REVIEWS

POPULATION GENETICS AND ANIMAL IMPROVEMENT. By I. M. Lerner. Cambridge Univ. Press, 1950. Pp. 342+xviii. 30s.

The author commences his preface with the statement that " The purpose of this book is to raise rather than to answer questions," and indeed it is not easy to see what other course is open ; for the subject of population genetics, in the sense that Dr Lerner uses the term, is full of unanswered questions, questions that only extensive experimentation can answer. They will be answered adequately and economically, however, only if they are posed correctly ; and they can be posed correctly only if the genetical principles at issue are made clear and the available information weighed and carefully sifted for pointers. This Lerner sets out to do, and, in the present reviewer's opinion, succeeds to a very great extent in accomplishing.

Dr Lerner has been associated since 1933 with the project for raising the egg production of the University of California flock of Single Comb White Leghorns by a systematic programme of selection. It is therefore with poultry breeding that he is chiefly concerned, and from poultry breeding, especially the breeding of the University of California flock, that he draws most of his experimental evidence. He devotes three chapters to the history of attempts to improve egg production by genetic manipulation, to the nature and components of the production index by which he measures egg production, and to an account of the University of California flock. These chapters will be of value in their own right to the poultry breeder, and indeed to all who have an interest (no matter how academic) in animal production. Their chief function, however, is to give the background against which the essential genetical principles of animal breeding are discussed in the remaining eleven chapters. They point the need for the genetical discussion and in some measure they determine the course which it will follow.

The primary genetical postulate, or limiting condition of the discussion as the author calls it, is that " characters of economic importance depend on large numbers of genes, whose individual effects cannot ordinarily be isolated." While, as the author points out, some economically important variation is of a simpler genetic nature, few with experience in plant and animal breeding will dispute the general truth of this primary postulate. This leads directly to Lerner's great point of emphasis, viz. that if the variation to be manipulated is polygenic, the methods to be used must be those appropriate to polygenic systems. The mendelian techniques of analysis and prediction, developed for and appropriate to discontinuous variation, fail when the variation becomes continuous. A polygenic approach is needed, with corresponding genetical theory and statistical technique.

The essential genetical principles are listed in chapter five. Then in the next eight chapters they are taken up one by one and discussed in detail, in the light of the available evidence (especially that from poultry) and in relation to methods of application. After a further chapter on

miscellaneous questions, the book concludes with a statement of the many questions upon which our knowledge is inadequate and which require experimental investigation.

In his statement of the principles involved, of their operation in practice, and of the genetical information which experiment must seek to provide, Lerner is clearly speaking from long and mature reflection. Much of what he has to say is perhaps common ground to all who are interested in this branch of genetics. The statement is, however, so scholarly, so comprehensive and so well balanced as surely to command respect from all who read it. Few will fail to find something new in treatment or emphasis, and the reader to whom this field is unfamiliar will have an admirable introduction to the principles and questions at issue.

It is, of course, impossible to discuss the principles and experimental needs without reference to methods of analysis. These are necessarily of a biometrical and statistical nature and require some mathematical facility for their understanding. Lerner has omitted from his account the derivation of the formulæ which he uses, as being extraneous to his chief purpose and in order to keep the book within manageable length. He includes, however, full references to the original sources and also a glossary of the many symbols which are used. The formulæ and methods are taken from Wright's original writings on the subject via the adaptation and elaboration of Lush and his school. Thus this part of the book is less particularly Lerner's own, and, to this reviewer at least, is less satisfying because more circumscribed than the parts for which Lerner can be held more specifically responsible.

Certain basic expressions will be generally agreed as common ground, since they are in essence the mathematical formulations of agreed genetical statements. We may, however, observe in passing that the notation in which these are expressed is not as clear as it could be made. Thus on page 84 we find the expression

$$\sigma^2_{G_e} = \sigma^2_G + \sigma^2_{G'}$$

indicating that the genetical variance ($\sigma^2_{G_e}$) is regardable as composed of two parts, the additive (σ^2_G) and the non-additive ($\sigma^2_{G'}$), which latter depends on dominance, epistasis, etc. Now the distinctive features of these three terms are to be found not even in the subscripts, but in the sub-subscripts (or lack of them). The implication of the expression is thus largely concealed from all but the closest scrutiny. Surely we may take it that having agreed to discuss variances and in particular genetic variances, we need not make the expression say all this again, but allow it to concentrate on its own task of clearly setting out the relations of the various types of genetic variance, by taking the σ^2_G for granted and writing, *e.g.* something like $G = A+N$ or (in a notation which I have used elsewhere) $G = D+H$.

This kind of criticism can be levelled at much of the notation. It is in a sense a trivial point. Clear notation can, nevertheless, be of great help not only to the reader, but also to the investigator concerned to manipulate the expressions, both in saving time and in avoiding misapprehension and mistakes.

