

HETEROSIS AND SELECTION IN THE DOMESTIC FOWL

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Summary

Hybrids, generated by crossing highly selected and mildly inbred strains from two distinct breeds (viz. Australorp and White Leghorn) of *Gallus domesticus*, showed appreciable hybrid vigour with respect to the trait used in the parental lines as selection criterion, and also with respect to certain other traits.

In the closed lines, bred from both hybrids, performance in egg-production traits showed a marked decline. As a result of subsequent conventional selection, different traits showed different response.

Models for the types of gene action contributing to hybrid vigour are suggested. Some of the objections to the proposed models, and the alternative models implied in such objections, are outlined. Further breeding experiments are tentatively suggested, with the intention of approaching a decision between these alternatives.

I. INTRODUCTION

It is widely held that the increase in performance obtained in the first cross between different strains, breeds, etc. (hybrid vigour) is largely lost on subsequent inter-mating (i.e. in passage from F_1 to F_2). In most models constructed to account for the type of gene action contributing to heterosis, one or more non-additive components of allelic action are assumed. Opinions differ, however, on the relative contribution of these non-additive components. For example, Jones (1917) asserted that the assumption of dominance of favourable alleles (at a large proportion of the relevant loci) is enough to account for as much hybrid vigour as is manifested in most observed instances. On the other hand, Crow (1948), using reproductive fitness as the measure of vigour, theoretically demonstrated that, on the accepted estimates of loci number and of mutation rates, such simple models of dominance can seldom account for more than a part of the observed gain in vigour. Hull (1945) interpreted his results as indicating that overdominance is a major factor. Other workers (e.g. Rasmusson 1933; Rendel 1953) found all the abovementioned *intra-locus* interactions insufficient to account for the degree of heterosis sometimes observed and assumed *inter-locus* interactions (epistasis) as a major contributing source.

Noting the agreement of most authors that (except on the rarest occasions) no single component is the *sole* cause of heterosis, it is seen that the attribution of the major role to one or the other component is of considerable importance, not only in the theory of quantitative population genetics, but also in the application of genetics to breeding. The fixation (or the potential fixation) of hybrid vigour is well known to be of great interest to the breeder; it can be seen that the hope—or lack

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of it—for such a phenomenon must be conditioned by the theory held about the proportions of contributions to heterosis, from various components. The portion of heterosis contributed by overdominance at single loci is unfixable (even in strict theory). On the other hand, the portions contributed by dominance, pseudo-overdominance, and some kinds of epistasis are fixable (at least in theory) and, if lost in the F_2 or subsequent generations, should be recoverable by judicious selection and mating.

In this paper we report observations which are hoped to contribute to the clarification of these problems, viz. observations of heterosis in the F_1 generation, of loss of some or all of that gain in the F_2 and of partial or total recovery of loss by subsequent selection. Consideration is given to the response to selection in the trait used as the selection criterion as well as to concomitant changes in correlated characters.

II. MATERIALS AND METHODS

Crosses between White Leghorn males and Australorp females ($L \times A$) and the reciprocal ($A \times L$), shows considerable hybrid vigour with respect to various characters, particularly egg production (Morley and Smith 1954; Morris and Skaller 1958). The pure breeds used for the cross-breeding study of Morris and Skaller were selected in an orthodox manner using a combination of individual and family performance. The method of “reciprocal recurrent selection” was brought into use for the two pure breeds in 1954 and both types of crossbreds were developed each year until the program was discontinued in 1959. In 1955 randomly chosen males and females from each cross were mated and two F_2 's were developed; these synthetic crosses remained closed thereafter. The two F_2 's, lines 73 and 74, resulted from the inter-mating of cockerels and pullets from the $A \times L$ cross and from the $L \times A$ cross, respectively. Both of these lines were subsequently selected for high *egg production index* (as defined by Lerner 1950) for five generations, selection being based on the record for the part period (i.e. first egg up to May 31). In 1960, these two lines were propagated for the last time; furthermore they were crossed reciprocally in duplicate: the cross 73×74 yielded lines 70 and 71, and the reciprocal cross, 74×73 , yielded lines 75 and 76. These four newly synthesized lines (F_1 's) were closed and F_2 's were developed in 1961. Thereafter, selection was practised in a manner similar to that described for lines 73 and 74 with the exception that some attention was given to egg size. A diagrammatic illustration of the actual development of these lines is contained elsewhere (Morris 1964).

