities in zygotes are *BB*, *Bb*, or *bb*, with the chance here of the emergence of a *red* offspring. These chances can, however, be given a simple numerical expression. With both parents producing *B* and *b* gametes in equal numbers, the total production of gametes is comprised of the two types in the ratio of 1*B* to 1*b*, so that with random fertilisation the relative frequencies of zygote formation are $(1B+1b)(1B+1b)$ or $1BB+2Bb+1bb$, *i.e.* 1 homozygous black : 2 heterozygous blacks : 1 red, or collectively 3 blacks : 1 red, which is a 1 in 4 chance for the red. An alternative method of arriving at this result is by means of a chequer board with the gametes arranged as the sides of the square, *e.g.*

	♀B	b
♂		
B	BB	Bb
b	Bb	bb

In addition to showing how the combination of genes is mainly a matter of chance, this example also illustrates some of the other simplest rules of inheritance. Just as it depends on chance which gene an individual may receive from either

parent, so also it depends on chance which gene of a pair may be passed on to any particular offspring. Thus, if the first offspring born of a $Bb \times Bb$ mating is Bb or BB, this does not affect the chances of the second offspring being BB, Bb, or even bb. The ideal or typical second generation (F_2)
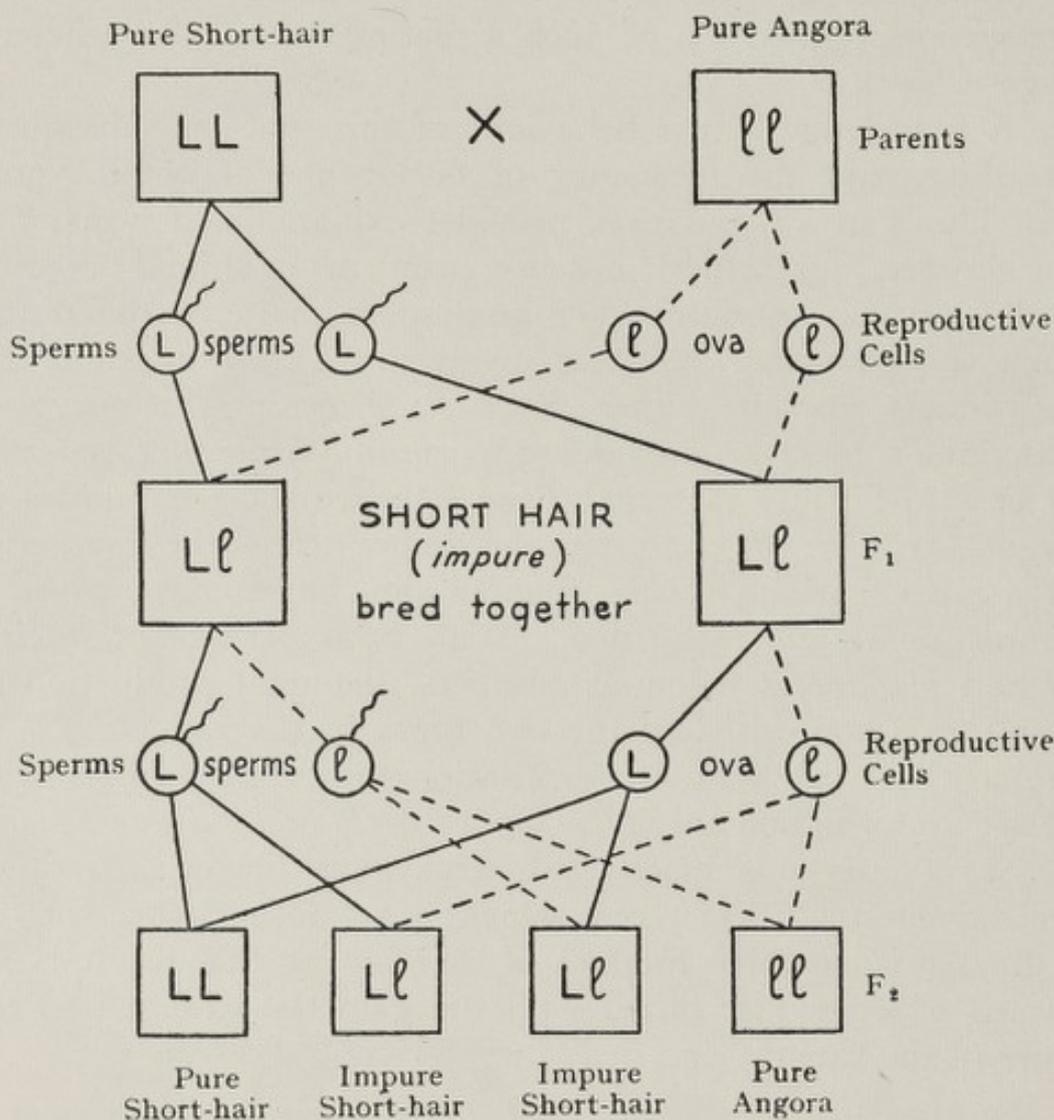
FIG. 1.—The inheritance of short-hair v. Angora (long) hair in the rabbit. *From* Pickard, 1943.

ratio is only revealed when large numbers of matings (or fertilisations) are made.

In the rabbit, short hair (L) is dominant to Angora long hair (l); the formation of the F_1 and F_2 types is shown diagrammatically in Fig. 1 (from Pickard, 1943).

If heterozygous blacks (Bb) are mated back to homozygous
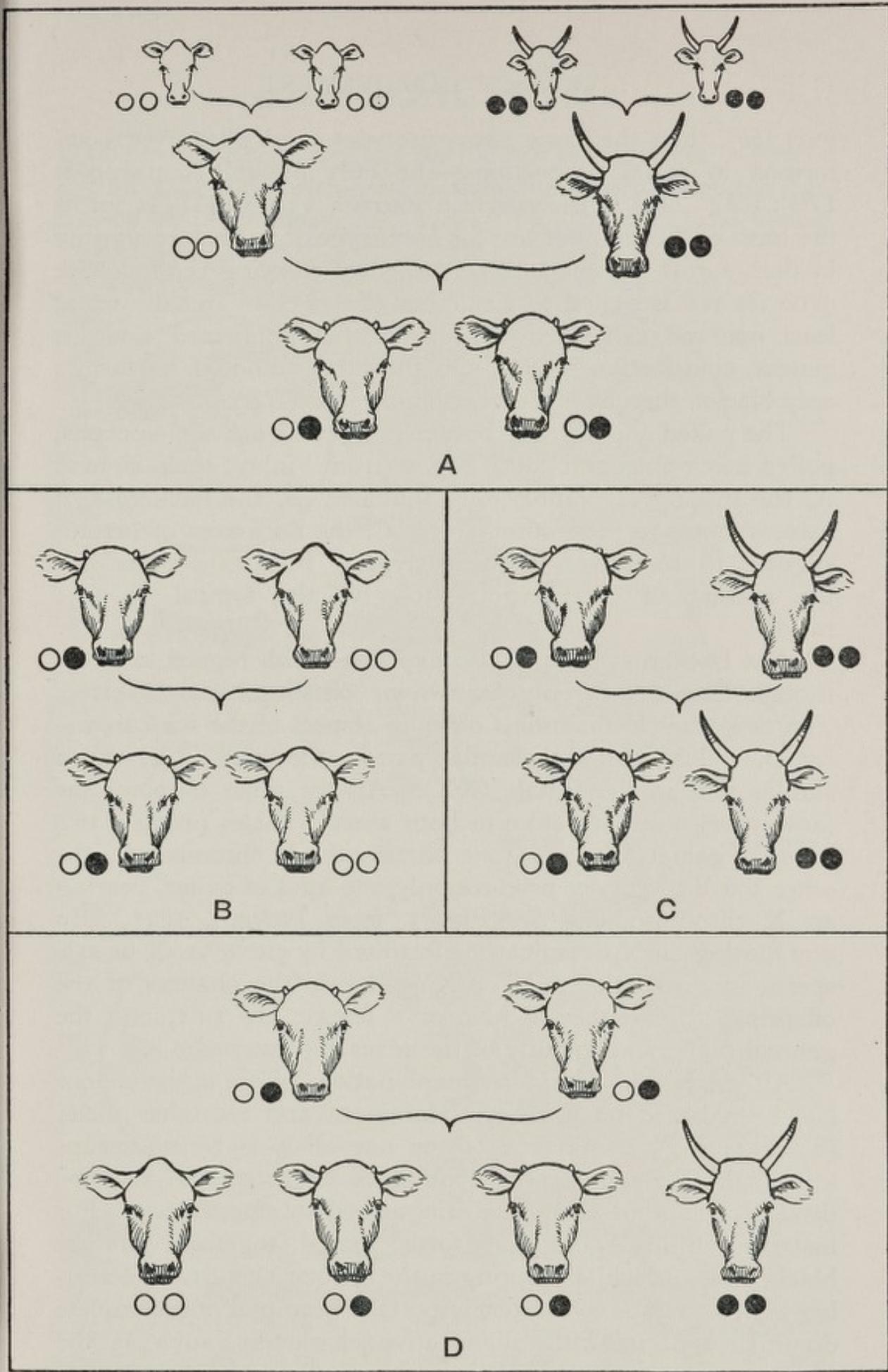
FIG. 2.—Inheritance of the polled and horned characters.
○ = " polled " gene ; ● = " horned " gene.   *From* Finlay, 1924.

reds (*bb*), then the same two genotypes, and phenotypes, are formed in equal proportions—the only possible outcome is 1*Bb* : 1*bb*. This is the single backcross 1 : 1 ratio. It forms the basis of the simplest test for homozygosity or heterozygosity in that, *e.g.* if a black bull suspected of carrying the recessive gene for red is mated to a number of red cows and throws at least one red calf, then the suspicion is confirmed, and his genetic constitution is *Bb*. On the other hand, if he throws only blacks, then he is clearly homozygous (*BB*).

The polled and horned characters in cattle are allelomorphs, polled being the dominant. Fig. 2 (from Finlay, 1924) shows : A, the mating of homozygous animals ; B, the backcross of heterozygotes to pure dominants ; C, the backcross of hetero-zygotes to recessives, with its typical 1 : 1 ratio ; and D, the mating of heterozygotes to give the typical F_2 3 : 1 ratio.

The backcross ratio is also expressed with regard to sex— though here a different *chromosome* constitution is involved. The two sexes in mammals differ in respect of the *sex chromo-somes*, which form a dissimilar pair in the male (XY) and a similar pair in the female (XX). All the other chromosome (autosome) pairs are alike in both sexes. Males produce two kinds of gametes (sperm), one bearing the X chromosome, the other the Y ; females produce only one kind of ovum, bearing an X chromosome. (*See* Fig. 3, from Pickard, 1943.) In any mating an X ovum can be fertilised by either an X or a Y sperm to give either XX or XY ; hence the chances of the offspring being either a male or a female are 1 : 1, and the general numerical equality of the sexes is preserved.

Although the foregoing explanation of gene behaviour has been based on a case of dominant and recessive alleles (black *v.* red), dominance of the one allele is by no means universal. In many cases dominance is incomplete and the three F_1 genotypes can be distinguished by appearance. For instance, Blue Andalusian fowls mated together produce black, blue and white offspring in the ratio of 1 : 2 : 1. Interest-ing and, as will be seen later, important examples of incomplete dominance occur with quantitative characters, such as the size of an organ ; *e.g.* Wriedt (1919) described long-eared, short-eared, and earless conditions in sheep which behaved

in this manner. If the gene for long or ordinary ear is termed E and that for earlessness e, then homozygous longs (EE) crossed with homozygous earless (ee) produce short-eared
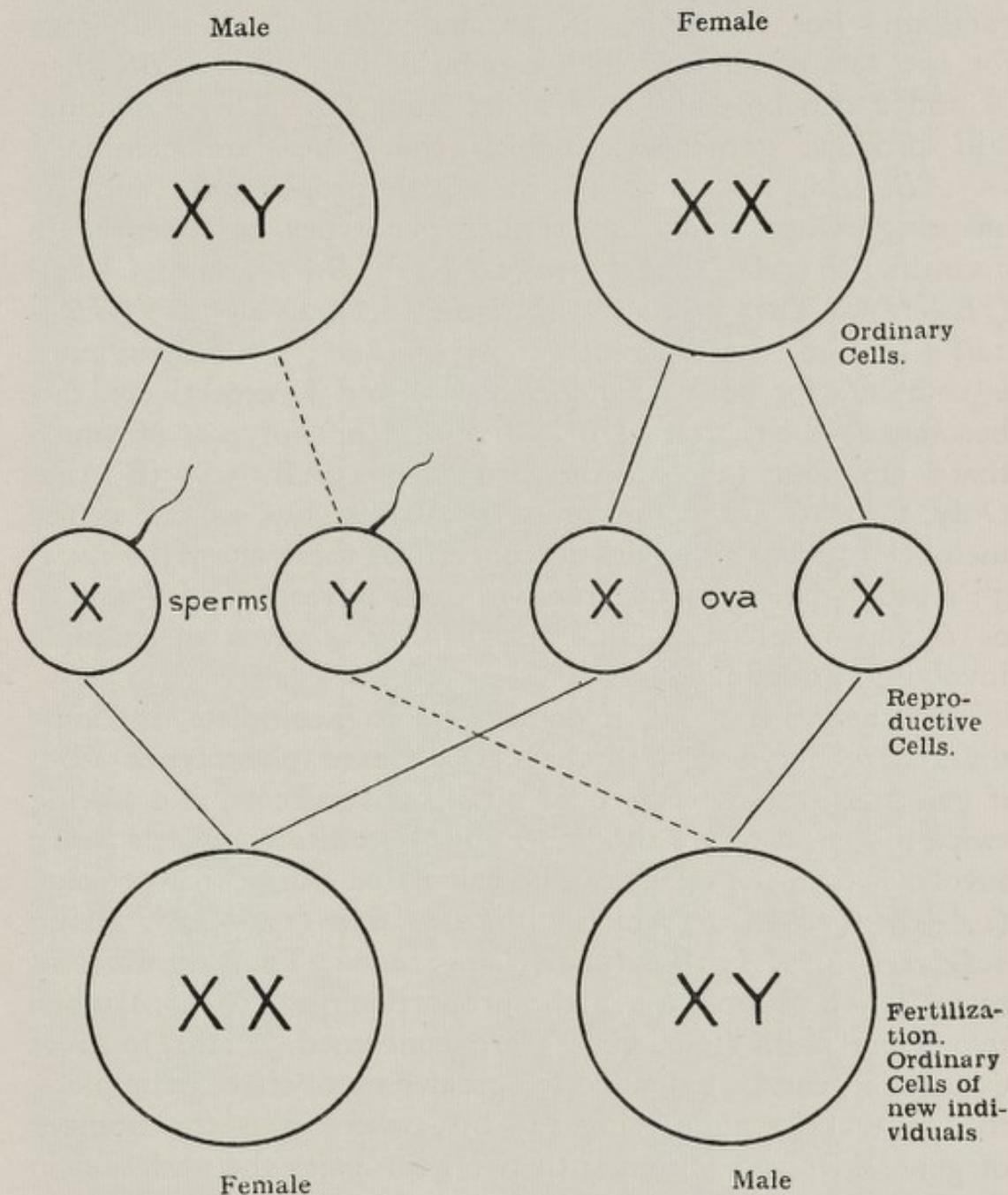
FIG. 3.—The inheritance of sex. *From* Pickard, 1943.

offspring (Ee); these F_1 intermated produce ($1E+1e$) ($1E+1e$) or $1EE : 2Ee : 1ee$ in the F_2. Further, if E were responsible for a certain *quantity* of ear length, say 2 ins., then the F_2 phenotypes would be EE, 4″ ears, Ee, 2″, and ee, 0 or earless.

Where more than two pairs of genes are involved, the important principle is that, with certain exceptions, different series of alleles behave independently, and are assorted at the reduction division quite independently, at random. For example, if an individual is heterozygous for two sets of alleles which can be designated Aa, Bb, then A and a can be considered apart from Bb. This individual will produce gametes in which the genes are combined as AB, Ab, aB, and ab in equal proportions, and its offspring, when mated to similar genotypes, will segregate according to $(1A+1a)(1A+1a)(1B+1b)(1B+1b)$, or $(1A+1a)^2$ $(1B+1b)^2$. That is, they will give $(1AA+2Aa+1aa)(1BB+2Bb+1bb)$ or nine different genotypes (*i.e.* 3^2). If dominance is complete for both A and B over a and b respectively, this becomes $(3A+1a)(3B+1b)$ in terms of phenotypes, of which there are four (2^2), in the proportion $9AB : 3A : 3B : 1ab$. Only 1 in 16 are homozygous recessives, but as far as the members of any *one* pair are concerned, these show the usual $3 : 1$ ratio (the $9 : 3 : 3 : 1$ resolves itself in respect of A and a, or B and b, into $12 : 4$, *i.e.* $3 : 1$). Fig. 4 gives an example involving 3 dominants.

On the other hand, if dominance is incomplete, the nine different genotypes give nine (3^2) different phenotypes; but if genes A and B have equal quantitative effects, AA having twice the effect of A, altogether four quantitative effects being involved, then the result can be calculated from the expression $(1A+1a)^2(1B+1b)^2$, which with $A = B$ is $(1A+1a)^4$, giving $1AAAA : 4AAAa : 6AAaa : 4Aaaa : 1aaaa$. Thus, the different quantitative groups are in the proportion $1 : 4 : 6 : 4 : 1$ when two gene pairs (four genes) are concerned. This form of calculation can be extended for greater numbers of gene pairs, the general formula being $(a+b)^n$, where n is the number of genes involved; even with two gene pairs the variation in the second generation, F_2, is considerable.

It has been pointed out that there are certain exceptions to this general principle.[1] There are many more genes than chromosomes; each gene occupies a specific position, or locus, on its particular chromosome. In cell division each chromo-

[1] For more adequate discussion reference should be made to any standard text-book on genetics.

27 9 9 3 9 3 3 1
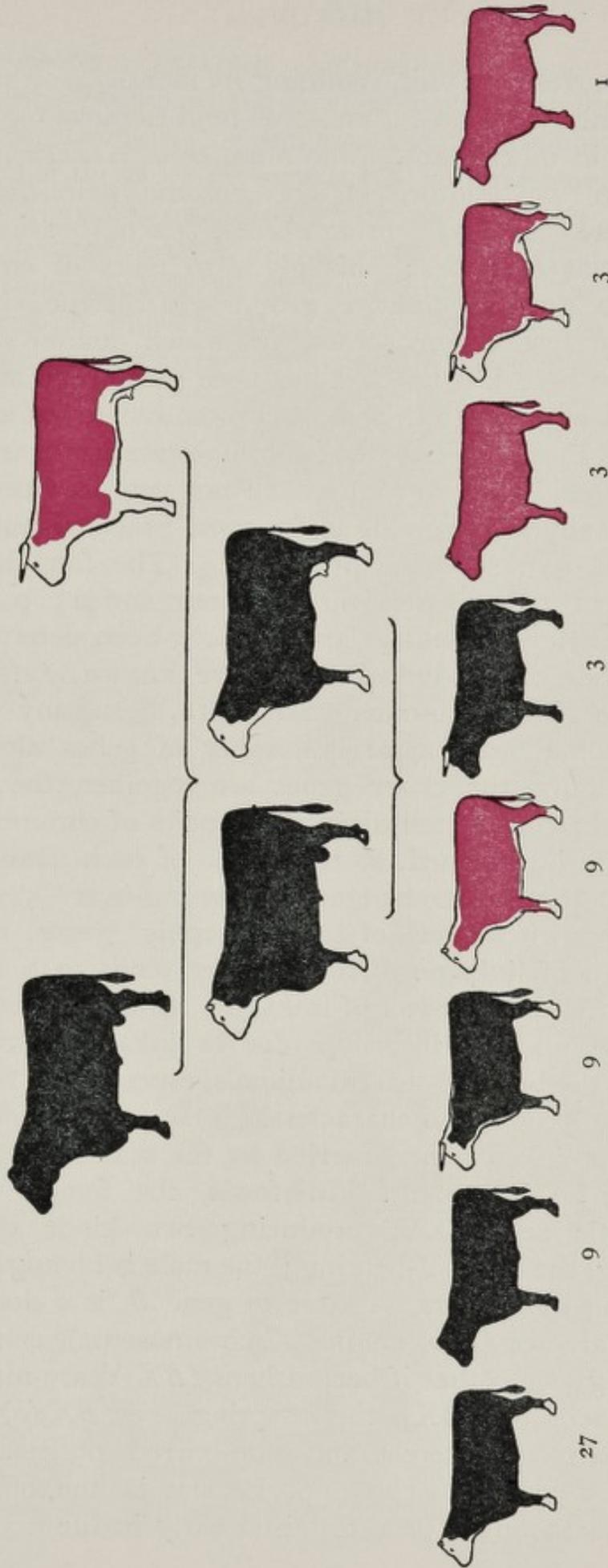
FIG. 4.—The Aberdeen-Angus has the black and polled characters which are dominant over the red and horned characters of the Hereford. The latter, on the other hand, has the white face pattern which is dominant over plain face. The three dominants appear in the F_1 progeny, but when these are interbred eight different types are possible, and the chances of each type appearing in F_2 is indicated by the numbers beneath the animals. The F_2 ratio can be derived from $(3B + 1b)(3P + 1p)(3F + 1f)$. *From Finlay, 1924.*

some usually moves as a unit, retaining its identity, so that the genes appertaining to each chromosome tend to move together, or are *linked*, in inheritance. The number of *linkage groups* corresponds to the number of chromosome pairs. Thus, in cattle there are 60 chromosomes, each bearing its own complement of genes; this gives 30 pairs of chromosomes and 30 possible linkage groups. In some species, with relatively few chromosomes, in which many genetic characters have been identified, it has been possible to allocate various groups of genes to their host chromosomes, but among larger livestock the numbers both of chromosomes and characters are so great that linkage groups have not yet been detected and it is generally safe to assume for most practical purposes that the genes segregate independently. (The fowl has 32 chromosomes, 1 pair of sex chromosomes and 15 pairs of autosomes; already 5 linkage groups have been determined, while a number of sex-linked genes are known, *i.e.* genes carried by the X chromosome. *See* p. 18.) In any event, each chromosome bears a large number of genes along its length. Generally, the closer genes are together, the closer are they linked; during cell division the pairs of chromosomes tend to become intertwined, so that parts of each member of a pair may become interchanged (" crossing-over "), with a corresponding switch-over of allelomorphic genes and a breaking down of linkage. Crossing-over tends to a certain extent to cancel out the effect of linkage; hence, the tendency of genes to be inherited in groups due to linkage is probably of little use to the breeder of farm animals, especially in relation to quantitative, production characters.

Yet the sex-linked genes, carried by the sex chromosomes (p. 18), can be important. In fowls, the female is the " heterogametic sex," XY, producing two kinds of ova, one X-bearing, the other Y-bearing; the male is homogametic, XX. Barring of feathers, say due to gene B, is a dominant sex-linked character (B is on the X chromosome), compared to non-barring, b, so that if barred hens (BX)Y are mated to non-barred cocks (bX)(bX), the offspring are (BX)(bX) and (bX)Y, or barred cockerels and non-barred pullets. The character thus passes to the opposite sex in the offspring, whose sex can therefore be recognised early in life according

to this feather character. Several other pairs of allelomorphic genes are known in the fowl and are used for chick-sexing. In the mammals, the male is the heterogametic sex (XY). The male therefore receives his X chromosome from his *dam*, the Y from his *sire*. Any genes borne by the X chromosome must therefore pass from father to daughter and then to half the grandsons. Y-borne genes pass only from sire to son. As yet, no important sex-linked genes have been clearly distinguished in farm mammals.

CHAPTER IV

GENE EFFECTS AND INTERACTIONS

As far as the inherited characters are concerned, an individual animal is to be regarded as the end result of the action of the genes it has received from its parents ; to its offspring it passes on a half-sample of its genes. Likewise a population of animals, such as a breed, can be considered as a population of very great numbers of genes. But any one character is not necessarily or inevitably attributable to one particular gene, nor does one gene of necessity affect only one character. The same character may be due to different genes ; for example, while the black fleece colour found in breeds of white sheep is usually due simply to a recessive gene, there is also a dominant gene which gives rise to black.

For a black individual to appear in a normally white breed a change must have occurred at some time in the original heterozygote, in the gene which governs the white fleece colour. When a gene changes, it is said to *mutate* and the resulting character is known as a *mutant*. If the mutant character is recessive to its normal allelomorph, then it may remain unexpressed until such time as two germ cells, each bearing the mutant gene, meet at fertilisation. If the mutation has a dominant effect, then it is expressed immediately in the offspring of the individual in which it has occurred. It can only be expressed, however, provided that the gene complex appropriate to its expression also exists. For instance, black fleece colour in sheep clearly depends not only on the particular gene for black but also on the *fleece, i.e.* the presence of skin, fibre follicles, etc. ; similarly, a gene affecting eye colour can only be expressed provided there are no effects of a gene or genes causing eyelessness.

The most easily recognised mutations are those which have gross effects ; many, in domestic animals, have been disadvantageous abnormalities and many of these are recessive. For these reasons it is often implied that gene mutations must be regarded as hindrances to the stockbreeders' efforts in selecting for improved stock. Where they have gross effects,

they may certainly be responsible for some loss, either in dead, infertile, or less productive offspring. On the other hand, it is relatively simple, when the mode of inheritance is known, either to test for the heterozygous carriers (*see* p. 18) and eliminate them, or, by not repeating the mating of known or suspected carriers, to reduce their occurrence to negligible frequency. In any event, the rate of gene mutation is low ; where it has been observed or calculated, in plants and animals, it is estimated to be only somewhere about 1 in 100,000, or even less, per gene per generation.

Gross abnormalities are usually recessive and one may occur in a strain or group of animals possessing other valuable characteristics, such as high production. In such cases the heterozygote, the carrier, shows no ill effects of the undesirable gene. The breeder then has to choose between sacrificing animals with the good points, enduring the loss from the abnormals, or take suitable precautions to lower the chances of the abnormality being expressed, *i.e.* for the homozygous recessive to appear. To take an example from the many cases known : a high producing champion cow of the Yaroslavl breed with a good constitution was used as a basis for inbreeding in the expectation that her good qualities might be fixed in the herd. When she, a daughter and a grand-daughter were mated with two of her grandsons, three out of six calves were found to be deformed, with short thick legs and small lower jaws, and of small body size. Meanwhile her sons were being widely used, so that the undesirable gene had good opportunities of spreading through the breed. The defect was considered due to a single recessive gene, and it could be recommended that the most valuable bulls of the strain should be progeny-tested to discover if they were heterozygous for the gene ; that the sons of bulls proved to be heterozygous should be culled ; and that sires unrelated to the original cow should be used (Ljutikov, 1937).

In other cases the heterozygote may show an effect. In Dexter cattle the short-legged character can be attributed to the heterozygous state of a dominant gene (say L) which, when homozygous, also causes the extreme " bulldog calf " condition, such calves usually being born dead or dying very soon after birth. The gene has, therefore, also a *lethal* effect.

The mating of Dexter bull to Dexter cow involves $Ll \times Ll$, to give $1LL : 2Ll : 1ll$. The homozygotes, LL, are bulldog calves and die, the surviving offspring are therefore short-legged and long-legged in the ratio of $2 : 1$. The intermating of Dexter types does not produce only the required short-legged type; the type is not pure-breeding, as 25% of the offspring are completely lost and of the surviving remainder 33% are off-types. A better practical result, though not an entirely satisfactory one in that the proportion of off-types is increased, is achieved by mating Dexter with long-legged (Kerry) stock, *i.e.* $Ll \times ll$, to produce $1 Ll : 1ll$ in each generation. This method is now exclusively adopted in Eire, where only Dexter $\times$ Kerry crosses are kept, not the " pure " Dexters.

The mode of inheritance of many abnormalities and lethal characters is known, and they provide useful information on how genes act. A wide range of expressions due to different genes is found, such as: hernia and imperforate anus in pigs; crippled forelegs and eyelessness in horses; a double-teat condition in goats; hairlessness in cattle and in rabbits. A gene may not always produce precisely the same effect, as Johansson (1939) has shown for two of the lethal genes occurring among Swedish Friesian cattle. One of them gives rise to " amputated legs " (different to the Dexter bulldog calf condition), which has a very variable expression, some cases showing only very short rudimentary legs, some having normal legs but " bulldog " heads, others normal heads and amputated legs. The seriously affected animals are still-born or die just after birth, less affected ones may live some time after birth. Johansson considers that the variable expression of the " amputated " gene may be due in part to modifying genes (*see* p. 30) and also to the time during development of the animal at which the main gene begins to operate. Time of action also most probably plays a part in the variable expression of another lethal gene which causes a dropsical condition of the foetus. Some foetuses are greatly enlarged by fluid accumulations and may be over twice the weight of normal calves; these may be carried for only 150 days of gestation or less. Others which are only slightly abnormal are carried to term. It is concluded that if the gene begins to operate earlier in development, it has a more pronounced effect.

A good example of time relationships of gene action has been described by Sturkie (1941) in the case of a recessive baldness in fowls. Here a defect in the epidermis (outer skin layers) allows it to separate from the dermis (lower skin layers), and fluid to form between, over the eye and brain regions of the chick during the eighth to eleventh days of incubation. This interferes with the development of the feather papillae, so that by about the fifteenth day of incubation, when the fluid is absorbed, bald areas are formed over these regions. In this case, a definite effect is produced by the gene coming into operation at a particular period of embryonic development. On the other hand, there are series of conditions, also in fowls, where differential effects are brought about by reason of differences in growth activity when the gene operates. Thus, while the general proportions of different parts of the body are remarkably constant in any species or race, abnormal forms, such as some kinds of dwarfs, are well known in which the usual proportions are considerably changed. In the Creeper fowl a lethal gene effect leads to a shortening of the long bones of the limb in heterozygotes; if any homozygous individuals do survive beyond the period during which the gene is lethal, they have the head affected as well as the extremities. The first effects of the gene are in a general slowing down of the development of the embryo, to give a smaller size. After that, the several long bones are affected in different degrees according to the times at which they are laid down in development; the later the bone is formed, the more it is affected and shortened. The toes are not affected in heterozygotes but the long bones are shortened; in the homozygotes the head is deformed and only rudiments of the extremities are found. A gene with similar action is also found in the Dark Cornish breed of fowl, but in this case there is no preliminary reduction in size of the whole embryo; this indicates that the gene present in the Cornish has a smaller total quantitative effect than that in the Creeper (Landauer, 1939). However, the lethal embryos in both breeds are alike in that the heart and spleen are enlarged, and later studies have led to the conclusion that the initial effect of the Creeper gene is exerted on the circulation mechanism to the end that the oxygen supply to the different parts of the body is reduced; this in

turn produces the result that the more rapidly growing parts, those requiring most oxygen, are severely affected (Cairns, 1941).

While these examples refer to lethal or grossly abnormal effects, it must be emphasised that such characters are often the most readily observed and are therefore handy tools with which to study gene action; enough is now known of other characters and other genes to allow of general conclusions.

Such work shows that a gene is capable of influencing more than one character, and it is indeed now considered that most genes affect at least several characters, although in many instances we are primarily concerned only with one, or a major, effect. It is frequently convenient, where a gene is known to have definite influences on several characters, to refer to its *pleiotropic* effects. Series of gene interactions and pleiotropic effects in the house mouse can be shown in simplified form in Fig. 5.
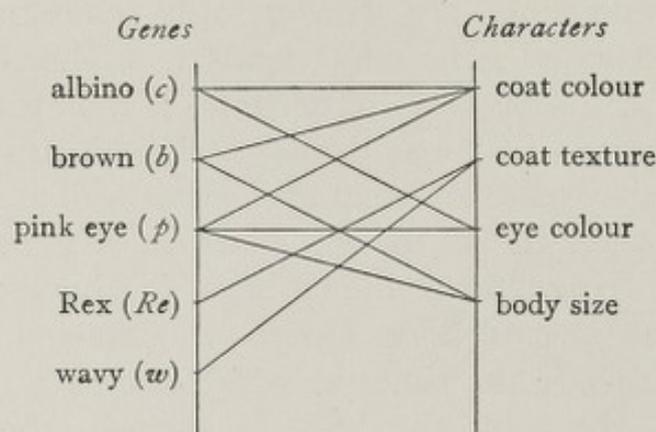
FIG. 5.

A further instance of a time relation may be quoted. White spotting in cats can be of various extents, ranging from the condition in which there is only a slight degree of white on the underside of the neck, through those in which white areas spread up the legs from the tips of the feet and from under the belly over the flanks and sides of the neck, to that in which the only area not white is a small spot on the back of the head. Now, in the development of the coat in kitten embryos the appearance of the hairs follows a similar general sequence, but in reverse order, gradually spreading out from certain centres over the body; if we work *backwards* from the stage

in which the kitten is almost fully covered with hair to that in which the kitten has only very few hairs, and compare the stages with the grades of white spotting, then the bald patches correspond closely to those of the white spotted pattern. From this it appears that the earlier the gene for white spotting begins to act, the more extensive the white spotted pattern, and vice versa; where white is only under the neck, the gene has come into operation late, where there is only a spot of pigmented fibres on the head, the gene has started early (Bamber, 1941).

So far genes in relation to their normal allelomorphs have been largely considered, but many cases are known in which series of genes are situated at the same position or locus on a chromosome; in this case an individual can carry only two of the series, which is known as a series of *multiple allelomorphs*. For example, three multiple allelomorphic genes are involved in the four blood groups found in man and termed the AB, A, B, and O groups. In this series the gene A is dominant to O, B is also dominant to O, and the heterozygote AB is distinguishable by blood agglutination tests in that it exhibits the results of the presence of both A and B genes. The only possible genotypes are the homozygous recessive OO, which gives an O group individual, the heterozygotes AO and BO giving groups A and B respectively, as do also the homozygotes AA and BB, and the heterozygote AB, giving the AB group. Paternity tests depend upon these situations, in that an AB group child cannot be the offspring of an O parent, nor can an AB parent beget an O child, and so on.

In this case the two genes A and B have produced in combination an effect that is clearly differentiated from the effects of either gene operating alone. A similar state of affairs can also be produced by the interaction of genes which are *complementary*, though not multiple allelomorphs. One of the earliest recognised instances of this kind of gene interaction is found in the different forms of comb in fowls. The single-comb condition can be regarded as the simple wild type or normal, and is recessive both to the rose and the pea forms. A breed with pea-combs must be either *PPrr* or *Pprr*, one with rose-combs is either *ppRR* or *ppRr*; when two such breeds are crossed, some of the offspring can have both P and R

genes and are neither pea- nor rose-combed, but have walnut-combs, being of the genetic formulæ *PpRr*, *PPRr*, *PPRR*, or *PpRR*.

The manifestation of a particular gene can be affected in various ways by the action of other genes, but it is not always easy or straightforward to identify or to classify the precise form of gene interaction involved. A character of variable expression can be attributed to a main gene, the different degrees of expression being influenced by a series of so-called *modifying* genes. Many cases have been studied, especially in the variations of colour and pattern in the coats of mammals : the basic colours are primarily related to the presence of dark (black) and red pigment granules, each of which are liable to alterations in intensity and distribution within the coat fibres by series of dilution effects which can give rise, for example, to the bay, brown, black sequence in horses as contrasted with the chestnut sequence. The basic colours can have patterns superimposed upon them, as in the white saddle of the Wessex Saddleback pig, where the " saddle " is due to a single dominant gene. The expression, in width, of the " saddle " varies considerably, even to the extent of a whole white pig, which is probably due to an extreme modification in one direction. A recent study (Olbrycht 1941) suggests that numerous other factors or genes affect the size, situation, and completeness of the saddle, as well as the presence of black spots within the white areas, or white ones on black areas. Although the numbers and precise effects of such genes are not easily determined, they are clearly of considerable importance in relation to selection (*see* Ch. VIII) in so far as they tend to influence its extent and the directions in which it can be applied.

In yet other cases the interaction is one of *epistasis*, in which the effect of one gene or series of genes is completely overruled by that of another. Some of the simplest forms of this interaction have already been mentioned, but as this general principle is also involved in questions of selection, it is necessary to emphasise it. In all mammals colour of any sort, as opposed to true albinism (complete lack of pigment), can be considered as due to a gene *C* in contrast to its allelomorph *c*, so that no matter what colour gene is present, if the

animal is genotypically cc, the homozygous recessive, it is always an albino. The albinism gene is, therefore, epistatic to other colour genes. Coat colours in horses provide an example of epistasis; while the basic colours are black and chestnut (red), black being dominant to chestnut, black itself can be modified to bay, and grey in turn is epistatic to bay and to black. Grey is the highest in the series and pure (homozygous) greys always beget grey foals irrespective of the colours to which they are mated; impure greys mated together produce greys to other colours in the ratio 3 : 1, or mated to other colours give grey : non-grey as 1 : 1.

The situation is not always clearly definable, as in the case of the red, roan and white colour series in Shorthorn cattle. All Shorthorns are basically red, which can be seen in the red eyelashes and hairs of the ear-fringes in homozygous white animals. The main series is attributable to the presence of an epistatic white gene (W), acting with the basic red gene (R), so that a red is $RRww$, a white $RRWW$, while the heterozygous white is roan, $RRWw$. (The white splashes or spots are due to another gene which can be neglected in the present connection, all red and white spotted animals being considered as reds, and roan and whites as roans.) The roan colour is very variable, ranging from almost red to almost white, due to either variable dominance of the white gene or, more probably, the presence of modifying genes. The calf in its early coat may have a few white hairs, leading it to be registered as a roan, whereas it may later be phenotypically a red. In the beef Shorthorn, moreover, it has been fashionable in recent years to favour the red or dark roan, so that breeders have tended to select the animals which are phenotypically red, although they may be either red or roan in genotype. That breeders have been able to select towards this end of the series indicates that modifying genes are involved and that selection has been effectively exerted on them, although basically the roan remains as an unfixable heterozygote, appearing from matings of red × roan ($RRww \times RRWw \rightarrow 1 RRWw : 1 RRww$), roan × roan ($RRWw \times RRWw \rightarrow 1 RRWW : 2 RRWw : 1 RRww$), and roan × white ($RRWw \times RRWW$), and always from red × white ($RRww \times RRWW \rightarrow RRWw$).

This interpretation also helps to explain what happens

when, as is common in practice, whole black beef cattle (Aberdeen-Angus or Galloway) are crossed with white Shorthorns. Here black being dominant to red, the contrasting genes may be denoted *B* and *b* respectively; any question of spotting is again ignored. The pure blacks, free of the epistatic white, can be denoted *BBww*, the whites are *bbWW*; the first generation hybrids (F$_1$) will be *BbWw*, the familiar " blue-greys ".

From the foregoing it will be seen that variations in character expression can follow upon the different ways in which the genes act and interact. In the first instance, the most striking and essential characteristic of the gene is that it can duplicate itself accurately and specifically, independent of the general characteristics of the individual animal in which it resides; it may, infrequently, mutate and give rise to another genetic character. Yet the action of any gene is dependent upon the action of other genes at other loci in the chromosomes; it is thus related to the internal genetic environment, or gene complex, of the individual animal. In considering the results of gene action, the results of gene interaction cannot be ignored. A gene can have multiple effects, sometimes depending on the time at which it begins to operate during development; it may have more or less gross discernible effects depending on whether dominance in relation to its allelomorph (or series of allelomorphs) is complete or incomplete, or upon its interactions with other series of genes which may be complementary, modifying, or involve epistasis. This concept is fundamental to an appreciation of how inheritance works but, while it provides a basis for explaining some of the variation in characters with which the stockbreeder is concerned, it does not explain all of it.

CHAPTER V

CUMULATIVE EFFECTS AND EXTERNAL FACTORS

THE effects of genes in combinations are very frequently additive or cumulative. This applies in many of the quantitative characters such as body weight and size, milk yield, muscular performance, conformation, fleece weight, and so on. Quantitative differences in such characters, which form graded series of expressions, are usually conditioned by numbers of genes, or are known as *polygenic*. It has been briefly shown earlier (pp. 18, 20) how even a few genes with quantitative effects can give rise to a variation in characterisation; this was related to the expansion of the formula $(a+b)^n$. A similar example, involving more gene differences, will tend to give a still better idea of the type of variation which may be found. Suppose the maximum difference in some measurable quantitative character, *e.g.* such as fleece weight, is attributable to four pairs of genes with equal additive effects and that of two breeds one, with the heavier fleece, carries all the additive genes, while the other has all their alleles. If the additive genes are denoted A, B, C, and D, then the first breed is of genotype $AABBCCDD$, with the eight additives giving the maximum effect, the other is *aabbccdd*. The F_1 individuals will be all $AaBbCcDd$, containing only four additives and therefore intermediate in fleece weight between the parents. The inheritance of fleece weight will have apparently blended in the first crosses. The second generation, by interbreeding F_1, will show greater variability, ranging from animals with eight additives, through those with fewer, down to those with none, *i.e.* from one parental genotype to the other. The extreme parental genotypes can each, however, be produced by only one type of mating, gametes $ABCD \times ABCD$ and *abcd* $\times$ *abcd* respectively. Each F_1 parent has also four possibilities of conferring *one* additive (either A, or B, or C, or D), so that F_2 individuals containing *one* additive can be produced by any one of eight possible matings.

C

Similarly, the F_2 individuals with one non-additive can also be produced by any one of eight possible matings; continuing this argument, the possibilities of F_2, with matings within the F_1 type quite at random, are—expanding $(a+b)^8$ with a for additive, b for non-additive genes—seen to be: 8 additives, 1; 7 additives, 8; 6 additives, 28; 5 additives, 56; 4 additives (and 4 non-additives—the intermediate form), 70; 3 additives, 56; 2 additives, 28; 1 additive, 8; no additives (8 non-additives), 1. There is uniform distribution of the variants about the intermediate form, which is the most frequent; if the number of genes were greatly increased, still more classes or variants would come between the parental types, which would become of progressively less and less frequency, forming smaller and smaller proportions of the whole generation population, so that the variation would tend to appear continuous, each variant grading imperceptibly into the next. (In the case of infinitely great numbers of genes, with relatively small additive effects, the distribution of the frequencies of the different classes would be of the so-called " normal " form.)

It is perhaps only of theoretical interest to the breeder to speculate on the numbers of genes in the various species of farm animals. In any species or variety the numbers which have been so far catalogued must represent only a very small fraction of the numbers present. More genes are continually being revealed by genetical investigation, but it is for the most part only genes which have a definite qualitative or spectacular quantitative effect which can be recognised, and the numbers recorded at any time do not give much foundation for estimating the total present.

The further the character differences are examined, usually the more genes are found to be involved, so that it becomes difficult to suggest that it will ever be possible for a breeder to be able to list all the economically useful or important genes in his stock. He can, however, acquire a sufficiently useful working knowledge of the ways in which his stock may be expected to perform in breeding, and of the mechanisms whereby the desirable or undesirable genes or combinations of genes may operate. To do this it is not necessary to know

precisely how many genes are involved in any particular quantitative characterisation.

Another way of stating the breeder's problems is to say that in ordinary circumstances he is concerned with larger or smaller differences or variations in complex physiological characters, not with " unit characters " in the old-fashioned sense. The complicated sequences of growth mechanisms and metabolic actions, which have interacted within the internal environment of the whole organism itself, tend to establish an *a priori* case against too simple an effect of any one gene.

Even simple characters, however, in the genetical sense, are subjected to differences in expression as a result of the action of external environmental factors. One of the earliest cases worked out is that of the Himalayan rabbit, with its light body and dark points. The body temperature is slightly lower at the extremities than over the body generally, and it has been shown that if the skin temperature is lowered by external means near the extremities, on the nose, ear, feet or tail, the coat colour changes from light to dark and the pattern is extended ; even on the body, dark patches can be made to appear. The typical Himalayan pattern (due to a single gene recessive to that for normal, wild type, agouti pattern) can be altered by changing the physiological environment in which the gene is acting, the pigment formation being stimulated by exposure to cold. It is suggested that a similar effect, but the other way round, is found in such animals as the mountain hare and the stoat, which assume a white pelage in winter, as contrasted with the normal coloured summer coat.