The chief criticism, or perhaps limitation would be a better word, of this mathematical approach springs, however, not so much from the way it is set down as from what it seeks to do. Any algebraic formulation must,

to be useful, be over-simple. Genes have too many properties of action and interaction for them all to be set out usefully in the formulæ we use. The system Lerner follows recognises this and deliberately concentrates (as most of us would) on the additive portion of the genetical variance. This course of action can, however, be misleading and there is obvious need for experimental work to test its validity or at least its utility—as indeed Lerner points out in his last chapter. In the absence of such information, which is gradually coming to hand for some species, even if for none that Lerner discusses, it is surely necessary to make provision in the mathematical formulation for a measure of the uncertainty in calculation and prediction to which the possible falsity of this simplifying assumption gives rise. The elaborate formulæ which are necessary for the interpretation of polygenic behaviour in stock animals can be no more reliable than the quantities which they combine and manipulate. To say that the experimental work necessary to give these measures of uncertainty cannot be carried out in large animals is merely to say that our large animal programmes need underpinning by experimental work with more readily handlable species. Again we feel that Lerner would agree—indeed some of the experimental designs he describes will give this type of information ; but the mathematical formulation he uses does not fully bring out the need for measures of uncertainty.

There are two basic quantities in all this mathematical elaboration, the heritability, as it is called, and the inbreeding coefficient. The measure of heritability must in general reflect departures from additive gene action, and if these are unknown must be treated with corresponding caution : and obviously so must any calculation based on it. The heritability has another limitation. It is essentially the ratio of the heritable to the total variation. It will therefore vary with changes both in genetical constitution and in environment. If, however, we seek to measure and use the heritable and the non-heritable variation as separate quantities, rather than relying on their ratio, we can go further towards understanding just what is changing the heritability of the character ; so that there is more chance of order coming out of what might be apparent chaos.

The inbreeding coefficient is suspect in another way. It is computed assuming uncomplicated Mendelian inheritance of the operative genes. But we have reason to believe, for example, that heterozygotes will enjoy an advantage over homozygotes in many species. In such a case the inbreeding coefficient as commonly computed must overestimate the actual effect of inbreeding. We need experimental evidence of just what does in fact go on. In the meantime major calculations derived from the inbreeding coefficient must be suspect, and minor corrections for it hardly worth the work of calculation.

All this is not to say that the sort of calculation Lerner describes is unnecessary. On the contrary it is essential to our understanding of those populations of domestic animals that we call flocks, herds and breeds. But our prime need now is for genetical experiments to test the assumptions on which these calculations are based and to measure the uncertainty which is inherent in them. The pleasure which many of us (including myself) get from the algebraic reduction of a complex problem must not blind us to this primary need of detailed, extensive and relatively tedious experimentation.

These considerations are clearly well to the fore in Lerner's mind, as any careful reader of his text will see. They are reiterated now with the sole purpose of emphasising that his text must be read and not merely the algebra enjoyed. One further point requires a little comment. It is assumed all through that the operative genetic system contains many genes, and that we can assume many units of segregation. This is doubtless well justified in domestic animals whose chromosome numbers are large. In species with lower numbers of chromosomes there also may well be many genes in the system ; but they appear often to segregate in a relatively small number of composite temporary units which I have called effective factors. In such cases the assumption or a large number of independently inherited genes could lead to error, especially in predicting behaviour under selection.

This having been said, the book can be heartily recommended to all serious students of production genetics, not only of animals but of plants too. For the plant breeder's problems, though differing in detail, arise from the same genic behaviour and involve the same essential principles.

Perhaps before concluding I may be permitted two minor personal comments, since they concern points on which Lerner specifically differs from me. He prefers the term " Population Genetics " to my " Biometrical Genetics." True, the problems he discusses are those of populations, though population genetics does not end with the study of polygenic variation. But, as we have seen, the study of polygenic variation must bring in controlled crossing experimentation more akin to the practical methodology of mendelian experiments than to the study and manipulation of populations of unknown genetic structure. The special feature of the work, whether on populations or on the offspring of controlled crosses, is that it is concerned primarily with continuous variation and therefore requires a biometrical rather than a mendelian analysis. So, as a general description, I still prefer Biometrical Genetics. And surely we have passed the time when the term biometry can fairly be regarded as having a dangerous anti-genetical flavour.

Secondly, in emphasising the polygenic point of view, Lerner expresses his feeling that I have been over-conservative in labouring its relation to mendelian genetics. Biometrical genetics would, however, be impossible if we could not start with the knowledge that the genes with which we must deal are transmitted exactly as are the major genes of mendelian genetics. Mendelian genetics is our sure and only foundation. Without it we should be no more able than Galton to make sense of continuous variation. As such it is worth a little acknowledgment, especially in an exposition of the methodology which our studies of polygenic variation entails.

These two points of difference are obviously minor ones. Lerner and I work with different characters in different species, but out problems are basically the same and we approach them with the same point of view. Our agrement is great and our difference small. *Population Genetics and Animal Improvement* has given me a double pleasure, of heartily recommending it as well as of profitably reading it. K. MATHER.