III. RESULTS

(a) *Manifestation and Loss of Hybrid Vigour*

An indication of the magnitude of the hybrid vigour encountered in our stock is given in Table 1. As there was a wide range in hatching dates and, in the case of egg production traits, since the part record terminates on a fixed date, only pullets having common hatching dates were used for the comparisons between cross-bred and purebred performance. The mean values for both production index and survivor production, as are all means reported in this paper, apart from those

referring to fertility, hatchability, and viability, are unweighted means of hatch means. From Table 1 it will be seen that the crossbreds exhibit considerable hybrid vigour in egg production when compared to the better purebred parental stock

TABLE 1
COMPARISON OF 1954 HATCHED GENERATION OF CROSSBREDS WITH RECONSTITUTED
PUREBRED PARENT STOCK FOR IMPORTANT TRAITS

		L × L	A × L	L × A	A × A
Production index	Part period	60.0	67.6	70.8	45.8
	Residual	88.1	111.7	96.7	53.7
	72 weeks	148.2	179.3	168.4	99.6
Survivor production	Part period	62.8	70.3	74.4	51.4
	Residual	132.2	137.6	122.2	93.8
	72 weeks	202.8	208.8	203.2	155.8
Fertility (%)		84.1	89.1	83.0	92.3
Hatchability (%)		86.8	93.9	81.4	64.6
Age at first egg (weeks)		24.4	24.0	23.6	27.1

(i.e. White Leghorn). The average hybrid superiority is 9.2 eggs for the primary trait, part-period production index, and 9.4 eggs for the part-period production of survivors.

TABLE 2
COMPARISON OF 1955 HATCHED GENERATION OF CROSSBREDS WITH SYNTHETIC
CROSSES FOR IMPORTANT TRAITS

		A × L	Line 73	L × A	Line 74
Production index	Part period	66.9	56.2	64.0	60.2
	Residual	130.5	115.5	112.4	113.9
	72 weeks	197.4	171.6	176.2	174.0
Survivor production	Part period	68.0	58.4	70.7	63.4
	Residual	145.5	132.7	147.4	130.7
	72 weeks	215.6	193.0	219.2	195.6
Fertility (%)		91.0	95.2	86.2	94.4
Hatchability (%)*		68.6	75.1	84.3	80.5
Age at first egg (weeks)		26.2	26.8	25.4	26.2

* Eggs stored for 1-14 days for lines 73 and 74, prior to incubation; for L × A and A × L, storage for 1-7 days only.

In Table 2 we can compare the performance of the next generation of reconstituted hybrids with the F_2 's, which had as their parents the original hybrids referred to in Table 1. If we assume that little or no change has been effected in the newly

constituted F_1 's as a result of the limited selection practised, then the difference in performance between the corresponding F_1 's and F_2 's, hatched and performing during the same period, provides an estimate of the loss sustained from the inter-mating of first cross-hybrids. The magnitude of a loss, if any, might presumably throw some light on the type of gene action responsible for the initial hybrid vigour. The results in Table 2 show a loss in production index of 10.7 eggs for line 73 when compared with its parent type ($A \times L$), and a loss of 3.8 eggs for line 74 when compared with its parent type ($L \times A$); corresponding losses in survivor production were 9.6 and 7.3 eggs, respectively. In all cases there was a tendency for F_2 production to regress back towards the level of the better purebred grand-parental stock.