Recently Sturkie (1942) has described a form of nakedness arising from a mutation in Rhode Island Red fowls, different to that discussed on p. 27 ; on certain areas of the body, but not over most of the head and on the alar tract of the wings, no feathers, down, or semi-plumes develop. The character varies in manifestation, is inherited as a simple dominant, and the gene has also a lethal effect in that, while hatchability is quite normal, there is a high mortality among the affected chickens in about the first ten to fifteen days. There is no relation between extent of nakedness and mortality, and the surviving hens produce at the ordinary level. The affected chicks are low in body weight and growth rate, on a dry mash

they have a low food intake ; if, however, they are fed a wet mash, their food consumption increases, although not to normal, they do not make up in growth rate and body weight, *but* the mortality is markedly reduced. From these facts Sturkie draws the conclusion that the lethality of the gene is the result of some basic derangement of the physiological processes related to a reduced consumption of food.

Many genetic characters have been identified in poultry ; workers of the Agricultural Experiment Station at Auburn, Alabama (1941), have studied the effect of differences in incubation temperatures on some of them, and have found that while the characters of Frizzled, naked-neck, crest, and comb type are unaffected, a low temperature at two and a half to three days of incubation tends to suppress the poly- dactyl character (supernumerary toes).

The experimental work necessary to establish clearly such effects on gene expression in the larger animals is naturally more difficult than in smaller stock and fowls, nevertheless instances are being found in which a suitable environment is a prerequisite for a particular genetic character to be manifest. That studied by Fourie (1939) in South Africa has considerable significance. He observed cases of the abnormality known as congenital porphyrinuria, or pink tooth, in cattle ; the condition involves the excretion of porphyrins (purple colouring matter) in both urine and faeces, the teeth are discoloured, and the skin develops lesions, due to photosensitisation, in intense sunlight ; these lesions lead to early death. From test matings of affected and related stock, in two groups each of both Shorthorn and Friesland, elsewhere usually called Friesian, cattle, Fourie showed that the character is inherited as a recessive, and that the Shorthorn groups had common ancestry, as also had the Friesland groups studied. Among the parent stocks of these breeds in Great Britain and Holland no marked lesions due to photosensitisation are found ; in South Africa, on the other hand, climatic conditions favour such lesions, and many affected animals were noted.

Such cases form part of the evidence that in considering the variation of characters and their expressions, the influence of external environmental conditions must be taken into account in addition to the effects of gene action, interaction,

and the genetic, internal environments. For some characters, especially the more simple, the genetic milieu of the particular genes responsible for those characters can be ignored; in others the external environmental influences may also be ignored. But where the genetically more complex characters are concerned, like those of economic production and performance, their expression is a result of the interplay of genetic and of environmental factors. Part of the problem of considering selection and improvement of livestock lies, therefore, in becoming accustomed to think in terms of these facts, as a corrective to a too facile assumption that progress in any direction can be attributed mainly to selective breeding or to changed external circumstances. Another part of the problem is to try to estimate the contributions of one or other of the broad groups of influences so that a reasonable assessment may be made of the possibilities and different methods of improvement.

CHAPTER VI

GENE AND CHARACTER FREQUENCY

IN a population of animals with entirely random mating, the proportion of recessives will depend upon the proportion of heterozygotes in the population; if only one animal in ten carries a recessive gene, the possible matings are homozygote $\times$ homozygote $\frac{9}{10} \times \frac{9}{10}$, *i.e.* 81%, heterozygote $\times$ heterozygote $\frac{1}{10} \times \frac{1}{10}$, *i.e.* 1%, and are homozygote $\times$ heterozygote $\left(\frac{9}{10} \times \frac{1}{10}\right)2$ or 18%. But only the heterozygote $\times$ heterozygote matings (1%) can give the recessive and that only in $\frac{1}{4}$ of the progeny (p. 15), so that in such a population the recessive character emerges only in $\frac{1}{4}$ of 1%, or once in 400. If, however, the heterozygotes had been recognisable by their appearance as such, *e.g.* in the Blue Andalusian fowl or roan cattle, and mating had been limited only to them, then the recessive would have appeared in 25% of the offspring. Further, if only the heterozygotes were always retained, the culling—for this character alone—would have to be 50% in each generation, homozygous dominants 25% and homozygous recessives 25%. This type of mating, of like to like, is known as *assortative* mating and of necessity involves an amount of culling or *selection* in so far as only certain individuals possessing the required character are allowed to mate. (*See* Chapters VIII to X for fuller discussions.)

The frequency with which a simple genetic character can be manifested, under any set of conditions favourable to its expression, therefore depends upon the frequency of the particular gene in the group of animals likely to mate; the frequency of combinations of genes is also related to the gene frequency and the kind of matings which occur.

Probably most individuals are heterozygous for a great number of pairs of genes; as it is, on the whole, a matter of chance which member of a gene pair may be transmitted to any one offspring, so also it is a matter of chance as to what half of the total inheritance of the parent will be passed to

one of the offspring. In dealing with inheritance in a quantitative way, we are confronted with various functions of the factor "$\frac{1}{2}$". Thus, two offspring from the same parents, that is, with the same pedigree, are not necessarily equipped with the same set of genes, their inheritances are not precisely identical.[1] On the other hand, having the same pedigree would increase the chances that the two offspring would exhibit a certain degree of likeness; and these chances would be still further increased if closely assortative matings according to pedigree had been made among the near ancestors, that is, if their near ancestors had been *inbred*.

With n pairs of allelic genes the possible number of gametes is 2^n, the number of different genotypes is 3^n (p. 20). If n is at all large, the number of possible genotypes is therefore much greater than the number of animals, of the larger species, alive. For all practical purposes it is virtually impossible to secure two individuals which are precisely similar in genetic constitution, so that there is always some genetic variation to be found. The chief exceptions to this are " identical " or monozygotic twins, which develop from the same ovum and are genetically alike. They are extremely rare; for example, Bonnier (1941), who has been collecting identical twin heifers for experiment, has calculated from calving statistics in Sweden that one half of one per cent. of all calvings are twin heifers, and 10% of the twins of like sex are monozygotic, so that the offspring of about 2000 calvings are required in order to obtain only one pair of identical twin heifer calves. With such exceptions, the greatest certainty in breeding is that no two animals will be alike. However, if large numbers of genes are present, a considerable proportion of them must be concerned in the generic and specific characters, *i.e.* in establishing the general gene complex upon which those genes of consequence to the breeder are expressed.

It is also a physical impossibility for any sire to mate with even a significant proportion of the possible combinations of those genes for which he is either homozygous or heterozygous.

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[1] This can easily be tested by writing down a hypothetical genetic formula, *e.g. AaBBCcdd*, . . . , and, at the toss of a coin, for each pair of genes noting which member would by chance be passed on into a gamete; then repeat for a second gamete, and so on.

Even with artificial insemination, which can greatly extend the use of a sire, the proportion of possible genotypes covered would not be greatly increased relative to all the different kinds of gene combinations that could exist.

A low mutation rate (p. 25) can have a significant bearing on evolution, but it is extremely doubtful if the stockbreeder can hope for any material progress by waiting for mutations, especially any with gross, quantitative, beneficial effects.

The groups of animals in which a breeder finds his material, whether they are called subspecies, races, or " breeds ", can be considered relatively small samples of all the possible gene combinations ; in them selection in some form or another has established a certain frequency of genes, and degree of genetic similarity.   Of these genes many influence general race or breed characterisation, the remainder (still probably a very large number) by recombination and assortment form the basis of the genetic variability to which the breeder can apply the several different methods of selective mating to bring about genetic change or improvement.

In this sense, therefore, and excluding environmental effects leading to modifications, breed uniformity is a matter of the frequency and the distribution of gene combinations among the animals forming the breed.   Lack of uniformity is due to differences in genetic constitution throughout the breed.   It is by rearrangement of gene constitutions and redistribution of them among the animals in a breed that breed characterisation and composition can be changed.   If a particular gene is not present in a closed breed, and the character to which it gives rise is desired, then no amount of selective mating can produce it, it must be introduced from some other breed.   If it is present as a rare recessive its frequency of expression can readily be increased by appropriate, and comparatively simple, means—such as back-crossing (p. 18)—which increase relatively the number of offspring of animals with the gene.

In some groups there are fairly simple characters, possessed by all members of the group, which serve as breed labels. Often these are whole colours, e.g. the black of the Aberdeen-Angus or the Galloway, the chestnut of the Suffolk Punch, the red of the Lincoln Red Shorthorn and other solid red breeds

of cattle, the black of the Black Welsh Mountain sheep, and so on ; here the first and last, blacks, are simple dominants, the others simple recessives. In many cases a colour pattern forms the breed label, as in the Friesian, Belted Galloway, or Hereford breeds of cattle ; but such a character frequently varies in degree of expression, and animals with the " standard markings" often acquire considerably enhanced value just because they are so marked, though their real productive or breeding value is no greater than that of their " mismarked " fellows.

It is necessary to offer a caution on the question of the significance of breed " labels " and of simple genetic characters. It may be that the epistatic grey colour of horses could be linked or closely associated with physiologically important characters or combinations, such as, say, speed in Thoroughbreds, but this is unlikely. On the other hand, grey colour is a breed label in the Percheron, a breed which has been selected for certain characters, other than speed, and it would be fallacious to assume that here grey has any particular virtue as an indicator of peculiar Percheron characteristics. At the same time, it is also unlikely that a Percheron breeder would have concentrated solely on a definite grey pattern or shade, and neglected all other points of conformation and constitution ; hence a particular kind of grey *might* indicate a general degree of careful selection, or standard of " purebreeding ". In certain cases, however, a label character can have a physiological significance ; the black coat colour of the Aberdeen-Angus is involved in the temperature-regulating mechanism and plays a part in exposing this breed to greater effects of intense solar radiation, reducing its suitability to tropical climates (*see* p. 47). Again, such labels may be of some importance as more or less significant indicators of a particular type of animal. For example, face-colour shade and pattern form an obvious part of the general characterisation of the British " grey-faced " or " Masham " sheep, crosses of Border Leicester on Scotch Blackface, and of Wensleydale on Swaledale, respectively, and in turn of the various dark-faced Down breeds on these crosses. In so far as the first or second crosses are favoured or desirable as meat producers, the face colour label can have a certain real or imagined value, although fleece and general body characters also come into the picture.

It has long been recognised in practice that certain breeds and types of animals have more or less distinctive general characterisations associated with functional or physiological differences and expressed as different levels of productivity. In economic characters breeds often differ markedly on the average, as for instance in the wide contrasts between beef and milk production of the Aberdeen-Angus and the Jersey, the hairy coat and the fine wool of the Scotch Blackface (or many " primitive " sheep types) and the Merino, speed and draft capabilities of the Thoroughbred and the Shire, and so on. Within one species a wide range of variation in any physiological character exists ; a type or breed, or even a group within a breed, covers a part of the variation and two extreme breeds may not even overlap, although some overlapping among breeds of the same type does occur and no one breed is absolutely uniform in any particular character. The genetic nature of many of these functional characters is not yet fully understood, but it is clear that these kinds of breed characteristics are of genetic origin, probably involving many genes, and subject therefore to some genetic variation as well as to environmental modification. In many cases the ways in which genetic differences affect the economic or productive characters are also not yet understood, in others a genetic basis for any difference is not fully established. A few examples serve to show the sort of conditions found.

In poultry, the associations of physiological differences and breed characteristics have been reviewed by Hutt (1939), who points out that many different kinds of mutations, sometimes even lethal ones, such as the Creeper (*see* p. 27), have been used by breeders to distinguish breeds, and, although breeders have always claimed some special virtues for their favourite breeds, only recently has it been shown that particular functional characteristics do appertain to certain breed types. These traits are not related to body size but are definitely inherited and may be either linked to a gene for a variation which has been used as a breed label or due to pleiotropic action (*see* p. 28) of such a gene. The White Leghorn requires less Vitamin B_1, and is not so susceptible to slipped tendon (a character of genetic basis and showing a high manganese requirement), as compared with the heavier Rhode Island Reds

and Plymouth Rocks. Also, Leghorns differ from these other breeds in responses to hormone treatments ; and, while they are more resistant to *pullorum* disease, they have a higher susceptibility to *Ascaridia lineata*. Further, Leghorns resist extreme heat better, and their body temperature more rapidly attains the normal adult state after hatching, showing thereby that they have a better heat-regulating mechanism than the Rhode Islands. Hutt suggests that these physiological expressions are probably not only between these breeds, but indicate fundamental differences between the Mediterranean types and those descended from Asiatic breeds, and may have been brought about by the different environments to which their prototypes were exposed after domestication. Another example in poultry is found in the low reproductive capacity of the White Wyandotte.

The modern development of pig performance testing at central stations, where feeding and management are closely controlled, has resulted in the collection of useful comparative data. At German stations groups of two piglings from each litter are compared according to their gains in live weight and to food consumption from weights of 40 kg. to 100 kg. ; breed differences in these characters are manifested, as well as in rates of gain. For example, the following figures summarise results at the Friedland Institute in 1938/39 :

Breed.	Daily gain.	Food consumed per 100 kg. increase.
Improved Landschwein	732·0 g.	367·6 kg.
Edelschwein	717·6 g.	356·6 kg.

At the Lentföhrden Station in 1939, Edelschwein took 209 days to increase from 40 to 100 kg. live weight, Improved Landschwein 212 days, and Angeln 216 days, while Berkshires took 226 days to increase from 40 to 80 kg. More detailed studies, such as those of Schmidt and Hogreve (1939), have also been carried out ; these authors made a series of critical observations on litters of five different breeds : Edelschwein, Improved Landschwein, Berkshire, German Pasture, and Mangaliţa. Under the same feeding and management the first three reached 100 kg. in 200 days, while the last two only attained 74-82 kg. The daily increase in weight did not differ significantly between individuals or sexes, but at the 200th day

there were marked breed differences in body measurements and amounts of back and belly fat, as follows : in body length, the Improved Landschwein were 21 cm. longer than the Mangaliţa, and the Edelschwein 17 cm. longer, the Berkshire 14 cm. longer, and the Pasture 13 cm. longer ; in chest girth and width the Berkshires came first and the Pastures last. Breed differences in fertility are also found ; for example, Phillips and Zeller (1941), dealing with the records of totals of 382 sows and 1354 breeding seasons among the six breeds, Chester White, Duroc-Jersey, Landrace, Poland-China, Tamworth, and Yorkshire (Large White), noted differences in failure to conceive varying from 13·9% in the Duroc-Jersey sows to 36·9% in the Tamworth, with associated differences in the average numbers of services required per conception, ranging from 1·28 in the Duroc-Jersey to 1·99 in the Tamworth ; there were also breed differences in average litter size and in average number weaned, the Poland-China being lowest and the Yorkshire highest in both characteristics. Another interesting case of varying physiological responses has recently been recorded, this time between two groups within a breed ; two inbred lines of pigs at the Texas Agricultural Experiment Station (1941) have shown significant differences in the times needed to exhibit symptoms of Vitamin A deficiencies when fed on Vitamin A-free rations.

Differences in fertility levels between sheep breeds also occur, though their expresssion is affected by the fact that the breeds are usually maintained under different, and varying, environmental conditions, including flock size. A study some years ago revealed the following differences among purebred flocks in the British Isles (Nichols, 1924) :—

Breed.	Number of Flocks.	Number of Ewes.	Lambs per 100 Ewes.
Border Leicester	32	651	207·0
Leicester	8	434	152·1
Dorset Horn	9	2096	150·9
Suffolk	9	1003	148·7
Oxford Down	34	3465	138·4
Lincoln	10	1375	128·1
Southdown	4	961	127·3
Hampshire Down	8	2328	121·7
Blackface	10	5768	91·75

In addition to such over-all differences, others relating to various reproductive activities are known; *e.g.* in the differences in breeding season and its length between the Merino and British breeds in Australia (Kelley, 1939; Pastoral Review 1940), and between the Dorset Horn and other breeds in Great Britain. The United States Department of Agriculture, Bureau of Animal Industry (1941), report that among large numbers of various breeds kept under range conditions, Rambouillets had the longest gestation period, averaging just over 151 days, and Columbias the shortest, about 148 days, with Corriedales and Targhees intermediate and averaging around 149·5 days. Moreover, it was found that, while ovulation usually occurred between 24 and 30 hours after the beginning of heat, Corriedale and Dorset Horn ewes tended to exceed Southdowns, Shropshires, and Hampshires in the time during which they remained on heat after ovulation. At the Department's Western Sheep Breeding Laboratory, at Dubois, Idaho, another kind of breed difference was exhibited in studies on selection, using related lines within each of the Corriedale, Columbia, Targhee, and Rambouillet flocks. The ewes were divided into three groups (according to weights as yearlings), formed of (*a*) the lightest quarter, (*b*) the intermediate half, and (*c*) the heaviest quarter; the average annual production of lamb over the lifetime of the ewe was determined, the lambs being weighed at about 130 days of age. The results can be summarised as follows :

Breed.	Lamb Production.		
	Group (*a*).	Group (*b*).	Group (*c*).
Rambouillet . .	55	60	69
Corriedale . .	62	68	75
Columbia . .	63	77	78
Targhee . .	71	81	87

In sheep, as well as in other animals, instances of differential resistance to diseases or parasites are found; Kent or Romney Marsh sheep are recognised in practice to have a relatively high immunity to footrot, just as the Shetland breed has to ticks; but

the precise reasons for these traits are not truly known. However, investigators in California have described results of experiments that indicate marked breed variation in susceptibility to the parasitic worm, *Ostertagia circumcincta*. Lambs to the total number of 2629, and of the Romney, Rambouillet, Southdown, Shropshire, and Hampshire breeds (together with three crossbreds), were kept continually exposed to infection by the parasite on an irrigated pasture; as judged by fortnightly egg counts, the Romneys were highly resistant to infection, the Rambouillets less so, and the three Down types were most susceptible, being closely similar in this respect. In addition to the pronounced breed difference in susceptibility, two other interesting points emerged: firstly, the Romneys varied little among themselves in susceptibility, whereas in the less resistant breeds there were significant variations, and secondly, the most highly resistant individual animals in the susceptible breeds showed a degree of resistance of about the same order as the average among the Romneys. The workers (Stewart, Miller, and Douglas, 1937) argued that these observations suggested that whatever the genetic factor, or factors, influencing the degree of resistance, they were present in all these breeds but had become more fixed in the Romney. This interpretation can be put in the form that whatever the gene effect or effects may be precisely, the genes involved have a higher frequency in the Romney, and are more frequently in homozygous condition, than in the other breeds.

Some of the physiological characteristics are important in relation to the question of adaptation to environment, which will be more fully discussed in Chapter XV; for the moment they can be regarded as conditioned, partly at any rate, as the results of prolonged exposure, or adaptation, to a particular environment. In this class are the traits whose significance is manifested when new or unfavourable environments are provided and comparisons with local breeds are possible. For example, Kaškarov (1940) quotes evidence from the Ukraine that at temperatures of 34-35° C. Karakul sheep had 60-120 respirations per minute, Lincolns had 120-210; in Lincoln, Romney Marsh, and East Friesian sheep respiration at high temperatures was so accelerated and carbon dioxide losses were so high that a pathological condition

followed, leading to death, particularly in lambs. Also, Lincoln sheep restricted their grazing to the softer plants along the river banks and would not eat dry herbage, while Kurduk sheep tended to restrict themselves to the dry grazing.

Differences in grazing habits are also exhibited in cattle ; in experiments in Louisiana involving Aberdeen-Angus and Zebu cattle, and $\frac{3}{4}$- and $\frac{1}{2}$-breds of these, it has been noted that the Zebus and the halfbreds on hot windy days will graze and rest in the open, while the Aberdeen-Angus and the $\frac{3}{4}$-breds (*i.e.* 3 parts A.-A. : 1 part Zebu) soon tended to seek shade and to rest (Rhoad, 1938, 1939). Similar observations have been made in South Africa (Bisschop, 1940) where, among cattle compared under the same conditions, the sequence of starting to graze in the mornings was according to breed : Afrikaner, Sussex, Fries (=Friesian), and Red Poll. The American experiments just quoted revealed other physiological breed differences ; for example, while the four types all showed increased respiration rates and body temperatures as atmospheric temperatures increased, the Aberdeen-Angus were most affected, the Zebus least. Again, in South Africa, at Messina in the Transvaal, the Afrikaner was found to be more resistant to heat than the Hereford, Shorthorn, or Aberdeen-Angus, and when it was very hot the British types stopped ruminating sooner than the Afrikaner (Bonsma, J. C., 1940).

Such features are of course covered in a general way by saying that one breed differs from another in some special characteristic—the Channel Island breeds of cattle have a higher butter-fat content in their milk than the Friesian, which in its turn far excels the Jersey and Guernsey in total milk yield. But such characters can often be markedly affected by environment, feeding, management, etc. The examples so far quoted illustrate, however, that the broad description of breed differences in physiological characteristics can frequently be restated in more specific and precise terms. Further, analysis of the differences helps considerably to define what part, or how much, of production can be attributed to environment and how much to genetic constitution and thus to indicate the lines which must be followed in order to achieve better and more efficient production. In many cases it is now possible

to measure production, or the physiological processes which lead to production, and to subject the data obtained to mathematical treatments so as to differentiate between the two main sets of influences. (The various statistical treatments will not be discussed here, only the results obtained.)

For instance, the " lowland " type of cattle is widespread in Europe, and a number of different breeds are recognised ; these have more or less distinctive breed characters, or labels, and the same general type of milk production, varying only in degree, with much overlapping from breed to breed and district to district. Milk production in four breeds of lowland cattle, the Black Pied Lowland, Red Pied Lowland, Shorthorn, and Angeln, was studied by Lauprecht and Döring (1940) in one district in Germany, the cows being grouped on their records into classes ranging in daily milk yields from 2 to 25 kg., at 1 kg. intervals. Daily milk yield, total daily fat yield, and fat content % were considered. Similar data were also available for cows in each of seven districts, so that environmental as well as breed variations could be assessed. It was found that for all districts and breeds, the daily milk yield and butterfat % bore the same general kind of relationship to each other ; the relationship between milk yield and fat content, i.e. fat yield, was simpler, and, in fact, was a straight line ; as one increased, so did the other with it by regular amounts. But when the relationships were analysed into their two component parts, namely, the part of daily fat production which was unaffected by, or independent of, milk yield, and that which was attributable directly to increases in milk yield, it was seen that environmental influences were less important than breed differences, which were consistently marked and particularly noticeable in respect of the Angeln compared with the others. In the Angeln the higher fat yields were less dependent on increased milk outputs than in the other breeds.

Important practical considerations are those of the way production is maintained throughout milking life, and throughout each lactation ; both these are also exposed to considerable environmental modification. One series of studies on highland and lowland types of cattle in Germany revealed only small breed differences in lifetime production, although cows of the

Middle German Red breed maintained their output better after maturity was reached than other breeds (Lange, 1941). The Oldenburg Black Pied Lowland was earlier in reaching peak production and then declined rapidly (for which a reason is suggested in that this strain contains some Shorthorn blood introduced early in its history), while the Angeln varied less in this respect. Persistency of production in a lactation is difficult to measure for purposes of genetical analysis, yet taken as a whole there are distinct breed variations. Two breeds which give closely similar lactation yields under ordinary conditions in England are the Red Poll and the Lincoln Red Shorthorn, but the Red Poll has a lower lactation peak which gives way to a slower decline (Sanders, 1930), and this may be related to the fact that the Red Poll is a late-maturing type compared with the earlier maturing Lincoln Red. The actual shape of the curve can be affected by management in that the early rise in production is often enhanced by extra feeding, and other factors which considerably influence the curve are time or season of calving, and also time of service after calving ; but, allowing for such modifications, there is evidence that form of persistency is to some extent a genetic character, probably with many genes involved.

Another possible form of physiological difference has been brought to light by Russian workers (Kushner, 1938, 1939 ; Patrushev, 1938, 1939, 1940) who have studied various blood characteristics in horses, asses, and mules. The numbers and sizes of the red blood corpuscles, their content of the active hæmoglobin pigment, and the capacity of the hæmoglobin to carry out its functions can be determined by suitable techniques ; these workers claim to have detected indications that greater vigour and performance are associated with higher values for these blood characters, which, except for red corpuscle size, tend to decrease with age. Kushner found, in comparing Thoroughbreds, Halfbreds, Anglo-Tekes, and draft type mares, that the Thoroughbreds had the highest and the draft mares the lowest rankings for blood values. Using other measures of blood metabolism, Patrushev noted that asses differed from horses in that the blood indices of the former were higher in young animals but showed a sharp drop at later ages, while those of the latter stayed at a fairly uniform

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level from about eighteen months to five years of age; he suggested that these differences were associated with the variation in growth rate between the two species, the ass having a high, intensive growth rate when young, finishing growth at about eighteen months to two years, while the horse has a slower rate of growth. Further, the same worker concludes from other studies that the earlier-maturing breeds of cattle show similar greater variation of blood characters with age than do the slower-growing forms, while extensive studies comparing imported with already acclimatised breeds in the Philippine Islands, which were conducted by Manresa and others (1940), established that the Philippine native and Indian Nellore cattle had significantly more haemoglobin in their blood than American Herefords and Holstein-Friesians.

No attempt has been made in the foregoing to give a complete picture of the situation; the examples given are examples only, and as such form part of the evidence in the first place that many of the production characters of farm livestock are genetically influenced, more in some cases and less in others, and secondly, that by processes of selection, certain groups of animals, usually designated and distinguishable as breeds, have been led to express particular levels of performance. The end results can be stated in terms of Ritzman's conclusions (1941) from the well-known studies on basal metabolism, carried out over a period of twenty-five years at the New Hampshire Agricultural Experiment Station, that the effect of selective breeding has been to set up adaptations of type, performance, and physiological activity in relation to special functions. The several species have been variously affected by this process, so that they now show differences in the ways their food intakes are utilised for particular functions, and hence in their adaptations to economic conditions and requirements. Seasonal factors do affect basal metabolism— the minimum energy output of an animal at complete rest and without food, just " ticking over "—but this is particularly under the influence of genetic factors which are necessary to set in motion the inherited function towards which the animal has been adapted.

Altogether the general situation can be broadly regarded

as one in which the various physiological characteristics are initially dependent upon the expression of a gene complex. This complex has been built up by a combination and inter-action of natural and artificial selection so that species and in turn groups of animals, such as breeds, have acquired different kinds of accumulations of gene combinations and frequencies. The form and degree of expression of the physio-logical traits depend in turn, and to different extents, upon environmental modification and genetic variation.

CHAPTER VII

ENVIRONMENTAL ASPECTS

THE two aspects, genetic and environmental, are not entirely distinct ; genetic constitution is a component of the general field or pattern of gene action. Nor is the distinction between external and internal environment always clearly discernible. It is convenient, however, to regard the situations described in the last chapter as if in the first instance the appearance and functioning of the individual—its phenotype—were more simply the effect of environment in " developing " its genotype, rather as a sensitised film is developed to give a photographic negative.

The fertilised ovum receives its set of genes from its sire and dam and grows, expressing its inherited attributes, exposed to a series of external influences. What it is seen to be, or how it performs, at any particular time in its life, is a sample, *at that time*, of the progressive developmental changes which it has undergone up to that moment. An animal can be regarded, in its course from early life through adolescence to maturity and then on through senescence to death, as passing over a continuous series of thresholds, its ability to respond at any one time being determined by its previous history and influencing in part its future development.

The changes undergone by the animal are best considered as taking place in two ways (Brody *et al.*, 1926 ; Hammond, 1932, 1940 ; Huxley, 1932). An animal *grows* in weight ; if its increases in weight are measured at regular intervals, it is seen to grow slowly at first, then more rapidly, and later at a diminishing rate as maturity is reached. The rapid stages are spread over the later prenatal and early postnatal periods. The rates of growth and the times at which maximum growth occurs differ in the various species and types of animals. The second group of changes are those in *development* of the different parts of the body ; as the whole body increases in weight, the proportions of its different parts alter relative to

SHIRE X SHETLAND

Birth

1 Month
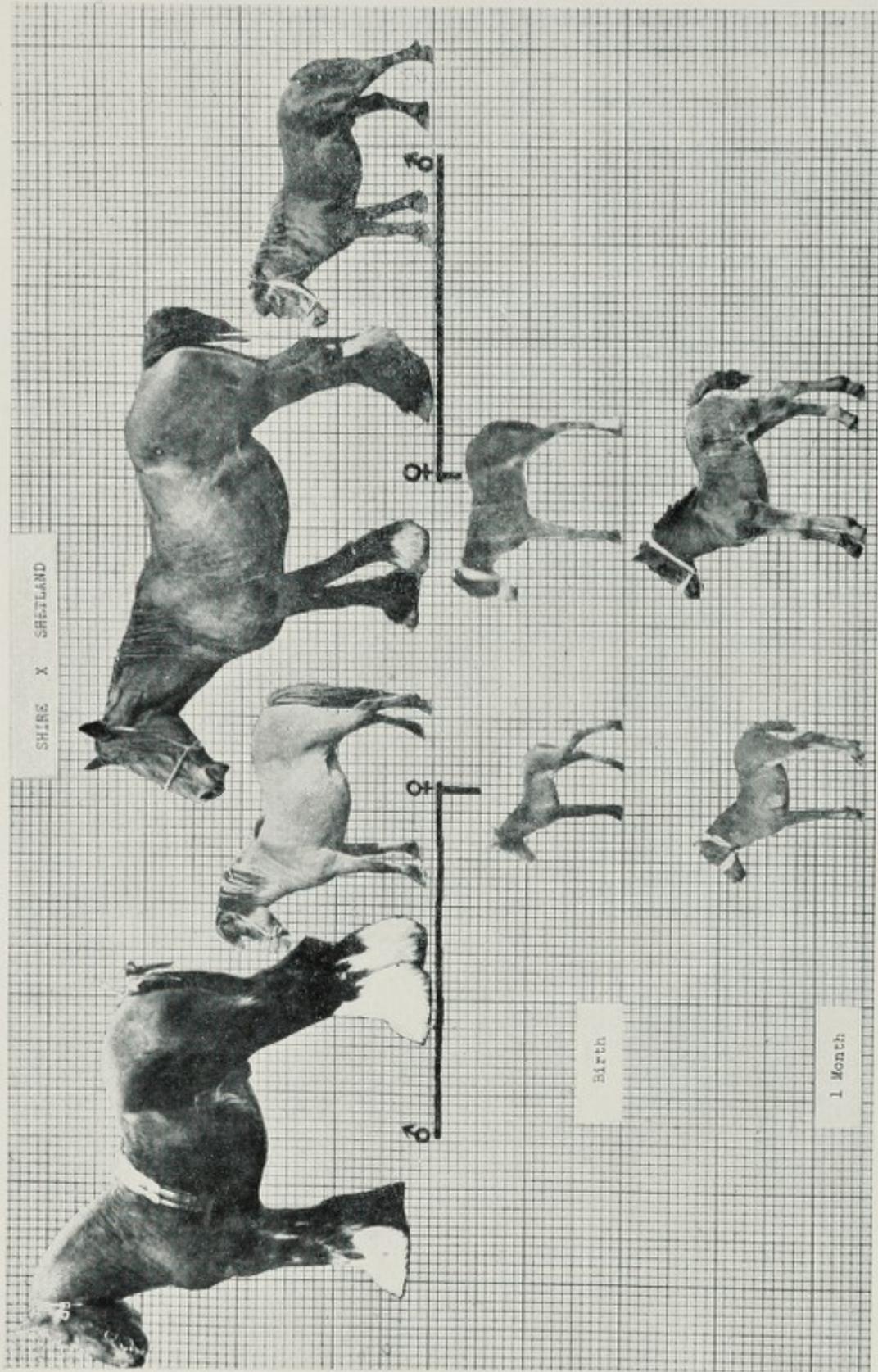
Fig. 6.—Reciprocal Shire×Shetland crosses. *From* Walton and Hammond, 1938.

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each other. For example, in early life the head grows most rapidly, next the trunk region, and, later, waves of active growth set in from the outer ends of the limbs. Thus, at first the head forms a high proportion of total body weight; its proportion progressively diminishes compared to that of the limbs, and so on. Hammond (1932, 1940) has shown that the same sort of *growth gradients* occur in the different tissues of the body, following the general sequence of brain : bone : muscle : fat. The whole of the gut develops early so that the very young animal is soon equipped with relatively high proportions of the organs necessary to sustain life —its head and brain, its alimentary canal, and its legs— while the " production " parts, the muscle, fat, and mammary glands, reach their full development and function much later in life.

This differential development of the body parts has a most significant bearing upon production, since it is by the response of the different organs and tissues, especially during the periods of their most active growth, and particularly to nutritional conditions, that the various functions and their performance are largely determined. The animal as a whole is fairly well balanced in relation to the conditions which can affect the relative growth of its parts, but a clearer idea of its reactions can be gained by noting the results of exposing it to comparatively severe or extreme conditions.

For example, wide extremes in maternal environment within a species are given by Shire as contrasted with Shetland mares. Walton and Hammond (1938) used crosses, produced with the aid of artificial insemination between Shires and Shetlands, to give a spectacular demonstration of the effects of maternal environment on the growth and development of foals. At birth the development of foals is well advanced, the rapid growth phases are early in life, so that the adequacy of maternal nutrition to the foal before birth and in suckling after birth are very important in relation to growth and size.

In this cross the foal by the Shetland sire borne by the Shire dam is much bigger than that from the reverse cross, actually about three times its size (*see* Fig. 6); and the difference in size persists for some time over the period of slower growth,

as at four years of age the offspring out of the Shetland mare is still only about two-thirds the size of that from the Shire mare. Further, as Hammond, Edwards, and Walton (1941) have emphasised, one of the other gradients, namely that of the limbs, is well advanced at birth in the horse—the legs are relatively full grown in length at birth—so that in these crosses the leg length of the offspring is also affected according to which way the cross is made, and, starting with the Shetland mare, it requires two crosses of Shire males to raise the size of the offspring in this respect to that of the first cross from the Shire mare.

The effects of maternal environment can be expressed in other ways and may persist for some time ; Šornikov (1941), in a series of studies in Russia, has shown that in a group of mares from which the foals were weaned at six to seven months of age, subsequent offspring had greater weights and body measurements at birth than had the offspring of a control group of mares which had suckled their foals until they were twelve months old. Again, Hámori (1942), comparing the offspring of old sires, over twenty years of age, with those from old mares, concludes that, while the offspring of the former showed no developmental deficiencies, bodily weakness or lowered resistance, those of the old mares were in more than half the cases inferior and showed themselves lower in fertility.

A great deal of our more precise knowledge of differential growth in farm stock is due to the work of Hammond and his colleagues. In sheep, the growth rate, and development, of the lamb depends largely upon the number of lambs at a birth (whether singles, twins, or more), the nutrition of the ewe during the later part of her pregnancy, and her milk supply. For instance, in experiments where some ewes were given rations which enabled them to put on weight during about the last third of pregnancy ($39\frac{1}{2}$ lb. in 53 days) and others kept so that they gained only 1 lb. in this period, single lambs from the two groups were very little different in average live weight at birth. The singles were adequately provided for by the maternal environment in both groups. The twin lambs, however, of the former group averaged 9 lb. in weight, and of the latter only 6·1 lb. (Verges, 1939, 1940). By good
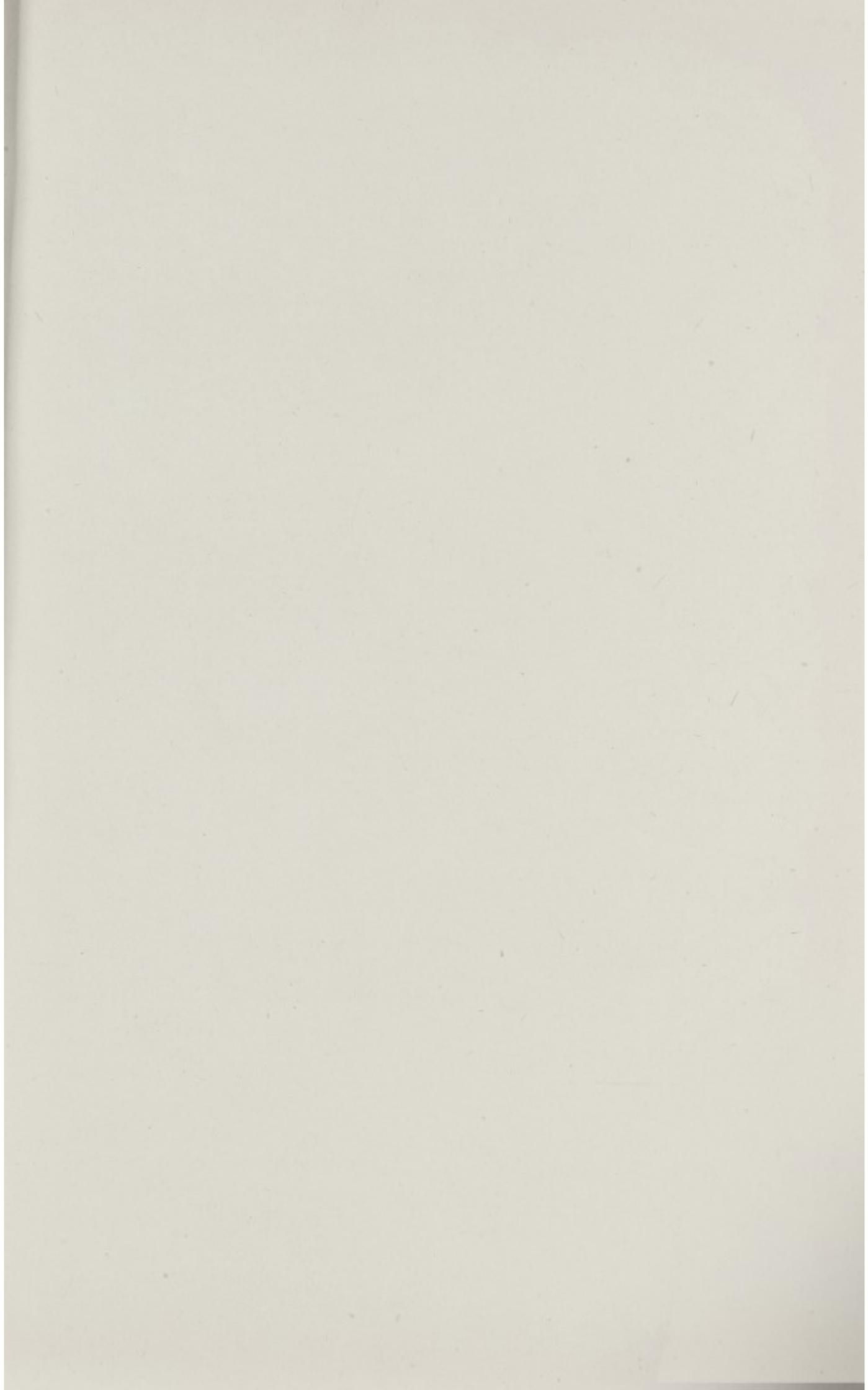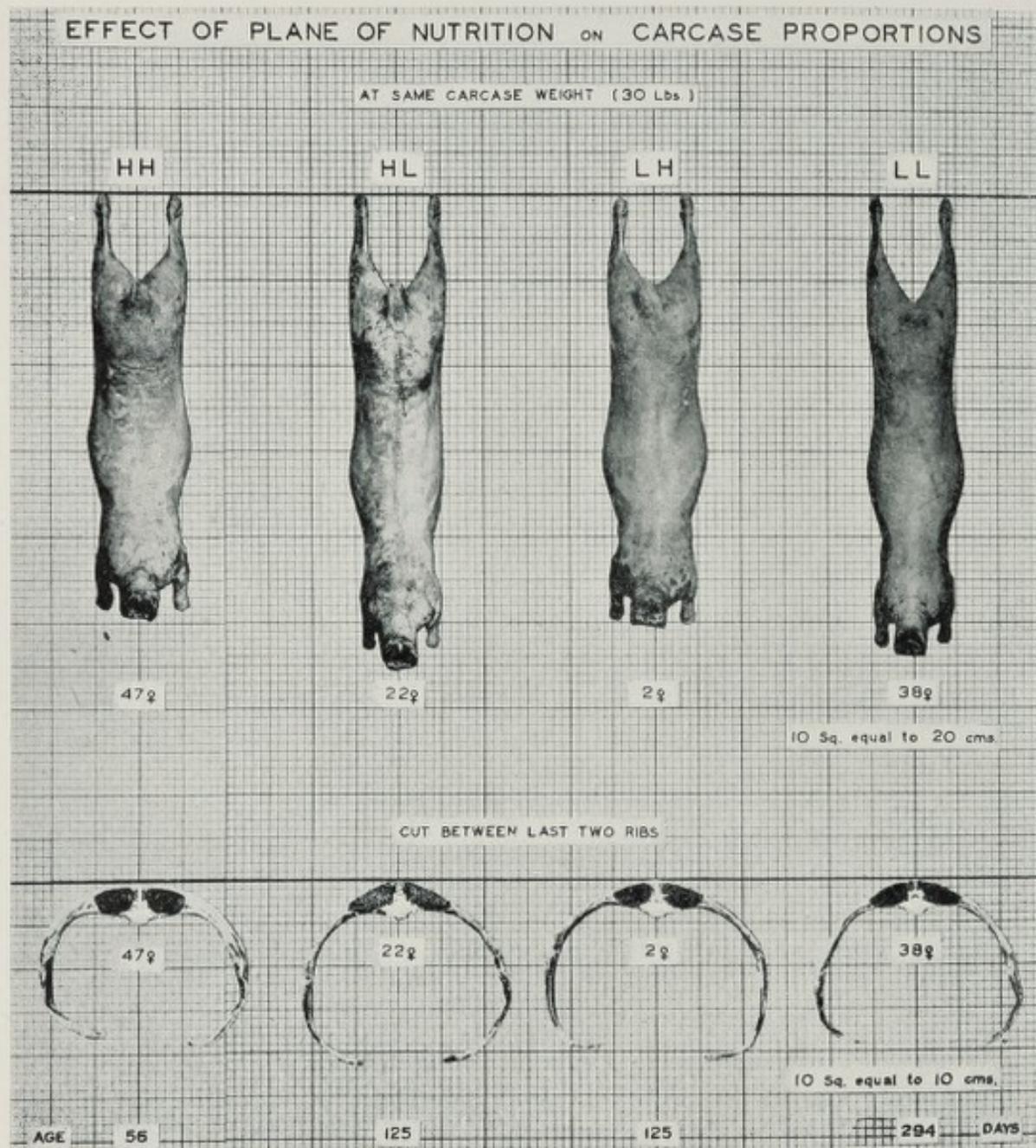
FIG. 7.—Carcasses of lambs reared on different planes of nutrition.
By courtesy of Dr. J. Hammond.

feeding in late pregnancy, the subsequent milk supply of the ewe is enhanced and as a result the lambs do better; with Merino ewes there is a strong correlation between the milk yield of the ewes and the growth of the lambs, particularly during the first five or six weeks, when the lambs are very largely dependent on their milk intake for nutriment (Bonsma, F. N., 1939). Also, twins reared as twins grow less rapidly than twins reared as singles; Hammond (1932) has suggested that a general assessment of the milk supply in a flock can be made according to the differences in size between twin and single lambs—if the singles are much heavier than the twins, then the ewes are yielding little milk.

The differences in growth rate are accompanied by differences in relative proportions of the body parts, the bone : muscle : fat relations being affected and hence the shape and production of the animal. Thus, the lambs from Verges' high and low fed groups of ewes showed differences in average carcass composition at birth; if the average weights of the various parts of the low plane lambs were expressed as 100% in each case, the relative figures for the high plane lambs were : live weight 150%, carcass weight 148·6%, skin and wool 142·8%, bone 130·9%, muscle 146·7%, and fat 284·7%. The better nourished lambs have markedly higher proportions of the edible parts to body weight than have the poorer nourished, the growth of the later developing parts having been accelerated. These differences are further expressed as a result of early postnatal nutritional conditions, for spectacular contrasts in body form and fleshing can be produced according to the levels at which early feeding is given. Typical carcasses produced from lambs of the same breeding in Verges' experiments are shown in Fig. 7.