Considerable hybrid vigour is also manifested in the concomitant characters, e.g. in production during the residual period; consequently, 72 weeks production shows a corresponding increase. Table 1 shows considerable hybrid superiority in 72 weeks production index and a lesser amount in residual production index. Table 2 facilitates a comparison between the crossbreds (F_1 's) and the F_2 's and shows that there has been a loss of high magnitude in 72 weeks production in all cases except for production index of line 74, which differed from the $L \times A$ by only 2.2 eggs. The results were quite similar for residual production, there being considerable losses in all instances except in the production index of line 74. When production of survivors only was considered, both lines 73 and 74 showed declines of approximately the same magnitude, when compared with their respective parent types, F_1 's.

It is a rare occasion on which the percentage hatchability of fertile eggs of the two first crosses, $A \times L$ and $L \times A$, does not exceed that of both purebred parent types (Morris and Skaller 1958). In the data in Table 1 of this study the White Leghorns had a higher hatchability (86.8) than the $L \times A$ (81.4). However, if the comparison is made in such a way as to avoid possible maternal effects, i.e. White Leghorn *v.* $A \times L$ and Australorp *v.* $L \times A$, the hybrid vigour manifest in hatchability is very obvious (93.9 *v.* 86.8 and 81.4 *v.* 64.6). When F_2 's are developed it is interesting to note that there is not a decline in hybrid vigour with respect to the hatchability of the F_2 's. From Table 2 it is seen that line 73 is in excess of its parent type, $A \times L$, by 6.5% and although line 74 is deficient to its parent type, $L \times A$, by 3.8% this deficiency is more than compensated for when it is realized that the fertile eggs of lines 73 and 74 were collected over a period of 14 days for each hatch and hence held in storage for 1-14 days prior to incubation, whereas those of the $L \times A$ and $A \times L$ groups were held only for 1-7 days. It would seem, then, that there is a very strong maternal effect of the hybrid dams which masks the loss, if any, in viability of the F_2 genotypes.

(b) *Subsequent Response to Selection*

Selection was imposed on lines 73 and 74, the 1955 hatched generations (the F_2 's) constituting the parental generations as far as the selection program was concerned. The selection criterion, as mentioned previously, was part-period production index. The progress recorded for this trait is diagrammatically illustrated in Figure 1 where the actually observed values are expressed as deviations from the randomly mated non-selected control. The similar deviations for the hybrids, reconstituted each year from the two pure flocks subjected to the recurrent reciprocal

selection program, are also shown up to the year 1959. The synthetic lines showed a steady gain in the selected character and had, by 1958, passed the production level of the hybrids. The evidence that the performance of the selected lines has exceeded that of the original F_1 's (i.e. their antecedents), as judged by their performance in 1958 and thereafter, is merely an indirect one. For every year, there is direct comparison with the reconstituted hybrids and certainly in 1958 and 1959