The lamb 47♀, H.H., was kept from birth on a high nutritional plane and attained a carcass weight of 30 lb. in 56 days; 22♀, H.L., was fed on a high plane until 42 days old and then switched to a low plane so as to reach 30 lb. at 125 days of age; 2♀, L.H., was on a low plane for 42 days and then changed to a high plane, finishing at 30 lb. carcass weight at 125 days, the same age and weight as 22♀; while 38♀, L.L., was kept on such a low plane throughout as to take 294 days to make a 30 lb. carcass. The second and third animals make a useful com-

parison—the former had a poorly fleshed carcass with good bone development, the latter had high fleshing on a relatively lighter skeleton.

The phenomena of differential growth and the growth gradients follow broadly similar courses in all mammals. In pigs, the proportions of the body parts have been altered experimentally by McMeekan (1940-41) and McMeekan and Hammond (1940), who, using animals of an inbred strain of Large Whites, were able to produce body forms like those in Verges' lambs by strictly controlling the nutritional levels. They have shown that by feeding on a high plane (H.) through the early stages, up until about sixteen weeks of age, and then feeding on a low plane (L.), the tissues, such as skeleton and muscle, which develop early are encouraged while the later developing parts, such as the fat below the skin, are proportionately diminished, so that a bacon type of carcass is obtained. (The lower bony parts of the leg are relatively well developed in the young pig ; but as the pig grows, the thigh regions begin to grow more rapidly and the ham becomes better shaped, especially if the rate of growth of this part is encouraged.) On the other hand, if growth is restricted by feeding on a low level (L.) for about the first sixteen weeks, the skeleton and muscles are relatively stunted, and if the animal is then transferred to a high plane (H.), the growth of the later developing tissues, the subcutaneous fat, is stimulated, and a lard type is obtained, with small frame and muscle and thick fat. Under these conditions the various effects can be summarised as : H.H.→pork type ; L.H.→lard type ; H.L.→bacon type ; and L.L.→bacon type, but not an economical one, as maturity is long delayed.

Within the fatty tissue there is also a sequence of development ; fat is first laid down as kidney and caul fat, then as the fatty subcutaneous layer between the muscle surfaces and the skin, and finally as " marbling fat ", which is interspersed between the muscle fibres themselves. In both cattle and sheep, the marbling fat, which is a valuable feature of meat, is laid down most readily in the types of animal which come earliest to maturity and are most readily fattened (Hirzel, 1939).

It has been pointed out that one of the growth gradients is that along the limbs, the bones towards the extremities develop-

ing earlier than the upper bones ; a bone also increases more rapidly in length earlier than in thickness. For this reason, the relative shape and development of the lower limb bones, such as the cannon, give useful indications of the stage of development of the animal generally, in that the shorter thicker cannon bones are related to a higher level of nutritional develop- ment, or to earlier maturity. Further, this type of bone growth in the lower limbs is associated with other changes in bone proportion, such as a short, wide but small head, a short neck, and short spinous processes on the spinal column, result- ing in a broad, instead of a peaked, shoulder (Pálsson, 1939-40).

Similarly, the proportions of bone to meat, or meat to fat, in sample cuts, give an indication of those of meat in the dressed carcass, or of meat to fat, provided that the cuts are taken from positions at which development is late. One of these regions is that of the loin, and the shape of the *longissimus dorsi* muscle (which forms the " eye " of the chop) in cross section at the level of the last rib, as well as the depth of fat overlying it, are good indices of the " quality " of the carcass (Hammond, 1932, 1936 ; Hirzel, 1939). The proportional thickness of this muscle can be shown as a shape index, this being expressed as $\dfrac{100 \times B}{A}$, where A is the width of the muscle from the side next to the spinal process of the vertebra to the end along the rib and B the depth of the muscle halfway along its width, *i.e.* from the upper part to the part lying along the rib. The earlier maturing, better finished carcasses have a higher shape index, the depth of the " eye " being relatively greater than its width. The relative thickening of the " eye muscle " is associated also with shortening and thickening of the bones. Moreover, in beef cattle studies it has been shown that the length of the metacarpal bone, thickness of meat over the sixth, ninth and twelfth ribs, and thickness of fat over the loin provide good indices (diminishing in value in that order) of the proportion of edible meat in the dressed carcass.

Body size and shape (conformation) are thus matters of growth (increase in weight) and of relative development. Weight at a given age is a useful basis for comparison of growth between types, and development, in terms of maturity, is responsible for the kind of meat produced. These conditions

can be widely affected according to the nutritional levels to which the growing animal is subjected, especially during the periods at which the various body parts are growing most rapidly. Character expression in these respects is under considerable nutritional, or external, influences.

Another group of characters which can show marked environmental responses are those which go to form the fleece of sheep. For example, in wool types such as the Merino, obvious differences in length of staple and/or in fibre thickness can result from changes in nutrition. Such changes have been studied by many workers (*e.g.* Ross *et al.*, 1937; Marston, 1937), and the effect of improved nutritional level on fleece weight is well recognised. An instance of wide differences in fibre growth within one growing season has been described (Nichols, 1933), where growth, measured by fibre volume output, first decreased by 29% and then rose by 142%, giving quality variations between average fibre diameters of $21 \cdot 98\mu$ towards the tip of the staple, $17 \cdot 57\mu$ in the middle portion, and $26 \cdot 92\mu$ in the basal portion (*see* Figs. 8 and 9).

The effects are not absolute, the direction, as well as the degree, of expression, are restricted by inherent propensities for differential development, that is, by the genetic adaptation to function (*cf.* p. 50) which has become established in the type or breed. If an extreme case is taken, American workers have shown that between the dairy and beef types in cattle, as represented by the Jersey and the Aberdeen-Angus, there are general similarities in skeletal form and any differences in respect of the size and weight of the internal organs are insufficient to indicate any difference in the work done (Swett *et al.*, 1928, 1937). The difference in external appearance and form is due more to the tendency of the beef type to put on flesh and fat, while the dairy type discriminates in favour of the development of the udder, which takes place after sexual maturity in response to the influence of the hormones, oestrin and progestin. (In the udder, the secretory portions, alveoli, are stimulated later in pregnancy by lactogenic hormones from the anterior part of the pituitary gland, and the subsequent milk production of the udder is strongly affected by the growth of the alveolar cells of the udder. The growth of the alveolar cells can be encouraged by suitable feeding—
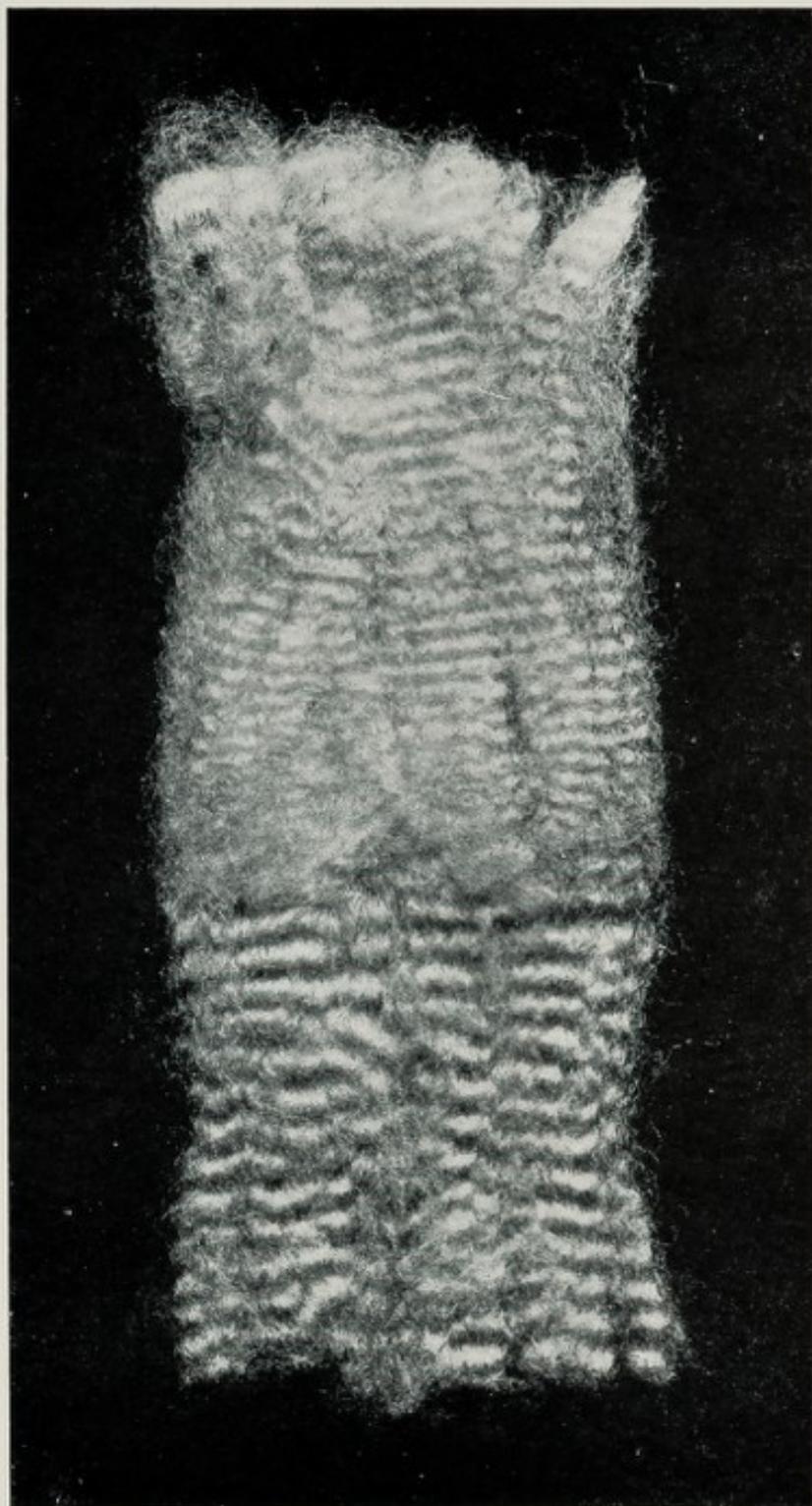
FIG. 8.—Sample of Merino wool showing growth changes,
From Nichols, 1932.

" steaming up "—during the last part of pregnancy, especially in heifers, not milking right up to the time of calving in older cows, and by not feeding a fattening ration to the cow after she calves.) Thus, there is a certain physiological antithesis between high meat and high udder performance, the fullest expressions and maturity of which are influenced by differences in time as well as form of development of the body parts concerned.

Yet these same production characters clearly have a genetic
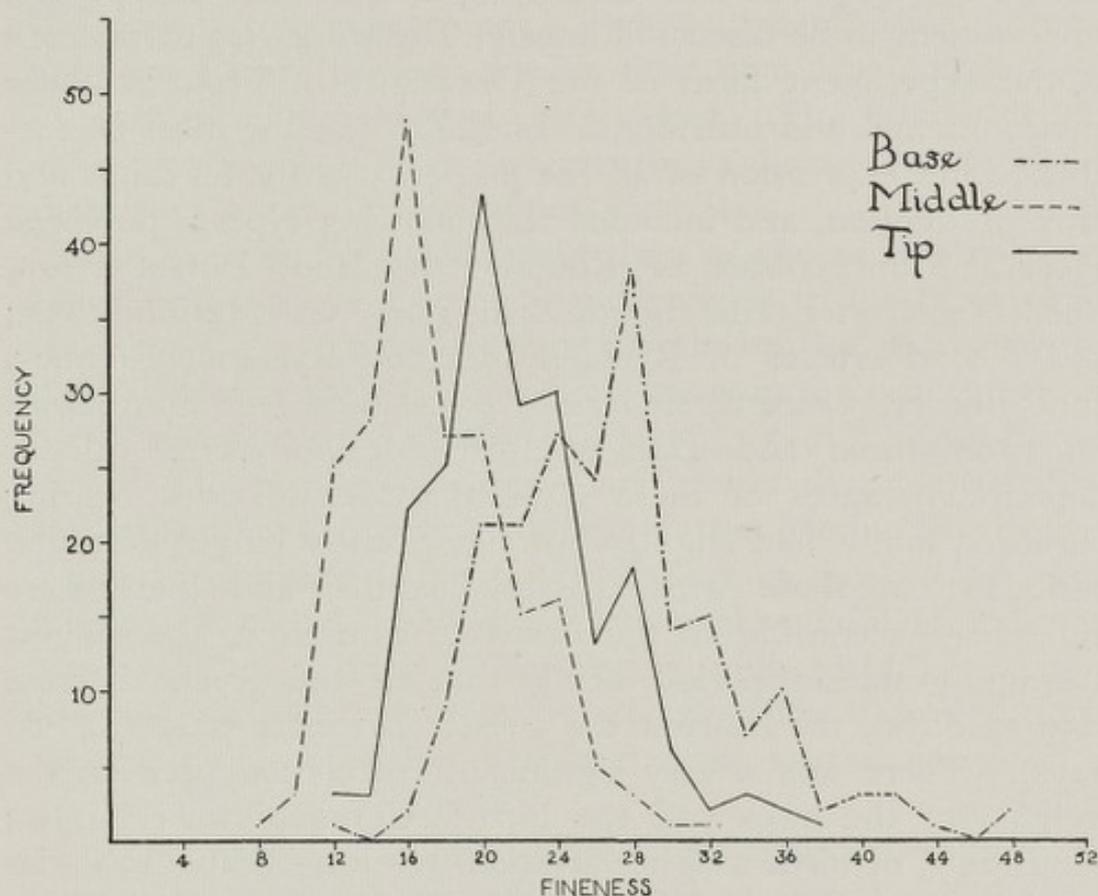
FIG. 9.—Fibre fineness distributions in the different growth phases of the Merino wool sample shown in Fig. 8. *From* Nichols, 1933.

basis also, in so far as breed differences are found, as in the body size of various cattle breeds (*e.g.* Myers, 1941). In two of the conditions which affect growth rate and development of lambs there are genetic differences : to a certain extent the number of lambs born is affected by genetic influences, as is indicated by the different levels of fertility in the various breeds (*e.g.* Nichols, 1924, 1926), while in F. N. Bonsma's

investigations marked differences in milk yield were found between the breeds and crosses studied.

Some of Bonsma's results may be quoted in detail as examples of the sort of information which can be obtained from observations with the practical aim of comparing the suitability of various breeds and crosses for fat lamb production. (Many investigations of broadly similar character have, of course, been made in other parts of the world, but Bonsma included a detailed study of the milk yield of the ewes. Moreover, his conclusions bear directly upon questions of type and environment to be discussed later.) The work was carried out at the experiment farm of the University of Pretoria under environmental and nutritional conditions not the most favourable to full expression of all the propensities for fat lamb and milk production, and included the following types : purebred Merino ; first crosses of Romney, Ryeland, Dorset Horn, Border Leicester and Southdown rams on Merino ewes ; and second crosses of Ryeland rams on Ryeland, Romney, and Border Leicester × Merino ewes, and of Southdown rams on these and Dorset Horn × Merino ewes. Under the circumstances of these tests, the Merino ewes bearing purebred lambs had slightly but significantly longer gestation periods than those with crossbred lambs, and there were differences according to the breed of ram used, the longest average gestation period being that of the Ryeland cross (150·27 days), the shortest the Border Leicester cross (147·86 days). There was a very significant correlation between the weights of the ewes and the birth weights of their lambs ; about 24% of birth weight variation was attributable to variation in ewe weights. The milk yield of the ewes—the most important influence on early growth rate of lambs—was found by weighing the lambs immediately before and after suckling their dams at seven three-hourly intervals throughout a 24-hour period, during which the dams and lambs were otherwise separated, once a week over twelve weeks ; the total of the differences in the lamb's weight before and after suckling was taken as representing the dam's milk production for the day. (A similar method has been used successfully for measuring the milk yields of sows.) For the eleven determinations on each ewe the average daily milk yields were :

Merino (70 ewes) . . . . . . 309·7 oz.
Romney × Merino (14 ewes) . . . . 415·5 oz.
Ryeland × Merino (16 ewes) . . . . 435·2 oz.
Border Leicester × Merino (11 ewes) . . . 473·6 oz.
Dorset Horn × Merino (6 ewes) . . . . 409·7 oz.

Yet the conditions were generally unfavourable to high milk production. The majority of the Merinos were in their second and third lactations, as opposed to the crosses, which were in their first. While the difference between the crossbreds and the Merinos was very significant (99 : 1 chance), those between the various crosses were not. Further, when individual cross-bred ewes were compared with their own Merino dams, the increase in milk yield was very marked. (However, individual ewes within one type varied greatly in yield, which indicates that from a practical point of view it is more important to choose ewes of high milk yield than to choose any particular breed or cross.) By correcting the yields to the basis of first lactations, the average increases shown by the crossbred daughters over their Merino dams were, in the order of crosses listed above, 92·3%, 106·9%, 110·0%, 58·0%. As Bonsma says, " The results indicate beyond doubt that the hereditary low milk producing potentiality of the Merino is the most important limiting factor for the failure of the Merino ewe to produce a well-finished first-cross sucker lamb suitable for export. The striking differences in milk yield between the Merino and the various half-bred ewes afford strong support for the policy of using half-bred ewes as the basis for the production of sucker lambs."

Apart from total milk yield, most important differences were noted in the shapes of the lactation curves and the times of maximum production. The Merinos produced maximum yields in the first week and thereafter steadily declined ; the crossbred ewes, especially the Border Leicester, Ryeland and Romney crosses, gave their highest yields in the third week after lambing, that is, during the time at which the lamb is particularly dependent on the milk supply from its dam the offspring of the crossbred ewes had a great advantage.

The lambs in these experiments were slaughtered when they had reached live weights of 60-70 lb. The average times taken from birth to attain these weights by the various groups

were, in days : Merino, 174·5 ; Border Leicester × Merino, 149·9 ; Romney ×, 149·5 ; Ryeland ×, 146·1 ; Southdown ×, 142·1 ; Dorset Horn ×, 140·8 ; Ryeland second crosses, 136·7 ; Southdown × Romney-Merino, 136·7 ; Southdown × Ryeland-Merino, 134·6 ; Southdown × Dorset Horn-Merino, 129·8 ; and Southdown × Border Leicester-Merino, 128.6.

Significant differences were found between the crosses, especially the Southdown, and the Merinos in respect of body dimensions ; the Southdown crosses were particularly favoured in transverse dimensions such as width of chest and of hook bones, the Southdown second cross lambs being better than the Ryeland second crosses. Southdown and Dorset Horn crosses were superior to the others in width of " eye muscle ", and the Southdown second crosses were better than the Ryeland second crosses ; in depth of " eye muscle ", the Ryeland first crosses had the greatest average values, while the Southdown × Border Leicester-Merino and Southdown × Dorset Horn-Merino were the best of the second crosses in this character. In both these respects the crossbred lambs were much superior to the Merino ; this was also the case in thickness of back fat, in which there was a wide variation among the crossbreds, as well as within the breeds.

The same kinds of breed variation exist in relation to performance type. Adult wild sheep, like the Mouflon, have body and shape and proportions similar to those which improved sheep, such as the Suffolk, have at about three months of age. This is an extreme case, but Hammond has also shown how gradations occur in the shapes and thicknesses of the limb bones, cannons and femurs, from the unimproved types, like the Soay, through the Shetland and Merino up to improved mutton breeds like the Hampshire and Suffolk. The bones become relatively thicker as the degree of mutton development increases. Again, from measurements on the carcasses of various breeds of sheep at the Smithfield Fat Stock Show, Hammond (1936) has demonstrated differences in the " eye muscle " shape according to breed as well as age ; thus, at about nine months of age the slower maturing mountain breeds showed a smaller average index than the early maturing Down breeds, the figures for Cheviot, Scotch Blackface, and Welsh Mountain being 52, 53, and 55 respectively, and for Suffolk, Hampshire,

and Southdown, 55, 56, and 61, while at about twenty-one months of age the corresponding average indices were, for the same breeds, 55, 57, 57, 58, 63, and 61 respectively. Similarly, among cattle the breeds most developed for beef and young beef production, such as the Aberdeen-Angus and Galloway, have greater depth relative to width of " eye muscle " than the Devon, or the dual-purpose Shorthorn and Red Poll breeds.

Much the same situation is found among the pig types ; an early-fattening pork breed such as the Berkshire has higher " eye muscle " shape indices than the bacon types like the Large White. It is possible to array the various British types of pig generally according to function in terms of meat production (allowing, of course, for the effects of different nutritional and management regimes). The sequence of breeds is : Berkshire and Middle White for pork, as opposed to Large White, Welsh and Tamworth for bacon, with " dual-purpose." types, capable of being more readily used for either bacon or pork, intermediate. The last group includes such breeds as the Essex, Large Black, Gloucester Old Spot, and Wessex Saddleback.

These evidences of a genetic background for quantitative production characters whose expressions are greatly affected by environment, must not be taken to suggest that the two sets of influences always bear the same relationship to each other. The genetic background cannot be considered either fixed, or always altered in the same ways by environment. The functional type of a breed may be changed over a period of years, or new environmental situations evoking different responses may be encountered, as in the transfer of a breed to new habitats. Also, the influences may have different relative importance at certain stages in the life of the individual animals. For example, McMahon (1940) has concluded that in the case of the fleece characters of the New Zealand Romney, while genetic influences are more strongly expressed in the early coat, environmental effects are greater in the adult fleece and can then override some of the genetic differences. On the other hand, in Barred Plymouth Rock cockerels growth rate and capacity to put on flesh are under a great measure of control by environment up to about twenty-four weeks, while

growth is proceeding most rapidly. After that stage, and as
the birds reach maturity, the inherited conditions become
manifested, with significant strain differences in body weight
and breast angle being established at the age of twenty-four
weeks (Gutteridge and O'Neil, 1942). As for various pro-
ductive characters in pullets of this breed, environment had
greater influence than inheritance on egg production and age
at first egg, while heredity was more important than environ-
ment in relation to maximum body weight ; egg weight and
also body weight when the first egg was laid are characters
which are apparently affected by environment and by inheritance
to about the same degree.

The considerations raised in this chapter have important
practical and theoretical implications. It is opportune now
to call attention to some situations that are frequently mis-
interpreted, though this anticipates the fuller discussion in
later chapters. It is obvious that so far as many physiological
traits are concerned, a certain level of environmental conditions
is necessary to their favourable expression. That is, the
breeder is confronted with two main problems, that of trying to
distinguish between the effects of heredity on the one hand and
of environment on the other, and that of providing an environ-
ment suitable or optimal for the expression of the particular
characteristics.

In the first problem there are many difficulties. The
amount of variation, due to all or any causes, in a population
can be measured by " variance " which, statistically, is the
average amount by which the individuals in the population
deviate from the average of the population. The best way to
estimate the extent to which a characteristic is inherited would
be to compare the variance in the population with that in
genetically constant lines derived from that population, but
such " isogenic " lines only occur with identical twins, which
themselves must be partly influenced by having the same
maternal environment ! Another method is that of taking
lines which have been selected towards extremes away from
the population average, and dividing the averages of those
lines by a measure of the amount of selection which has taken
place. In most cases, however, the heritability can be assessed
by comparing the degrees to which related animals resemble

each other, although it is still difficult to decide how much of the resemblance is due to similar environments. If the variance in the offspring is designated σ_O^2, that due to heredity σ_H^2, that due to environment σ_E^2, and that due to the correlation or interaction of H and E, σ_{HE}^2, then $\sigma_O^2 = \sigma_H^2 + \sigma_E^2 + \sigma_{HE}^2$ and the actual amount gained owing to selection is approximately assessed by the fraction $\dfrac{\sigma_H^2}{\sigma_O^2}$; as selection proceeds, σ_{HE}^2 can be considered as becoming much less in amount. The closer the relationships between animals the better for the purpose of estimating heritability, and a good way of eliminating most environmental effects from the reckoning is to consider the correlation in the observed characteristics between dams and offspring among groups of offspring, in different herds, by the same sire. The effect of a common environment is more likely to be seen in the degree of resemblance between full brothers and/or sisters, *i.e.* full sibs, than in that of parents and offspring or in maternal half-brothers and/or sisters, *i.e.* maternal half-sibs, as compared with paternal half-sibs. In such estimations individuals which are further away than half-sibs are not much use (Lush, 1939).

In the second problem an important point is that unless a suitable environmental level is provided, there is a distinct possibility that animals which are culled as poor performers may actually have had a superior genetic constitution to those which have been kept; this has the effect that the offspring of those retained will tend to slip back, or " regress ", towards the average because of the error in selection that has been made. In any event (as is shown on p. 72) the offspring will not, *on the average*, be so high above the population average as their chosen parents were; they will only have a fraction of their parents' superiority (Lush, 1937, 1939).

The clear case that a *suitable* environment should be given to allow physiological characters to be well expressed is sometimes extended to imply that the best possible environment should be provided. In this there is the assumption that better and better environments will themselves encourage the accumulation of adaptive changes by favourable gene mutations. There is no direct or experimental evidence that improved environment actually evokes " improved " genes, and there is no need to

E

make such an hypothesis to interpret the facts, but better environments in themselves do offer the possibility of selecting those gene combinations which are capable of responding in them. Moreover, if this assumption is also taken to imply that animals kept under extremely good conditions of feeding and care have thereby of necessity better genotypes than animals not so favoured, then disappointment in their breeding performance is certain, unless their offspring are raised in similar conditions—in practice genetic differences are often masked by such high treatment. With progressive improvement in environment, it is more difficult to assess the environmental effects unless the variance due to heredity is also more accurately determined. Further, an extreme " improvement " in environment may in effect mean exposure to highly artificial situations such as either the bulk of the population would rarely encounter in practice or would amount to a new environment requiring a different gene complex for a successful fit. The safer general course is to keep the animals as far as possible under those environmental conditions in which they are expected to perform, in which they are to be used, and therein to consider the possible relative significance of the genetic and the environmental influences. (*See* Hammond, 1935 ; Smith, 1935 ; Greenwood, 1935 ; Lush, 1935 ; and Nichols, 1935.)

CHAPTER VIII

GENETIC ASPECTS. (1) SELECTION

IF mating were unrestricted in a large population, the proportions of the genotypes would undergo little change, provided also that all the different genotypes present had the same chances of producing offspring. This situation never obtains in practice ; there is always some interference with any tendency to unrestricted mating, the animals to be the parents of the next generation being chosen by either nature or man. This choice of parents is *selection* and affects the distribution of genes in the group in different degrees and ways according to the mating systems followed. The number of animals in any group or breed is small relative to *all* the combinations which could exist of the genes present in the group (p. 39). The breeder cannot alter the genes, but he wishes to increase the frequency of those considered desirable.

Breeds frequently overlap in their characteristics, or breed differences may be very small and not of great importance. There is a tendency for breeds to drift apart in genotypes —because of the sampling of genes which takes place at each formation of the gametes—if the ancestor groups have been and are kept distinct. In some cases, however, the selection in two breeds has had a common aim, so that the two breeds, with separate ancestry, have been drawn together to a common general type ; this has happened with certain pig breeds, for example, the Large White and the Landrace in Sweden have approached a common performance level as a result of selection for bacon type. (Other examples will be given in Chapter XIV.) But in these cases the resemblance need not be even largely due to close genetic similarity, it may be predominantly one of appearance, that is, of phenotype.

The genetic differences between breeds are probably due partly to homozygosity in respect of opposite members of gene pairs and partly to wide differences in the relative proportions of the alleles. In any case the differences can

usually be recognised on the basis of the average conditions regarding many characters, the more the better, even if there is a good deal of overlapping in many of them. This is what the breeder or judge is automatically, and more or less subconsciously, doing when " typing " animals according to descriptive standards. In measurable characteristics the distinctions can be made more precise, though admittedly often at considerable labour, and this is one of the major justifications for the biometrical description of breed and performance types which has been widely applied in recent years, especially on breeds or strains in Europe, involving many measurements of body characters such as heights, lengths, widths, etc., in various directions.

In so far as a breed can be defined as a group whose ancestry has been kept largely or completely distinct from other groups, and which possesses traits more or less distinguishable on the average, a similar definition can be extended, and these general considerations applied, to sub-breeds, varieties, or strains.

Selection and mating system are the main tools available to the breeder to enable him to alter gene frequency and combination. Matings fall into four main categories : those between relatives—inbreeding in some form ; where the parents are unrelated—outbreeding ; those in which the parents are chosen because of similar appearance, *i.e.* " like-to-like " or " assortative " ; and those where parental selection is based on dissimilarity of appearance, *i.e.* of unlike to unlike. The distinctions are not always clear cut. The systems have different effects but it is unusual for any one to be followed consistently, for a sufficient length of time, or far enough, to change the breed characteristics compared to what these would be if once those animals selected to become parents had in fact been allowed to mate quite at random. It is only in the case of inbreeding that mating is sufficiently restricted to be considered not at random for each pair of genes considered separately. (Unless, of course, a breed is 100% pure for a simple dominant gene, such as that causing black colour in cattle, in which case all animals possess the gene in double condition, the frequency of that gene is 100%, and so far as that gene is concerned, it does not matter what matings are made.)

All these kinds of non-random mating involve selection, on which much of our knowledge is derived from mathematical analyses of various gene situations and populations (*e.g.* Lush, 1937), backed by experimental evidence.

First of all, in the simplest cases selection cannot fix a heterozygous condition such as red- or blue-roan in Shorthorn or Blue Albion cattle, and if selection is applied against a recessive character, it is fairly rapidly successful in the early generations but then slows down. These are cases of *mass selection*, taking the animals on their individual merits regarding the desired or undesired traits. Mass selection also fails where it is for a simple dominant, *e.g.* for black as against red in black cattle breeds. These three situations are all shown in the following table, *a* being an undesirable gene, strictly culled when appearing in its homozygous state, or then eliminating itself if it has a lethal effect, and with every genotype retained having equal chances of reproducing.

Beginning with a heterozygous population, culling only the homozygous recessives and thereby retaining the genes A and a in changing ratios, say of X to Y, for producing offspring in the succeeding generation in proportions $(XA+Ya)^2 = X^2AA+2XYAa+Y^2aa$, the effectiveness of selection in each generation is as shown in the third column.

Generation.	Genotypes.	Culling of aa, as % of total.	Gene ratio among parents of next generation.
F_1	Aa	0	$1A : 1a$
F_2	$AA : 2Aa : 1aa$	25	$2A : 1a$
F_3	$4AA : 4Aa : 1aa$	11·1	$3A : 1a$
F_4	$9AA : 6Aa : 1aa$	6·3	$4A : 1a$
F_5	$16AA : 8Aa : 1aa$	4·0	$5A : 1a$
F_6	$25AA : 10Aa : 1aa$	2·8	$6A : 1a$
...	...	...	...
F_{10}	$81AA : 18Aa : 1aa$	1·0	$10A : 1a$
...	...	...	...
F_n	$(n-1)^2AA : 2(n-1)Aa : 1aa$	$\dfrac{100}{n^2}$	$nA : 1a$

It would take ten generations in this situation to reduce the proportion requiring to be culled to 1% of the total number of individuals in a generation, and in the tenth generation

there would still be 18% of heterozygotes remaining to produce 0·8% of homozygotes in the eleventh generation. This is in terms of generations—the time required in years would depend upon the average interval between generations, which in cattle is roughly about five years. Hence in cattle the time needed to attain an equivalent amount of culling would be about fifty years.

The case illustrated in the table begins with a frequency of the recessive gene of 50% in the first generation; a given gene might have a frequency of 100% or of 0%, but these extremes would not usually be achieved in practice except for single pairs of genes. For the usual genetic situations, the range of frequencies would be intermediate, and it can be shown that selection is most effective when the frequency of any gene is somewhere about the middle of its possible range. Selection of the kind discussed above can lead, though slowly, to a given recessive gene becoming very rare in a population, but it probably cannot succeed in eliminating the gene because at low frequencies the possibility would begin to appear that mutation (itself extremely rare—*see* p. 25) from dominant to recessive would help to counteract selection by replacing in the population some of the recessive genes lost.

If for any particular reason the heterozygous condition were favoured, *e.g.* as a desirable type or because of a more satisfactory adaptation to environment, then a situation of equilibrium would be achieved.

As has been shown, many of the characteristics of animals in which the breeder is interested are no doubt affected by many genes; for these such extreme conditions of gene frequency and selection must be very unusual. Further, the breeder is rarely in the favourable position of being able to consider only single and simple character differences; in many cases he cannot cull animals which are below standard in one or two traits because they are at the same time good in others. This has an important practical bearing on the possibilities of selection, but its importance is overshadowed by another consideration.

The chief limit to selection lies in the need, in most species of farm animals, to keep relatively large numbers in order to replace the animals lost from the herd or flock by reason

of disease, infertility or sterility, and other wastages besides old age. The replacements in many kinds of farm animals are high and much work remains to be done in practically every species, and under the various conditions, to assess and to reduce those attributable to preventable causes. At present only rough general estimates can be given, but they show how serious this is as a limiting factor in selection. In the United States, about one-third of the dairy cattle which pass out of the herds are culled because of low production, another third because of disease and similar disadvantages, and the remainder for these two classes of causes in combination. In Great Britain, the number of lactations per dairy cow averages only about three or four, disease being the most important source of wastage; just over 20% of wastage is due to sterility and just under 20% to low yields. In Denmark the average number of lactations in a herd is about four, and somewhere about 80% of the wastage is due to sterility. In the herds of the Norwegian Agricultural College, during 1896-1940, only 49·2% of all the cows had up to 3 pregnancies; infertility gave rise to 37·6% of the total culling, and handicapped selection for milk yield (Berge, 1942). Also, there are losses among the young stock coming forward as replacements, so that altogether the breeder has to keep a high proportion of his heifer calves for no other reason than that they are heifers and will be needed to keep up his herd numbers; generally something over 50% of the heifer calves must be kept in any case, and probably about 5% of the bull calves, purely as replacements. This means that, so long as these wastage rates hold, there is very little prospect of useful genetic selection among female dairy cattle. In the more rapidly reproducing species, and those which show a shorter time interval between generations, measured by average age of parents when their young are born, and higher fertility, such as pigs and poultry, the proportions of females needed for replacements are much less than in cattle and can be put at about 10%. Even such a level is still a serious handicap to selection, in that it is very little use claiming great benefits from selection for high production, on the basis of homozygosity for desirable genes, when only 1% of animals may be of homozygous genotype and 10% must be kept for breeding replacements (Lush,

1935). Obviously the intensity of selection which could be applied in such circumstances would be very small. (In such species as pigs and poultry, with short intervals between generations, the proportion of animals actually replaced in each generation—the replacement rate—is high.)

Intensity of selection can be indicated in terms of the difference between the average of the animals chosen to be parents and the average of their own generation (Lush, 1937)—this measure is termed the *selection differential*. It is affected by the replacement rate necessary, in that if more parents have to be kept, in order to replace numbers, than would be chosen on merit, their average merit is lower than the desirable. Further, not all of the selection differential is actually achieved in the next generation; the offspring tend to regress towards the breed average and will only achieve a part of their parents' superiority over the breed average. (The actual gain made by selection is about $\dfrac{\sigma_H^2}{\sigma_O^2}$ of that " reached " for; that is, the gain depends upon the amount of variance in the population which is due to additive actions of genes.) Lush (1935) gives an illuminating example of this limitation, in that, excluding environmental effects, he shows that if only those cows which exceeded the rest by 150 gallons were kept for breeding and one-third of the variance of milk yield were due to additive genetic effects, then their offspring could only be expected to be better than their parents' generation by 25 gallons, *i.e.* half of one-third of 150 gallons, when no attention is given to selection among bulls. Another example is that provided by McMahon (1940), who concludes from his studies on fleece weight in the New Zealand Romney that only some 10% of the variation in that character is attributable to additive gene effects (50% is due to seasonal influences); this would imply that, excluding environmental effects, for a gain of 1 lb. in superiority of the offspring over the average of the parents' generation the parents would have to be chosen among those animals which exceeded that average by 10 lb.

Under most practical conditions, one set of productive characters often appears incompatible with desirable expression of another set. There appears to be a general physiological disability in associating even moderately high

performance in two or more respects, *e.g.* early beef maturity and draft, fine fleece and high fleece weight, and, possibly, high butter-fat content and high milk yield. A common difficulty is to combine high quality beef characters in the male with high milk production in the females of the dairy breeds. In such cases, where series of genes which do not have additive effects are involved, selection may result in rapid progress at first until the desirable genes become so distributed among the breed that they give rise to desirable performance on the average but will not necessarily be combined in individuals ; any further progress by selection will only be very slow. Once this average performance is reached, it can be said that further selection will serve to hold the gains made but not lead to much more progress. Breeders, however, will recognise that some individuals do occur, though relatively rarely, in which high performances in two traits are combined, so that it is unwise to dismiss the desirable combinations as physiologically impossible. What can be said is that selection alone for such combinations will not be likely to achieve much progress.

It must be stressed again that, for the moment, environmental effects are being neglected. Early maturity, of lamb or beef, requires a high nutritional level in early life ; without it, the growth and development factors cannot be adequately expressed. Delayed growth and development lead to a different form, less desirable for meat but not so disadvantageous in the case of animals wanted for milk production. But the differences in growth rate and development depending on environmental factors do not themselves convert an animal of early beef type into a milking type. There is an association of genetic conditions which decides the initial performance type ; upon this background the environment acts, and, excluding the environment, selection can in turn serve to mould the genotype, but only in a limited degree.

Excluding environment as far as possible, there is then a "peak of desirability" for each performance type (Lush, 1937) ; within each species of farm stock there is a series of peaks of desirability, with an array of breed types conforming generally to the series of peaks. One series has already been given for pigs (p. 63). Others can be

broadly described on a topographical analogy to series of mountain chains, with high peaks joined together by lower intervening saddles or passes. The chains need not be straight but may branch, with each branch having its own peaks, spurs, and cols; each peak can be pictured as the highest expression of some desirable performance type, found in one or more breeds. The peaks are not all of similar height or equidistant in the chain, or evenly defined; the intervening country is not all alike. The skyline presented is broken; the peaks of desirability for genetically determined breed productive characters may not grade imperceptibly into each other. Milk and beef are two main peaks in the cattle chain; early lamb, adult mutton, Merino type fine wool are main peaks in the sheep chain; and so on. " Dual-purpose " performance occupies the lower slopes in most cases. Such a picture might be called a selection landscape, in which the effects of selection are for the most part limited to holding the types within the marches of their own particular peaks; selection may draw the type uphill and thus restrict its range, but selection alone cannot move a type across an intervening gap on to the lower slopes of a neighbouring peak. (For more detailed accounts of the conception of " peaks " and " surface " of desirability, see Lush, 1937.)

If selection on any peak could be absolute, it would be like running a definite line at a certain level around the peak and discarding all animals which fell below it on any flank or slope. But criteria of selection are not absolute in practice; some flexibility has to be allowed, either deliberately or because of the breeder's inability clearly to distinguish genetic differences. If, however, selection has been applied drastically and for so many generations that the favourable genes are isolated, the stock can have been restricted in range to such a narrow part of the peak that any later counter-selection, for a closely allied performance type, may be ineffective.

In relation to this aspect, the question of suitable rather than the best environments again rises (*cf.* p. 65). The best possible environment may serve to restrict response in performance characters so that either a narrow field for selection is presented or else other essential background traits, such as hardiness, are neglected. The poultry industry possibly

provides examples of this effect, in that the highly controlled environment of specialised poultry flocks, with its great emphasis on production, has opened the way to increased susceptibility to disease, etc. ; on the other hand, it must be admitted that poultry have a very high reproduction rate, which allows very rapid expansion in numbers and thus a field for less rigid selection for general physiological characteristics in combination with high egg yield.

Other reasons why selection is usually not very severe are also important : first, the optimum level of production is often not the maximum level, so that the practical criteria of selection are less strict than if maximum performance were the chief aim ; and second, that very rarely can only one set of criteria be applied, as several characteristics must be considered. In the former, the highest performance may be uneconomic in terms of requirements of food or handling, as in the case of high-yielding milch cows, in which the secretion of milk may be so rapid that frequent milking is needed to reduce udder pressure periodically, or with high fat deposition in beef cattle, which can interfere with reproduction. Again, the trait itself may be a complex one. The second reason is probably of greater practical significance and can apply where the characteristics are not mutually exclusive. It operates in every case where a breeder is seeking to improve performance in his stock ; it is always necessary to regard a particular desirable trait in relation to its general physiological background, the animal which bears it. Because it is so universal an influence, it is important that its effect on selection and breeding methods should be clearly recognised.

Two examples show the kind of problems involved.

Greenwood (1935) has discussed the genetic factors concerned in egg production and reviewed the results of various workers. For a hen to have a high annual egg production five desirable qualities are necessary, apart from traits not directly connected with production. These are early sexual maturity, high intensity of production, no winter pause, non-broodiness, and high persistency of production ; all are subject to genetic control. Two independent dominant genes affect sexual maturity ; one gene is sex-linked and the other is autosomal, but either can cause egg-laying to begin (*e.g.* in

Rhode Island Reds) before the age of 215 days. Two dominant genes, which have an additive effect, together increase the winter clutch size up to three or more eggs and thus bring about high intensity of production. Winter pause is due to a single dominant gene, so that hens with no winter pause must be homozygous recessives. Broodiness is affected by two dominant genes (A and C), complementary in action ; birds with neither A nor C are non-broody, so are those with only A or only C, thus broodiness is difficult to breed out, since an A and no C (non-broody) type can produce a broody when mated to a C and no A (non-broody) type. Persistency is apparently due to another single dominant gene ; it involves no break in production due to an early moult. There is no known reason why these traits cannot be combined in all the birds, but with the different genes concerned Greenwood calculates that the number of possible genetical classes for these five characters reaches a total of 10,935, one gene being sex-linked, therefore there are different numbers of classes in males and females ; only one class would give genetic fixity of type. Hence, for this reason alone, progress by selection must be slow. Actually, Hays and Sanborn (1934) found in their flock of Rhode Island Reds that while 59% of the birds showed three or four of these desirable characters, and 16% all five, the rate of improvement during five years was only one-sixth of that which could be expected on theoretical grounds.

The other example gives an idea of the relative frequencies of unrelated characters which sometimes have to be taken into account. Terrill (1939) analysed the records of the Rambouillet flock at the United States Department of Agriculture Sheep Experiment Station at Dubois, Idaho, to examine the reasons for culling range ewes. The study was a retrospect of the selection which had actually taken place among 757 ewes born between 1925 and 1933 ; the records were supplemented by information (*a*) on the reproductive history of other ewes, to an overall total of 1,290 ewes, (*b*) on the body weights at weaning, just after shearing early in June, and at culling in early October, of 305 ewes which had been kept in the flock for five years or longer, (*c*) on score for mutton conformation in 747 ewes, and (*d*) on the unscoured fleece weights and lengths of staple for 323 ewes. The amount of culling

for low quality, in several characters, at an average age of about three years but including some animals up to six years, was altogether 29%; this was made up of 14% culled for inferior mutton type and small size, 11% for light fleece weight or short length of staple, and 4% for having excessive skin folds. During the period of fifteen years, about a quarter of the ewes were culled because of age, another quarter were dead or missing, and unsoundness and low fertility were among the reasons for culling the remainder. It was found that ewes which had been culled for inferiority in a particular characteristic at any time later had usually been deficient in that respect when they were a year old; further, they were frequently below standard in other characters also. In general, the condition of body weight, fleece weight, and staple length as yearlings gave useful predictions of the lifetime performance, particularly if comparisons were made within groups of ewes born in the same year. Younger ewes, at two and three years old, produced a lower percentage of weaned lambs than did ewes aged four to nine years, so that it was apparent that the general reproductive rate in this flock could be increased by having a higher proportion of older ewes in the flock at any time. This could be achieved by the process of culling a greater proportion out of the young ewes for low performance in any trait, and by so doing the effectiveness of the selection practised for all characters would not have been lessened.

When a breeder is confronted by the problem of improving several characters in his stock, he can adopt one of three methods: he can either select for one character at a time, or treat the characters independently of each other, or else he can select on a total score for desirability. In practice, breeders probably tend to adopt the first method, starting with the characteristic in which the stock appears most defective and then taking the others in turn. The third method, based on a total score of desirability, or a general evaluation, is, however, more effective because high merit in one trait tends to even up weaknesses due to another trait in the evaluation.

This method, using a total score, has another advantage, based on the fact that, although the selection differential for each character separately is decreased whenever several characters have to be taken into account, the decrease is not

so great when the characters are balanced up in a total score as it is when they each have an independent culling level. The mathematical basis for this difference lies in the fact that if n independent characteristics are to be watched, then on a total score evaluation the selection applied to each will only amount to $\dfrac{1}{\sqrt{n}}$ as much as for each taken separately. On the other hand, with n characters on independent culling levels and x the proportion of animals which must be retained for replacements, the intensity of selection for each character separately can amount roughly to $x^{\frac{1}{n}}$. For example, suppose a pig breeder were obliged to retain 10% (*i.e.* 0·10 proportion) of his young sows for replacements and that he was taking into account four characteristics such as fecundity, estimated carcass quality, economy of food utilisation, and constitution and disease resistance. If he set up a total score criterion for these four traits together, the intensity of selection in respect of each would be $\dfrac{1}{\sqrt{4}}$, or $\frac{1}{2}$, of what it would be if each trait separately were the basis of selection. On the other hand, if he were to work on four different and independent levels of performance in the traits, he would derive his 10% for saving from among the animals which were $\sqrt[4]{\dfrac{1}{10}}$ of the best for each trait separately; this is about the 0·56 proportion, or 56%, so that he would have to get his 10% out of the best 56% in fecundity, the best 56% for carcass quality, the best 56% for economy of food utilisation, and the best 56% in respect of constitution. That is, the intensity of selection possible to apply to any one trait is much lessened, as for each he can only eliminate the lower ranking 44%.

This has a significant practical application, in that for many types of animal breed points, or labels, may have no direct relationship with production characters or even with each other. But each breed point adds yet another character to be considered in selection, and therefore introduces a further lessening of the intensity with which selection can be applied. With selection in itself slow and difficult, the fewer extraneous

or subsidiary points demanding attention the better. Nevertheless, a certain qualification to this must be made ; if breed labels are allotted points in a score card so that their maximum contribution to a total score is fixed relatively to other more useful characters, and so that they cannot be unduly stressed, then assessment of an individual against an inflexible standard has advantages as an aid to selection. This does not amount to a justification of score cards, it merely implies that, under certain circumstances, they have a distinct virtue in limiting the emphasis that can be laid upon a few minor characteristics. Also, breed points may by custom have a cash value.

The measurement of progress in relation to selection differentials is not always possible for practical purposes ; there is another measure which is often useful provided it is applied and interpreted with caution. This involves an estimate of the degree of progress per generation ; for example, in the Swedish Landrace pig the thickness of the back fat has been reduced by about 9 mm. between 1924 and 1940 (Johansson, 1943), which represents about 1·5 mm. per generation. Such a statement, however, does not mean that this progress is attributable only to selection ; it describes the result of a number of generations over which both selection and some degree of designed matings have been carried out, and therefore knowledge is required of the systems of breeding followed, their effects combined with selection, and also of any changes in husbandry and environmental influences which may have operated, before it can be properly interpreted. Further, the particular trait may have an optimal economic level—in this case back fat could become too thin—so that the limit to which the characteristic can profitably be taken must also be considered. Again, the optimal expression of the trait may have altered during the period for which information is available ; fashion or economic value may have fluctuated so that for a number of generations selection may have changed its direction. These aspects severely restrict the use of this method for comparative purposes between breeds, or for the same breed during different periods of its history.

CHAPTER IX

## GENETIC ASPECTS. (2) INBREEDING AS A MATING SYSTEM

THE general concept of relationship conveys the idea that if two animals have a common ancestry, the chances will be increased that their genes are the same. The closer the relationship, the smaller the fraction of their genes that are probably dissimilar, and vice versa. In any population such as a breed there is a certain likeness of gene constitution; relationship therefore refers to the amount of similarity *above* the average of the population. Hence, only animals within a breed can strictly be compared in terms of relationship; the average amount of relationship will differ from breed to breed, depending upon the width or narrowness of ancestry and the ways in which the ancestors have been mated together.

Selection is the choice of animals to be parents and thus provides the basis for mating; it and the way the selected animals are mated affect the distribution of genes within the next generation. A breed has a very restricted ancestry compared to the whole population of the species, and as any system of mating involves animals which are related or are unrelated in the above sense, the idea of relationship and its meaning must be understood before the results of the various mating systems can be properly appreciated.

The more distant the ancestor, the less chance it has of contributing any particular genes to its descendants. On the average a parent contributes about half of its gene complex to its offspring, a grandparent about one-quarter, and so on; every generation which comes between any one ancestor and its descendants reduces by half the proportion of genes which are likely to be exactly duplicated in the descendants. There is a major exception to this general rule, apart also from the sex-linked genes; in the case of a parent in which many of the genes are in a homozygous state, there is a much greater chance that many of the genes in any two of its offspring will be more alike than in the average of the population.

In assessing relationship to a common ancestor there is no need to go back further than about four or five generations to find one, since at that distance, owing to segregation of genes, there is a high probability that some ancestors will have contributed nothing at all to the genetic make-up of the descendants being considered. The method of measuring relationship can be most simply illustrated by comparing half-brothers and brothers whose parents are not related and not inbred, in the sense that they are not descended from related stock. In the diagram, A and B are brothers out of a sire S and a dam D, and C is a half-brother to A and B, being out of the dam D by another sire. There is *direct* relationship between
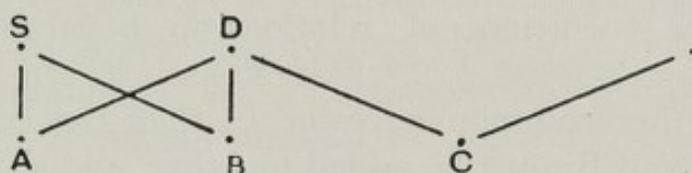
parents and offspring (S to A and B; D to A, B, and C), the latter being descendants of the former. There is *collateral* relationship between A, B, and C, but the amounts of this differ. The direct relationship may be measured in the familiar way by " percentage of blood ", A and B having 50% of the " blood " of S and 50% of that of D; C has 50% of D and none of S. Similarly, in " percentage of common blood " A and B have 100%, A or B and C 50%. But on the genetic basis, and as a measure of relationship, " percentage of blood " is clearly misleading, for B and C are each separated by one gene segregation from D, B and C each receive half of their genes from D but the two halves are independent and unless D were homozygous for large numbers of her genes, the genes going to either B or C are just as likely not to be duplicates as they are to be the alleles. That is, B and C (and also A and C) are only $\frac{1}{2} \times \frac{1}{2} (= \frac{1}{4})$ related, or 25%. A and B, on the other hand, are genetically related in that they get $\frac{1}{4}$ of their similar genes from S and another $\frac{1}{4}$ from D, giving a total coefficient of relationship of $\frac{1}{2}$ or 50%.

This can be stated more directly by saying that two segregations separate A and B via S and two via D; as at each segregation relationship is halved, their relationship is $(\frac{1}{2})^2 + (\frac{1}{2})^2 = \frac{1}{2}$

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or 50%. Skeleton pedigrees, such as that given above, will show, for example, that two animals having one grandparent in common are related $(\frac{1}{2})^4$, two segregations up from one animal to the common ancestor and two down from that ancestor to the other animal, or 6·25% ; two animals with two grandparents in common, two segregations up and two down via *both* grandparents, are related $(\frac{1}{2})^4 + (\frac{1}{2})^4$ or 12·5%.

In actual practice, among farm stock the relationships are not usually so straightforward as these, but the general rule for calculating this coefficient of relationship, suggested by Wright (1922), between two animals X and Y is to count the segregations separating X from the common ancestor A, calling this number n, and those separating Y from A, called n^1, when the coefficient of relationship between X and Y through A $(=R_{XY})$ is $(\frac{1}{2})^{n+n^1}$; if X and Y are also related through another common ancestor B, then the coefficients in respect of A and B must be added together, and so on for other common ancestors. The actual formula, in this form, is stated as $R_{XY} = \Sigma(\frac{1}{2})^{n+n^1}$.

" Percentage of common blood " is inadequate as a measure of genetic relationship because it makes no allowance for collateral relationship, and the chances of gene likeness depend upon how many generations away the common ancestor is to be found. On the same basis the frequently quoted Galton's Law is only partly true, in so far as the relationship is halved by each generation which comes between ancestor and descendant, but is incorrect in suggesting that an individual's genotype is determined by its ancestors, as this does not allow for segregation.

Genetic relationship is, however, affected if there are closely related individuals among the ancestors. If close relationship means greater possibility of similar genetic make-up, then the mating of close relatives together still further increases the possibility of genetic likeness. This effect will be considered more fully later, pp. 83, 94. But if there has been no inbreeding, no two animals, except identical twins, can be related in terms of Wright's coefficient more than 50%. Also, sex-linkage introduces a minor complication, in that a son receives his sex chromosome (X) from his dam, and is therefore more like her, so far as sex-linked genes are involved, than like his sire ;

a daughter is for the same reason and in the same sense a little more closely related to her sire than to her dam.

A measure of genetic relationship has a certain practical value, as it provides a means of estimating the probable worth of an animal whose near relations have known performances, and its usefulness in this respect increases as the number of these known relatives increases, especially if the relatives are close, such as half-brothers or half-sisters. For example, if a Merino ram has a fleece weight 6 lb. heavier than the breed average, then any one of his offspring, most of which are half-sibs and the rest full sibs, might be expected to be 3 lb. over the breed average because they are 50% related to him. But this sort of estimate has to be interpreted very cautiously for many reasons, the chief of which is that half-sibs are frequently kept in the same environment, which may induce a certain amount of apparent similarity. Also, the comparisons are in any case based on appearance and cannot be taken directly as indicating genetic worth. The fact of relationship alone cannot greatly simplify the estimation of the genetic constitution or breeding worth of the parent from the offspring's performance, especially as the parent is likely to be heterozygous at least for some genes. But, to the very limited extent that some characters may be considered as due to additive genes and completely unaffected by environment, the average inheritance received from two unrelated parents can be more accurately gauged as the numbers of their offspring, full sibs and 50% related, increase, that is, the larger their family.

Compared with the average of their population, close relatives have a greater chance of being similar genetically, so that when close relatives, more related than the average of the population, are mated together, there is a yet greater chance that their offspring, on the average, will be still more alike so far as their genes are concerned. The mating of close relatives is *inbreeding*, and its main effect is to increase the amount of homozygosity, and therefore lower the proportion of heterozygosity, in the offspring.

Inbreeding is a system of mating which has frequently been used among farm stock, for which great advantages are claimed, and which is also frequently decried. The various opinions regarding inbreeding and the varying results obtained

by it have led to much discussion. Yet its action and results can be readily appreciated on general grounds which should admit few differences of interpretation; for this reason no attempt will be made here to review the very extensive literature on the subject.

In the first place, inbreeding involves a definite form of selection, in that mating is restricted on a basis of relationship—it is severe pedigree selection. When the members of a breed in a particular country are all descended from just a few animals, they must all be related in some way, but this does not necessarily mean that inbreeding has been or need be carried out within the breed, since, by our definition, for inbreeding to occur it must be by mating animals which are more closely related than the average breed members. Although all the Brown Swiss cattle in the United States are descended from imported animals numbering only 21 bulls and 129 cows (Prentice, 1942), inbreeding among them need not be frequent.

Secondly, inbreeding without any other form of selection does not affect gene frequency in the group to any great extent, it only lowers the proportion of heterozygosity; it only secures a rearrangement of the genes with which the group began, leading to a general separation into lines which are homozygous for particular genes. Moreover, once homozygosity for some genes is attained in an inbred line, it cannot be lost, although *complete* homozygosity for all genes is never attained among animals. The practical outcome is that with close inbreeding, such as brother × sister matings, the lines tend to separate towards homozygosity, the original gene balance being upset. If close relationship, therefore, is the sole or main criterion in the selection used, inbreeding will quickly reveal the recessive combinations, dividing the population up into distinct lines or families. If undesirable genes, such as lethals or those leading to infertility, to weakness of conformation or of performance, are present in the original selection, they will be uncovered, and the lines in which they are most frequent will obviously be " degenerate " compared to other lines as well as to the original group. This is the most probable interpretation of what happened in the Duchess Shorthorns, inbred by Bates for eight generations in all and on a basis equivalent to brother × sister for two generations.

As inbreeding proceeds, the lines will become more uniform and, if no other form of selection is applied, the population, as a result, will become more variable. This distinction is important: a population or breed may lack uniformity because of genetic variability; this variability may be the result of widespread heterozygosity or may be due to the existence of uniform and fairly homozygous families, groups, or sub-breeds that are widely different from each other. Selection will have different possibilities and results in the two cases, but inbreeding is the only practical tool that the breeder has to bring about genetic uniformity.

Another important feature of inbreeding alone is that it requires no judgment of genotypes or, alternatively, of environmental effects, so that it can be usefully applied in regard to characteristics which are not largely due to additive combinations of genes. This is one of the ways in which inbreeding differs from the mating of " like to like ", where the selection for mating is that of similar phenotypes.

It must also be pointed out that, in tending to increase the proportion of homozygosity for some gene combinations, inbreeding may lead to an additional source of deterioration, in so far as desirability may be due to several combinations of genes. For example, constitution and thriftiness in dairy cattle may be broadly considered attributable to one set of gene combinations, milk production to another set; highly desirable milch cattle express the most favourable conditions or balance of both sets, but continued inbreeding of such stock may upset the combinations, destroying the desirable balance, and thereby reduce the average desirability of the stock.

The reasons for the possible dangers and disadvantages of inbreeding are now apparent. If undesirable recessive genes are common in the original stock or have marked effects—as the recessive genes in farm animals often have—inbreeding reveals or fixes them so quickly that the breeder, faced with the problem of replacements, cannot afford to cull the affected animals heavily. Also, the effects of inbreeding in producing variability are often soon noticeable, so that heavy culling is necessary to retain only desirable lines. Depending upon the genetic situations involved, it may be some time, in terms of generations, before sufficient uniformity in any trait is

attained (the early generations of inbreeding among pigs are often highly variable) and intense selection is necessary to achieve this. Further, the disadvantages are more likely to appear when inbreeding is sporadic or desultory, and undesirable genes not easily recognised may become relatively fixed throughout the animals in the herd before their effects are fully appreciated. In relation to such disadvantages close inbreeding may be either a risky or an uneconomic project for an individual breeder, because (1) undesirable genes may be present in the stock with which he begins, or (2) the desired characteristic is a complex of several sets of additive gene effects, or (3) his resources for a sufficient degree of culling are inadequate, or (4) because of a combination of these reasons.

Contrary, however, to much of popular opinion, the question of the practical application of inbreeding cannot logically be decided on these disadvantages. The same genetic effects lie behind its main advantages, but what may be an advantage under some conditions may be a disadvantage in others.

When a superior individual has been found, inbreeding is the only method of keeping stock closely related to it. This holds good whether the desired characteristics are highly inherited or not. Genetic relationship cannot be more than 50% unless some inbreeding takes place. This situation can arise in the formative period of a breed, when animals with the desired combination of traits are relatively rare; for instance, the Colling brothers mated Favourite to his own daughters for four generations. Unfortunately, inbreeding is sometimes made to animals which are only ordinary specimens, as in small herds or flocks, where it is cheaper to put a sire to some of his descendants rather than replace him—this leads to bad results. Inbreeding is also useful as a means to reveal any comparatively rare recessives so that they can be culled from the stock, but culling may be an expensive process if the number of undesirable recessive genes is great, and in any event the selection should also be made against the heterozygous parents of the recessives. If no undesirable characteristics emerge, there is evidence of the absence of the causal genes, so that in this sense inbreeding can also be considered a test of genetic worth.

Greater homozygosity is important in a direct practical

way, as it is the main reason for *prepotency*, which may be briefly defined as the capacity for deciding that the offspring shall be either more like the parent or like each other than the average resemblance of parent and/or offspring in the breed. It may be due to dominance of particular characters or to homozygosity. From the point of view of production the latter is probably the more significant of the two reasons, although dominance can lead to spectacular results and thus sometimes be misleading. Thus, in cattle polled animals, of any breed or type, will always produce some polled offspring when mated to horned stock. They may be called prepotent for this character, but this does not mean that they are also homozygous for other characters; whether they are or not depends on their degree of homozygosity for the genes concerned in the other characters.

Wentworth (1925) quotes the difference in breeding results between two Red Danish bulls to show how prepotency should be regarded as a property of the character, not of the individual. The effects of the two bulls were as follows :

		Average Milk Yield. lb.	Average Fat %.	Average Butter Yield (89% Fat).
Bull DAN 450.	Dams (44) .	9,413	3·44	360
	Daughters (44) .	10,126	3·89	440
„ HERMOD.	Dams (21) .	9,730	3·81	413
	Daughters (21) .	9,301	4·35	453

Dan 450 would justifiably be called prepotent for both milk yield and butter-fat content; Hermod's influence is not so marked, particularly in terms of increased butter yield by his daughters. The cows to which Hermod was mated had higher milk productions, with higher fat content, which would tend to make his influence appear comparatively less than that of Dan 450. At the same time, Hermod's daughters yielded less milk than their dams but this milk had a much higher average butter-fat content. In terms of average fat content and average butter yield Hermod has as much right as, if not more than, Dan 450 to be recognised as prepotent, but if he is, then he must also be termed prepotent for lower milk yield.

Simple dominance, or the behaviour of obvious characters, often distracts the breeder's eye sufficiently for him to miss the real significance of what has actually happened. A form of prepotence due to homozygosity is often seen where one breed which has been closely selected and bred for a particular combination of characters is crossed with another which is more variable or inferior for the same characters. Here the first-cross offspring tend to throw more towards the more prepotent parental type rather than to be strictly intermediate. Examples of this are found when improved breeds are crossed on " primitive " breeds, unselected for improved production. In crosses between such breeds as either the Leicester or the Lincoln and the commercial Merinos, mutton conformation tends more to the longwool parental type ; on the other hand, if the Merinos are of the types highly selected for uniformity of fleece characters, the F_1 tend rather towards this uniformity than to be just halfway between the parental breeds. In the same way, the Scotch " Halfbred " tends towards the Border Leicester parent (Nichols, 1925, 1933). However, within a breed prepotency in a parent can be recognised by the extent to which its offspring resemble each other when contrasted with the similarity of other sets of half-sibs in the breed, although it must be remembered that, depending upon herd size and management, there may be a tendency for half-sibs to be reared in the same environment, and the effects of this have to be discounted.

In any case, two features of prepotency must be stressed. Firstly, the breeder's only means of setting up and influencing prepotency is by inbreeding. Secondly, prepotency as such cannot be transmitted from parent to offspring, except in so far as it is due to dominant genes ; if, as is more usual for productive characters, it is based upon homozygosity, then this is the property of the individual, or to a less extent of a highly related strain. Prepotency as a general character cannot descend from a sire to his son or any other offspring unless the matings involve inbreeding, that is, are among animals of close genetic relationship. This means that any cases in which prepotency is claimed must be carefully examined to see if that is the real explanation. Often the claim is made that prepotency is passed from sire to son in some noted " sire

lines ", as is commonly said of certain Thoroughbred lines ; such cases are not due to prepotency, but if the crucial tests are made of finding out what kinds of females were selected to mate with him, and what happened to the half-brothers of the favourite sire in any generation, the most frequent and most satisfactory reason for the " sire line " appears in the severe selection used in each generation to decide which of the half-sibs will remain to be the next outstanding sire.

The effect of inbreeding in encouraging distinct " families " to drift apart in average characteristics can be of great practical use because selection based on a family is more accurate than selection based on individuals. The differences in performance between the distinct families resulting from inbreeding, there-fore, give better opportunities for picking out the different genotypes successfully ; and if the desirable characteristics are not all found within one family, then they can be brought together by making suitable crosses between families. To bring about the separation into distinct families, inbreeding must usually be carried out for some time, and must be con-sistent ; if the inbreeding is towards several ancestors, varia-bility will tend to persist. Also, where inbreeding has gone on for several generations, there is usually some deterioration, in practice, for the reasons given above. This can also be got rid of by a suitable cross with another family, but a result-ing improvement is not shown unless there has actually been a sufficient amount of prior inbreeding. Crosses between inbred families are forms of *outbreeding* (*see* pp. 68, 101).

Just as with relationship, a measure of inbreeding is useful, provided that it is clearly understood that the measure can only apply to the *average* condition of any pair, or combination, of genes. A satisfactory measure has been proposed by S. Wright (1922) and is founded upon the fact that inbreeding reduces heterozygosity. The " coefficient of inbreeding " of an individual is about half of the relationship which exists between its parents ; each parent may be highly inbred, but the offspring is not inbred unless its parents are related to each other (the offspring of an inbred Jersey mated to inbred Friesians are not inbred at all). If X represents the individual and A an ancestor common to both sire and dam, the formula for the coefficient (F_X) is $F_X = \Sigma[(\frac{1}{2})^{n+n^1+1}(1+F_A)]$, where n is the

number of generations from the sire of X back to A, n^1 the number from the dam to A, and F_A is the coefficient of inbreeding of A. As with the coefficient of relationship, all the ways in which the sire and dam are related to common ancestors are included in the sum. In practice it is unnecessary to go back for more than three or four generations to find A; if it is more remote than this, its contribution is likely to be immaterial.

The coefficient of inbreeding has several uses; one is in the analysis of the methods used in building up breeds (Chapter XIV). Others are in making an estimate of the results, good or bad, of a mating, when the worth of the common ancestor of the sire and dam is reasonably known, and in assessing, before an animal has actually been used for breeding, the possibility of it being prepotent.

The coefficient is not very convenient to determine under the ordinary systems of mating which are followed, as sire and dam may be related in many different ways to a common ancestor, and in small groups or herds the animals may also be related collaterally. Moreover, it is in the relatively small groups that a definite plan of inbreeding is frequently followed, either deliberately or of necessity, and once the relationship of the individuals within the group becomes complicated, the calculations are not straightforward. In small groups situations may be found like that shown in the following pedigree, which is based on an actual case in dogs (after Kelley, private communication; other cases in Kelley, 1942).

```
                                    ┌─ G
                          ┌─ D ─────┤
                          │         └─ I
                ┌─ B ─────┤
                │         └─ E   ┌─ G
        A ──────┤           ┌─ F ┤
                │           │    └─ H ──┐      ┌─ G
                │    ┌──────┤           └─ D ──┤
                └─ C ┤      └─ E              └─ I
                     │
                     └─
```
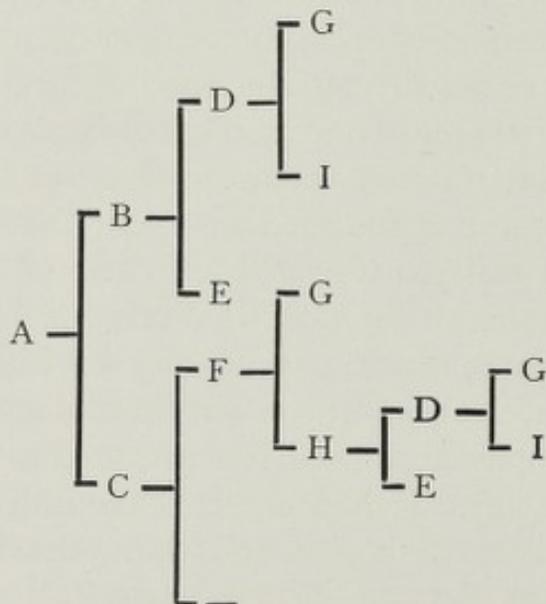
Here the bitch, H, was mated to her grandsire, G, and a granddaughter of this mating was in turn mated to a full brother, B, of the bitch H, thus there are several lines of descent from G to A; A is 3·1% inbred to G, but altogether is 9·4% inbred.

Very often it is useful to have an idea how the proportion of heterozygosis may change in a small group of animals kept isolated from the general run of the type, as for instance in a numerically small breed, whose herd book is closed, or in a flock to which no outside breeding stock is introduced (as occurs fairly commonly in Australian Merino flocks), or again in small herds of cattle where only a few sires, bred within the herd, are used. Lush (1937) has derived a simple formula to estimate for most practical purposes the loss of heterozygosity in each generation in such a group when mating is at random, but where of necessity some relationship between mates occurs. If M is the number of males in use, and F the number of females, the reduction in heterozygosity, due to the small numbers of the group, is roughly $\frac{1}{8M} + \frac{1}{8F}$. Actually, M or F should be the numbers whose offspring will attain breeding age in the group in every generation; these will fluctuate owing to a variety of causes. In any case, F is usually large compared to M, e.g. in sheep, M is usually 2-2½% of F, so that the contribution due to $\frac{1}{8F}$ can be neglected for ordinary purposes.

This formula can be applied as follows: the Polwarth breed of sheep in Australia is a numerically small one. In 1930 twenty-eight stud flocks (out of thirty-two) stated the numbers of rams used and the numbers of ewes put to the ram. The totals were 531 rams and 25,918 ewes. If the breed were kept at such a size by culling on a basis of selective registration and with a closed flock book, the reduction in heterozygosity would only amount to $\frac{1}{8 \times 531}$ or 0·024% per generation; or allowing four years per generation, probably conservative, it would take over 160 years to bring about 1% of inbreeding with such numbers. A certain amount of

inbreeding would almost certainly be carried out in practice, but if it were strictly and deliberately avoided, the rate would be still further reduced by about a half. On the other hand, certain flocks rigidly exclude the purchase of breeding stock, but even in a flock where twenty-five homebred rams were used, the loss of heterozygosity for this reason alone would only be about $\dfrac{1}{8 \times 25}$ or 0·5% per generation, or with five homebred rams 2·5%. As yet there is no definite evidence as to the amount of inbreeding which can be sustained over a number of generations without some disadvantages cropping up, but it is suggested that somewhere about 5% is generally safe. This would certainly imply that in such a breed as the Polwarth, which incidentally has an open flock book, there would be no danger from the amount of inbreeding that would result from the smallness of numbers. (Also, in relation to the fears expressed that severe restriction of sires under any system of artificial insemination in a breed or part of a breed would lead to high inbreeding, this point deserves attention ; it is most unlikely that the restriction would ever be so great as to result in a dangerous level of inbreeding throughout the breed.)

However, some further selection, other than that of restricting the males used on account of numbers, is usually applied ; particular sires may be favoured because of show-ring performance or of successful breeding history, etc. This leads to a further reduction in M, and so tends to increase the loss of heterozygosity. Also, inbreeding towards favoured sires or dams tends to increase the rate, though not so much as might be expected, since the direction and degree of this extra selection and inbreeding would not always be the same for every breeder or in every flock. Unless the ideal sought were relatively simple, as for instance in mutton conformation, and were accepted completely by all breeders, there would be a tendency for the different forms of selection to cancel each other throughout the breed. Several studies which have been made on various breeds suggest that the general increase in homozygosity because of inbreeding is about 0·5% per generation.

Altogether, the breeder has two tools available to alter gene

frequency and gene distribution towards homozygosity in his stock—selection and inbreeding. In practice neither tool is used to the exclusion of the other, but the effects differ. Selection in itself has only an indirect influence in bringing about homozygosity, through its effect in altering gene frequency ; this effect is only slowly manifested, many generations being required to produce a significant change unless the character is due to only very few genes and is one to which selection can be heavily applied. Where the character is due to one or a few recessive genes which are relatively rare, the quickest way to increase the frequency of the desirable—with culling of the undesirable—genes is to inbreed. In this situation, if the character concerned is not much affected by environment, the inbreeding can be between close relatives, with selection based on the progenies, and extensive strains need not be developed. If, however, the character is one which shows wide variation due to environment, it is better to develop separate inbred strains, which need be only temporarily kept distinct by inbreeding, and base selection on the average performance of the strains.

Many production characters are, however, probably due to more complicated interactions of gene series, and where the desirable form involves a combination of genetic effects, the situation is quite different. Here the approach is to select different strains, each sufficiently numerous to allow selection within it. When the strains have become widely separated with the aid of inbreeding, the inferior ones can either be discarded or graded up by outbreeding (Chapter X) and the better strains used for interbreeding to find those that *nick* together to give the most desirable combinations, which in turn can be made the basis for new strains. That is, direct selection first, followed by inbreeding, selecting, and then interbreeding the inbred strains (Wright, S., 1939).

While mild forms of this latter method are sometimes adopted, it seems most probable that breeders are generally not taking sufficient advantage of this effect of inbreeding in giving rise to distinct strains. The inbreeding practised is probably more often for other reasons and is not taken far enough to establish separate strains before an outcross is made. An outcross is made before it is really necessary, in the belief

that inbreeding has already proceeded too far, and certainly well before the strain has been enabled, by the amount of inbreeding used, to attain anything approaching the genetic stability possible or desirable.

Appendix to Chapter IX

Inbreeding among the ancestors affects the question of genetic relationship among descendants ; as inbreeding increases homozygosity, the more inbred an animal is, the greater the chances that its descendants will have genes which are duplicates rather than alleles. For this reason the coefficient of relationship given on p. 82 must be corrected to allow for the extent to which the common ancestor is inbred, *i.e.* has lost heterozygosity compared with other animals of the breed. The corrected formula is

$$R_{XY} = \frac{\Sigma[(\tfrac{1}{2})^{n+n^{1}}(1+F_{A})]}{\sqrt{1+F_{X}}\sqrt{1+F_{Y}}}$$

where F_{A}, F_{X}, F_{Y} are the coefficients of inbreeding of A, X, and Y, respectively. The factor $\sqrt{1+F_{X}}\sqrt{1+F_{Y}}$ corrects for inbreeding tending to increase the variability in the population, unless both X and Y are in the same inbred strain. Uncorrected in this way, the coefficient is an index of the proportion of genes in X and Y likely to have come from the common ancestor ; with these corrections it becomes an estimate of the extent to which the genotypes of X and Y are probably the same. If two animals, say B and C, were directly related only, B being a descendant of C, the formula for

their relationship becomes $R_{BC} = \Sigma(\tfrac{1}{2})^{n}\sqrt{\dfrac{1+F_{C}}{1+F_{B}}}$; $(\tfrac{1}{2})^{n}$ is the

" percentage of blood ", so that it is only when the two animals are equally inbred that relationship is expressed by " percentage of blood ". But the difference between F_{C} and F_{B} is usually not great, hence " percentage of blood " is ordinarily a measure of relationship provided that the animals are directly related, without any collateral relationship (*cf.* p. 81). However, little error is introduced by neglecting $\sqrt{1+F_{X}}\sqrt{1+F_{Y}}$ in the formula, and, except when both sire and dam are much

inbred, it is enough for most purposes to say that an animal is inbred about half the extent of its parents' relationship.

In studies of breed history it is obvious that a great deal of computation would be necessary if the full pedigrees of animals were considered; it has been shown that tracing pedigrees from sample animals back to foundation animals by way of randomly selected parents gives sufficiently accurate results (McPhee and Wright, 1925, 1926). When inbreeding percentages for breeds are given in later chapters, the values have usually been determined by this means.

CHAPTER X

GENETIC ASPECTS. (3) LINEBREEDING

THE outstanding consideration in inbreeding is that the animals to be mated are close relations. Linebreeding differs from inbreeding mainly in degree so far as relationship is concerned, but the greater freedom of choice among ancestors and collateral relatives allows also a greater opportunity of exerting selection for other characters than pedigree alone. Hence it has distinct advantages over inbreeding for some purposes. The object of linebreeding is to keep the offspring more or less closely related to a particular ancestor which had the desired characteristics ; it involves a certain amount of selection among ancestors and at the same time permits more selection among the offspring, since greater numbers can be considered, except when a small group, herd or flock, is the breeding unit.

As the near-relationship criterion is not so important as it is in inbreeding, the breeder should have a clearly defined aim to substitute as his main basis for selection. For linebreeding to an ancestor it is essential that he or she should have left many offspring, otherwise the linebreeding will soon reach a stage when it is not in effect to the chosen ancestor but to one or other of its descendants, *i.e.* it becomes secondary linebreeding. If limitations of numbers of available offspring, or lack of success in finding the suitable characterisation among them, prevent linebreeding to the chosen ancestor, an outcross is necessary and the advantages due to linebreeding will thus of course be lost. For these reasons it is difficult but not impossible to linebreed satisfactorily in a small group ; Lush (1934) has described a herd of Beef Shorthorns in which linebreeding to a bull, his son, and his grandson was practised successfully for twenty years, with the members of the herd becoming in effect full sibs. On the other hand, the number of relatives of the chosen ancestor can be increased by linebreeding to it, and hence the field for selection widened, so that it can be readily followed in a community or association of groups.

Obviously, among the possible ancestors only those will be chosen as pre-eminent that have left some desirable offspring, so that linebreeding is a system which selects among ancestors those which are progeny-tested.

Its effects upon homozygosity and on prepotency are essentially similar to those of inbreeding, though not so rapidly attained; the slower progress, however, is more likely to incorporate also generally desirable characters. Linebreeding thus gives the best practical combination of inbreeding and selection and should be used as a mating system whenever animals with superior characteristics, and also good breeding results, have appeared. If their descendants are not kept in close genetic relationship to them, by linebreeding, then their influences will be halved at each generation of mating to unrelated animals, and in a few generations so distributed among many animals as to be negligible. But if the descendants are linebred so as to make their genetic relationship to a chosen ancestor high, the effect is to draw together again the influence of that ancestor.

Like inbreeding, linebreeding tends to set up separate families and to isolate them from the rest of the breed, and as it gives scope for selection for production characters, it is particularly suited to those situations where the more complicated gene interactions are involved. For instance, there are practical difficulties in combining good beef qualities with draft capabilities among the cattle in those parts of the world where this is the dual-purpose aim; yet, as Pontecorvo (1939) has pointed out, individual animals which actually combine high performance in both respects *do* exist, so that the desired combination is physiologically possible. Where such desirable combinations do occur, the chances of regaining them in the stock are increased by linebreeding to them, and only by linebreeding. Moreover, because linebreeding of necessity involves selection for characteristics, and not just for pedigree, the two processes help each other. The selection as such becomes more effective in leading to progress, in addition to merely holding the progress gained. In terms of " peaks of desirability ", selection itself cannot achieve much in moving gene constitution from one peak towards another, but combined with linebreeding, the two together can move the effect of selection on from one to another peak.

G

Many of the above effects of a linebreeding system and selection are well illustrated in a herd of Holmogor cattle, described by Messing (1940). This was descended from a small group which had been bred for a long time on the Solovetsky Islands; and in the years 1933-38 the average milk yield had increased from 3922 kg. to 4513 kg. (about 8646 lb. to 9949 lb.), the average butter-fat content from 3·29% to 3·44%, and at the same time the average body weight had increased to 580·6 kg. from 532·7 kg. (to about 1279 lb. from 1174 lb.). But the breeding system had involved the use of few sires and heavy culling, so that distinct lines had been set up, the chief factor in establishing them being uniformity of quality or genotype, not the particular ancestry. The lines differed in milk yield, in fat content, and also in body weight; branches of the same line also differed in these respects. Messing points out that under such circumstances it is not necessary to aim at homozygosity; if the desired combination of traits is due to heterozygosity, then the aim of linebreeding and heavy culling will be to retain and hold it. In this herd three lines were more important than the rest; one-quarter (25%) of the animals belonged to one of these three lines, 27% were derived from triple crosses among them, 31% from crosses between two lines, and more than 10% were animals bred by crossing another two of these lines; the remainder of the herd belonged to other less important lines. Linebreeding to two of the foundation sires had been carried out so that one bull occurred in 70% of the pedigrees and the other in 77·3%.

It will have been noticed that the groups of animals separated from the rest of the breed by inbreeding and linebreeding have been referred to as " strains " or " lines ", while in relation to assessing genetic effects the term " family " was used. It must be emphasised that these terms have genetic implications; the same terms are often used by breeders in such ways as to have very little, if any, genetical significance at all. The distinctions in use and meaning are best appreciated if the question of genetic relationship is borne in mind. In a broad sense, all members of a breed which is descended from a relatively few ancestors must be related in some way, but as the common ancestors become more and more remote, their

genetic influence upon their descendants must average less and less, and in fact is almost insignificant at three or four removes of generations. Only if there has been inbreeding or linebreeding, which keep genetic relationship high and increase the chances of similarity in genotype, can the genetic influence of an ancestor be considered of much account; such groups are best called " strains " or " lines ".

" Family " can be used to describe two different kinds of groups, both of which have high average genetic relationships, *i.e.* high as compared with the average condition among the rest of the breed or major group. These are: (1) A group of close relatives in which there has been no or little inbreeding, such as the ordinary human family, but preferably covering only parents, sibs, half-sibs, cousins, grandparents and grand-children, and not extending beyond great-grandparents and great-grandchildren. This kind of family surrounding an individual has a definite use in enabling hereditary worth to be estimated, particularly in connection with characteristics which are greatly affected by environmental conditions. Selection in respect of such traits can be inaccurate when based only on individual appearance or performance, unless their expressions in the animal's close relatives are also taken into account. (2) A group in which linebreeding, with selection, has been practised to a sufficient extent to separate the group from the rest of the breed. This kind of family has a relatively high genetic relationship but can sometimes be numerically large and, in effect, amount to a sub-breed. In this sense the term could probably be justifiably applied to such " types " as the Scotch Shorthorn, as compared with the Shorthorn breed, or to some of the stud types of Merino sheep in Australia, especially those which have been kept quite distinct in ancestry from the rest of the breeding studs. Moreover, in such cases members of the same family have frequently an enhanced cash value, in so far as the particular family genotype and performance may justify a discrimination in capital value, because they are genetically related.

On the other hand, " family " has no special genetical significance as commonly used, when based only on a family name which may trace back either along the dams or, less frequently, back through the sires. Here there may be a

purely speculative value attached to the name, but this has only a very slight basis unless the original holder of the family name is not more than three or four generations away (when its average contribution will be 12·5% or 6·25%, and halving at each remove). Sometimes the speculative value may be enhanced, as when the number of females entitled to this kind of family name is small ; the rarity factor, however, may even then be due to undesirable traits, such as low fertility. But occasionally the favour of a family name has encouraged breeders to undertake some linebreeding, using fairly closely related sires on females with the family name ; when this has happened, it is the linebreeding that confers some additional worth.

Another distinction must also be made. There is no general connection between what is commonly covered by the term " blood line " and the genetic meanings of strain, family, or line. In fact, " blood line " may have different meanings in different contexts. In some, it may be useful if it refers to a specific concept, such as when it is used in the sense of either kind of family ; but even here it does not usually imply close genetic relationship. In others, it is too indefinite to have any real significance, as when it includes distant ancestors in any consideration of pedigree. It can be grossly misleading when it suggests some degree, usually a high one, of prepotency. In this last connection it is often used with reference to the so-called " outstanding sire lines ", and completely neglects the fact that prepotency is a property of characteristics, not of individual animals (p. 87). However, " blood line " is sometimes a convenient term to convey a general picture of ancestry, provided that the persons using it are familiar with the ancestry concerned and the mating systems followed, and are prepared to give a pinch of genetic salt to any conclusions drawn from it.

CHAPTER XI

OUTBREEDING AND HYBRID VIGOUR

MATING systems which are based on unrelated animals, *i.e.* less closely related than the average, are more commonly used than inbreeding or linebreeding. They can be considered as various forms of *outbreeding*, although in many cases the original outbreeding is followed by a certain amount of subsequent in- or linebreeding. In relation to terminology, an *outcross* can be regarded as outbreeding, but with the direct implication that after one or a few outcrosses some form of linebreeding will be resumed. In this sense the term has been used in earlier chapters, and it obviously applies to matings within a breed, between animals of different strains or lines. Where an outcross to another line has been made, this is frequently called a " topcross ".

Outbreeding also involves mating within the breed, but with no intention to return to systematic breeding towards a particular level of genetic similarity. When animals of different breeds, and hence with major differences in genotypes, are bred together, the mating is a *cross*. In terms of genetic relationship, therefore, the systems of outbreeding, and crossing, bring together representatives of increasingly wider genotypes. Also, outbreeding cannot strictly occur unless there has been some prior separation of genetic lines, either by inbreeding, or linebreeding with selection, or else by long-continued isolation acting as a form of selection.

The effect of outbreeding is to increase the heterozygosity of the individual offspring. As it tends to make all the offspring on the average heterozygous for the genes of their parents and, when used among large numbers of mates, to spread this average heterozygosity throughout the offspring, a secondary effect is thereby to increase the uniformity of the breed. In marked contrast to inbreeding, there is no separation of different genetic lines ; if outbreeding is continued as a general policy throughout the breed, the increased heterozygosis and the initial greater uniformity will only be held. Some selection

will no doubt be brought into play, but in the first generation of outbreeding about half of what may have been previously gained by selection will be lost. Similarly, because of the increased average heterozygosity the breeding value of the individuals will tend to be reduced, owing to segregation and genetic variation in their offspring, and any prepotency for a particular character will be lost. But the system has a definite practical value in providing starting-points for future inbreeding, or linebreeding, and selection, in that it brings about fresh combinations of genes—this is the advantage in an occasional and judicious outcross. For the same reason, largely, the system increases individual merit or performance, since genes favourable to production are generally dominant to those which are less favourable. It thus lends itself well to the production of good commercial animals or to outstanding individuals.

Whatever the characters concerned, the performance of outstanding animals in a breed must be carefully examined in relation to their probable genotypes. Such animals can arise in two different ways : either as a result of inbreeding tending to segregate out highly desirable gene combinations, or from outcrosses which combine favourable genes from two or more lines. The former will have prepotency and high breeding worth from their homozygosity ; the latter will not, although their descendants, if inbred or linebred to them, will tend to repeat their performances. Consideration of the animals' pedigrees will provide a reasonable clue to the situation, so long as their ancestors' performance is also known. Also, it is necessary to examine the reasons for breed uniformity in the same light, since a breed or sub-breed can either be kept at a high degree of uniformity by a general adoption of mating unrelated animals on the one hand, or attain this end as a result of prolonged inbreeding plus rigorous selection. In most of our breeds the reason for such uniformity as exists is probably due to the former cause rather than to the latter. Moreover, the early breeders could probably choose from a wider range of genotypes than later breeders who have a relatively restricted field of choice imposed by the pedigree system.

The possible and probable effects of inbreeding as well as of outbreeding have to be taken into account in examining the

practical results which ensue from the latter, otherwise apparently confusing interpretations can be drawn from the many comparisons which have been made. Willham and Craft (1939) studied reproductive capacity and growth rate in a herd of pigs including two lines of sows, one outbred and the other inbred for eight generations so that the average percentage of inbreeding increased from 15·6% to 45·6%.[1] The inbred sows farrowed fewer and smaller young than the outbreds, and they weaned on the average 3·1 pigs, each weighing 23·8 lb. at 60 days, compared with 5·4 of 26·7 lb. The better growth of the outbreds continued after weaning, although after 180 days the inbreds improved relative to the outbreds ; when mature, the inbreds were shorter and thicker than the outbreds, and in maturing had been less efficient in utilising their rations. In regularity and length of breeding life, the inbred sows were as good as the outbreds, but owing to their lower reproductive rate it was more difficult to select breeding stock among them. Generally, therefore, the inbred were inferior to the outbred sows ; also the boars of the inbred line did not produce more uniform or such quickly growing offspring when outcrossed as did the outbred boars. Although in these experiments inbreeding had distinctly disadvantageous results, yet the conclusion was drawn that this was due to gene combinations with unfavourable effects having been concentrated in the few generations of inbreeding. A broadly similar set of results from inbreeding, but with different outcome when the inbred animals were outcrossed, was observed by Kolesnik (1939) in a large group of cattle of the Yaroslavl breed. Among the inbred animals in the group there were a larger proportion of calves with low birth weights, which therefore were of inferior vitality, but, within the same group, there were wide differences in birth weight, some bulls tending to sire heavier, others lighter calves than the average. Moreover, some of these bulls when outcrossed sired much heavier calves than those from other outbred matings. The daughters of one cow produced light weight calves by one bull, which begot heavy calves from other cows, yet these daughters gave heavy calves by other bulls. The results in respect of live weight at birth

[1] This use of the term "lines" is justified, *cf.* p. 99, as the two groups had been separated in respect of the mating systems followed.

were therefore affected by the particular outcross made and could not be consistently regarded as disadvantageous due to inbreeding. Further, there were little differences in adult live weight, milk yield, or fertility between the inbred and the outbred cows.