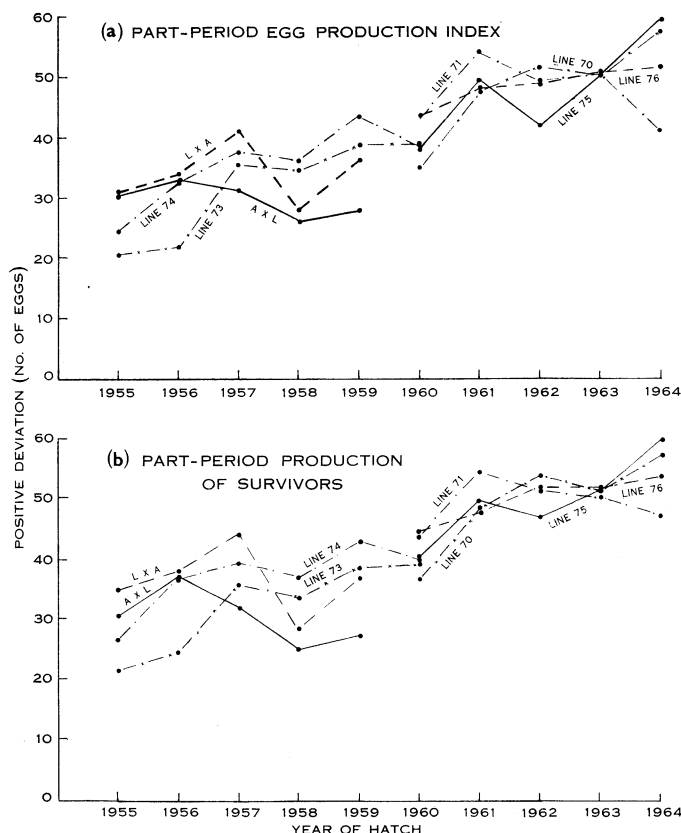


Fig.1.—Part-period egg production index (a) and part-period production of survivors (b) for crossbreds and synthetic crosses—expressed as a deviation from the randomly mated non-selected control flock and based on the mean of two hatches.

the selected synthetic lines were superior to them. However, relating this comparison back to the original F_1 's (performing in 1955), so as to validate the claim on recapture of lost hybrid vigour in performance, implies the assumption that the loss in performance of the reconstituted hybrids (as a side effect of the recurrent reciprocal selection) is negligible; and this assumption is far from proven. Alternatively, one may avoid the difficulties involved in this indirect comparison: i.e. one compares directly the performance of the selected synthetic lines with that of their actual hybrid antecedents in 1955 (see Fig. 1); such use of a direct comparison implies the assumption that the elimination of the main effect of seasonal variation did

not generate genotype \times environment interaction of objectionable magnitude. Observations obtained by crossing lines 73 and 74 in 1960, and by subsequent selection of the resulting four new lines, add further to the belief that the original hybrid level has been surpassed. Similar trends are evidenced for the part-period egg production of survivors and these are also shown in Figure 1.

Interesting trends are provided by a concomitant character, residual egg production (production from June 1 to 72 weeks of age) and these are shown in Figure 2. The initial loss, as a result of intermating F_1 's, was more consistent for

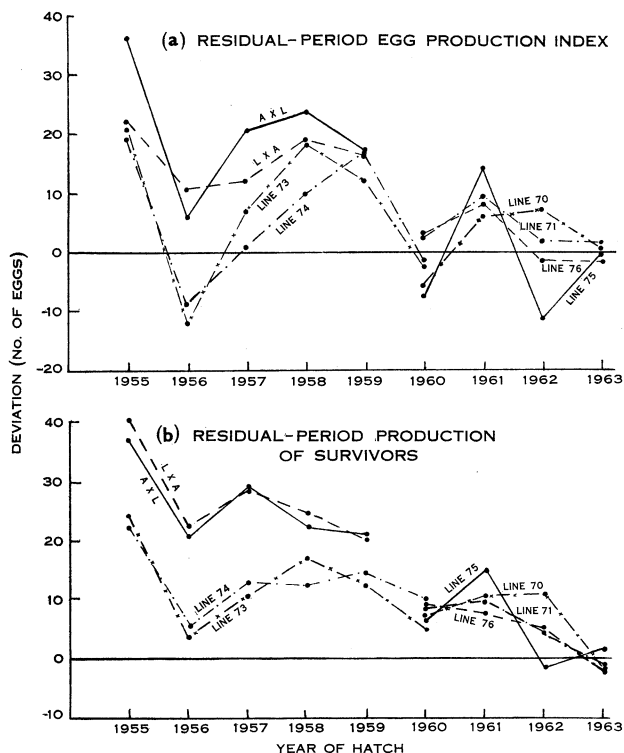


Fig. 2.—Residual-period egg production index (a) and residual-period production of survivors (b) for crossbreds and synthetic crosses—expressed as a deviation from the randomly mated non-selected control flock and based on the mean of two hatches.

the production of survivors than for production index and this loss was not made good, as a correlated response, in the case of survivors. Although no recovery took place with respect to the individual production rate (as measured by survivor's production), some of the loss in the average rate of production (as measured by production index) was recovered. This discrepancy is accounted for by the mortality rate in the reconstituted hybrids exceeding that in the synthetic crosses.