When outbreeding or crossbreeding occur, the offspring of the first generation are heterozygous for more genes than either parental stock, and, in so far as the more favourable genes are dominant over the less favourable, a greater array of dominance is set up, with individual dominants coming from both parental stocks, so that the F_1 hybrids tend to exhibit what is known as " *hybrid vigour* ", or " *heterosis* ". This is commonly shown in hybrid plant stocks, and is frequently thought to occur widely in outbred or crossbred animals; that is, that the hybrids have an enhanced capacity for performance due to the fact that they are hybrids, with the associated heterozygosity. When the hybrids are interbred, this heterosis tends to be diminished owing to the segregation of gene effects in the F_2 generation, which is also responsible for the greater variability of the F_2 compared with the F_1. Where hybrid vigour exists, it appertains essentially to the first hybrid generation; the good results in commercial crossbreeding are often attributed largely to this effect, and on it also rests part of the argument for continuous crossing. Yet, in animal breeding, the part which heterosis can play in enlarging the individual merit of the outbred or crossbred stock must be accepted with some reserve, for various reasons.

Lush (1937) concludes that heterosis is not likely to contribute in physiological characters more than about 2% to 8% increase above the average of the parental breeds. If these are widely separated in performance, then that of the hybrids will not approach closely the standard of the better parental type, although it will greatly exceed that of the inferior parent. This is probably most frequently seen in commercial sheepbreeding, especially where range types, *e.g.* the Merino, are crossed with mutton breeds, as in Bonsma's experiments (*see* p. 59). And if the lines mated are within a breed, an increase of this order is not likely to be very obvious, though sufficient, other things being equal, to give some outstanding

animals compared with the average of the breed, or their parents. Also it is conceivable that heterosis may be more readily expressed in such characters as hardiness which in themselves have not received so much attention in some classes or breeds of stock, where productive characters like milk yield or racing ability are the major aims.

The last consideration is possibly the significant one in the mule, the result of mating two widely different genotypes; this animal has distinct advantages over the horse and the ass for special purposes, but it is worth remarking that these special purposes occupy a particular environmental niche in the sense that the mule attains its best use and performance under conditions which are not optimal for either the horse or the ass. The work of Kušner (1938) and Patrušev (1938) demonstrates that mules are definitely superior to the parental species in various blood characters, especially in the capacity of the haemoglobin to function, in which the mule is 10·5% higher than the horse and 13·5% higher than the ass. This indicates a physiological basis for the mule's endurance and relative resistance to environmental factors such as temperature, when compared with its parents.

In the comparison between parental and F_1 performances, the conditions under which they are made, or for and in which the parental forms have been selected and bred, cannot be properly excluded, although these factors are often overlooked in claiming a clear-cut hybrid vigour effect. For example, Asmundson (1942) studied heterosis as shown in the growth rates of turkeys during their first thirty-two weeks, using crosses between the Black and two other small and two large varieties. All the crossbreds showed growth heterosis for the first four weeks, and the females up to eight weeks; later the purebreds grew faster than the crosses. The offspring of the Black and the other small varieties (Bourbon Red and Lilac) surpassed both their parents, particularly after eight weeks of age, and those of the Black × larger varieties (White and Black-winged Bronze) matings exceeded the growth rate of the Black parents; but the latter group, small × large, were not significantly different from the large group in weight throughout. Thus, while it could be said that " heterosis " was shown by the hybrids from small parental types when

compared with their parents, there was none in the small × large hybrids compared with the large parents.

Until more is known of the genetic situations affecting broadly similar physiological characters in the different species, it is also unsafe to generalise regarding possible heterosis effects. A comprehensive study of poultry growth involving Barred Plymouth Rocks, New Hampshires, and crossbreds of the two breeds (Hess, Byerly and Jull, 1941) showed that the crossbreds were generally more efficient in using their food intake for growth and flesh production than were the purebreds, but the valuable point emerged that a cock which produced efficient progeny in purebred matings tended also to produce efficient progeny when crossed on hens of the other breed. At the same time, detailed comparison carried out by Phillips and his collaborators (1942) of purebred Hereford steers and those from Hereford cows by Shorthorn bulls showed no significant superiority of the crossbreds in efficiency of weight gain, although they were markedly better in weight at birth, carcass weight, dressing percentage, and actual gain while being fed for finishing. The purebreds were better than the crosses in respect of grades at slaughter and of carcass, but not significantly so, while the crossbreds were more uniform than the purebreds.

Johansson (1939) has suggested an interesting indication of heterosis in regard to milk yield in his studies on dairy cattle in Sweden. From just prior to the end of the nineteenth century, the Swedish Ayrshire and the Red and White Swedish breeds, originating in crosses of imported Ayrshires and Shorthorns, respectively, on native types, began to be bred with the same objectives ; in 1928 the two were amalgamated in the " Swedish Red and White " breed (S.R.B.), and, in the amalgam, bulls of Red and White Swedish (R.S.B.) lines of descent have been favoured. The Ayrshires are rather smaller than R.S.B., F_1 hybrid cows of the two types are intermediate in size ; F_1 bulls are nearly the same size as R.S.B. In milk production the Ayrshire, R.S.B. and F_1 stock compare as follows : milk yield 100, 102·8, 107·5 ; butter-fat content (%) 100, 96·6, 99·3 ; and butter-fat yield 100, 100, 105·4.

Comparisons of this sort obviously exclude possible environmental effects in the sense that each group must contain animals

kept under a fairly wide range of conditions. Allowance must therefore still be made for the possibility that the different levels of performance may also, in part, express different interactions of genotypes and environments. Much further work needs to be done before the question of how far responses to environment may affect heterosis in animals can be answered with any certainty. That environmental effects are involved can be deduced from general observations, and in this connection some recent Russian work may also be suggestive. Lebedev (1940) concludes that an adaptational effect is necessary to explain the observation, made at the Uzbekistan Institute of Sheep Breeding, that where ewes are mated to rams imported into the flock, their progeny in the first year is usually superior in birth weight to later progeny. The suggestion is that the dissimilar environments in which the parental stocks have been reared tend to reduce the effects of genetic similarity so that at first the matings are equivalent to outbreeding, while later, with the parents kept under the one set of conditions, their genetic similarity is more fully expressed and a depressive influence, as in inbreeding, is manifest in their offspring. Further, Lebedev advances experimental evidence from inbred and outbred strains of rabbits, in which the results of mating males bred under the same conditions as the females were compared with those where the males were raised in separate environments ; in all the inbred and outbred stocks the litters from similarly raised parents were inferior to those from differently raised parents. He infers that heterosis may be produced in the one inbred strain if the parents have been kept under different management, but until these results are confirmed it would be unwise to draw the practical conclusion that some of the disadvantages that can accrue from inbreeding can be sidestepped by the simple device of keeping the related parents under different conditions. As yet such a direct environmental influence is not established ; these phenomena can be interpreted equally well on the grounds that even within a generally inbred stock differences in environmental conditions can give rise to sufficiently wide variations in characterisation to allow scope for selection of mates on other points than genetic relationship, and so lead to the mating of dissimilar genotypes within the one inbred strain.

On the whole, it can be said that wherever anything of a heterosis effect is seen, there is evidence that the parental stocks do not carry *all* the favourable gene combinations, but that some of the genes require a milieu different to that provided by either parent for their optimum or maximum expression. Again, the practical problem resolves itself into finding the most suitable milieu, whether genetic to fit the environmental or environmental to fit the genetic. The former alternative is frequently met in practice by appropriate crossbreeding, mating purebred animals of different breeds, and more could no doubt be done by appropriate outbreeding of strains within breeds.

This form of commercial breeding to enhance individual merit amounts, when continued, to using a kind of " controlled heterosis " to produce the desired traits from breeds or strains each possessed of some of them, and to gain afresh in each generation whatever may be due to the heterozygosity of the F_1 individuals. Anything due to heterosis will be lost on interbreeding the hybrids, and the F_2 will also be more variable than the F_1. This variation in F_2 may even extend over the whole range shown by the parental types taken together, as, for example, in the F_2 obtained by interbreeding Scotch Halfbred sheep (Border Leicester × Cheviot), where individuals predominantly Border Leicester in characters emerge, as well as those of Cheviot type (Nichols, 1925, 1933). In many cases, however, the range of variation in F_2 is not evenly around the strictly intermediate form, but tends to swing towards one of the parent types ; thus the F_2 of the Halfbred is not intermediate between the Border Leicester and the Cheviot, but is distributed more towards the Border Leicester type. The distribution curve is not normal but is " skewed " in one direction, in this case towards the grandsire's breed. This cannot be attributed to any virtue of the male side of the pedigree as such, but is explicable on the grounds that, again in this case, the Border Leicester as a breed has been more carefully bred and selected, and is therefore relatively more homozygous for many of the genes involved in the cross, so that the frequency of the genes in the F_1 is biassed towards that of the more homozygous parental breed, and in the F_2 the chances are greater of securing gene combinations which tend to recapitulate that parental genotype. Figs. 10 and 11
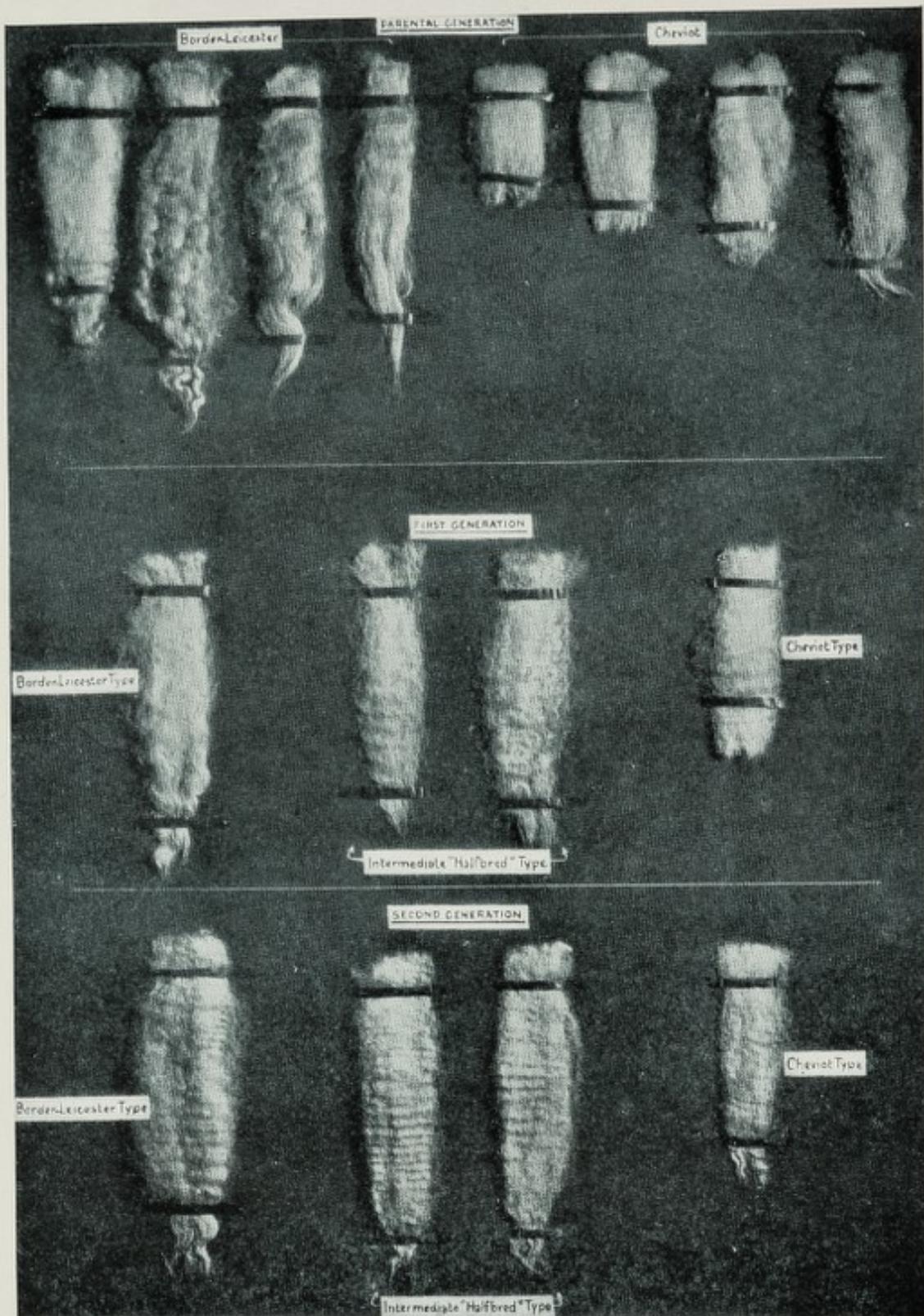
FIG. 10.—Shoulder samples indicating range of wool types in parental, F_1 " Half-bred ", and F_2 generations. *From* Nichols, 1933—*J. Agric. Science.*
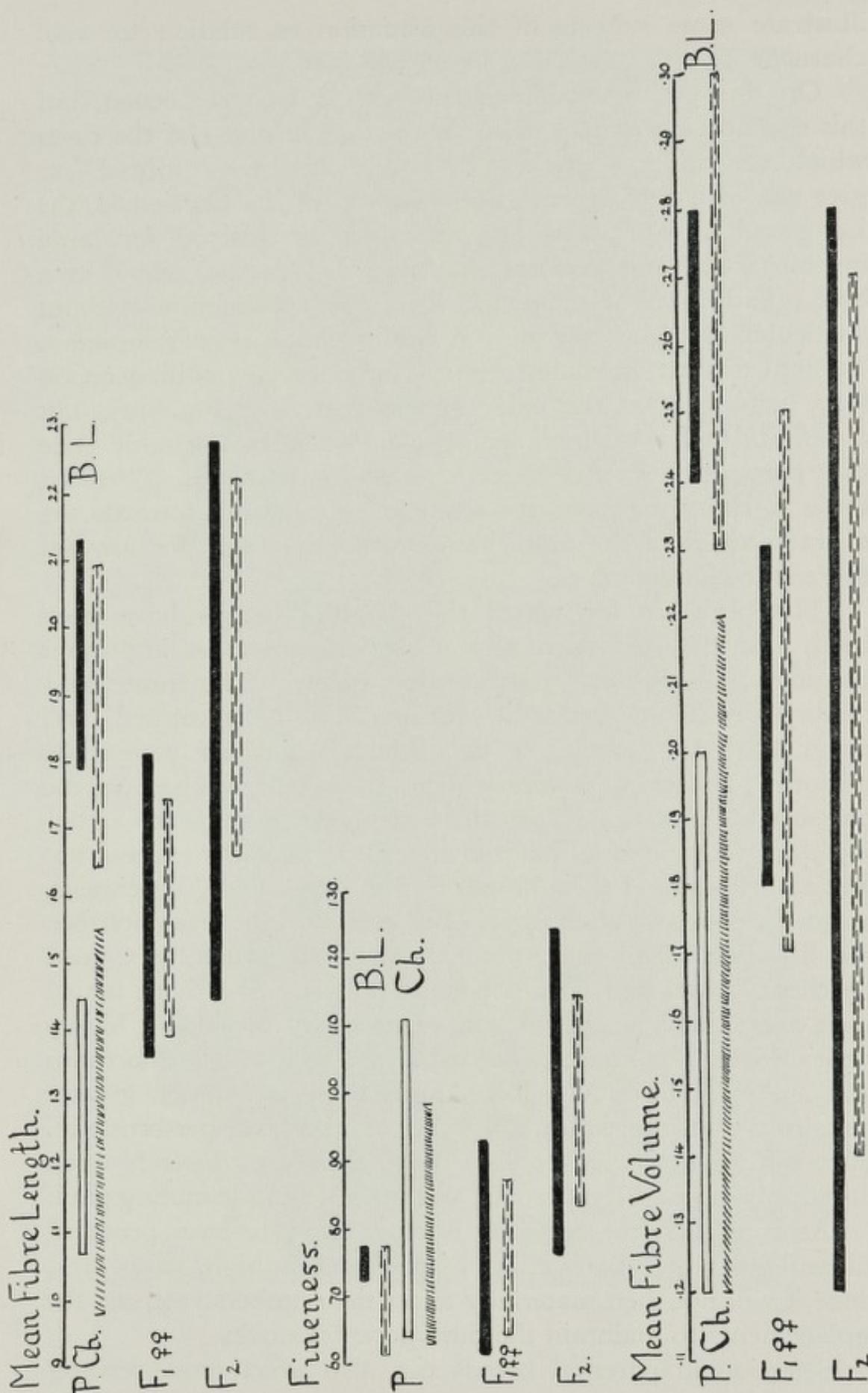
FIG. 11.—The ranges of variation of fibre characters in parental Border Leicester and Cheviot, F_1 "Halfbred", and F_2 animals. Shoulder samples above, britch below, for each type. *From* Nichols, 1933—*J. Agric. Science.*

illustrate some aspects of this situation in relation to wool characters.

On this point also much further research is needed, but this explanation is reasonable in relation to many of the cases which are found, where a hybrid form has been " inbred " to give rise to a new breed. For instance, in the Corriedale, the Longwool ancestry was one more highly selected for large mutton frame and performance than the Merino, which as a breed had been selected for fine wool production without particular emphasis on mutton conformation or development. To hold the intermediate form not only is heavy culling necessary, especially in the early generations, (*see* Fig. 12), but a definite policy of linebreeding would also be desirable once the particular intermediate objective is defined. Without these working together, the tendency is to swing towards the characteristics of the more homozygous condition for any set of genetic characters.

The purposes for which the parental breeds have been bred, and the success in that direction, are most important considerations in any crossbreeding policy. The most satisfactory result, so far as its repeatability is concerned, will come from the crossing of two breeds which are genetically uniform for the characters which are to be combined in the crossbreds. For this reason there are good grounds for asserting that the individual parents should be carefully chosen, not just as members of their breeds but as " wellbred " specimens, of good geno- and phenotype. Because, say, the cross between the Shorthorn and the Aberdeen-Angus is generally a good butcher's beast, that does not mean that any Shorthorn mated with any Aberdeen-Angus will of necessity produce a highly desirable beef animal ; but with a " wellbred " Shorthorn and a " wellbred " Aberdeen-Angus there is a much greater certainty that the hybrid will be of excellent performance. Successful continuous crossbreeding, therefore, depends upon the supply of purebred parents, and upon a definite mating plan.

As a policy, crossbreeding is most likely to have practical advantages where the fertility of the stock is high, as in pigs, since it will not then materially affect the numbers required for replacements to maintain the pure parental stocks.

Selection in parental breeds can also affect crossbreeding

Fig. 12.—A group of F₁ and F₂ animals from English Leicester × Merino, showing variation.

as a policy in a negative way, tending to eliminate it as a practical proposition, if a definite market demand has set up a common form of production. This is well illustrated in Sweden, where formerly crossing the Large White pig and the Swedish Landrace was a common procedure to get a utility pig. However, the development of pig recording and testing, with the objective of improving bacon production, has given the two breeds the same aim, and crossing has lost favour. The first impetus has been to selection on performance, *i.e.* phenotypic selection, so that while the two breeds have similar bacon characteristics, there may still remain a certain genotypic difference between them, hence Large White × Landrace crossbreds may still have a certain advantage in the strength, vigour, and growth rate of the young pigs.

While interbreeding hybrids, as a commercial proposition, is generally unsatisfactory because of the greater variation in F_2, there are many cases where the crossbred female is successful as a dam. In pigs, the early growth of the litter is greatly influenced by the mothering ability and milk yield of the dam, more than by the genetic constitution of the young themselves ; the same applies in sheep for lamb production. Quite apart from any question of adaptation to particular practical conditions, the crossbred dam allows advantage to be taken of any heterosis for these characters, either by backcrossing to one of the parental breeds or by mating to a male of a third breed, as in second and higher crossing. That is, there is an initial advantage in making the original cross, followed by a subsequent backcross or triple cross. With a backcross, some of the heterosis effect will be lost ; with a second or triple cross, heterosis will be retained and possibly augmented.

Under certain circumstances, mainly where there is a good market outlet for different classes of the same general product, continuous crossbreeding to produce the F_1 hybrid gives place to a system of *crisscrossing*. An outstanding example of this is in the " comeback " type of sheep in Australia, some flocks of which are still maintained by utilising sires of the parental breeds alternately. The effect, however, is not to establish an intermediate type, but after a few generations to set up a flock in which two distinct forms are maintained, each with a high degree of uniformity.

The system adopted in a well-known " comeback " flock in Victoria is essentially as follows : good fine-wooled Merino ewes were mated to specially selected Lincoln rams, the F_1 females backcrossed to Merino rams to produce a " comeback " with a fleece of about 58s-60s quality ; the ewes of this cross were mated to Lincoln rams of 36s fleece, giving " second cross " offspring with 46s-56s fleece, which were in turn mated back to Merino rams of 64s-70s fleece. The scheme can be shown diagrammatically as :

Parents	Lincoln ♂ × Merino ♀	Type
Generation 1.	$\dfrac{L \cdot M}{2}$ × M ♂	Halfbred
2.	L ♂ × $\dfrac{L \cdot 3M}{4}$	Comeback
3.	$\dfrac{5L \cdot 3M}{8}$ × M ♂	2nd Cross
4.	L ♂ × $\dfrac{5L \cdot 11M}{16}$	Comeback
5.	$\dfrac{21L \cdot 11M}{32}$ × M ♂	2nd Cross
6.	L ♂ × $\dfrac{21L \cdot 43M}{64}$	Comeback

etc.

The flock includes about 10,000 breeding ewes, of which about half are " second cross " and half " comeback " ; culling amounts to about 33% of the ewe crop in each generation and there is a good market for both types of surplus stock. The project is mainly for wool production and the careful selection of rams and culling of ewes enables the main wool lines to be held at a high level of uniformity. It must be noted that at about the fourth generation the comeback type approached a composition of one-third Lincoln to two-thirds Merino ; the next Lincoln cross brought this to nearly two-thirds Lincoln

to one-third Merino. Continuous crisscrossing stabilises these two ratios, with the result that the production of the " comeback " part of the flock is no longer equivalent to that of the usual three-quarter Merino " comeback " which when inbred is the Polwarth. Also, the products are clearly distinguishable from those of the other commercial cross of the two parental breeds, the halfbred.

Crisscrossing as a definite policy for combining the commercial qualities of two breeds and sustaining any advantages from heterosis could probably be adopted under many practical circumstances. For example, in Sweden a crisscross of Large White and Swedish Landrace pigs would appear to offer distinct possibilities for utilising any advantages of the crossbred sow for mothering ability and milk yield ; in this case, as the parental types have already been made closely similar for productive characteristics, the system would allow more scope for higher fertility and greater early growth. Another direction in which crisscrossing could be used is in relation to the choice of a suitable crossbred type for commercial use, for comparing with the ordinary first cross or halfbred types, as it can provide at various stages, three-quarter, quarter, two-thirds and one-third types, according to how the first backcross is made and how long crisscrossing is continued.

Another breeding system which can be considered as a form of outbreeding in its early stages is *grading*, though after a few generations this becomes more like a system of inbreeding to a type. Grading is directed towards the improvement of common or " breedless " stocks by continued mating to purebred sires, but should only be admissible when the superiority of the chosen pedigree stock is clearly established. When the productive merit of the purebred is definitely higher than that of the commercial stock, grading quickly brings the level of the latter up towards that of the former. (*See* Fig. 13.)

Some pedigree breed societies, with " open " books, admit grades to registration after some generations of topcrosses to registered stock. This policy has some advantages, from the genetic point of view, probably not envisaged by many who support it as a means of increasing the numbers and popularity of their favoured breed ; it allows the introduction into the breed of additional genes and thus contributes to the available

H

$\frac{15}{16}$ GRADE

$\frac{7}{8}$ GRADE

$\frac{3}{4}$ GRADE

$\frac{1}{2}$ BRED

SCRUB
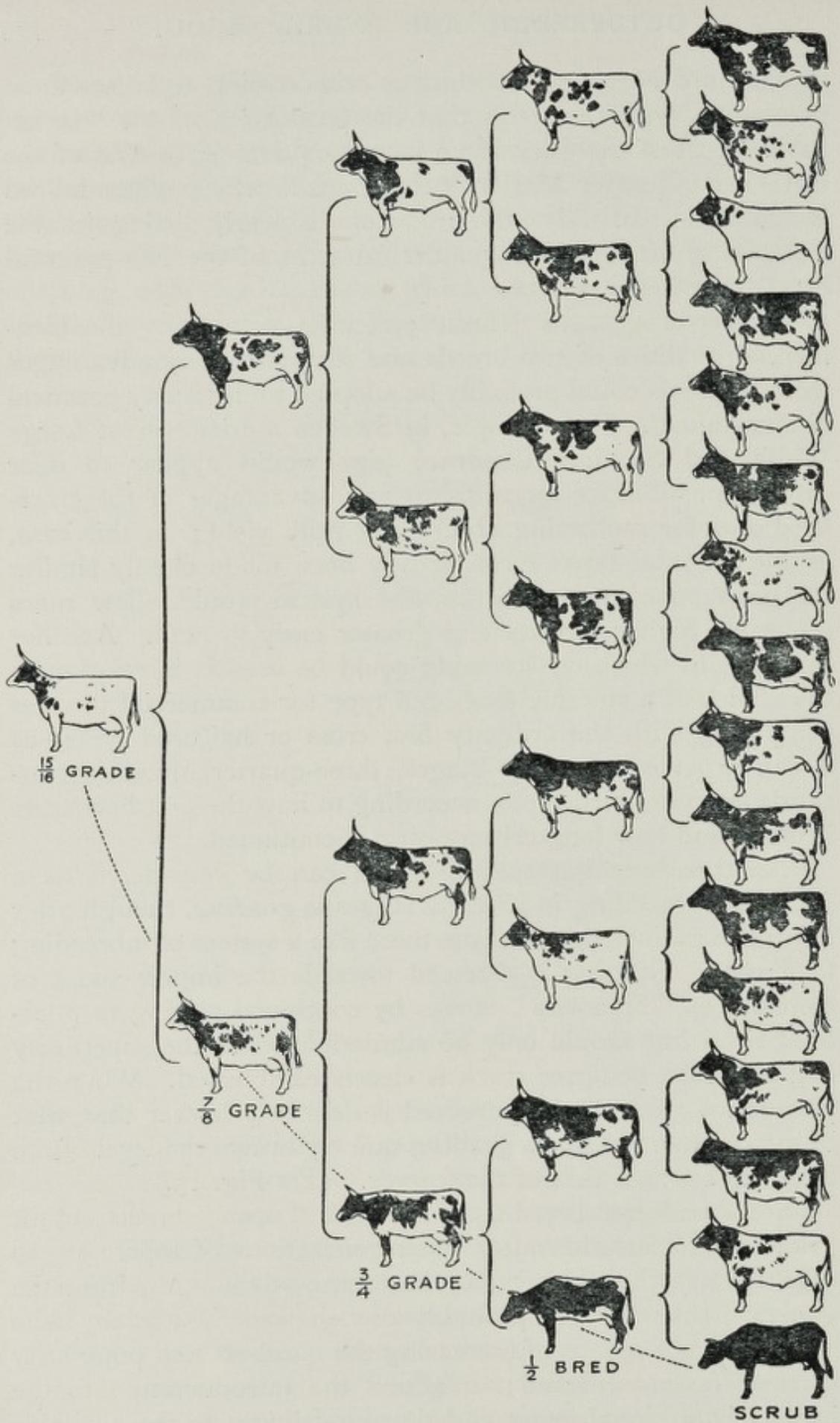
FIG. 13.—Grading. *From* Finlay, 1924.
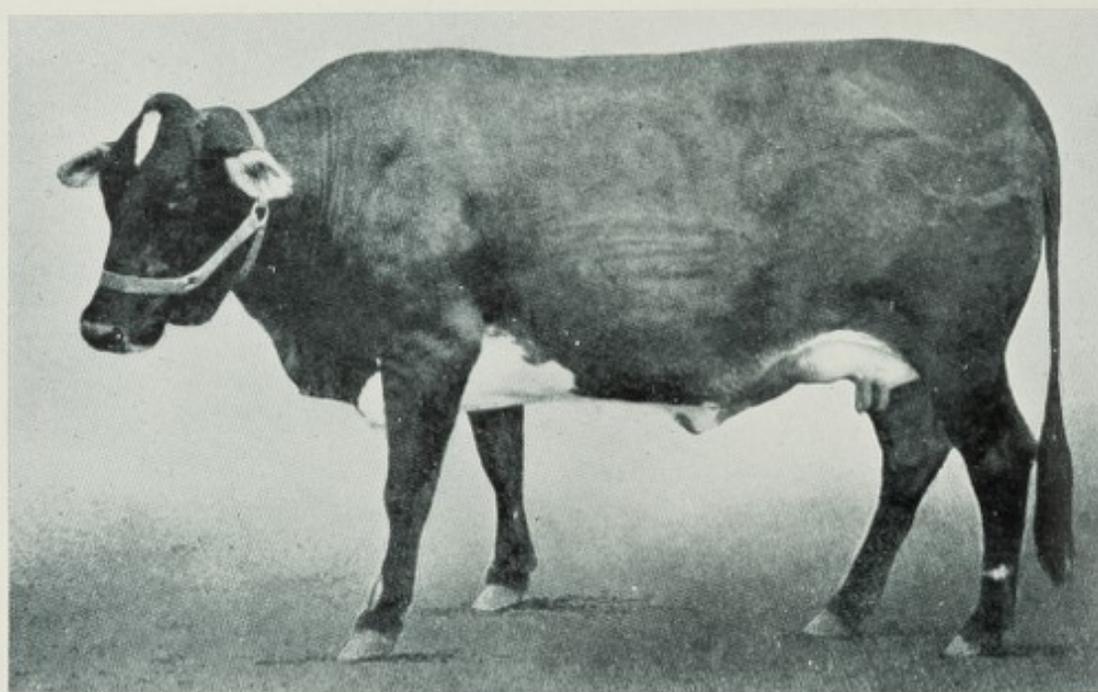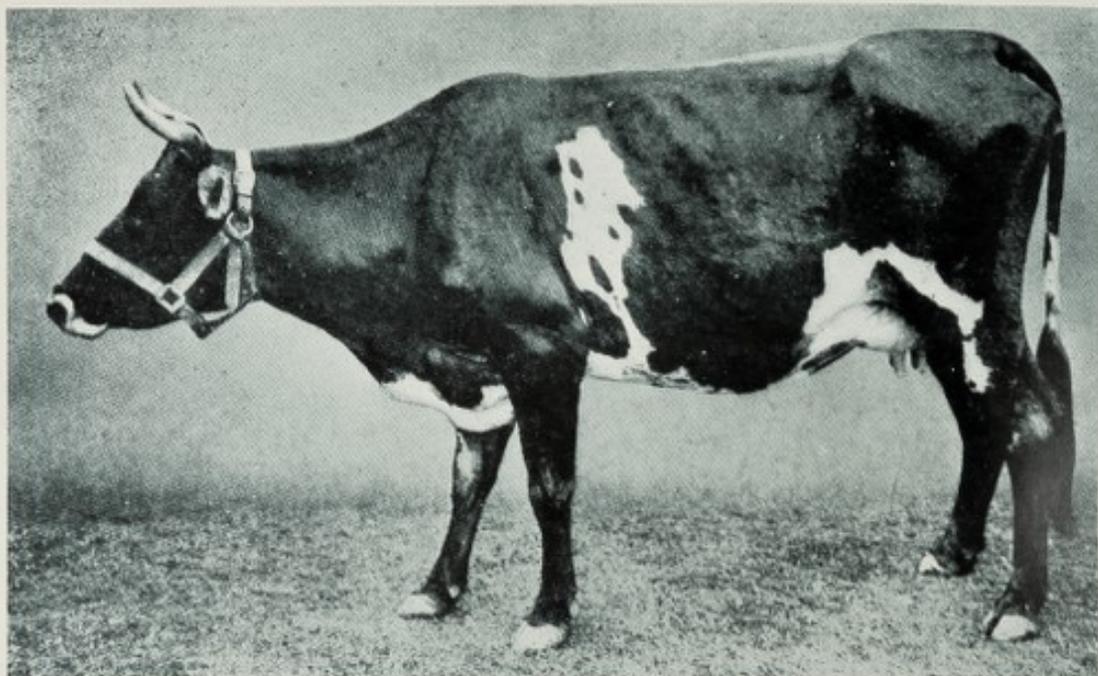
FIG. 14.—Degeneration in a high-grade Jersey cow (above) in the Tropics. Her daughter (below) by a Zebu bull is not only of better constitution for tropical conditions, but has also given higher milk yields. *From* Hammond *et al.*, 1941.

store of heterozygosity among which further selection, line-breeding, and inbreeding can be used to effect improvement within the breed. If favourable genes are contributed by outside animals, there is no genetic reason why the higher, registered grades should not be linebred towards the " outside " individuals, or strain, from which they came, although this is more unlikely in ordinary pedigree breeding practice than continuing to breed towards some supposedly outstanding animal of unimpeachable recent ancestry. In any event, some allowance should be made for the possibility that some of the phenotypic superiority gained in the first cross may be due to heterosis.

In the process of grading up to a pure breed there is no necessity to inbreed provided that fresh purebred sires are available, but equally, if a potent sire is found, there is no reason why he should not be used on his own descendants. His first few inbred matings in this way serve as test matings and so help to prove his worth for further use.

At the same time, there are definite limitations to the widespread adoption of grading as a means to improve commercial or " breedless " stocks. The significance of these limitations is not always appreciated. A common assumption has been that purebred stocks which give high performance in one set of environmental conditions are necessarily of superior genotype to other stocks and hence can be used for upgrading them. The qualification has already been made above that grading is justifiable when the purebred stock chosen are definitely superior ; this superiority must also be shown under the conditions in which the grades are to produce. Frequently the apparent superiority of the purebred type, or " improver ", has been exhibited in conditions widely different from those of the " unimproved " stock, and grading has led to unsatisfactory results. For instance, numerous examples are found of the failure of dairy cattle of temperate climate origin to improve native types in the tropics and subtropics, because the constitution of the grades is inadequate to sustain increased production in the tropical environment. This occurs with British breeds of dairy cattle used for grading in Ceylon and the West Indies (Hammond, 1932 ; Edwards, 1932). (See Fig. 14.) Similar difficulties have given rise to the policy of

preferring selection among the indigenous stock, which has brought such outstanding results among certain cattle breeds like the Sahiwal in India (Olver, 1938, 1942), or of grading back towards the indigenous forms after a single outcross to an imported breed, made with the purpose of introducing fresh genes to the available complex.

Moreover, the same qualifications should be applied where narrower differences occur in the environmental factors of the chosen types, or when the stocks are effectively of the same general type or breed, as in many livestock improvement schemes. The environmental and the genetical backgrounds to the real or apparent inferiority of the forms to be " improved " must be closely examined, as well as those of the breeds to which grading up is proposed. It is a common fallacy to attribute improvement in the basic local types to the " improver " breed and to the policy of grading, when there has also been a simultaneous change towards better care, feeding and management in the local stocks. The application of a grading-up policy in any area of relatively low production is not a cure for the inferiority of the stock, though it may help if better stock management is also developed ; and in some cases an improved environment may not only render grading unnecessary but even produce a situation in which grading to a particular purebred type would be a disadvantage. Grading as such is usually only one among a complex of factors which operate in a stock improvement policy. Very often, e.g. in pastoral sheep flocks, it is accompanied by a change in breeding policy or culling within the flocks, and the better results, say in the wool clip, are just as, if not more, likely to be due to the change in breeding aims and methods as to the introduction of rams of the particular chosen strain. This somewhat sceptical view of the claims sometimes made for grading is enhanced by the fact that often the " improver " stock must be so heterozygous, and its characteristics so influenced by its home environment, that the breeder of the " inferior " stock is actually introducing successively heterozygous genotypes, whose main effect is to increase the genetic variability of his stock, and thereby providing himself with better material among which to select for improved production in any direction he may choose.

CHAPTER XII

MATING LIKES AND UNLIKES

Two other main systems, commonly used within breeds, involve mating according to appearance, *i.e.* of like to like, and of unlikes. The former is of historical interest, as it was undoubtedly used widely in the formation of present-day breeds, but is also of practical importance because it is often followed partly in association with other systems ; in this case it is brought in as the basis of a method of selection whose effects are superimposed on those of the breeding method followed. Its effects can, also, be considered separately from other factors.

As its name indicates, like to like mating depends upon choosing animals which closely resemble each other in outward appearance or performance, *i.e.* are of similar phenotype. It is thus clearly distinguishable from inbreeding, which is mating animals likely to have similar genotypes. Actually, of course, like to like, or assortative, mating is always accompanied by some other selection of mates, in that the animals which are alike in a breed are not all able or all allowed to interbreed. Also, the similarity of appearance of two animals is never complete although it may be very nearly so in identical twins. To appreciate the outcome of assortative matings in terms of genetic results it is, therefore, necessary to examine how the resemblance of possible mates is made up.

The resemblance in respect of visible characteristics between the mates may be high if the breeder's judgment is accurate. Among the stock concerned there can be a high correlation between the characters, which are each the outward expression of all the gene effects present but may yet have different genetic formulae, involving different sets of genes. In assortative matings, the external resemblance will usually be greater than the genetic resemblance, so that for any particular character the correlation between the hereditary constitutions, for that character, of the prospective mates will not often be high. The effect, therefore, is broadly the same as mating hetero-

zygotes, and if mating like to like is continued the net result is that the variation of the whole population is increased.

Like to like mating not only does not fix an intermediate type but also does not fix any type to any appreciable extent, unless the number of genes is very small and their effects in no way influenced by environment. Where many genes are concerned, a great deal of heterozygosity must remain. But this system does have a valuable effect in that, because the parents are deliberately chosen for the reason that they both exhibit the same gene expressions, it increases the extent to which the offspring will resemble their parents and each other. As a practical means of securing the appearances that the breeder requires, assortative mating is therefore useful, but the desired phenotypes can only be fixed by inbreeding.

However, some other selection will inevitably be applied, so that some of the variability of the population will be removed and the group of retained animals will show great uniformity, due to this selection and not to the mating system. Moreover, this additional selection will tend to change the gene frequency in the population which will therefore not be able to recapitulate in later generations the precise form of character variation originally shown.

These considerations help us to appreciate the systems followed and the results obtained by the early breeders, so far as their results can be judged in retrospect, and also to assess the contributions being made to breed improvement by breeders who now use this method. The early breeders' choice of animals to mate was relatively unrestricted by pedigree and could be freely based on resemblance; assortative mating increased the degree of resemblance between offspring and parents, and also increased the general scattering of more extreme types in the population. But heavy culling was also comparatively unrestricted by the requirements of registration and could be freely practised; its effect was to make the individual breeder's group (herd or flock) of animals highly uniform. This uniformity could not be fixed, nor could the desired types, without some inbreeding being adopted. If, however, only a few genes were concerned in the desired character, and their effects were not confused by environment— as in the case of genetically simple breed labels—progress

would be fairly rapid but would not reach completion. Once the purebred idea is established, breeders who mate like to like without any inbreeding do not reduce the heterozygosity of their breed or secure any genetic fixation of type ; if they can cull heavily, they can ensure great uniformity in their own studs, with a high resemblance of parents, offspring and full sibs, but their culls are adding to the diversity of the breed.

On the other hand, the breeding aim may be to hold the general type so far achieved. This favours a policy of mating unlike individuals, *i.e.* of *negative assortative*, or *corrective*, *mating*, by which the shortcomings of one parent in a particular trait are more or less corrected by the excellence, or over-expression, of the same trait in the other parent. This form of mating is very commonly employed where an intermediate type is desired, as in dual-purpose cattle, or in large sheep studs where uniform appearance of sale stock leads to enhanced cash returns so that culling, in the usual sense, is distinctly unprofitable. Its effects are to reduce the correlation between parents and offspring, and between sibs, and also to make the population as a whole more uniform. It forms another contrast with assortative mating in that it actually leads to only a very small increase in heterozygosity ; its greatest possible effect, even assuming the unrealisable condition that the two parents should be of completely different hereditary values, would be to increase heterozygosity compared with a system of random mating by $\dfrac{1}{4n-1}$ where $n =$ the number of genes involved (Lush, 1937). That is, if a difference of so few as five gene pairs were responsible for the dissimilarity of the parents, corrective mating would only increase heterozygosity by one-nineteenth, and for most traits, involving many pairs of genes, the amount would be quite negligible.

Because of its wide application, some of these effects of mating unlikes merit further consideration. The system has a definite use in enabling a type, especially an intermediate one, to be held, without any fixation whatever, until it is possible to carry out close inbreeding for the special purpose of fixing the desired type. Uniformity of type being held high, few extremes emerge and the group as a whole is not split into separate sub-groups ; thus numbers can be held, or

increased, and any surplus stock have a reasonable commercial value as individuals. At the same time, especially in large groups, *e.g.* flocks, experimental or test matings involving inbreeding can be carried out within a section of the group. Within limits, it is possible to establish several sections inside a stud, where numbers are sufficiently large, whereby inbreeding or linebreeding is followed in some, and the culls from these utilised to breed phenotypically uniform " lines " in the others. Such a system is followed in some Australian Merino studs, where it has been noticed that the variation in the higher stud animals (forming the " specials ", " selected studs ", etc.) is frequently greater than that in the general stud " flock " from which sale rams are sold for use in commercial flocks. The practical result of such a compound system is to make possible a consistent output of groups of sale rams, of perhaps different types according to the demands from different districts, but it may be that this output is possibly more an indication of successful use of genetic variability among the " tops " than of genetic improvement of the sale rams in relation to their use under commercial conditions. To the latter, progeny testing under these commercial conditions is probably a much better guide than phenotypic resemblance in the environment of the parental stud (Nichols, 1940).

Also the effect of corrective mating in setting up general uniformity in the population is only temporary ; if the system is discontinued, the original variation reappears. This, partly, may explain the situation sometimes noticed in practice when a phenotypically uniform line of females bought from a stud, mated to a sire emanating from the same stud, throw very variable offspring, even although the females have been released from the parent stud for reasons of age and have therefore presumably been successful breeders previously while inside the stud.

CHAPTER XIII

PERFORMANCE AND PROGENY TESTING

To distinguish differences between individuals, the means the breeder uses to measure or estimate performance must be as accurate as possible and must be strictly applicable to the trait in question or to a closely linked character. For example, it is not of the slightest practical use to have accurate methods of measuring the shape and form of a cow's escutcheon as an indication of her yield when there is no real relationship between escutcheon form and milk yield. There has been a great deal of wasted effort, and of misdirected selection, owing to fancied relationships of external and productive characters; yet, because many of the imagined correlations have been shown to be spurious, that is no reason for ruling out the possibility that some external or easily appreciated characteristics may be useful as indicators of productive ability.

Another difficulty lies in the fact that rarely is only one kind of performance required; many animals are expected to produce, to go on producing, and to reproduce. To a great extent, however, the ultimate decision as to which of the many characteristics is most valuable has to be made by the breeder himself. He is concerned mainly with the ways in which the results of performance testing can be interpreted and applied to the benefit of his own breeding programme, and is interested in how the performance of his stock can be repeated by the stock themselves and in their progeny. In this sense, *performance testing* applies to methods of assessing performance worth, while *progeny testing* involves the estimation of breeding worth on the basis of the performance of the offspring. The success of each depends largely upon the precision with which the methods of test can be used, but the conditions under which the records of performance are obtained must be closely considered, since the performance level is almost invariably controlled by environmental effects such as those discussed in Chapter VII.

Environmental influences cannot even be dissociated in

the classical comparative forms of performance tests, such as races and shows, where the virtue of a record of competitive results depends on the numbers and "quality" of the competitors, *i.e.* on the "company" among which the record is achieved, and the extent to which the conditions of test are repeated. Generally, the conditions—such as company, weights, distance, course, state of ground, etc., in horse races—are not precisely repeated in successive tests, and there is thus a severe practical limit to the conclusions to be drawn from competitive results, though not to the possibilities of speculation. A degree of more objective measurement has been introduced into such contests by means of the stop watch for timing speed, and score cards for show animals, but even with the latter repeatability of the record is also affected by the consistency of the judging standards.

Livestock shows have useful functions under certain circumstances. They have assisted the development of breed type by imposing standards at which the breeders, or a proportion of them, can aim, and thus have pointed out a general direction for selection on appearance. Where the phenotype broadly indicates performance or economic worth, as in meat animals, the direction set by the breed standard may be satisfactory, but there are at least three main groups of objections to accepting a show standard as the pre-eminent breeding aim : (1) it often tends to overemphasise appearance or points of conformation of the individual that require a very high standard of feeding and husbandry, which cannot generally be sustained for commercial production, and thus it sacrifices some of the utilitarian traits ; (2) it lends itself to varying shades of interpretation, among which that favoured in any period by a relatively exclusive, small group of breeders can become dominant ; and (3) it is not necessarily consistent with the physiological balance for production, or stresses fancy points, and adds to the number of characters which have to be regarded in selection. Examples of these can be seen in the prevalence of nurse cows for the young bull classes of the highly developed early-maturing beef breeds, the changing fashions in show types, and insistence on colour, set of horns and ears, etc., in many breeds, when such points have no relation to productive characters.

Yet, on the whole, shows play an important rôle in emphasising the results of, and the need for, good husbandry, and this educative function is the more valuable in regions where the general standards of the stock and of its husbandry are low. In this respect they have proved a useful method in stock amelioration which cannot be severely criticised, even when its limitations, of emphasis on individual merit and of inconsistency with some of the practical requirements, are recognised. Allowance must also be made for the fact that any flexibility in interpretation of a show standard does enable show requirements to be adjusted or adapted to give greater weight to production, but how far this is achieved depends largely upon the extent to which production is measurable by objective means, as in the introduction of milk or butter-fat yield classes for dairy cattle.

The development of more objective tests of performance has been the most important single factor in stock improvement. But there is still much scope for improvement in the tests and in their wider application. The idea of setting up a yardstick against which performance can be measured is not a new one ; it is expressed to some extent whenever an " ideal " is established. But the yardstick only becomes of real use when it incorporates some factual basis for estimating performance, and its worth increases as it becomes more precise. Ellman of Glynde set a standard for his improved Southdowns by noting the differences in price, charged by the local butchers, between legs and loins, neck, and breast of mutton, and, having seen the advantage of a type with hindquarters heavier than forequarters, recorded the weights of the quarters and the various joints in the carcass (Lloyd, 1933). He was thus one of the early users of the carcass measurement method of judging meat type.

Performance for meat production can be measured in various ways on the carcass, and carcass competitions have become popular. As usually conducted, however, they suffer from some disadvantages, especially in that they refer to relatively few and not necessarily typical animals, and these animals are, of course, dead when judged. There is also the disadvantage that they depend largely upon differences between animals as assessed by judges. Greater precision and objectivity

has been introduced in recent years by means of detailed measurements, such as those of " eye muscle " shape, length, etc. (pp. 57, 62), but these are often laborious and impracticable on any large scale, though necessary for many scientific purposes. Also, and to obviate some of this disadvantage, comparisons of the carcass cuts with photographic standards have been introduced, as in the method of scoring bacon carcasses proposed by Davidson *et al.* (1936-37), where photographs of highest quality, medium, and poor shoulders and hams are used as the judging standards against which to allot marks for the carcasses or cuts exhibited. Such methods also tend to reduce the errors arising from the differences in the judges' opinions, particularly in enabling the same standards to be observed over long periods of time, as from one evaluation, or competition, to another.

In this connection, great practical advantage accrues from an organised marketing system for meat animals which includes a standard system of carcass grading. Where such a system operates, as in exporting countries like Australia and New Zealand, for fat lambs, series of records of carcass weights and qualities are made available to the breeders. A high degree of proficiency is attained by the graders; this is encouraged, and to a large extent fixed, by supervision and inspection and by the necessity of turning out level lines of weights and qualities, irrespective of the particular flocks from which the lambs come. Hence, the records have high merit as less subjective standards than could be applied by the individual breeder to all his lamb product; they have a definite value as performance tests in enabling the breeders to judge the results of their breeding policies.

The inconvenience of dealing with whole carcasses in detail leads to the search for adequate indicators, like sample joints, which can serve to give a fair assessment of some aspect of quality of the dead beast (*see* pp. 57, 62). For example, the length of the metacarpal bone and the thickness of meat over the sixth, ninth, and twelfth ribs have been found to be useful indices of the proportion of edible meat in beef carcasses (U.S.D.A., 1941), while in sheep the shorter and thicker the shank bone, the better the quality of the carcass. But however accurate this class of indicator may be, the breeder will generally

prefer means of forecasting from the live animal its performance when dead, or gauging subsequent live performance from juvenile or adolescent characters. In these respects there is a profitable field for further study, not only in examining the real predictive value of some of the criteria commonly used but also in devising new ones.

Many aspects of these questions obtrude themselves, and sufficient work has been done on them to warrant general conclusions. The precise problem varies of necessity according to the animal and the products concerned ; in light horses it is that of assessing speed and stamina, in heavy horses of judging power, from external features in both young and old ; in meat animals, whether beef cattle, mutton sheep, or pigs, of relating conformation and " condition " to carcass characters, and of estimating economy or efficiency of gain in weight on the young beast ; in wool sheep, of forecasting adult per-formance from the early coat characters in the lamb ; and in milk-producing animals, of considering external form as an indication of yield, present or future. Many different kinds of indicators have been suggested and used in the past, a limited number of them have some validity on general grounds, such as the shape of a meat animal in relation to its carcass and its " feel " as a pointer to its condition, but many have no practical significance and have been exposed as fallacious once an actual measure of production has been set up, e.g. the " escut-cheon theory " in dairy cattle had to be dismissed when the technique of weighing or measuring the volume of milk produced was adopted.

A common difficulty here is also that of establishing reason-able methods of measuring the indicator character. Score cards help partly to overcome this in many instances. Their use is limited, because, even with a definite system of allotting points, experienced judges are liable to error in not repeating the same scores for the same animals at different times. Knapp, Black and Phillips (1939) analysed the points allotted by seven competent judges to each of fifteen beef Shorthorn females in respect of twelve external features, the scoring being carried out three times at intervals of about a week ; they found the errors were of sufficient size to warrant the conclusion that, while scoring gives a reasonably simple method of recording

and measuring wide differences in conformation between animals, it is unreliable as a measure of small differences. Although more precise methods are therefore needed for evaluating small variations, the score card still provides a better basis for recording characters and type than do ordinary verbal descriptions or memory pictures ; moreover, they have a definite advantage as a basis for selection (p. 79).

An example such as the above for beef conformation introduces another important aspect of the problem ; no doubt should be allowed as to what the records of characters or performance actually are, and how far they constitute an accurate measure of the performance in question. Some of the difficulties here have already been indicated but can be illustrated further by considering the case of milk recording, in which direct measures of the yield at a milking or in a day are easily made, or the fat content of the milk estimated. But the performance of a cow is not just based on one or a day's milking, it is affected by such factors as the length of lactation, the calving interval, the cow's age or number of lactations, and the number of times she is milked per day. The daily yield varies also according to the stage of the lactation. Further, it is impracticable in most herds to weigh the milk at every milking, so that for record purposes sample days are necessary, from which the total or lactation yield is estimated. The estimation of total yield depends not only on the accuracy of the individual test but also on the accuracy of the samplings as measures of the total, so that the computed total yields are at best only estimates and not actual totals. The objective and direct nature of the sample records, however, makes them more satisfactory for all practical purposes than other indirect estimates based on indicators and also gives an opportunity for establishing correction factors by which allowance can be made for the several influences causing variations in yield.[1] Quite apart from the restrictions placed by recording agencies on what is the " recording year " or the length of lactation for recording purposes, the actual fact of the existence of a method of milk yield test has necessitated adjustments for age and so on. These correction factors are derived from average influences and do not apply with equal

[1] *See also* Sanders, 1927.

validity to individual cows, or even between cows of different breeds. Thus, from the American Dairy Herd-Improvement Association records it was recommended that the " mature " ages for Ayrshire, Guernsey, or Jersey cows were 6-7 years, for Brown Swiss and Milking Shorthorn 7-8½ years, and for Holstein 6-6½ years ; the various age conversion factors to be applied in these groups ranged from 1·343, 1·718, and 1·515, respectively, for 1½ years down to 1·000 and then up to 1·199, 1·192, and 1·378, respectively, at 16 years. The range of the conversion factors in a mixed average of these breeds was from 1·429 at 1½ years to 1·000 at 6 and 6½ years, and then to 1·288 at 16 years. To convert a 365-day record to the basis of a 305-day one, the conversion factor is 0·85 ; vice versa, it is 1·17. Since four times milking daily increases a cow's yield over twice daily milking, a record obtained on the first basis must be multiplied by 0·74 to render it comparable to one obtained under the latter conditions ; vice versa, the factor is 1·35. Similarly, the conversion factors respecting three and two times daily milkings are 0·83 and 1·20 (Kendrick, 1941, quoted by Rice, 1942).

The establishment of conversion factors does not dispose of all the difficulties in interpreting the records. In the long run it is the efficiency with which a cow produces milk from the food supplied and the length of her productive life that are of major importance. In both these, and especially the former, feeding and management are closely involved. A great advantage of milk recording is, of course, that it enables the poorer producers to be recognised, and within a herd this can probably be accurately done without using complex conversion factors. Official testing also provides a stimulus to better husbandry, and the often quoted good results of milk recording schemes are due to a combination of better management and elimination of the low producers without of necessity any accurate or fine distinctions made between the good and the slightly less good. The Chief of the Bureau of Dairy Industry (U.S. Department of Agriculture, 1941) has reported that the 763,502 cows in Herd-Improvement Associations in 1940 (less than 3% of all cows) produced on the average 8133 lb. of milk and 331 lb. of butter-fat as compared with 4575 lb. and 181 lb. for all cows. Fraser (1941) instances the fact that while 205 Ayrshires

in U.S.A. have produced over 100,000 lb. and 4000 lb. of butter-fat in their lifetimes, out of this total 37 cows were in the one herd. But in relation to improving the cow population the replacement rate is a limiting factor—so long as the average complete life of a dairy cow is six years, then her average production of heifers is only about two, and possible selection among replacements is very restricted. The average rate of replacement in U.S. dairy herds is about 20% (U.S.D.A., 1941).

While milk recording and testing provide by far the best means of assessing production, their use is limited in another way. Production alters with succeeding lactations even under consistent management; each additional lactation provides additional evidence of the cow's real producing ability. Although the first lactation is often used, of necessity, as an index of future performance, it is in fact very inadequate; the second and third lactations greatly improve the reliability of the estimate of lifetime yield, both for milk and fat production (Ashour, 1939; Berry, 1940). Again, management factors come into play; by intensive steaming up of the heifer before she calves it is possible to force up her milk production sufficiently to reduce the difference between her first and third lactation yields.

To some extent, in assessing a cow's real performance ability, it is possible to make corrections for environmental factors with temporary effects by considering only lifetime records, though here it must be remembered that with increasing numbers of records the variability will appear to be reduced. That is, animals with extreme high, or low, records are those with only a few records; a cow with a few high records will appear a higher producer than a cow with many records smoothing out her few individually high ones. The lifetime record does not, however, dispose of other environmental factors of longer influence, such as the effects of poor growth in early life, or consistent bad husbandry; nor does it discount those parts of the genetic milieu due to the effects of dominant genes or those whose action depends upon epistasis (Lush, 1937).

The single record can be misleading as an index of production ability, whether it is of the individual cow or of only one of her lactations, as it does not allow for environmental

effects. A comparison with other cows is necessary, especially in relation to the rest of the herd. It is here that the herd test has great advantages over tests of individual, selected cows within the herd, particularly if the complete records of the herd are made available. In U.S.A. the official herd test has become greatly developed, while in various European countries some form of " byre average " is commonly used as the basis for comparison, at least for scientific purposes. This enables the performance of single animals, or a group, to be assessed against the average production of the herd of which they form a part, and the general trend of production from year to year ; it is, however, open to the objection that one influence which is included in the general environment is that of the genetic constitution of the herd, which may change appreciably over a period of years and must therefore be taken into account.

The interpretations to be placed on herd tests, in which all cows in the herd are recorded, are far more valid than any that can be placed on single or a few records. The herd test has usually a different purpose to that of ordinary cow testing, in so far as it aims at presenting a reasonable picture of the total production in a herd, or group of herds, against which the standards of performance of the individuals and of management can be assessed. Its object is not necessarily that of extolling the performance of a few animals. Actually, the herd test as a basis for measuring economy of production in terms of feed is not a new technique ; weekly records of milk weights of all cows were begun in 1843 in one herd in Denmark, and in others there in 1853 and 1854, but for a long time the system was restricted to larger herds. It was not until 1895 that the first co-operative society for herd testing was organised in Denmark (e.g. see Anthony, in Prentice, 1942). This delay was partly attributable to the lack of quick and convenient methods of estimating butter-fat content, as were provided by the Gerber and Babcock tests, developed towards the end of the nineteenth century. On the other hand, somewhat sporadic attempts were made earlier to show the outstanding production of particular animals, usually for short periods, as in the " churn test " over a few days suggested in the U.S.A. in 1853, or the milking trial held at Ayr in 1860, when eight cows were judged according to the weight of milk

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yielded in five days, the winner giving an average of 26 lb. 5 oz. of milk for the ten milkings (Ayrshire Cattle Society's Journal, 1939).

It is often enough to have performance recorded in terms of either butter-fat or milk yield, depending upon which is the main market product, but more frequently a method of expressing production of both together is needed. This can be done by giving the records as so much milk of so much fat content per cent., or as total milk and total estimated fat; in both cases it is left to the person interested to make his own evaluation of the differences between two cows or two groups. Yet for the purpose of standard comparisons, especially in regard to efficiency of production, it is better to set aside the fluctuations in fat content and milk yield by combining the two forms of production in terms of a standard milk. A reliable method of doing this is to give the records as pounds of fat-corrected milk (F.C.M.), the fat contents being reduced to the common basis of 4%. The necessary calculation is by the formulae: F.C.M. $= 0\cdot4M + 15F$, or $= M(0\cdot4 + 0\cdot15f)$, where M is the milk yield in lb., F the total fat in lb., and f the fat content %. This method is satisfactory because, while it appears to neglect the solids-not-fat, the fat content is a good measure of the properties of normal whole milk, so that the F.C.M. figure is a fairly accurate estimate, for comparative purposes, of the energy value of the milk produced. On this basis the difference in average performance between D.H.I.A. cows and all cows in the U.S.A. as quoted above (p. 127) is still more striking, being 8218 lb. $v.$ 4545 lb.

While a lifetime record gives also a general indication of the state of the animal in respect of the other physiological characteristics which sustain production, such as constitution and consistent reproduction, it is achieved only in retrospect. For a more complete record of the general attributes of an animal, a combination of scores for bodily characters and production data is required. In young dairy heifers, prior to production, conformational score is not a good indication of future production; the first lactation is better, but still not very satisfactory, but the second and third lactations improve the basis of estimation. A knowledge of ancestor performance (provided it is at least reasonably complete, which it rarely is,

as yet), and of the breeding system followed, gives some further indication of probable performance. Yet all these considered together do not give a definite guide to the level of production to be expected. In any case, there is still the difficulty of deciding how to combine the data available under various circumstances.

From a study of data from the American Jersey Herd Classification Program, in which scores of conformation are kept, as well as production records, Copeland (1941) found that there was some relationship between conformation and producing ability, but that conformation rating was not a reliable index to production. High score and high performance can be shown together in one animal and are therefore not incompatible ; where breed type is an economic consideration, breeders are obliged to take it into account, though to what extent will depend upon the relative importance attached to type or to production in the breed standards, in prevailing fashion, or according to the level of performance in either respect desired by the breeder. Swett and Graves (1941) have proposed an ingenious method of combining score and production which allows for different relative weightings of the two ratings, though it is directed primarily to show-ring conditions and is still open to some of the objections mentioned above with reference to score card records. The principle is that the group of animals should be scored according to production, the points allotted being a set proportion of the performance record (*e.g.* 10% of the butter-fat yield) ; if production and type are considered of equal importance, then the top animal on type score is given the same points for type as the top animal for production and the lowest animal in type the same points as the lowest producer. Thus the same range of points applies between the top and bottom animals for both type and production, and the type scores of the intervening animals can be adjusted by the type judges to place them in appropriate order of merit. The final scores, and the placing of the animals on the combined basis, are obtained by adding the two series together. If different values are to be placed on type relative to performance, then the ratings can be adjusted by simply correcting on the basis of the relative importance, *e.g.* for production twice as important as type, the type scores

could be halved relative to the production scores before the final summation is made.

Even though neither type score nor a production record may be highly accurate in indicating performance ability, the two considered together form a better guide than either separately to real productivity over a lifetime ; but in relation to selection of breeding stock, the more the attention that is paid to one, the more the amount of selection that can be applied to the other is restricted (p. 78).

The limitations of the performance tests discussed above have to be borne in mind when uses of the records are considered. The main uses fall into two groups. In the first place, records provide an objective basis for distinguishing between individuals, and hence for selecting animals to be registered or to form an élite group within the breed. Some form of *selective registration* no doubt applies very generally among the breeds of all classes of stock, in that where any option remains to the breeder as to whether he registers a young animal or not, he tends only to register those obviously of breed type. Where points of disqualification are laid down in breed standards, selective registration is fairly definite and can cut across productive characters. Exceptions to the general situation are found, for example, in Thoroughbreds, where all foals must be recorded in the Stud Book, and also in practice among those breeds, usually new ones, where there is a real or an artificially-stimulated demand for breeding stock, so that all animals with the appropriate parentage can be and are registered.

Selective registration can take many forms but its results in respect to selection can be briefly stated. It is a form of official mass selection, which, if it were conducted according to absolute standards accurately indicating breeding value, would eliminate all individuals falling below a certain performance level ; under these circumstances it would tend to increase the intensity of any selection for desirable genes and hence the rate of improvement within the breed, though, because of the small effects of selection alone, the acceleration in improvement would only be slight. (Fairly strict selection has been carried out for the " saddle " pattern in the Wessex Saddleback pig, but has got practically nowhere.) If all

possibly eligible animals were submitted for registration, it would involve the admission of some useful animals which would not otherwise be registered and thus help to contribute some desirable genes to the available store. However, the standards in practice would not be so rigid as to exclude all the animals deemed below the minima ; the accuracy of the standards is not so high as to permit no mistakes, and, where scoring by inspectors or judges is a condition, would be sufficiently flexible to allow registration to a proportion of animals significant enough to provide some useful genetic variation on which to work. There would be a distinct disadvantage in having the standards too high or too rigid, as this would narrow the peak of desirability too much, prevent breeders from developing their own ideas of improvement, and restrict the possibilities of moving type and performance towards meeting changes in demands for production and in environment.

Selective registration within breeds is expressed in the various systems of advanced registry, or " registers of merit ", now being widely adopted. Again these take many forms, but the various kinds of register usually include animals outstanding in one or more respects, e.g. the recently introduced Register of Merit scheme for Red Poll cattle, where qualification for a cow depends upon her having been inspected in terms of the breed standard, produced three live calves within three years, and given six, seven, and eight thousand pounds of milk of minimum average fat content of 3·25% in her first three lactations of 365 days. A purpose of this élite registration is to indicate the highly desirable animals to become ancestors of the following generations by providing further and more accurate information in the pedigrees. But in many forms of production it is impossible to state the actual performance of the male ancestors ; their probable genetic equipment can only be indicated indirectly by reference to their near relatives, particularly their offspring. In some cases discrimination of males is made in favour of those whose dams meet a selective registration requirement more stringent than the normal ; e.g. in Germany only those bulls can be licensed as first-class breeding animals whose dams produce annually 10% more butter-fat than the minimum.

The second use of performance records is therefore in relation to progeny testing, which is the most accurate guide to breeding worth. No perfectly reliable valuation of genetic merit is as yet possible in farm stock, and generally the least reliable is that of individual performance. Pedigree is of some value as an aid to selection in so far as it enables some discrimination of the effects of environment and would also help to eliminate inaccuracies due to dominance and gene interactions if full information as to the breeding behaviour of the ancestors were always declared. It also enables the breeder to estimate the probable genotype of an animal, for example to decide, from the study of the mating system that has produced it and a knowledge of the performance of its ancestors, whether an outstanding animal is likely to be highly heterozygous or not. At the present stage of pedigree records, this knowledge is likely to be very incomplete, because the ancestors themselves are a selected group, the records pertaining to them are often derived from selected groups and also include the inherent inaccuracies discussed above. Moreover, there is always one genetic segregation between parent and offspring, and it is only in a mating between two complete homozygotes that the genotype of the offspring can be estimated with great certainty. Improved methods of making performance records have provided the opportunity for more complete statements of the merit of ancestors and their collateral relatives, but this opportunity has not yet been utilised as far as is desirable in many classes of stock. The information is, in fact, frequently grossly misleading, as when it refers only to heavily selected near relatives, i.e. to the performance of only a few out of the many near relatives of the ancestors. For the information to have real value it should refer to unselected groups of related animals, and should be as comprehensive as possible for the nearest ancestors. If complete data are available for near ancestors, they are of much greater significance than any referring to animals more distant in the pedigree; in fact, if comprehensive information exists on the animals one or two generations back, *and on their near relatives*, there is no need to go any further back in the pedigree.

A vast amount of work has been done on the question of progeny testing and a voluminous literature has accumulated,

but in view of the various forms of production, the measures and their inaccuracies, involved, much further investigation is still required to add greater precision to its application. The scope of the problem and the general conclusions so far valid can be outlined by reference to some of the methods of performance testing, of using " indicators ", and of analysis of records, employed or suggested in the different species. In all species of farm stock the selection applied to mates falls most heavily on the males, few of which are retained for breeding purposes. The main points, therefore, of progeny testing are to find measures of assessing a male's genetic merit from the performance of his offspring and to discover those males which can be regarded as " improvers " so that they can be suitably exploited.

Most work has been carried out on these questions in dairy cattle because of the direct importance of milk and fat yield, and of the development of suitable measures of performance. (Although the early progressive breeders of other kinds of stock are reputed to have used kinds of progeny test in their operations, and no doubt did to a certain extent, we lack sufficient evidence of the precise ways in which they interpreted their observations to warrant speculation as to their methods or to the degree to which progeny testing contributed in the formation of their breeds.) A number of different treatments of milk production data have been suggested to give a measure of the bull's genetic worth. He can be assessed on the average production of his daughters, or on how the daughters differ from their dams, the various records being adjusted in several ways. The records should in any case be converted to a reasonable comparative basis, *e.g.* as F.C.M. at mature age. No index can be absolutely accurate owing to the segregation of genes and to the fact that the various measures, and their adjusted forms, include some errors of determination.

A first essential is that the records should be of animals as unselected as possible. The simple average of daughters ($\bar{O}$) alone has the weakness that unless all the daughters are concurrently in one herd, they are under different environmental conditions, and also that any differences due to their dams are neglected. If the measure is that of the difference between

the averages of daughters and of dams ($\bar{O}$—$\bar{D}$) this also suffers in that the daughters may not have been exposed to precisely the same environments as their dams, and that the dams are probably a highly selected group ; but in this any errors due to environmental differences from herd to herd are most reduced. Probably a generally adequate bull index is that known as the American, or the Modified Mount Hope, which gives a bull an index figure, for either milk or butter-fat, so that his daughters are strictly intermediate between their dams' average and the sire's index (*i.e.* Index = $2\bar{O}$-$\bar{D}$). This is in effect the sum of the two former indexes, and has the advantages and disadvantages of both of them. (For fuller discussion, *see* Lush, 1937, 1939.)

Whatever the index, there are inaccuracies due to gene sampling and segregation and also to the imponderable errors arising from inadequate allowance for environmental effects. The accuracy of the index can be increased, especially in regard to the former, by increasing the number of offspring considered ; when this reaches three or four, the progeny test becomes more accurate than any pedigree estimate, when it becomes five or more, the errors from gene sampling are made small. But with these low numbers of offspring there is a tendency for them to be within the same environment, which thus assumes a consistent significance as an error. (Actually, maternal grand-daughters tend to have the same herd environment, to remain in the same herd, while paternal grand-daughters tend to be in different herds.) At higher numbers, eight to ten or more, little further accuracy is gained. The interpretation of the index is also affected for comparative purposes by the group of dams—if its average is similar to that of the breed, the dams forming a fairly representative or random sample of the breed, then the dams' averages can be neglected, say, in comparing the breeding performance of two bulls, but if the groups of dams are selected, their averages must be included and the existence of a large error recognised. In view of these sources of error the question of how many offspring are necessary for an adequate progeny test or sire index can only be answered in an arbitrary sense that it should not be less than about five unselected animals, although some registry schemes require up to ten.

The higher the production average among the dams, the less chance there is of finding a sire which is superior in the sense that he will improve production in his get. Also, in a heterogeneous stock the correlation between parent and off-spring tends to be high, but as the stock becomes more homo-zygous through inbreeding and linebreeding, and selection, the correlation between dam and daughter tends to become less. These considerations introduce further qualifications into the way sire indices may be interpreted, while an important practical limitation in regard to dairy sire indices is that of the delay before a sufficient number of daughters have acquired their own performance records; this means that the bull is aged before he is proved on the basis of his offspring, so that the number of proved sires available for further use is low at any time. An idea of the magnitude of this problem is given by the fact that during the year ended 1st April 1941 the records of 3519 proved sires were listed in U.S.A., but by the time the list was complete only 16% of these sires were still alive. (Artificial insemination offers a means of extending the use, as well as of early testing, of sires in this connection.)

If circumstances are against waiting for a progeny test before a young bull is selected for trial, a good method of combining pedigree evaluation with available records is to choose a young bull which is by a proved sire out of a dam which has at least one daughter, but preferably more, with good records (West Virginia Agricultural Experiment Station, 1941). But in such predictive estimates, as with using indices, allowance should be made for the general tendency of the offspring to regress towards the breed average.

In the long run, and in most cases, the individual breeder has to interpret the progeny test in relation to the environmental conditions in his own herd, and among his own stock; that is, he has to attempt to allow for and discount the environmental factors concerned. Because these introduce imponderable but appreciable errors into sire evaluation in terms of an index, there are good arguments for presenting the breeder with the official records of dams and offspring on a comparable basis and allowing him to draw his own conclusions in the light of his knowledge of the herd environment. This course is followed in several recording schemes.

Much use is made in European countries of the so-called "heredity grid", in which for each bull the daughters' productions are plotted graphically against their dams'; from the graph the tendency of the bull to raise or to lower production can be assessed. In connection with these, it is claimed that comparison of a cow's production with the byre average enables a better indication to be obtained of her inherited ability, more so with butter-fat per cent. than with total butter yield, and that her average production, in absolute figures or expressed as a percentage of the byre average, is a simpler basis for studying her inheritance than the heredity grid (Pallavicini, 1942).

A similar system is used in the sire survey work under the Herd Recording Council in New Zealand; the requirement here is that all cows in the herd must be under test. The production records of dams are based on all their available records, and corrections are made only for young (two and three-year-old) cows and in case of exceptional seasons; lactations not reaching a length of 200 days, and any parts of lactations over 320 days, are omitted. The surveys are made in a progressive form for each bull at intervals of one year. When the daughters' first lactation records only are available, they are included in a "Preliminary" survey; as second lactations become available, they are added, together with fresh first lactations, into an "Intermediate" survey, while the "Final" survey for a bull includes third, second, and first lactation records of his daughters (Ward and Campbell, 1940).

Where advanced selective registration is carried out, some evidence of progeny performance is required before males are admitted; in the Red Poll scheme quoted above (p. 133) a bull can be accepted for the Register of Merit when he has sired six daughters who qualify for the Register.

Progeny testing with records of performance in beef cattle is complicated since early growth, up to weaning, is influenced by the dam's milk yield, and throughout growth the proportions of the carcass parts change relative to each other (see Chapter VII). American workers suggest that there should be incorporated, in the final valuation, data on rate of gain of live weight during the nursing period and during fattening, the feed utilisation for 100 lb. gain in live weight (though rate

of gain is an indicator of economy of gain), and on carcass grade or score (*e.g.* Winters, 1940), but the necessary recording of such data is beyond the resources of the ordinary breeder. One difficulty is that the dam cannot be recorded concurrently, as a dairy cow can ; another is that the environmental conditions vary considerably, especially in regard to feeding practices during fattening. Recent work indicates that six to ten offspring, steers, are sufficient to provide a progeny test on the basis of efficiency of feed utilisation, during a feeding period of 168 days after weaning at 180 days, provided the data are adjusted for differences in the initial weights (Knapp *et al.*, 1942). In beef cattle, however, appearance and conformation are generally better guides to performance than in dairy cattle, and these are capable of evaluation in some way relatively early in life, so that a form of progeny test can be more readily applied for beef bulls than for dairy bulls, especially since the aim has become early maturity under high feeding, in which cost of feed is relatively unimportant, as a high-quality carcass is sought. In this sense selection of " proven " sires is simpler and quicker in beef cattle, and this has probably been an important factor in some of the improvement achieved in beef breeds.

Similar difficulties in detailed recording, and also advantages from judging on appearance, occur in regard to mutton and lamb performance. (The marked advantages of carcass grading in giving a bulk form of progeny test have been noted, p. 124.) From the outlines already given of environmental influences and developmental processes it is obvious that many different factors have to be taken into account ; the practicability under ordinary flock conditions of making sufficient records to do so is very doubtful. None the less, Christgau (1939) has proposed a system which goes further than rating the ewes according to the weight of lamb produced per ewe or per 100 lb. of ewe per year. He suggests a record of performance which combines wool production, lamb production, and estimates of feed consumption, but which requires careful control of husbandry and breeding practices in the flock from year to year, records of fleece weights, ewes' weights at shearing, and lambs' weights at birth, 15 weeks and 23 weeks. Wool production is converted on a grade and

price basis to its equivalent in terms of weight and quality of lamb, also corrected for grade and ruling prices. It would appear questionable how far the errors of the various corrections and estimates balance out in such a record, and how far they tend to obscure the main issues, particularly when factors like weight at birth, sex, single or multiple births, season of birth all have some effects upon selection, survival, and production, as Phillips and his collaborators (1940) point out. These authors studied body weight, fleece weight, and fleece length at first shearing, in groups of Columbia, Corriedale, and Rambouillet ewes, whose sires were known. They found significant differences in all these characters from year to year, so that in any comparisons of rams it is necessary to use progeny which have been born and reared in the same year, or else to make allowances for these differences between years as well as for any due to the dams within comparable groups of dams. Ordinarily, young rams are not tested on sufficient ewes to ensure that they get enough offspring to form a representative group, including equal numbers of the two sexes, of singles and twins, and of lambs with heavy and light birth weights ; this fact limits the value of early progeny and performance testing with regard to body conformation and meat characters. If, however, the way in which the population is made up in any character is plotted as a frequency graph and the same is done for ram progeny groups of about twenty individuals, a useful and rapid comparison can be made.

With regard to fleece characters generally the situation is also complicated by environmental factors and development and age changes. Samples of each year's production are obtained at shearing, and where the fleeces are adequately " classed " or graded on standard lines, the data so available are useful as records of mass performance ; but the contributions made by fibre fineness, length, strength, crimp, etc., and by clean fleece " yield " to final appraisal vary in the different wool types and according to breed. A complete microscopical and physical description of fleece character is impracticable for most of the breeder's purposes, although in certain traits, such as " yield ", fineness, length, and hairiness or medullation, fairly speedy and accurate methods of sampling and appraisal have been developed. Moreover, other characters of the

growing fleece have functional or economic significance to the breeder beyond that which they have in the shorn fleece to the wool buyer, *e.g.* fleece density, or the lamb's coat. Much attention has been directed to the question of indicators of future production both as guides in early selection and as aids to early progeny testing of rams ; thus, for instance, Dry (1934) uses the fibre constitution of the lamb's birth coat as an index of subsequent fleece composition in the New Zealand Romney, Pohle (1942) finds a high correlation between weanling and yearling Rambouillet, Corriedale, and Columbia ewes in respect of fleece length and yield, but a barely significant correlation for density, Roberts (1926) examined the various kinds of lamb coats in the Welsh Mountain sheep in relation to adult fleece quality, Nichols (1927) suggested that change of colour in the head tuft of the Suffolk lamb gives some indication of the freedom of the adult fleece from dark fibres, and Thomasset (1938) proposed that the degree of hairiness on the tail of the lamb is a guide to that of hairiness in the later fleeces. But in view of the apparent wide influences of environment on many fleece characters, much more work remains to be done before standard or reliable methods of shortcircuiting the making of detailed records, or of adding precision to those so far available, can be adopted by the breeder in practice. There is, also, evidence that the environmental and genetic relationships vary in the different breeds, or groups of breeds.

McMahon (1940) has thrown a valuable light on the problem of progeny testing in respect of fleece characters as a result of his study on fibre medullation in the New Zealand Romney, where he found that about 40% of the total variation was due to year-to-year variation and only about 10% to inheritance. Also, other results suggest that about 10% to 15% of the variation in fleece weight, and possibly in body weight, too, is attributable to simple genetic effects. Provided that the ewes have not been specially selected for pedigree or strain, their genotypes can be considered as at random for the purpose of progeny testing in characters of low heritability, and the offspring alone can serve as a measure of their sire's breeding merit. For this purpose, seven offspring are sufficient and give a better indication of genetic worth than does the sire's phenotype ; this allows young rams to be used safely. The

rams should be tested with groups of ewes sired by different rams ; the highest rate of improvement in fleece weight of the flock can be achieved by culling 50% of the ewes and 80% of the rams, progeny testing the remaining 20% of rams and retaining 3% on the basis of the tests. On his data for fleece weight in this breed, McMahon calculates that, with culling rams and ewes in this way, the fleece weight of the progeny can be improved 0·86 lb. per generation, *i.e.* only 1·16 generations, or four years, will be required to gain one lb. improvement as opposed to a gain of 0·162 lb., needing 6·2 generations or 24 years for one lb. increase, if the more usual practice of culling 50% ewes and 97% rams directly were followed.

Selective registration is not widely applied in sheep. Flock inspections are obligatory in some breeds before a flock can be registered, that is, the requirements constitute a bar to the open flock or stud book. In Russia, standards for registration are, however, being rigidly enforced even within the purebred flocks, although definite standards are also used among the high-grade animals to aid selection of improved breeding stock ; *e.g.* purebred rams and ewes of the various breeds are admitted to the District Flock Books at two years of age provided they have progeny which have been graded as first-class, and meet the breed standards for live and fleece weights. Older sheep must themselves be first-class before they are accepted, or, if they are graded second-class, must have produced two first-class offspring (Esaulov, 1940).

Performance and progeny testing in horses are at an interesting stage. In this animal more than any other there has been a greater insistence on pedigree, and performance tests have been almost entirely on a competitive basis, particularly in the form of races for the light breeds. The attempt by Laughlin (1934) to elaborate a measure of racing performance, incorporating many corrections for age, weight carried, distance, and speed, and to derive a " futurity index " for the racing potentialities of offspring, is practically an isolated case, and his system is little used. Dynamometer tests for draft horses have been introduced in several countries but suffer from the disadvantage that they do not simulate practical working conditions. Yet in areas where the horse is still of great practical

utility for many purposes and the common horse stock is relatively unimproved or not collected into defined breeds, performance tests are being strongly developed, especially as a means for selection of breeding stock. For instance, in Finland horse stud books began in 1907 and separate books for heavy and light types were started only in 1924. The horse population has increased very rapidly since 1917, and up to the end of 1934 over 3000 stallions and nearly 42,000 mares had been registered; admission to the stud book depends upon performance tests, in which draft horses of four to six years old weighing 470 to 610 kg. must be able to move 900 to 1350 kg., with a tractive effort of 200 to 450 kg. (Niklaus, 1941). The light horses must trot for one kilometre with a coach bearing two people.

In Germany, the Sachsen-Anhalt Horsebreeding Association has qualifying tests for light carriage horses which involve 2000 metres being covered in not more than $6\frac{1}{2}$ minutes at the trot, and 300 metres walked in 3 minutes. On the basis of tests with varying loads for different ages, it is suggested that for the Hafling breed in Germany a minimum requirement should be ability to cover a vertical height of 500 metres per hour with a 110 kg. load (or between 100 and 200 kg.), the distance traversed not being so important. In that country tests for various attributes have been investigated by Krüger (1939); endurance is estimated from the results of three days' tests; tiredness and willingness are also estimated. Three other tests, for utility, work, and speed, are combined to give an index. The first involves strength exerted in ploughing, measured by dynamometer, time, and distance; the second includes load-pulling over distances of half a kilometre up to the point of refusal, the load beginning at 60 kg., increasing by 30 kg. after a five minutes' rest at the end of each half kilometre. When a weight of 180 kg. is attained, the distance is split into five equal parts with one minute's rest after each. The speed test is performed on a track over distances of between two and fifteen km., with loads of 30 to 60 kg., at the walk, trot, and gallop.

Russian workers are using standard tests to help define the desired type of working horse, combining them with score systems. Trotters are widely used in U.S.S.R., and regulations

introduced in 1938 provide for a method of complex, or combined, scoring on scales of ten points for each of the following traits : conformation, as judged by measurement and by eye ; speed ; origin ; type ; and progeny. According to score the animals are allocated for different grades of breeding or use, and an examination made by Vladykin (1940) on 377 Russo-American Trotters showed that real differences were discriminated by the scoring system. The Élite are allocated to the improvement of purebreds, they are the tallest (height, 160·2 cm.), fastest as a group (1600 m. in less than 130 seconds to over 150 seconds), and have no defects of conformation ; the lowest group, Class III, have no use in breeding—their heights averaged 153·2 cm., their times for the same distance ranged from 2 minutes 15 seconds upwards, and they showed a high proportion of conformational defects. Classes I and II, comprising stallions and their dams for mass breeding studs and for mass improvement, respectively, had the same speeds as Class III, average heights of 157·9 cm. and 156·5 cm., and exhibited no and few defects, respectively.

For the improvement of the range horses in Soviet Central Asia a simple form of selection by registration has been developed, the record cards bearing statements of identification, faults, condition and general type, constitution, and a detailed tabulation of conformation points, with an evaluation of each entered in five columns reading from poor to good from left to right. This enables the general ranking of the animals to be assessed rapidly, those with entries predominantly to the left being inferior, those to the right superior (Barmincev and Hitenkov, 1939).

In pigs, as in dairy cattle, a great deal of investigation has been conducted on methods of testing ; here progeny and performance testing are essentially the same thing, as the function of a sow is to produce young and her performance is expressed in her prolificacy and mothering ability (including milk yield and teat number), and in the survival, growth rate, economy of gain, and eventual carcass quality of the offspring. Many of these attributes can be adequately tested on the young pigs, or reasonably predicted therefrom, since the piglings which are heavier at birth generally grow faster and attain market weights earlier than those which are of low birth

weight, while there is also a correlation between rapid growth and the efficiency of food utilisation with which it is achieved. Pig testing schemes, and official stations for conducting them, have been firmly established in many progressive countries, in particular those where a standard export product has been the objective, and have been responsible for great developments in pig breeding. In other lands this activity has not been so widely stimulated, and it can be generally stated that it is in these countries that breeders are the most handicapped in their selection and breeding systems by the lack of adequate performance records; indeed the records made available along with the pedigrees are frequently misleading or almost meaningless.

The testing techniques followed vary somewhat in different countries, for instance, some state pigling weights at 56 days, others at three weeks, and there is still room for further investigations as to the accuracy and significance of some of the criteria employed. Also the minimum requirements for qualification—litter testing is frequently used in selective registration—vary in different countries and breeds. In Germany an objective is a total litter weight of 60-70 kg. at 4 weeks, with the piglings averaging between 6 and 8 kg. and with little variation among them; the official testing stations in that country accept two piglings between 10 and 12 weeks old from each litter and the test begins at the age of 92 days, being carried on for the period necessary for the pigs to increase 100 kg. in body weight under the standard conditions of feeding and management (Haring, 1939). The results are expressed in terms of the number of days needed to make this gain, the daily gain, and the food utilisation required. When the test is combined with a carcass show, the lowest carcass losses, the proportion of meat to fat, and the meat quality are taken into account. In contrast to this method, the official tests in Sweden, where they have been compulsory since 1923, record different data. The sample of each litter sent to the station is of 4 piglings, which is probably a satisfactory number, and these are slaughtered at 90 kg. live weight. The records required from the breeder are the number of piglings born per litter, the mortality between birth and 3 weeks, the number alive at 3 weeks and their collective (litter) weight

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at this age, together with the mean weight per pigling. The weights of the heaviest and lightest pigs in each litter furnish an indication of the variation within the litters. The sow's production is expressed as the average weight of the three consecutive litters which had the highest total weight, on the condition that these were produced within a period of less than 16 months. This, however, favours the older sows, because they have had a better chance than younger sows to produce three consecutive heavy litters, and also for the reason that litter weight generally increases from the first to the third litter (Johansson, 1943). While the litter weight at 3 weeks may not give an adequate indication of the genetic merit of the sow or her mothering ability, it probably gives useful information on the genotype of the offspring in respect to growth rate. As the Swedish tests are now used primarily as progeny tests for the boars, they are therefore valuable, especially since for this purpose it is better to take a few sample piglings from many litters than many piglings from a smaller number of litters, three or four groups being the minimum.

The question of the accuracy of numbers and weights of piglings at birth and three weeks of age is being examined at the Iowa Agricultural Experiment Station, where, in relation to American requirements, the best measures of performance yet developed comprise weight at 180 days, score for market standards at about 225 lb., and the number in the litter and weight at weaning (Rosenfeld, 1942).

For egg production in poultry, performance testing is relatively simple and cheap; complete records of daily and lifetime egg-laying can easily be kept without much addition to the ordinary routine, but accurate recording had to wait for the development of the trapnest in the late nineties of the nineteenth century. Egg grading by weight gives another measure of quantity and quality of production, while large-scale hatching by incubator provides opportunity for testing fertility and hatchability as factors in the production of particular matings. Thus all the major aspects of egg performance can be adequately covered, especially by the large-scale breeder himself. Egg-laying trials, and their competitive element, under standard conditions enjoy considerable vogue; the entries are selected groups, chosen on different bases and repre-

sentative in varying small degrees of the parent flocks. Their results have distinct propaganda value, but little merit to the individual breeder unless he can interpret them in relation to the performance of the stock from which the trial birds are derived. To do this he requires records of that stock, which means that if such records exist in adequate form, then the trial records are unnecessary. On the other hand, standard trials have brought special emphasis to actual production and placed other points in proper perspective, so that they have performed a valuable service in aid of progressive breeding. At the same time they have emphasised performance under particular sets of environment and husbandry conditions, which are possibly not equally applicable or desirable throughout the industry generally, and hence set standards in other characters such as constitution and disease resistance which may not be conveniently emulated, or the most profitable, in more ordinary flock circumstances.

Other standards also apply in exhibition poultry, so that conflicting breeding aims are found within some types. On the whole, breeders of poultry have readier opportunities than breeders of other species for incorporating valid data in their records of breeding stock, though these opportunities are not so fully seized as is desirable, and weaknesses often remain in the usual methods of expressing the indications of genotype from progeny tests and performance.

For table birds, which are usually sold before growth is completed, indicators of performance are desirable. These have been found in the relations between shank length, least body depth, and length of keel, all expressed in relation to body weight (actually to the cube root of body weight, which reduces this measure to a function of linear dimensions). The proportional shank length is the best of these three, and since female birds achieve mature shank length between 16 and 22 weeks after hatching, males being about a month later, it is thus possible to predict the adult body size and market conformation from the live bird some four or five months before its growth is finished. This criterion applies in both egg-laying and meat types, and especially when a breed or strain is fairly uniform in body shape (Jaap, 1939, 1941 ; Jaap and Penquite, 1938).

A recent development in the poultry industry has been for commercial flocks not to do their own breeding but to receive their stock from hatcheries. In certain circumstances the stock favoured are F_1 hybrids of two breeds; for example, Bonnier (1941) mentions the superiority of certain crosses of White Leghorns and White Wyandottes in Sweden and stresses the need for progeny testing the parental strains to discover the best " nick " to produce offspring of high performance. As the parental birds are two or three years old before their daughters have been proved, the practical difficulty of securing large enough numbers of parents is being overcome by an ingenious imitation of plant breeding methods, whereby large groups, or populations, of the parental types proved most successful for crossing are multiplied in mass, their genetic constitution being held fairly constant over a few generations by the device of mixing sperm from many cocks and using the mixed sperm in the artificial insemination of many hens.

Commercial livestock industries generally incorporate some form of crossing between breeds, the proportion of registered purebreds in a livestock population is usually low, and for commercial production all the desired attributes are not necessarily combined in the one pure breed. The question of progeny testing for hybrid performance is therefore by no means confined to poultry but calls for wider attention. In many cases the actual production can be measured in the same ways as for purebreds, *e.g.* meat, milk, eggs, but the problem is to combine, or make correction for, records of other physiological traits such as prolificacy, efficiency of production, hardiness, or constitution, which may be the properties of the mixed genotype of the hybrid. Further, in all progeny testing the probable genotype of the parents is being assessed from the phenotype of the offspring, so that in testing crossbred offspring we are in effect setting out to assess the probable behaviour of samples of the parental genotypes as contributions to a heterozygous genetic complex. In this sense the progeny test results of, say, a purebred Jersey bull from his purebred offspring might form a less adequate basis for predicting his merit in crossing with Friesian cows than of his worth in mating to other Jersey cows. For some types of crossbred performance the technique of producing pure and cross offspring in the

same pregnancy, as in the mixed litters of pigs obtained by mating a sow during one heat period with boars of two different breeds, offers possibilities of eliminating some of the environmental variables, though it does not preclude the contingency that the different genotypes may show different responses to the one maternal and early postnatal environment.

In any event the interpretation of progeny test records for this purpose would be similarly exposed to the qualifications and limitations which have been discussed above.

CHAPTER XIV

BREED CONSTRUCTION

A BREED can be regarded as a group of animals forming a selected small sample of the species, which has been held more or less separate from other groups. The genes present in the breed are also a sample of those of the species, but occurring in combinations much less numerous than all the possible ones. Separation of groups by natural and/or artificial means will have tended to make them drift apart in genetic constitution and characters as a result of the sampling process in inheritance or of selection. The ways in which a breed can differ from other groups may be almost insignificant—breeds may overlap—but if a sufficient number of characters are taken into account, the average characterisations of the breeds may be recognisably distinct. The frequency of each of a pair of genes in a breed and the combinations in which the genes exist are largely affected by the systems of selection and, in particular, of mating to which the breed has been subjected. No group of animals, large or small, is unselected ; environmental as well as genetic influences having operated, the only fair way of considering the performance and breeding merit of a breed is to regard its probable genetic constitution, making due allowance as far as possible for environmental effects.

In many cases the relative smallness of a breed as a sample of its kind has been established or preserved by superimposing further restrictions according to the requirements of some association or society of breeders. These requirements can be based upon pedigree, conformity with certain " ideals " (which may or may not be closely related to productive merit) or on a combination of these. This process of breed recognition has had important practical results in such matters as emphasising breed type, in publicity and propaganda, in affecting breeders' policy and even general livestock policy, and in encouraging better husbandry. The assumptions made regarding the significance of these results are not always valid, however, nor are their implications in livestock improvement satisfactorily appreciated.

The existence of a system of registration itself confers no inherent advantage in genetic constitution, although the existence of a registering society may profoundly affect the part played by a breed in relation to a livestock producing industry. The foundation animals themselves were only samples of the original populations of animals, and could not have included all the most favourable genes available; moreover, the foundation stock were often chosen from among local, indigenous groups (previously, at least, exposed to natural selection) and could therefore be possessed of no more than a sample of their genes. In other cases the foundation animals were obtained by interbreeding among representatives chosen from two or more previously separated breeds, *e.g.* the Corriedale from Longwool and Merino. Whatever the precise origin, and whether or not its history has been recorded, the present-day members of a registered breed are descended from stock possessing only a relatively limited number of genes and gene combinations. No breed has therefore the prerogative of including all the necessary genetic potentialities for maximum or even optimum performance. Yet some breeds, or some individuals within them, can be considered to be relatively highly homozygous for, or with a high frequency of, some of the favourable genes present in the original stock, if and only if the systems of mating and selection followed down the generations have been sufficiently consistent to bring these genes together in suitable combinations and to spread them suitably throughout the breed. Deliberate breed construction for any particular purpose involves the choice of foundation animals likely to contribute the appropriate genes to their descendants and the adoption of methods of selection and mating likely to bring the genes together in suitable combinations.

From what has already been said regarding environment— and more will be added in the next chapter—it is clear that the genetic constitution of a breed must also be considered in relation to the conditions in which the breed is to perform. Whether or not a breed includes the necessary genetic capabilities for performance under conditions other than those in which it has been bred can be discovered only from its behaviour when submitted to the new circumstances. The

more adequate the tests of performance and progeny that can be carried out, the better the discrimination between suitable and unsuitable genotypes.

Various examples of the ways in which these general considerations apply in established breeds or in mixed livestock populations have already been given ; the following instances illustrate some of the particular problems and applications encountered in practice.

A single gene effect can be brought in from another breed. New poultry breeds such as the Legbar, Dorbar, and Buffbar have been introduced with the purpose of including the sex-linked barring factor enabling the sexes to be distinguished at hatching, or soon afterwards (Pease, 1943). The polled character has been introduced likewise into horned cattle breeds, such as the Shorthorn and the Hereford. Similarly, the genetically simple Rex and Chinchilla coat conditions have been added into various rabbit breeds. In such cases, even if the original cross required is a wide one, the general characteristics of the receiving breed can rapidly be regained by grading the descendants of the donor stock for a few generations (p. 113). Simple dominants can rapidly be spread through the receiving breed, and fixed if the appropriate test matings are made to pick out the homozygous animals and these only are used ; numbers and other considerations often affect the culling rate which can be applied, so progress is usually slow. Where genetic methods are not used, the proportion of off-type heterozygous individuals, and of homozygous recessives, can remain high.

The breeders who began selecting for improved types among local indigenous breeds had some advantages in knowing their own and their neighbours' stock intimately, so that their selections on appearance could be reinforced by direct observations on breeding results. The histories of many breeds show that the early stages were carried out by groups of breeders who interchanged stock to a considerable extent ; good examples occur among British sheep breeds, many of which still retain their local breeding areas. Bakewell's practice of letting rams constituted in effect a refinement of this community breeding. In more recent years, the Duroc Jersey and Chester White breeds of pigs were largely developed

by local communal effort, while new breeds like Polwarth sheep have a strong local background. Under such circumstances, and especially where the herds or flocks are of small size, some linebreeding to superior individuals is almost inevitable, and will accelerate improvement, without of necessity developing into inbreeding close enough to expose any undesirable homo-zygous recessives.

The direct opposite of this situation can obtain where registered stock are frequently transferred and widely dispersed among small units. For example, Donald (1940) found that among a sample of 365 boars and 1900 gilts of the Large White breed described in the sale catalogues of 33 leading herds in Great Britain, about one-third of their sires and one-half of their dams were homebred. There was a wide variation in the practice of using homebred stock either as sires or dams ; taking the total figures only about 18% of these animals had both their parents homebred, while 30% had parents bred outside the herd. Obviously these figures indicate that outside blood was being continually introduced into these herds at a very high rate, so much so that practical limits were placed on the opportunities of discovering individuals of, or strains with, superior performance.

The societies controlling breed registration have different requirements for admission. A number of registries are closed, so that only the offspring of fully pedigreed parents can be entered ; others are open to the admission of high grades. In any case, the great majority of societies were formed some time after the breed was recognisable as a distinct group or as having the possibilities of becoming one. Where stock of a particular type had been exported from one country to another, registration in a closed book frequently was started in the second country and thus stimulated the formation of a society in the original home of the breed. Breeders and importers of Jersey, Guernsey, Holstein, and Ayrshire cattle in America anticipated the founding of herd books for these breeds in the ancestral parts of Europe (Prentice, 1942). Thus at the outset a registry could be open in one area and closed in another. A closed book may have some influence in encouraging breed-ing for homozygous strains or general homozygosity in the breed ; whether this is achieved will depend on the mating

systems generally adopted. Open books, on the other hand, at worst allow the possibility of some loss of homozygosity, and a chance of undesirable genes also being introduced, but their chief effect is to permit probably favourable genes to be admitted through the high grades qualifying for entry. Selective registration demanding superior qualifications on the part of the grades approaching admission forms a useful filter, and various forms of it are now being widely used in provisional and supplementary registers (p. 113, and *e.g.* Esaulov, 1940). Further, the satisfactory results of selecting among indigenous types individuals with superior performance to form the basis of improved strains or breeds, like the Sahiwal and other breeds in India, is a modern and spectacular use of this method (Olver, 1938, 1942 ; Wright, N. C., 1937).

Some societies have practised selective registration in a negative sense, using points of disqualification to preclude otherwise satisfactorily pedigreed animals from registration, *e.g.* red or red and white calves in black or black and white breeds of cattle ; in such cases the disqualification could as logically be applied to the parents for being heterozygous for the causal gene. Selective registration, however, is usually applied positively, and in some instances requires evidence of actual productivity before final admission, as in the dairy breeds in Denmark, where a cow must have had at least three lactations and a yearly average of over 400 lb. of butter-fat production. Where official pig-testing stations operate (p. 145), *e.g.* Denmark, Sweden, Germany, etc., definite standards of record are required before a sow is registered—these requirements may vary according to breed.

The nature of the demand for a particular product has no doubt always been a predominant influence in the development of breeds, particularly if developments in husbandry have also allowed a higher level of response in production. This effect has been noteworthy in meat animals even from the days of the new Leicester and the improved Southdown. But the series of problems set for the breeder have not always been easy to solve ; the extent to which he can change his basis of selection may be severely limited by the fact that the other products of his stock may be important economically or physiologically, or he may be handicapped by the type and standards

of the available breeds and their registrations. The balance of requirements of type and production vary in the different breeds, and in relation to general conditions, but only the former situations will be considered for the present.

The fewer the characters to be considered, the simpler the problems of selection and the more rapid the progress which can be achieved ; the more production characters are obscured by other points, such as breed labels, the less intensive the selection that can be applied to them (p. 78). The progress towards early maturity attained in beef breeds like the Aberdeen-Angus can no doubt be attributed to the relative freedom enjoyed by the breeders to concentrate on beef conformation at an early age as contrasted with the more difficult task of the breeders of the Podolian types in Italy and Eastern Europe to regard also draft characters ; further, the restriction imposed by the need to maintain milk yield as well has been partly removed in herds where very high feeding and nurse cows are integral parts of husbandry.

A recent move stimulated by economic conditions stressing the importance of efficiency of production has occurred in U.S.A., with particular bearing upon milk performance. Herd testing has shown that unregistered cows, of mixed breeding, are often superior to pedigree cows of the various breeds. To enable breeders to focus attention on performance, irrespective of any fancy points or breed origin, and to take full advantage of progeny testing for this purpose, the American Dairy Cattle Club has been established, with four " orders " for registration.

For cows there are no pedigree requirements for the first order ; for higher orders their parents must have been recorded at least in the next lowest order. The performance require-ments for cows are in terms of 305-day, twice daily milking, mature equivalent lactations, and for the various orders are : 1st, a complete lactation, of no specified quantity, or two daughters each with 300 lb. butter-fat records ; 2nd, a pro-duction of 350 lb. fat ; 3rd, 375 lb. ; 4th, 400 lb. fat. The requirements for bulls are based on their American indices (p. 136), based on five dam-daughter pairs, as follows : 1st order, an index of 375 lb. ; 2nd, 400 lb. ; 3rd, 425 lb. ; 4th, 450 lb. Indices of 450 lb. on a 10-pair basis, or 500 lb. on a

15-pair basis, will admit bulls without the pedigree requirements to the 2nd and 3rd orders respectively (R. Prentice, in Prentice, 1942).

Lewis (1942) has been able to throw some light on the changes in conformation by selection in a dairy breed from a study of the ratings of registered Island Jerseys during five separate periods spread over the years 1866 to 1935, the animals being recorded as " Highly Commended " or " Commended ". As between the first and last periods, 1866-82 and 1930-35, respectively, the matings of " C " sires to " C " dams decreased from 27% of the total to 17·5% ; of " H.C." sires to " C " dams from 43·6% to 17·5% ; and matings of " H.C." parents increased from 21% to 73%. Yet the proportions of progeny classed as " H.C." to " H.C." parents, which increased from 23% to 43% between 1866-82 and 1890-93, did not show any consistent increase afterwards, hence there appeared to have been no increased homozygosity in this population in respect of the genes affecting " Highly Commended " conformation.

In the early days of stock improvement, if it was considered that all the potentialities were not represented in the nearest available local type, there was little restriction on bringing in representatives of other types, and selection could proceed among the widened genotypes resulting from the crosses, favourable combinations being chosen from the later crossbred offspring. Rapid improvement was possible, but heavy culling was necessary, under such circumstances. Also, without any rigidly common standards of selection, the existing variation allowed a considerable choice of types, so that subsequent selection and linebreeding could lead towards different peaks of desirability and a divergence of the new breeds. A good example of this occurred with the Hampshire Down and Dorset Down breeds of sheep, which sprang from a common stock in crosses of improved Southdowns on old Wiltshire Horns and Berkshire Knots ; after a time two of the leaders in this move, Humfrey and Saunders, exchanged rams but the Humfrey flock developed into Hampshire Downs, the Saunders into Dorset Downs.

Mixtures of previously formed breeds are a common source of origin of new breeds ; in recent times the urge to form a fresh breed frequently comes from the success of an established

practice in commercial crossbreeding, especially if any change in type or availability of the parental breeds appears to be making it more difficult to obtain the desired first-cross animals. Males of breed A crossed on females of breed B may have produced "halfbred" $\left(\dfrac{A \cdot B}{2}\right)$ animals in large numbers suitable for commercial production on a large scale; the types of A and/or B may change, so that $\dfrac{A \cdot B}{2}$ are not quite the same as formerly and less suitable to the old purpose, or the supply of surplus B females may have been reduced in numbers, by displacement of B by some other animal or type, but if there is still good scope and demand for the $\dfrac{A \cdot B}{2}$ type, then there is a distinct stimulus to some breeders to attempt to create a breed $\dfrac{A \cdot B}{2}$. Among sheep, such breeds as the Corriedale and Columbia are well-known examples of this development.

The obvious genetic problems in such cases have been dealt with already; but other aspects must be mentioned. The second stage is usually the interbreeding of F_1 stock and selection among the F_2. The intermediate forms are the most frequent but provide much choice for the breeders in selection and subsequent aims, so that there are possibilities of a variable breed with many subtypes, according to the range of breeders' ideas, unless a rigid breed standard is set up and selective registration adopted. If the new breed has access to a wide range of environmental conditions for which some subtypes are more suitable than others, then this tendency will be encouraged. If the new breed meets a popular demand early in its development and is encouraged to increase rapidly in numbers, then the necessary strict and heavy culling tends to be discouraged and the greater variability remains. This great variability may itself be an advantage to the spread of the unformed breed in numbers and areas, as a greater flexibility of use and distribution is possible to a genetically variable than to a more homozygous breed. (This last consideration may lie behind the wide dispersion of some old-established breeds.) And there is also the major question as to whether

the strictly intermediate form, halfway between the parental types, is truly the desirable one. The F_1 form is not of necessity the best guide to the practical answer, since its apparent advantages *may* be attributable to some heterosis effect (p. 104); in some crosses, as between an " improved " breed and non-descript, breedless or primitive types, they could follow from the heterozygosity of both parental forms allowing in some offspring a greater accumulation of dominants, and fresh combinations.

In some cases the intermediate form is not the objective. The Polwarth breed in Australia is made up of $\frac{3}{4}$Merino $\frac{1}{4}$Lincoln (this may also involve some heterosis); registration is by successive stages. A standard of type is laid down by the Polwarth Sheepbreeders' Association, with provision for flock inspection. The stages covered from an original cross between Merino (M) and Lincoln (L) are : $M \times L$; $\frac{M \cdot L}{2} \times M$ ram; $\frac{3M \cdot 1L}{4} \times \frac{3M \cdot 1L}{4}$, which are equivalent to " come-backs " (*see* p. 112). The progeny of this mating are called the first generation and are eligible for recording in the Flock Book of the Association. (*See* Figs. 15, 16, and 17.) After this no animals can be introduced into a registered flock except from another registered flock. At the third generation, stock can compete in Polwarth classes at shows, but not until the fifth generation of $\frac{3M \cdot 1L}{4}$ breeding is attained is registration admitted to the Association Stud Book.

A similar backcross type is being developed in Russia to combine egg production and body weight in hens. The off-spring of Light Brahma cocks × White Leghorn hens exceeded White Leghorns in both characters, the F_1 were backcrossed to White Leghorns and the new " Heavy Leghorn " breed developed from the offspring of this mating ; its egg production is 127% that of the White Leghorn, and its average weights at nine months of age surpass those of White Leghorn males and females by 215 grams and 140 grams respectively (Alihanjan, 1941).

Even in old-established breeds much variation still remains,

FIG. 15.—The construction of the Polwarth breed ;
Stage 1—F$_1$ Lincoln × Merino.
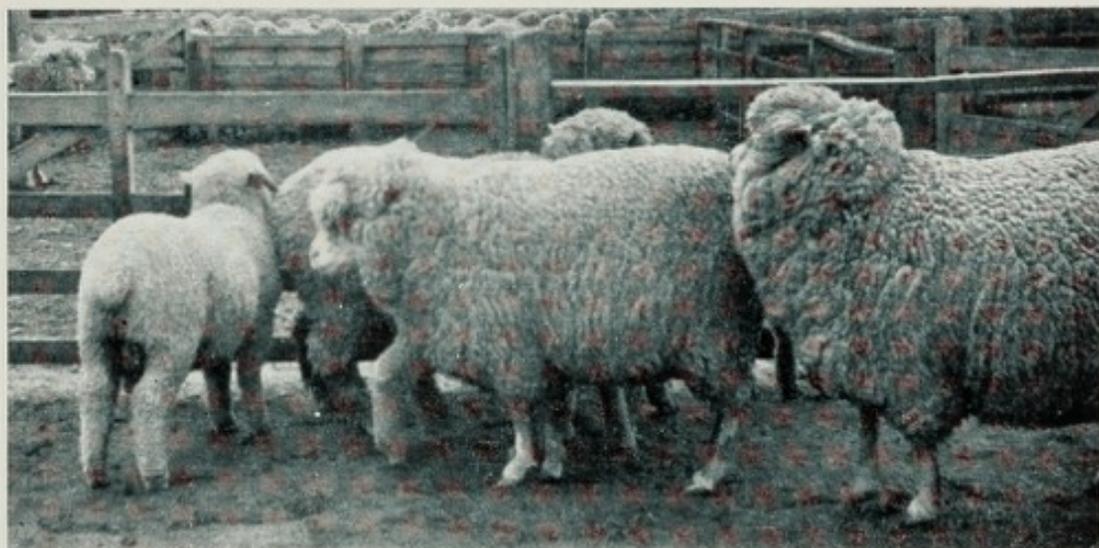
FIG. 16.—Stage 2—The " comeback " type.
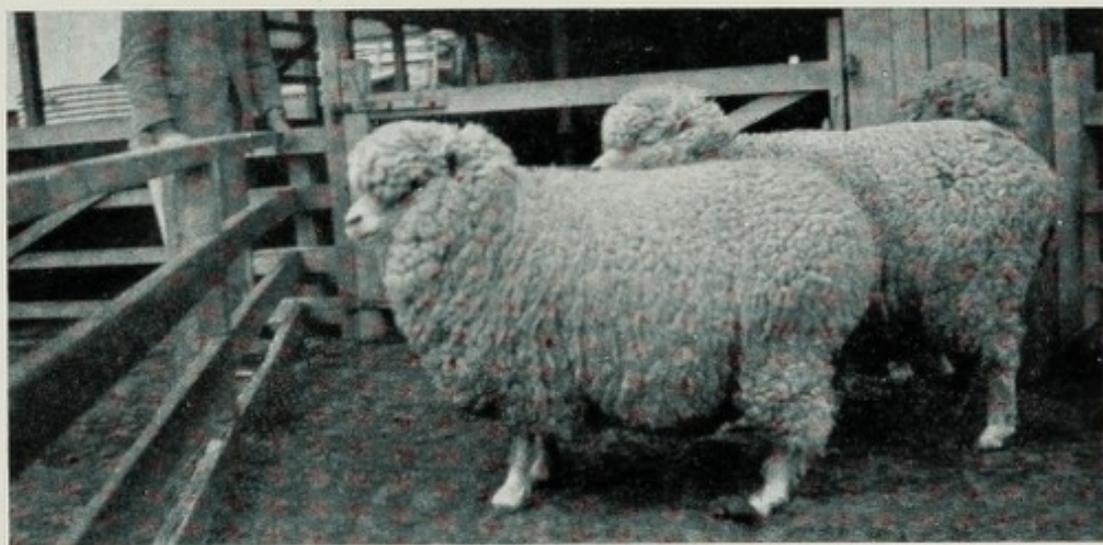
FIG. 17.—Polwarths.

and further progress towards the breed aim depends upon how the variation is made up. For instance, Cole (1940) has noted more variation between individuals within breeds than between breeds, under similar conditions in Michigan during 1939, in respect of daily increase in live weight of lambs up to 135 days of age among Hampshires, Oxfords, and Rambouillets, the respective ranges being 0·42-0·62 lb., 0·4-0·737 lb., and 0·4-0·66 lb.; he concludes that lengthy selection has not led to much uniformity in this production character. Probably no breed has yet attained a state when only a negligible amount of genetic variability can occur except possibly in respect of a single gene effect, free from genetic modification. The genetic basis for further progress may be lacking; the genetic constitution may not be sufficiently fixed by the breeding systems followed; environmental conditions may not allow the desired combinations to be suitably expressed; or the breeders may require a more precise means of detecting the remaining variation. As an example of the last, the case of fibre variability in Merino wool can be cited : Merino breeders have been highly successful in considering fleece characters such as density, length, weight, and yield, but the ordinary methods of judging such characters do not apply with any precision to the question of the variations in fineness from fibre to fibre within parts of the fleece. In spite of the fact that even fairly narrow differences can be distinguished in general fibre fineness (as a part of fleece quality), as, for instance, between shoulder and britch regions, local differences in fibre uniformity are not readily appreciated, *e.g.* on the britch or on the shoulder. (*See* Fig. 18.) In so far as this fibre variability is a fault in the clip, its recognition is necessary before steps can be taken to reduce it; this can be done by microscopic analysis of the fleece. (For the practical application of such methods, *see* Lefroy, 1942.)

A change in breeding aim can lead to increased variability of performance or tend to split a breed, as in the Berkshire and Canadian Berkshire pigs. Inconsistency of aim over a long period of time can cause fluctuations; cattle breeding in East Friesland began with breeding for performance, then came a phase in which conformation, colour, and other breed characteristics were emphasised, later performance testing brought back the former aim to prominence, but even with
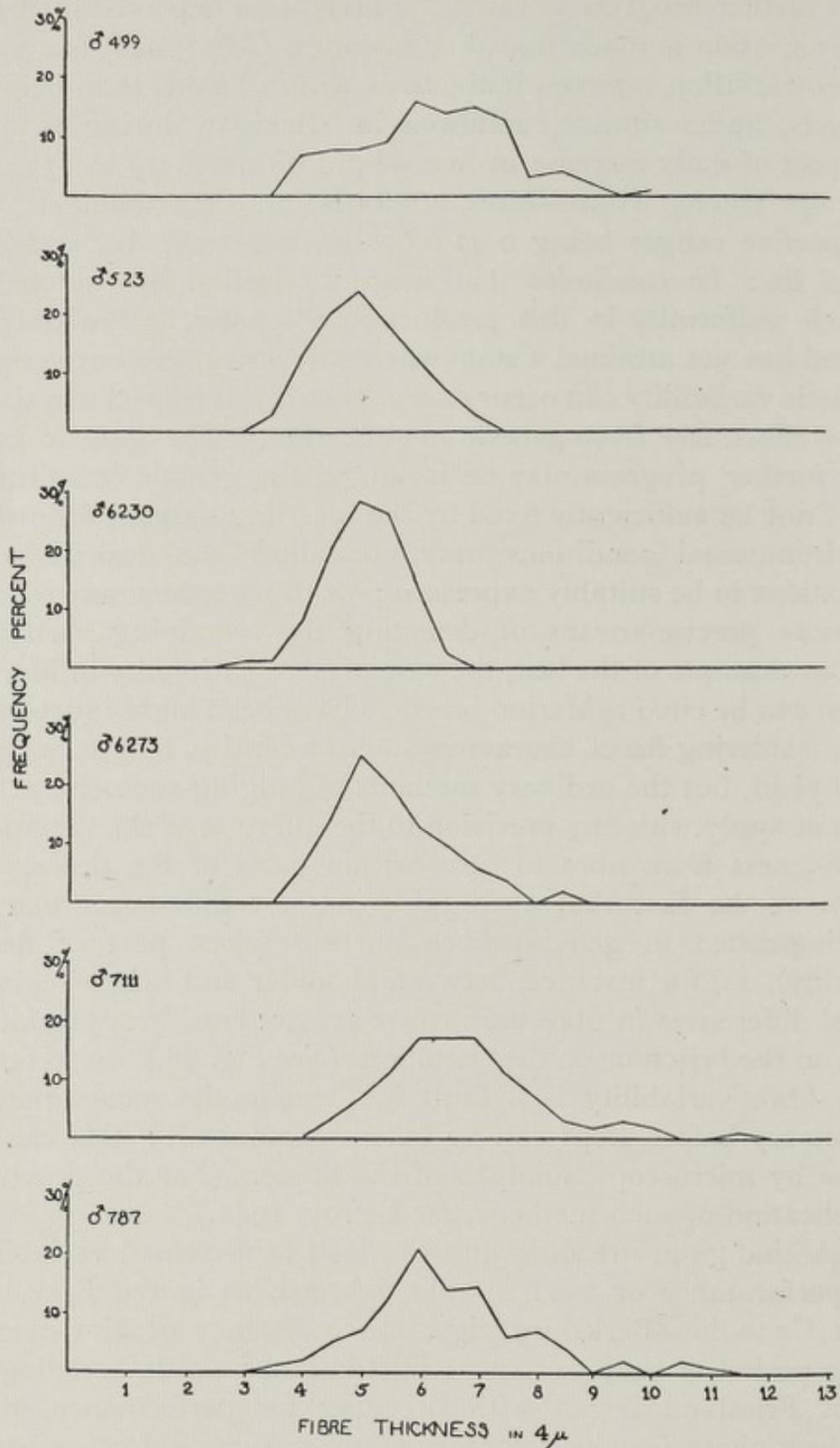
FIG. 18.—Fibre variability in high-class stud Merinos (shoulder samples).

the great advances in husbandry in recent times and their effects in raising production, the early high performance has not yet been achieved again (Osterkamp, 1942). The Poland China breed of pigs was founded among many types in about 1850 and formed into a breed in 1878. Between 1900 and 1920 the breed interests became divided between the lard or " hot blood " type of small animals and the " big type ", with larger frame and more rapid growth at weights between 200 lb. and 250 lb., at which weight it fattened. After 1920 the ideas came together towards an intermediate, " meat " type. Lush and Anderson (1939) examined 400 sample pedigrees, tracing back to about the year 1886, for each of four periods, 1900, 1910, 1920, and 1929, and calculated the inbreeding and relationship coefficients (p. 95). Inbreeding increased steadily from 2·0% in 1900 to 9·8% in 1929, but there was little tendency to form separate families which did not interbreed. The ancestors of the widely differing " hot bloods " and " big types " were closely related, so that the types had become distinguished mainly as a result of phenotypic selection. The inbreeding which had taken place was mostly due to the use of sons, daughters, and grandsons and granddaughters of outstanding animals, but the favoured ancestors were continually changing and were never closely related to each other.

This method of studying breeding systems has been applied to several other breeds and shows that different procedures have been followed. The imported Hampshire breed of sheep expanded slowly in the U.S.A. until 1906 and then increased very rapidly by growth, and with fresh importations, until 1912 and up to 1927, after which it became fairly stabilised numerically, about 20,000 being registered each year. Carter (1940) shows that the inbreeding was about 1·4% in 1925 and 2·9% in 1935, though at these times the relationship coefficients between animals chosen at random were 0 and 0·5%. This indicates that a certain amount of separation into families had taken place, probably as a result of the geographical isolation of parts of the breed following its rapid expansion, rather than any definite or deliberate line- or inbreeding. The large numbers of importations, and their recent dates, explain the fact that very few prominent animals were found in the pedigrees ; only two rams, father and son, were related to the

breed more than 2%. On the other hand, among American Hereford cattle the inbreeding coefficient increased to 8·1% in 12·9 generations of average length 5·4 years, between 1860 and 1930, in which year relationship within the breed was 8·8% (Willham, 1937). There had been a tendency to form distinct families, which never went far before crosses with other families were made. Most of the animals showing high relationship were ancestors, or descendants of one animal, Anxiety 4th, or were his mates. Among the foundation animals, to which the lines chosen at random traced, over 80% were bred by twenty breeders in England, three of whom actually bred 38% of these animals.

A similar tendency has also been revealed in the Aberdeen-Angus in U.S.A., where the breed is tending to separate into groups largely because of linebreeding and the use of home-bred animals or stock bred in near localities (Stonaker, Holbert, and Lush, 1942). In samples of 2000 cattle born in 1900, 1910, 1920, 1930, and 1939, the average inbreeding and relationship coefficients were, respectively: 8·9, 9·4; 12·7, 16·3; 10·8, 12·2; 14·2, 16·1; and 11·3 and 13·3. If mating were entirely at random, it is calculated that only 38 bulls would have been needed to cause an increase of inbreeding at this rate, whereas somewhere about 2300 bulls are used in each generation. One bull, Black Prince of Tillyfour (77), is almost a grandsire of the whole breed, which is related to him 24·1%, while over 60% of the foundation animals were found in five herds in Scotland, 50% of them being bred in the Watson herd alone.

It would appear that inbreeding has not played so much part in dairy stock, possibly for the reasons that in beef cattle the phenotypes of both bulls and cows can be readily assessed and a bull can be judged by his progeny test at about 4-4½ years of age, while the dairy bull cannot be assessed on phenotype, and must wait till he is 6½-7 years old for his progeny test. Also dairy cattle breeders tend to have had the idea that inbreeding is detrimental, though Fowler (1932) has shown in the Ayrshire breed that cows producing over 1000 gallons were just as inbred as the average producer with under 800 gallons, though they had an inbreeding coefficient lower than the breed average. In the Jersey also (Smith, 1929) high

yielders averaged 1·845% inbreeding as opposed to the breed average of 3·9113. Yet it should not be impossible, though more difficult, for the breeders of dairy cattle to secure greater genetic uniformity for high production by selection and inbreeding on similar lines to those used by beef cattle breeders.

A contrast in breeding policies is also found between heavy and light breeds of horses as represented by the Clydesdale and the Thoroughbred. In the former, Calder (1927) shows that selection, favoured by the numerical smallness of the breed, its local popularity, and the high numbers of progeny which can be got by a sire, has helped to build up the breed type, without much inbreeding (6·2% in the period 1920-25) but with definite linebreeding, particularly towards the Darnley line. On the other hand, the pedigrees of 556 winning and 395 beaten U.S. Thoroughbreds gave no signs of the formation of well-defined lines ; selection had played a greater part than inbreeding in any fixing of standards that had been achieved (Steele, 1942), and, not surprisingly, the "tail-male" or "tail-female" ideas received no support whatever.

That so many of the pedigrees trace back to so few individuals in many registered breeds is no evidence in itself that any particular foundation animal confers more merit upon his later descendants than any other. Nor is the fact that the apparently outstanding animals, with a marked influence in the breeds, are frequently males any direct evidence that the male has a greater influence than the female. As individuals the males have greater numbers of offspring and can be culled more heavily than the females. It is usually only when a dam has several sons that become widely used (e.g. the Holstein-Friesian cow De Kol 2nd—Lush, 1937) that she can have any appreciable influence as shown by her frequency in the pedigrees of far-off descendants.

The development of dual-purpose breeds presents somewhat different problems, largely because it covers the attempt to combine two major forms of performance, but with each not expressed to a maximum or even an optimum. The aim is usually to obtain a balance of standards so poised that either one product can be increased according to particular demands and in response to a particular direction of husbandry, or else

a more or less fixed combination can be secured of the two physiological characteristics which will move well together under a fairly wide range of conditions. The distinction may be a fine one, but has practical significance, in that the latter would require a closely linked genetic combination to be discovered and fixed by linebreeding, while the former might be satisfied by a heterozygous type whose more homozygous offspring could be readily, and with equanimity, disposed of as animals suited to one or other kind of performance, only some being used in corrective matings (p. 119) to reconstitute the intermediate heterozygous " breed " type. The nature of the ecological niches to which dual-purpose ideals are adapted will be indicated in the next chapter ; it can be said at this stage that at low levels of husbandry, either socially or technically determined, a dual-purpose combination is sometimes warranted, but if the productive potential is raised, then the choice has to be made between increasing the dual-purpose level as such or distributing the effort over two performance types. For instance, while in India it is now considered preferable to select superior producers among the native stock and thus to improve the indigenous breeds for milk production rather than to import European breeds, it is also considered inadvisable to attempt to secure a true dual-purpose type to meet all the demands of draft and milk which may be better met by separate draft and dairy breeds (Olver, 1942).

Sometimes contributions from several established sources are necessary. Ranch sheep production on the Western ranges in U.S.A. covers a wide range of conditions throughout which vigour, wool, and lamb are important and often large size of ewe is required. While the Columbia breed $\left(\dfrac{\text{Lincoln . Rambouillet}}{2}\right)$ is designed to meet the need for size, the Targhee breed is also being developed to provide a standard type where a smaller ewe is wanted. It can broadly be described as the product of mating Lincoln rams to Rambouillet ewes and backcrossing to Rambouillet rams (i.e. it is $\dfrac{\text{1L . 3R}}{4}$, cf. the Polwarth, p. 158), although some Corriedale blood has also been used. More complex methods have been used in combining thriftiness, disease and pest resistance, and improved

performance for tropical conditions ; for example, the Philamin breed of the Philippine Islands combined Philippine native (P), Indian Nellore (I), and Hereford (H) blood for improved beef-draft purposes, as follows (after Manresa, 1939) :

$$P \times I$$
$$|$$
$$\frac{P \cdot I}{2} \quad \times \quad H \quad \times \quad I$$
$$| \qquad \qquad |$$
$$\frac{P \cdot I \cdot 2H}{4} \quad \times \quad \frac{H \cdot I}{2}$$
$$|$$
$$\frac{4H \cdot 3I \cdot 1P}{8}.$$

There are sufficient indications generally—only some have been quoted above—to warrant the conclusion that all the established breeds retain enough genetic variability to make some change in type possible, provided that the tools of line-breeding and selection can be freely and accurately used. This proviso requires also that a sufficient number of animals are available on which to work, otherwise inbreeding may perforce have to be used to an extent which might be dis-advantageous or dangerous in inflicting undesirable character-istics on too great a proportion of the stock to allow them to be culled. Also, numbers are necessary to ensure that the requisite genes have reasonable chances of being brought together in the desired combinations frequently enough for the combinations to be recognised. Again, as increasing the number of characters for consideration greatly decreases the selection differential possible for each one of them, and hence extends the time in generations needed for progress, it is essential that the aim and the methods should be consistently observed over many generations if uniformity is desired. These considerations apply also to the development of new breeds ; and just as a breed is a group or a sample of the population, so is a herd or flock a sample of the larger group.

Suggestions for breeding policies for improvement cannot, however, be advanced until further interrelationships of the problems of type and environment are examined.

CHAPTER XV

TYPE AND ENVIRONMENT

BROAD associations of type and environment are recognised in breed descriptive terms or in some of the classifications frequently used, such as " lowland " *v*. " alpine " or " mountain " cattle, " lowland " *v*. " mountain " sheep, " steppe " cattle, and, to a less degree, in the " land " races of various species. The implications are that selection in one form or another has led to the establishment of more or less distinct types or breeds which differ in adaptation to certain sets of environmental conditions, and also that farm stock are similar to other animal species in having optimal environments for their growth and reproduction. For farm stock, the environmental complex is, however, more intricately woven than for other, wild species, in that a network of man-made economic and social factors is superimposed on the biological, climatic, geophysical, and other influences which affect their distribution.

From early records and descriptions it is clear that local types or breeds adapted to particular ecological niches made up the livestock population ; and to a great extent this view of the constitution of livestock populations still holds good, although the interrelationships involved are more complicated and can vary even within narrow geographical limits. Moreover, the dominant features of the environmental complexes differ from one set of conditions to another, and may change in time according to the stages of social and technical development attained in the human population owning the stock. Religious considerations can decide against a particular species—Islam excludes the pig. In parts of India where there is an important demand for ghee, buffaloes are favoured rather than cattle because the she-buffalo gives more milk of higher fat content than the ordinary village cow (Wright, N. C., 1937). Primitive standards of wealth recognise numbers rather than quality or production merit of stock. The kinds of products and their uses have obviously great effects : a relatively inflexible demand for mohair has restricted Angora

goat raising broadly to parts of the U.S.A., South Africa, and Asia Minor, while the rapid rise and decline of the ostrich industry in South Africa with the changes in fashion for the ostrich feather are well known. The effects of a consumption trend from beef to mutton and lamb in Great Britain, of a realisation of the possibilities of pasture improvement and of methods of increasing stock-carrying capacity in New Zealand, together with the technical advance of refrigerated transport to get the meat from one country to the other, inter-locked to stimulate lamb production in favourable regions in New Zealand and to change the composition of its sheep population from predominantly wool-producing Merino to predominantly Romney. But the influence of the form of production can be seen in less obvious ways; for example, the increase of about 10% in the lowland cattle population of Germany, at the expense of the hill breeds, since the end of the nineteenth century has been deplored because of its effect on the leather trade, the lowland cattle having hides suited only for making flat leather, for cowhide and boxcalf materials (Grassmann and Trupke, 1942).

Pontecorvo (1939) has described a sequence of inter-relationships between density of human settlement, topography and soil, systems of cultivation, and dual-purpose beef-draft cattle, which have been usually developed from primitive draft types of pronounced hardiness. The beef-draft types are frequently associated, especially in Europe, with dense human settlement, difficult topography and soil conditions, and culti-vation methods with high animal labour requirements. The sequence begins with agricultural systems of discontinuous farming and wide unimproved grazings, when oxen do the work, the cows produce only replacements, and low-quality beef is obtained from old mature animals; at the other extreme are closely settled agricultural systems and high densities of both human and cattle populations, in which the cows work and males surplus to reproduction needs are finished for beef. Through the intervening stages the ratio of working cows to working oxen progressively increases.

The nature of the product can also affect the course of selection in the stock, in that it can introduce a real trend to confuse the apparent aim; for instance, a difficulty in horse

selection arises from the low fertility of mares, which is influenced partly by the fact that a mare has a use and value for work even when she is barren (Cummings, 1942). A similar situation probably holds to some extent in Merino sheep kept under pastoral conditions for wool production, where the dry ewe can survive and produce a profitable fleece when a pregnant or milking ewe is at a disadvantage. These contrast with the case of the range beef cow, whose main function is to produce and rear a calf, on which basis culling is made.

The general distribution of stock populations as such, *i.e.* in numbers, is decided by a complex of environmental factors (as considered and analysed by geographers, *e.g.* Huntington, 1925), but the question of type and environment in relation to stock selection and improvement is that of how the complex, or any component, affects the composition of the populations in terms of breeds or types. While extensive spheres of influence can be outlined for particular equilibria of the main factors, within such spheres the local conditions may vary greatly, even down to significant differences between neighbouring farms. In this sense the question is ultimately that of the internal herd or flock environment, which can decide, for example, that the system of sheep husbandry shall be on the basis of a flying flock kept for only part of a year, but the problem of adaptation still remains, as in any particular locality a flying flock cannot be made of any kind of sheep, some kinds being better suited to its demands than others. Similarly, in cattle herds the choice of stores, or of feeders, is not entirely free but is usually restricted to the most readily available stock types; again, the highly " artificial " conditions of intensive poultry husbandry for egg production have emphasised the necessity of regarding male chicks as useless surplus and have thus encouraged their elimination from the individual flock, by chick-sexing methods which, when sex-linked characters are used as criteria, introduce some restriction of choice based on genetic characters, *e.g.* of plumage, that have no direct relationship with the main enterprise of egg production (*see* Pease, 1943).

The objection that an ecological approach to the problem based on the adaptations of breeds is unjustifiable because so many stock populations are crossbred, is not itself valid, since

crossbreds are also affected by the same environmental complexes as apply to purebreds, and the fact of crossbreeding serves to merge or to extend the spheres of influence of the dominating factors operating on the parental breeds.

It is interesting to note the parallel in plant breeding, where it has become almost axiomatic that the forms suited to the particular conditions, of soil, climate, demand, inter-relationships with partners or competitors, etc., must be selected, so that the fine adjustment or adaptation of species or strain to environment can be achieved. Yet it is sometimes held that this aspect can be neglected in animal breeding, improvement and introduction, presumably in the belief that the techniques of husbandry can completely override all other factors. (This theory is frequently advanced in relation to the restocking of devastated regions.) Furthermore, the plant breeder and grower recognises that the different species and strains do not respond uniformly to changes in habitat; a variety which is, for instance, highly productive, or is disease resistant, in one locality is not necessarily superior in production, or may be susceptible to disease, in another area. The animal breeder has frequently overlooked the similar situations which can apply in his stock and has yet to gain the same precision as that of the plant breeder in dealing with this phase of his work.

The environmental complex is never static, either in localities with an established stock population or in those gaining a new one. Stock improvement, in so far as it is a matter of securing more satisfactory adaptation, is a continuous process of importation : of new ideas of the desirable gene complexes and frequencies from among the existing genes, or of fresh genes or gene combinations, to established populations or breeds ; of stock with the desired genes to new countries and developing populations ; and to both these, of new ideas and progressive methods in husbandry. The last can have major effects, and it is usually difficult to assess separately the parts of progress or improvement attributable to genetic or to husbandry effects. In many cases it is almost certain that improvement has been attributed to breeding when it is largely due to better husbandry, as when the gain has been so rapid at first as to be virtually impossible of attainment by genetic

means and has then only been maintained, *e.g.* in milk yield in the latter part of the nineteenth century (Prentice, 1942), or possibly in recent years in the fleece weight of the Australian Merino (Nichols, 1940). Also, the success of some official livestock improvement schemes which provide for the subsidised males being maintained and used under prescribed high standards of care, merits examination as to whether it is due to the introduction of better standards of husbandry rather than to that of any specially advantageous genotypes.

To some extent lack of adaptation can be overcome by appropriate management, and though in many cases this may require uneconomic, intensive methods, it may sometimes be justified by returns, as for example with the installation of humidity control to render conditions more comfortable for high-yielding milch cows in some tropical regions (Singapore). Generally, as conditions improve minor differences become more important, *i.e.* the expression of adaptational traits is not overridden by environment. For most practical purposes it can be considered that, while a favourable environment is necessary to allow favourable genetic situations to become expressed, once the physiological limits to performance of a particular genotype are attained—the " ceiling values " of production reached—further amelioration of environment yields no further increase in production. Thus, from experiments at the Institute of Animal Breeding, Wiad, Sweden, it is concluded that, while good environments accentuate inherited differences in milk production more than unfavourable environments do, no more increase in yield is obtained with a very high nutritional regimen (Bonnier, 1940, 1941). The ceiling value can be in respect of a fairly simple character, such as that of the butter-fat colour in cattle, which cannot be pressed beyond a certain intensity by increasing amounts of greenstuff in the rations (Thompson, A. A., 1931) ; or more frequently it is related to a complicated series of physiological interactions, when the optimal performance for a combination of products may be below the ceiling values of each independently. When stock developed in good conditions are exposed to less favourable environments, in which their original level of performance cannot be sustained, those traits which are least adapted to the stress in the new habitat tend to break down. This is usually

stated as " the constitution breaks down ", as with temperate climate milch breeds taken to the tropics (Hammond, 1932). (*See* Fig. 14.)

The conception of importation outlined above can be used as a basis for considering the course of " improvement " and the breed composition of livestock populations. The processes of development are essentially similar both in countries where the stock population has attained a numerical equilibrium within the prevailing agricultural and pastoral systems and those where open country is being exploited ; the former areas can be considered *saturated* so far as their stock are concerned, the latter *unsaturated*. But the make-up of the stock population in respect of breeds and types at any time can be regarded as a question of " *maturity* " of the population in relation to possible improvement—stock populations may be called " young " or " immature " while improvement or adjustment to prevailing conditions is not far advanced, " mature " when the stock types have achieved a high degree of stability. (The idea is somewhat analogous to that of young and old soil types.) Obviously, both saturation and maturity are relative ; also, the stock population of a country need not be homogeneous in either respect, the dairy cattle portion may be relatively immature and their average production low, while the sheep fraction may be mature, and so on. A primitive stock population may be saturated and mature, but the importation of new concepts of performance, of new techniques of husbandry and agriculture, may set it off along a new phase of development and improvement, in relation to which it may be saturated in numbers but very immature. Yet better varieties and better management may lead to a reduction in stock numbers or stem production decreases in a population declining in numbers, *e.g.* Payne (1941) notes that, in Kansas, while poultry stocks had decreased by about 32% on 250 representative farms between 1926 and 1941, output had not diminished to this extent because of more productive varieties and improved housing and feeding.

Changes in saturation and in maturation are well shown in sheep populations, as this animal is usually kept under less artificial conditions than other species and so exhibits more freely the effects of the natural controls. In the simplest case

of a natural pasture area the saturation density of a sheep population is decided by the carrying capacity of the grazings in relation to their feeding value and regrowth, and in a new country increases in numbers tend to follow a well-defined " growth curve " (the Verhulst-Pearl logistic curve); in Tasmania during 1817 to 1926 the sheep population first increased rapidly until late in the 1840's, when it reached about 1,670,000 as its saturation density. After the early 1850's it fluctuated around this number, made up almost entirely of Merinos, until 1925, when fresh increments began, owing to the spread of improved pasture management and a greater market for fat lambs (Davidson, J., 1938). These two factors co-operating imposed a change also in breed composition, encouraging the development of crossbreeding the Merino with longwool rams, and the halfbred ewes with Down type rams to produce the fat lamb crop, in the favourable areas.

The British Isles could be said to have a mature sheep population at about the end of the eighteenth century, composed of numerous local types, and no doubt many crosses, for the most part with characteristics sufficiently distinct to warrant a breed classification (*e.g.* Youatt, 1837, Low, 1845), but falling into fairly well-defined groups, such as mountain longwools, lowland longwools, Downs, heath breeds, etc., according to habitat. Among the lowland longwools and the Downs were developed the improved Leicester and Southdown, respectively; their influence spread rapidly, so that by about 1840 they had been tried as " improver " breeds on many of the old local types. Some time about 1870 their spread had probably reached a maximum extent and signs of recession had become apparent because other " improved local " breeds were being developed, each owing something to either the Leicester or the Southdown, and also because it became recognised in certain cases that replacement of the old breed by the new was not advantageous. Among the lowland longwools, for example, while the old Lincoln and Romney Marsh " breeds " were subjected in part to new Leicester influence, its effects in lowering fleece weight and in reducing the suitability to local conditions caused breeders' aims to revert to the older forms (Nichols, 1928). The stimulus

to improvements of husbandry as well as of breeding spread also, and the wave of development of most of the present

	IGNEOUS	PRE CAMBR	CAMBRIAN	SILURIAN	O.R.S.	CARBONIFER	PERMIAN	TRIASSIC	JURASSIC	CRETACEOUS	TERTIARY	RECENT
HERDWICK	■			■								
CHEVIOT	□			■	■							
BLACKFACE	□	■			■	■		□				
SWALEDALE				□		■	□	□				
GRITSTONE						■						
LONK						■						
BORDER LEICESTER		▲		△	▲	▲						
WENSLEYDALE				△		▲						
LEICESTER									▲	▲		
LINCOLN									▲	▲		▲
COTSWOLD									▲			
ROMNEY MARSH										▲		▲
RYELAND				●	●				●	○		
SOUTHDOWN					○				●	●	○	
OXFORD					●			●	●			
SHROPSHIRE						○		●				
HAMPSHIRE									●	●		
DORSET DOWN									●	●		
DORSET HORN									●	●	○	
SUFFOLK										●	●	
WELSH MOUNTAIN		■		■	■	■						
KERRY HILL				■	■	□			■			
CLUN FOREST				■	■							
DARTMOOR	△				▲	▲						
EXMOOR					▲				△	△		
DEVON CLOSEWOOL					▲	△						
SOUTH DEVON					▲							
DEVON LONGWOOL					△	△	△					
WILTSHIRE	○	●		●					●			

FIG. 19.—Geological environments of aggregations of purebred flocks of sheep in the British Isles.

British sheep breeds had begun. The extent of spread of the new breeds and any recession bore some relation to the degrees to which the environment of the original focus of development
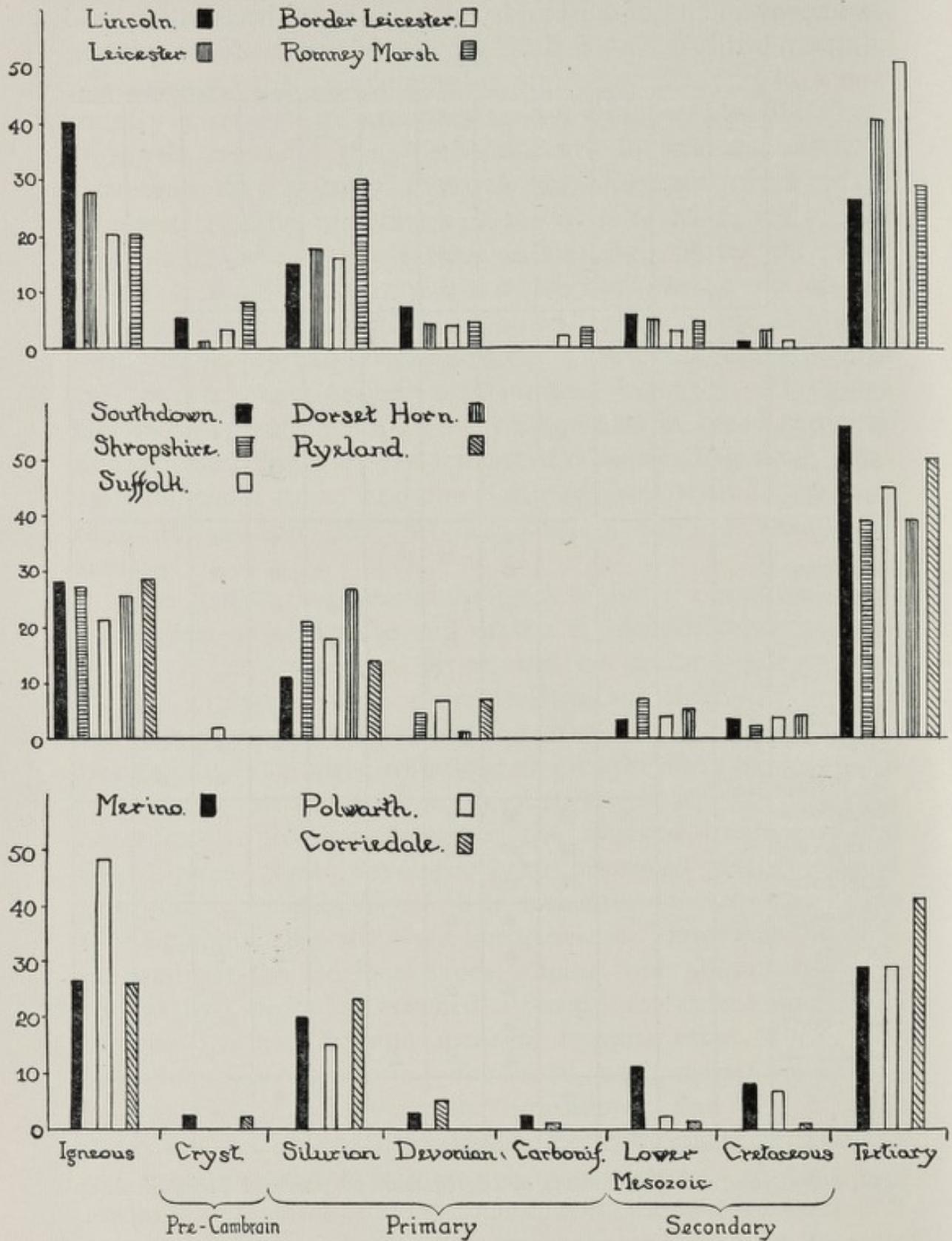
FIG. 20.—Geological environments of sheep breeds in Australia; columns indicate the percentages of the registered flocks of each breed that occur on the different formations.

was distributed or could be recapitulated in other areas. The new Leicester was developed in its name county but its main breeding area is now in the eastern parts of Yorkshire. If the natural environmental complex is considered according to its components, the main breeding areas of the various breeds and types can be distinguished, *e.g.* the Southdown flocks, and their close relatives, retain their densest aggregations on the Jurassic and Cretaceous formations, mainly in the South of England. (In Fig. 19 the solid dots represent the densest aggregations of purebred flocks, the outlines less concentrated aggregations or areas into which the breeds have spread recently.) In so far as, for sheep, the general characteristics of the grazing are controlled by temperature and rainfall, to which the animal's physiological processes also respond, the conditions of these factors in the prevailing climate of the ancestral homes of the breeds can also be distinguished and used as a broad basis for forecasting the response of a breed when exported to another area or country (Nichols, 1933). The ways in which registered flocks of various types in Australia are distributed according to geological environment and to annual rainfall zones are shown in Figs. 20 and 21.

It can be suggested that an adaptability to varied environmental conditions in its original home confers an advantage on a breed in its adjustment to and use in other areas, as has been suggested by geographers regarding human populations, whereas original restriction implies less plasticity. If this is so, then a breed in which little attempt has been made to mature its capabilities in relation to special demands or performance, *i.e.* of " general utility " type, can be expected to have possibilities for wide distribution ; or, alternatively, a wide distribution indicates no particular aim towards greater specialised performance, or definite peak of desirability, unless the conditions in which high performance are achieved are closely recapitulated in many other localities.

While the local environmental complex may change, some of its basic natural components, such as geological conditions, climate, altitude and topography are fixed, and alterations in others are likely to be slow. The idea that over a long period of time, and in respect of the major environmental factors, close harmony between a breed and its habitat is desirable

has led to practical emphasis on the advantages of " soil-stable " breeds (" bodenständig ") in many countries, especially in Europe, and on improvement by selection within the " land " races or breeds of most classes of stock. The latter is well
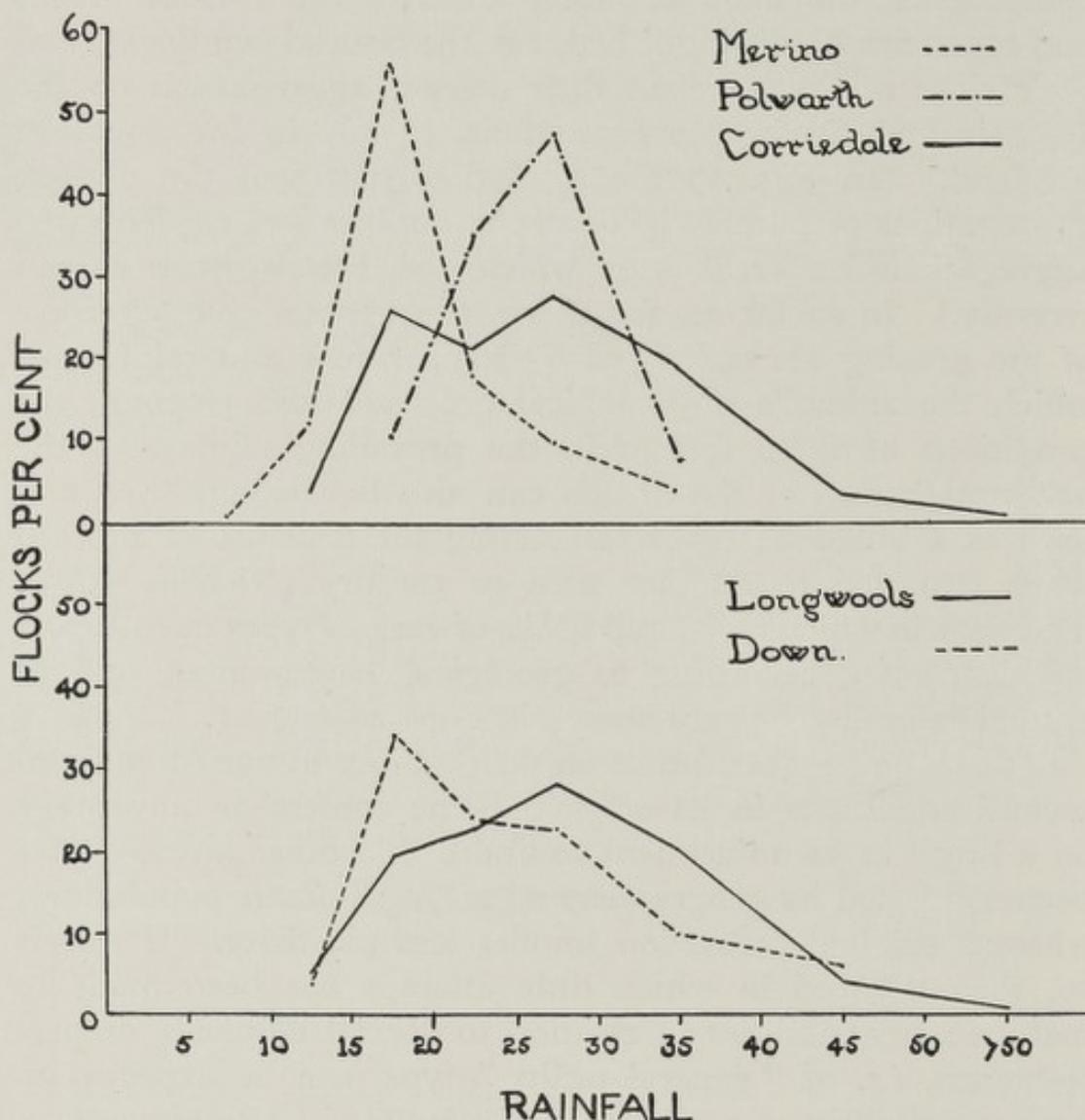
FIG. 21.—Sheep types and annual rainfall zones in Australia ; vertical scale—the proportionate distributions of registered flocks, horizontal—annual rainfall in inches, thus, about 25% of the registered Corriedale flocks, compared with over 50% of registered Merino flocks, occur in the 15-20″ rainfall zones.

seen in tropical and subtropical regions, which present the most severe changes in environment to improved breeds, most of which so far have been developed in temperate climates.

Just as the particular environmental factors which have predominant influences can vary from one locality to another, so also can the response of the physiological traits that are

apparently most important. Some of these have already been discussed in Chapter VII. From a review of detailed studies by many workers with different species in various countries on the direct and indirect effects of climate and the separate climatic factors, Rhoad (1941) concludes that these constitute the major part of the natural environment where it limits the extent to which an artificial environment can be made favourable to production. J. C. Bonsma (1940) has considered the questions of heat tolerance, grazing habits, skin thickness and hair characters, lowered reproductive efficiency in hot temperatures,[1] and food requirements in relation to the distribution of the Afrikaner and exotic cattle breeds in South Africa and the effects of climatological factors ; in that country, he suggests, underdevelopment due to high temperatures will occur where average monthly maximum temperatures are 90° F. or over, and no underdevelopment will be found where the average monthly minima fall to 32° or lower. Moreover, it appears that degeneration as a result of high temperatures and small fluctuations will occur generally in areas of the world lying between the north and south isotherms of average yearly temperature 68°, except where the altitude is over 3500 feet or local geographical factors produce cooler local conditions. Exotic breeds in these areas will degenerate even if well fed ; outside these regions, if cattle do not develop well, this is due to improper feeding and not directly to climatic factors.

An example of geological influences on cattle breeds and type is provided by Fleckinger (1937) from studies of the distribution of local French breeds in Corrèze ; among the varieties of the Limousin breed, the Vendonnais is raised in districts with basic argilosiliceous soils, the larger Meyssac in Permian and Liassic districts, and the smaller Treignac on areas deficient in lime and phosphorus. Three varieties also occur in the Salers breed, the classical type associated with volcanic soils, a larger with Tertiary, and a smaller, long-legged form, of inferior conformation and production, on granite.

Among other physiological attributes involved in adaptation generally are : body size—smaller types of cattle with lower

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[1] See also Gunn (1936 ; —— et al. 1942) for this effect in sheep.

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maintenance costs are more profitable in South Africa (Burger, 1941), Jerseys are preferentially distributed in the southern states of U.S.A. because of their size in relation to heat tolerance (Davidson, F. A., 1927); digestibility and food consumption— European type cattle consume somewhat more food in relation to their weight than Zebu cattle in Trinidad (Harrison, 1942); time of most productive heat periods in relation to lambing or calving when growth and quality of natural grazing are high (*e.g.* Thompson, D. S., 1942); and those concerned in the early growth and development such as considered by F. N. Bonsma (1939, *see above*, pp. 59-62).

As a consequence of the varied interactions the different breeds and types are distributed in zones, within which their main breeding areas are still further concentrated. The process of maturation of the stock population involves a settling-down of productive types to zones with readjustment and redistribution in response to changing demands and standards of performance, especially among the types least limited by natural environmental factors. Where local conditions within a zone are favourable to a special breeding aim, the tendency is generally to attempt to create a new breed, or modify an old one, so that the trend would seem to be usually to develop a pattern of breeds each restricted to a special ecological niche. The gaps between the special breed zones tend to be saturated by means of crossbreds, crossbreeding as a policy being directed towards securing both plasticity in relation to environment and flexibility of production; these are enhanced when more breeds rather than few are available for crossing.

Sheep populations, again, provide good examples of the patterns which develop with maturity to set up a *stratification* of the industry (Nichols, 1932; Hammond, 1936). In Figs. 22, 23, 24 the schemes of stratification in three countries, each having a wide variety of environments, are shown diagrammatically. The stages by which the maintenance types or breeds occupying the pastoral areas, named opposite the topmost rectangles, are converted and adapted to higher forms of production follow a definite sequence. In the diagrams the products at each stage are indicated in the lower rectangles by the ends of the broken vertical lines, the dotted continua-

tions of which end at the final dead product where an animal has two main products; to the left of each diagram the con-
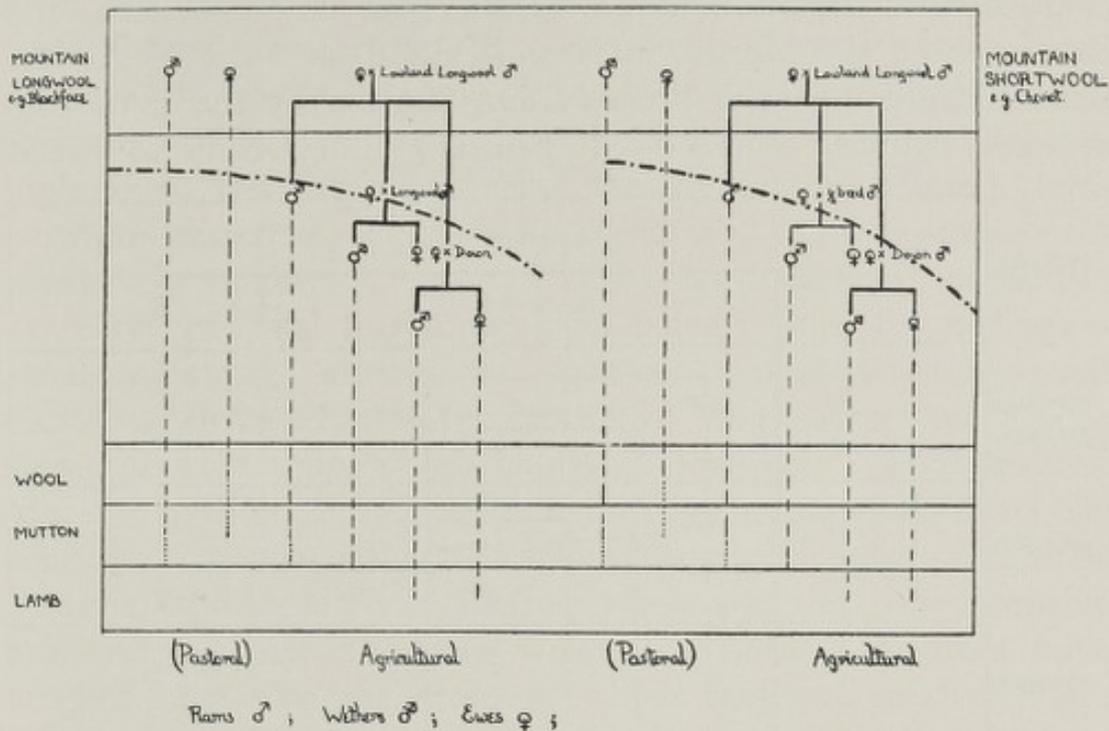
FIG. 22.—Stratification of the sheep industry—British Isles. *From* Nichols, 1932.
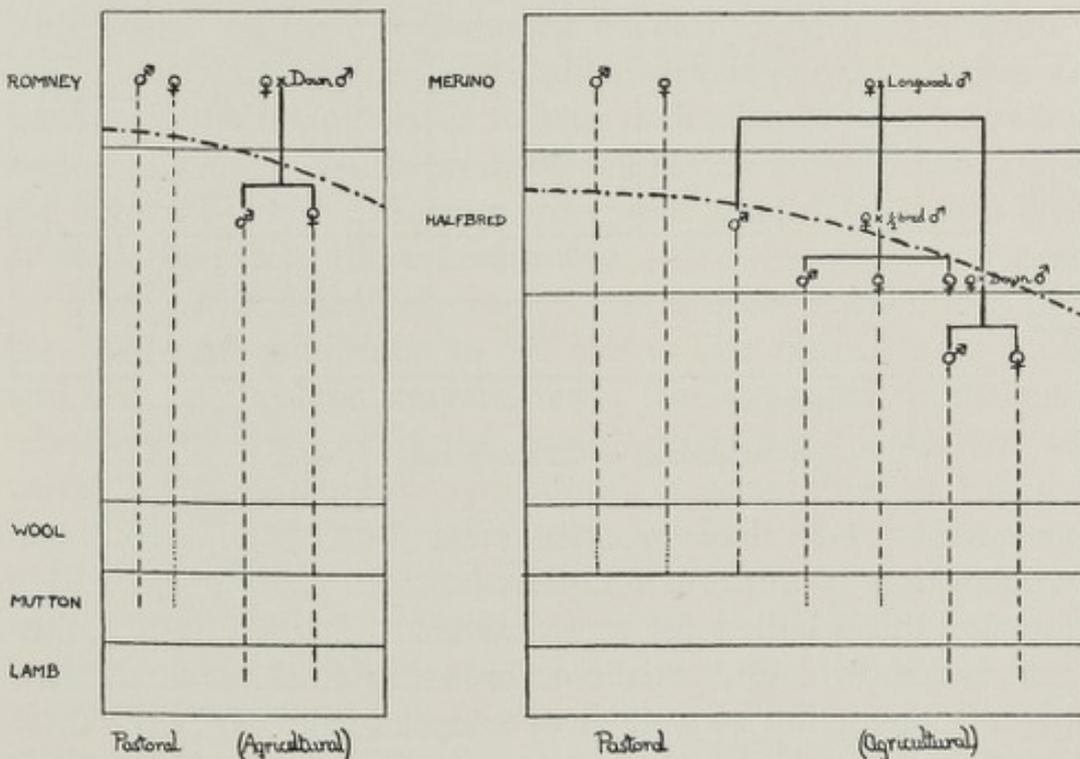
FIG. 23.—Stratification of the sheep industry—New Zealand.

ditions are "pastoral", to the right "agricultural", while the broken dash-dot line which curves across each diagram

from left down to right represents in an arbitrary way the trends of the various factors in the scheme. Thus, the various characteristic mountain types of sheep in Great Britain, the Romney and the Merino in New Zealand, and the Merino in Australia are the *basic* breeds filling essentially the same rôle in each country—their ewes' primary function is to breed
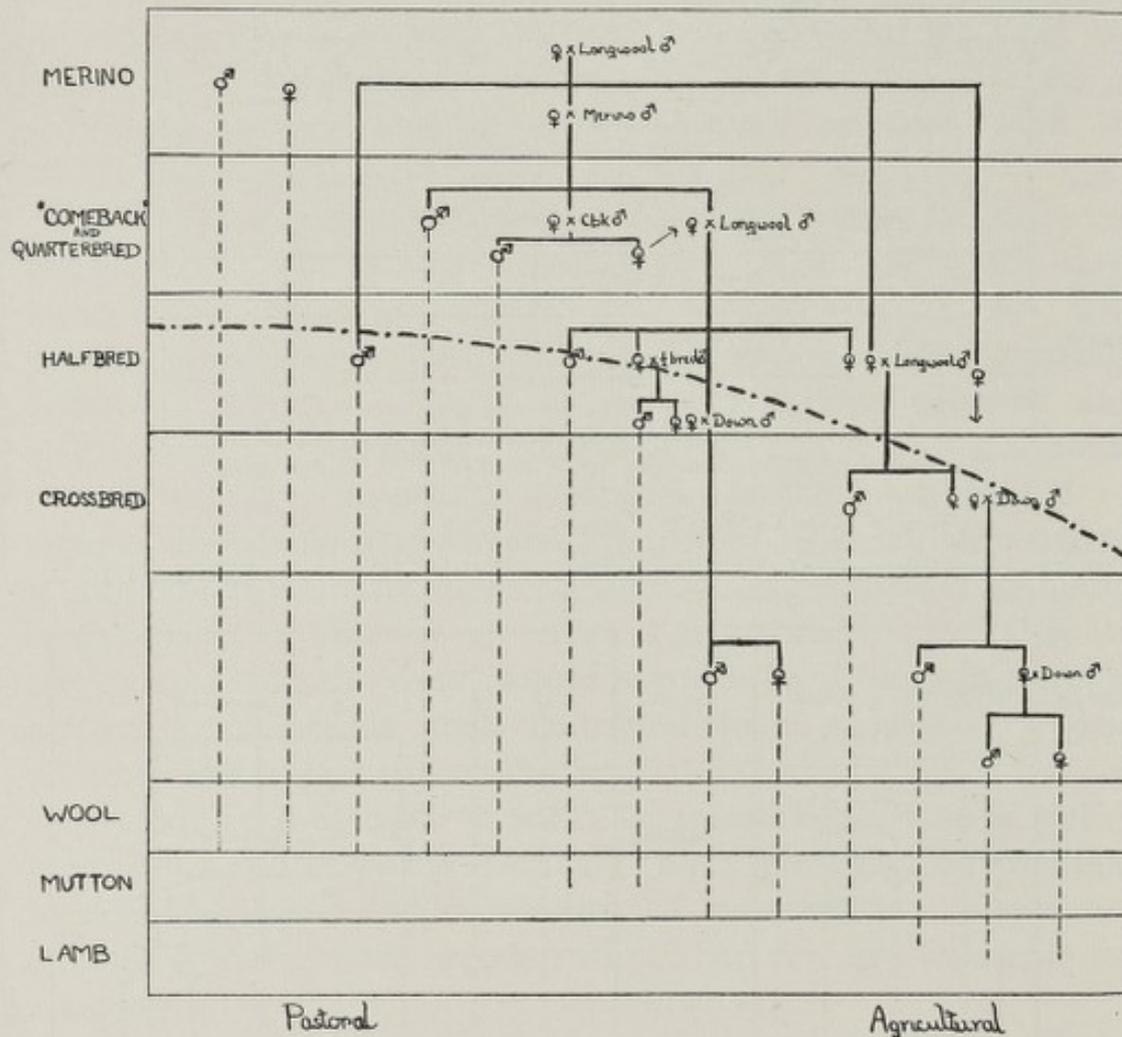
FIG. 24.—Stratification of the sheep industry—Australia.

replacements, but they produce annual wool clips and are of some value as mutton if fattened before slaughter, surplus ewes, and those culled for age, are crossed to rams of other breeds, as shown, and this crossbreeding initiates successive stages of production as well as of adaptation towards the final fat lamb product in which both ewe and wether lambs are all slaughtered.

An industry is mature in so far as it embraces those portions of the range allowed by the predominant natural controls;

a breed is mature in so far as it is developed to meet the requirements of a particular part of the general scheme. The trends need not have the same starting-points in all countries, yet they follow similar relative courses. Among them are : altitude, in Great Britain and New Zealand, high→low ; rainfall, *e.g.* in Britain and for the Romney in New Zealand, high→low, but for the Merino usually low→medium ; temperature, extremes→equable ; poor natural pasture→improved, intensively managed grazing ; low→high carrying capacity ; extensive pastoral husbandry→intensive ; finer or medium→ stronger wool ; slow→rapid growth ; poor mutton→good mutton→lamb ; low→high fertility ; high→low mortality ; slow→rapid turnover on capital ; low→high land values. Moreover, there is generally a movement of stock from the conditions on the left to those on the right, surplus animals being constantly transferred from the less to the more intensive husbandry areas, *i.e.* from where the natural controls have more influence to the areas in which they are relatively less significant. Also the stratification can be accomplished in time as well as in space. New Zealand was first stocked with Merinos ; as the industry developed with expansion of settlement, improvement of natural grazing, refrigeration and transport, the change-over to longwool crosses and longwools, and finally to fat lamb production became superimposed upon the original wool-producing enterprise where conditions were, or could be made, more favourable.

The stratification can vary in complexity, depending upon the range of conditions to be met. The numbers of breeds and crosses involved may be few if the range of conditions is relatively narrow, or if the basic breeds are themselves very variable and not highly specialised in adaptation or function. For the industry to mature, the breeds must be improved towards better performance in relation to their particular environmental demands and functions, and this applies to the basic breeds as well as to the others. The whole of it can often be achieved on one farm when the scheme is comparatively simple and local environment permits ; and this situation frequently applies in the modified systems in other species, *e.g.* beef cattle raising and finishing, although more usually the various stages are dispersed over different farms and areas.

The idea of stock improvement can thus be considered in relation to the complete framework of the industry, and performance merit viewed in regard to function as a part of the structure, the whole process being of continual adjustment to more or less fluctuating environmental influences. Within breeds the problem is largely that of increasing adaptation to, and efficient performance in, definite zones restricted to parts of the general scheme ; between breeds, that of the appropriate choice of crosses to occupy the zones not adequately met by the available pure breeds. Where an industry is still unsaturated, deliberate zoning of breeds in respect of prevailing agricultural or pastoral conditions provides a direct means of increasing saturation as well as of achieving greater maturity. This has been the principle followed recently in Russia, where breed regionalisation schemes, for all classes of farm stock, allocated breeding zones to native and imported types, *e.g.* the Large White has been established as the main " improver " pig breed and widely distributed, the Ukrainian White Steppe, a pork and lard type, has been extended over the steppe regions, the Livny and Breitov local breeds are being improved by selection as fat pigs for central and northern regions, while the indigenous Lesogor breed is being improved (with Berkshire and Large White " blood ") in size and quick maturity but retains its traits of hardiness and adaptability to wooded, hilly, pasture lands in the Caucasus (Kačalov *et al.*, 1938 ; Unanov and Sokolov, 1941 ; Smirnickiĭ *et al.*, 1941).

In industries more mature in types, also, the breeding aims should give prominence to functions relative to the general stratification, especially where the rôle is that of a basic breed ; this implies attention to better performance within the zone conditions. In primitive societies an intense negative selection can result from the practice of selling the best animals to traders, as has been noted among the local sheep in Syria (Schuler, 1937), and insidious ill-effects no doubt occur even in more advanced regions. For instance, in range sheep areas, while body weight is an important factor in selection for fertility and lamb production (Terrill and Stoehr, 1942), and the milk yield of the ewe has a profound influence on early growth of the lambs (F. N. Bonsma, 1939), there is a tendency, emphasised in times of economic stress or prolonged adversities

such as drought for breeders of basic types to realise their best grown lambs and thus to allow a negative selection to operate behind their attempts to emulate the meat production of more favourable areas. Also, in range beef cattle the development of early beef characters on the range, as in parts of U.S.A. and Australia, requires satisfactory milk production in the dams, which is not always consistent with beef type conformation or performance in those dams.

There is also a general tendency for the pedigree breeding units to be aggregated in favoured localities—very few leading, or stud, herds or flocks of the basic types are situated in localities typical of the areas in which their stocks are expected to perform—so that breed standards are dictated by what can be achieved by relatively few breeders under environmental circumstances quite different to those of commercial production. From these centres breeding animals emanate to influence the similar stocks of the other, less favoured areas, grading them up to standards which may be inconsistent with their real performance functions. It is thus important that progeny testing should be based upon, and selection directed at, performance in the commercial areas rather than in the stud localities (for a discussion of this situation in Australian Merino sheep, see Nichols, 1940).

Even in conditions highly favourable to one form of production the real course of selection can be obscured by environmental effects ; thus Phillips and Dawson (1940) have shown that among Southdown, Shropshire and Hampshire flocks, when selection was made at an early age, lambs which were singles, or born early, or of heavy birth weight, were favoured against twin lambs, or late born, or of light birth weight, respectively, though none of these characters can be considered predominantly controlled by genetic influences, so that the animals showing them have no genetic advantage for superior mutton performance. Hence the actual selection followed lowers in effect the chances of choosing animals of superior genotype. This situation can be remedied by comparing only animals which are alike in any one of these respects, i.e. singles with singles, etc., by making selections at a definite age and making allowances for the variations due to these birth factors,

or by delaying them until the effects of these environmental factors have worn off, as at about a year old.

The question of the appropriate progeny testing, made in the environmental complex in which the offspring are expected to perform, arises also in relation to the breeds to be chosen for deliberate crossing for particular purposes, while the function of a breed in respect of those to which it can be crossed can be important. These points can be illustrated by reference to the stratification in sheep-breeding industries. A broad classification of sheep breeds can be made according to whether they are ram- or ewe-producing; the basic breeds are, or should be, ewe-breeding, with emphasis on the attributes of the females which render them most fitted for breeding replacements. The crossing breeds have a definite rôle in breeding rams for mating with ewe-producing types. The Border Leicester breed has been developed in its main habitats largely for crossing with Scotch Blackface or Cheviot ewes, the Wensleydale for the more restricted purpose of producing rams mainly to " nick " with Swaledale ewes; and the more catholic functions of the Border Leicester, together with its wider spread, may be partly responsible also for its greater use on other basic types, such as the Merino, as compared with the Wensleydale. Some breeds give more successful nicks at particular stages of the crossing process than others (*cf.* Bonsma, 1939, p. 59, and *below* p. 186) and this is also noticed in crossbred pigs. Moreover, the discrepancy between the aim of stud breeders in concentrated favourable areas and the requirements of the breeders in the commercial areas is widened if the emphasis in the former is placed on male phenotype or standards in contrast to the basic female characteristics needed in the latter.

Under some circumstances the improvement policy involves replacing the indigenous, or native breedless stocks, either by grading them up to another type, or by introducing new genotypes. Official livestock policies are frequently based on grading up, as in the stock premium or licensing schemes. Some of these ostensibly take the variations in local requirements into account but frequently do not go far enough in recognising that the local needs may involve distinct features in adaptation. Others go too far in assuming that the high

grade, almost " purebred ", is the most desirable objective. In many cases there are, however, fairly definite limits of " blood " or performance beyond which grading should or need not be taken, although much more study is required to decide, for instance, the appropriate stages in the various conditions, *e.g.* to retain hardiness and disease resistance in African grade cattle or in grade Merino sheep in Kenya.

In grading up the local shorthorned Zebu of Tanganyika with European breeds, while the F_1 stock are much better than the Zebu in size and productivity, the higher grades do not improve in milk yield, growth rate, or development. Their breakdown is encouraged by low nutritional standards, though these are not the cause of the inferior performance (nor is their longer coat, which embarrasses them). French (1940, 1941) suggests that the higher grades have higher nutritional requirements or cannot use the digestible nutriment so well as the lower grades and the Zebu, in spite of the fact that their digestion is about as efficient. The possible alternatives to continued grading are (*a*) selection and pure breeding among the native Zebus, (*b*) degrading some of the high grades with Zebu bulls towards the level at which inferior animals do not appear, but with selected superior native cows continually introduced for grading up, or (*c*) inbreeding at this level and culling undesirable progeny. Another instance of a limit to grading has been indicated recently by Harlamov (1941) from his experiments on improving the wool production, body weight, and fertility of the coarse-fleeced Kurduk (= fat-rumped) sheep in Kazakhstan by grading up with the Précoce ; animals from inbreeding the third generation $\left(i.e.\ \dfrac{7\text{P}\ .\ 1\text{K}}{8}\right)$ were little inferior in the desired fleece characters, and of high fertility, body weight and vitality, compared with fifth generation grades $\left(\dfrac{31\text{P}\ .\ 1\text{K}}{32}\right)$.

Some of the methods adopted in replacing low-producing types by more mature forms have been discussed under " Breed Construction " (Chapter XIV)—various aspects of the problem outlined in the last three paragraphs are illustrated in the

experience extending over twenty-five years at the Iberia Experiment Farm with hybrid cattle for the Gulf States of U.S.A. Rhoad (1942) has stated that the best results have been obtained by grading the foundation stock (say " F ") with beef bulls (" B "), mating the F_1 cows $\left(\dfrac{\text{1F . 1B}}{2}\right)$ to Brahman (Zebu, " Z ") bulls, and backcrossing the female offspring of this mating $\left(i.e. \dfrac{\text{1F . 1B . 2Z}}{4}\right)$ to beef bulls, to get $\dfrac{\text{1F . 5B . 2Z}}{8}$.

Otherwise, good results came from backcrossing $\dfrac{\text{1F . 1B}}{2}$ cows to beef bulls and then putting the offspring to the Brahman to obtain animals of the constitution $\dfrac{\text{1F . 3B . 4Z}}{8}$. The introduction of a beef cross before bringing in the Brahman was better than first using the Brahman cross followed by the beef breed, although making the Brahman cross for the F_1 generation was better than not using the Zebu at all, i.e. better than grading the foundation types direct to the " improved " beef breeds. In the case of straight-out replacement of the local stocks by animals of only beef and Brahman ancestry, good results accrued from backcrossing F_1 stock $\left(\dfrac{\text{1B . 1Z}}{2}\right)$ to the beef breed to obtain quarter-bred Brahmans $\left(\dfrac{\text{3B . 1Z}}{4}\right)$, but if other combinations were required, superior stock resulted from mating the quarter-bred Brahman bulls to halfbred cows $\left(i.e. \dfrac{\text{3B . 1Z}}{4} \male\male \times \dfrac{\text{1B . 1Z}}{2} \female\female \to \dfrac{\text{5B . 3Z}}{8}\right)$ than from using half-bred bulls on quarter-bred cows.

These considerations show that the general problem of livestock improvement cannot reasonably be stated just in the simple terms of seeking suitable types, fixing or holding them, and filling the gaps in commercial production by appropriate crossbreeding. Even if an arbitrary distinction is drawn between the genetic and the external environments, then the performance of the stock is a function of the interactions of the gene complex within itself and with the external factors,

some of which can be more or less controlled by man and others are relatively free from his influence. If the problem is stated as that of identifying and choosing the most favourable gene complex for efficient performance in a particular environment, then the question of the choice of the environment favourable to satisfactory expression of the genotype is also involved. The question of type cannot be dissociated from environment, of which the surrounding or neighbouring stock and their functions can form an important part. Further, the ideal of performance is never a simple one, but is compounded of many genetical and physiological characteristics. For these reasons, the particular inflexions imposed on the trend of improvement change from one character, gene complex, or environment, to another.

The aims of the breeders of purebred and of crossbred commercial animals differ in so far as the former require breeding merit as well as performance, while the latter are mainly concerned with performance. The advantages of objective and standard methods for assessing performance, especially that based on complex gene interactions, lie in the better basis for selection which they provide. Selection alone, however, is not a very efficient means of altering the genetic constitution of the individual animals or the gene frequency in their group. The different mating systems, together with selection, have different effects, in degree or in kind, on genetic constitution, and there are limitations on their use according to the end desired. Apart from the extremely simple cases in which the matings are between animals homozygous for one or a few pairs of genes, the genotype of the individual offspring cannot so far be forecast with certainty, but the probable or average genotypes can be assessed by taking into account the performance merit of the *near* ancestors and collateral relatives, together with breeding merit as revealed by the performance of the progeny.

The breeding merit of a breed depends upon the frequency of the desired genes and the ways in which they are distributed among the animals of the group. As has been shown, it is most unlikely that any isolated breed is sufficiently homozygous, for the large numbers of genes involved in establishing its typical or desired qualitative performance characters, to be

of such genetic uniformity that further improvement is impossible in the direction of discovering superior gene combinations. (If it were, then improvement in such a breed would have to wait upon the probably exceedingly rare favourable gene mutations.)

Greater genetic uniformity or homozygosity within a breed is therefore often a legitimate breeding aim, though the extent to which it can be agreed upon and approached depends upon how closely the policies of the individual breeders and the mating systems they use can conform to the general systems needed for the whole breed. For reasons enunciated in earlier chapters, an individual breeder carrying out an inbreeding or close linebreeding system might have to resort to outcrossing with some other strain before he could have had time to bring about a degree of homozygosity advantageous to the breed as a whole.

Because of the distinct possibility of this sort of conflict, and since the number of stock generations covered by the individual breeder of the larger farm animals is in any case comparatively small, plans for genetic improvement are usually considered in relation to a whole breed. Lush (1937) suggests, as an ideal plan for rapid breed improvement, a system by which the breed is divided into local groups, each of which would follow a common linebreeding policy interrupted by outcrosses from nearby groups when required. Each group should have about three to five males, so that a midway course could be struck between too high inbreeding with too few males and too slow progress towards group uniformity and differentiation. As the groups would tend to become distinct from their neighbouring groups, the possibility of effective selection between them would also increase and exceed that which could be carried out in ordinary circumstances.

On the other hand, Hagedoorn (1939) has proposed a " nucleus scheme ", by which the main steps for improvement would be concentrated in a few specialised units, somewhat on the same lines as have proved successful in plant breeding, with especial care taken to ensure that the selected top stock should be free from undesirable recessive genes and lethals ; further, this nucleus would be isolated from any possible introduction of such genes. The nucleus would be formed

only of a few superior males as assessed by progeny test, utility points only being considered, and the males used throughout the breed would be exclusively the sons, or sons and grandsons, of the small number of nucleus sires. It is claimed that the rigid progeny testing would prevent any disadvantageous effects from that degree of inbreeding which would inevitably occur under this scheme.

Hagedoorn's plan differs from many practical systems already in use in the degree of its rigid exclusiveness to a sample of the genes present in the breed, and in the implication that such a sample would provide the necessary gene material to accommodate changes in environment or of demands of performance in response to them. The suggestion of Lush superimposes a structure whereby genetic methods are given wider opportunities for improvement by selection and line-breeding as well as allowing scope for the progeny test to be carried out in environments in which the stock are called upon to perform.

The requirements of adaptation to environment—including that of the market demands for the particular products—are continually changing in some degree, so that standards of performance are not persistent unless they relate to conditions in which the natural environmental factors predominate, as in many of the basic breeds, or are so artificial as to be highly monotonous and uniform. As a stock industry approaches maturity, the tendency appears to be that either the range of conditions to which a breed is best fitted becomes more restricted or the breed's functions and performance in relation to its neighbours require greater recognition. In either of these cases, the breeding aim should take account of the physiological and genetical traits involved in function and, in so far as this is to be specialised, genetic uniformity is a justifiable objective, provided that it is also recognised that adjustment to a new demand of environment would then involve the introduction of new genes from some other genotype, and thus the end of the old breed as such. If a flexibility of performance in a variety of environments is desired, some genetic heterogeneity can equally well be accepted as the deliberate aim; this may be achieved by encouraging the development of distinct local groups or varieties (which ultimately means the establishment

of separate breeds and thus has the same end) or by drawing on two or more differentiated breeds in deliberate crossbreeding.

Whatever its direction, the policy of improvement should be re-examined in relation to the general pattern of the environment, and the appropriate mating systems and selection methods chosen according to what is known of their effects, of which an account has been attempted here.

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