Figure 2 also provides supporting evidence for the argument adduced by Morris (1963) that continuous selection, based on part-period records of egg production only, will eventually result in a plateauing of residual egg production and very

likely a subsequent decline in this trait. This phenomenon has been observed for the two synthetic lines, 73 and 74, and the trend is continuing for the four more recently synthesized lines, 70, 71, 75, and 76.

A close examination of Figures 3 and 4 reveals that the major contributing factor towards the increased egg production during the part period has been an increase in rate of lay whereas the slight decrease in age at first egg has been of minor importance. From Figure 3 it can be seen that the two synthetic lines had rates of lay

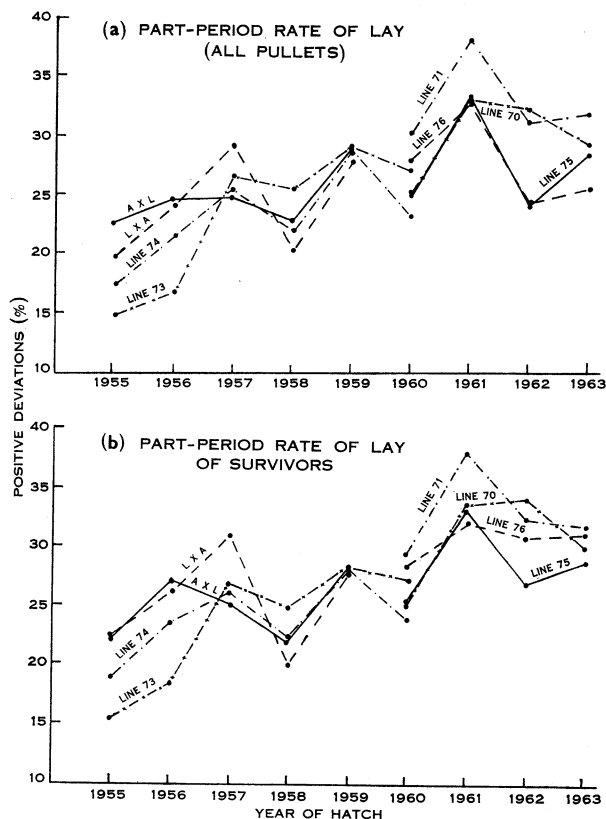


Fig. 3.—Part-period percentage rate of lay of all pullets (a) and part-period rate of lay of survivors (b) for crossbreds and synthetic crosses—expressed as a deviation from the randomly mated non-selected control flock.

equivalent to those of the reconstituted hybrids of 1959 and that after this there was a slight increase up to 1963. Rate of lay has not been plotted for the residual period as the egg production graphs are a precise representation of the rate trends for that period.

(c) Occurrence of Heterosis in Subsequent Crossing of Lines

Little hybrid vigour was observed as a result of the crossing of lines 73 and 74 in 1960. Some of the more important traits are set out in Table 3 both for the reconstituted parent lines, 73 and 74, as well as for the cross-lines. It will be noticed

that half-sib comparisons are available between lines 73 and 70, as well as between lines 74 and 75. The only character exhibiting hybrid vigour was percentage hatchability of fertile eggs, all the four cross-lines being superior to both parent lines. On the other hand, in the case of all "egg production traits" the individual records of each of the four cross-lines is very close to the average performance of the parental lines. The absence of hybrid vigour in traits other than hatchability may well be due to the similarity in genetic composition of the two parental lines. They originate from the same ancestral strains and the duration of their genetic isolation was merely for five generations during which period their differentiation, if any, originated from random causes only.

IV. DISCUSSION

From Figures 1 and 2 it is seen that the response to "subsequent" selection is rather different for the different traits observed. In part-period production—as far as one can accept the indirect evidence outlined in Section III(b)—the performance level of the F_1 has at least been attained, and has most probably been surpassed.

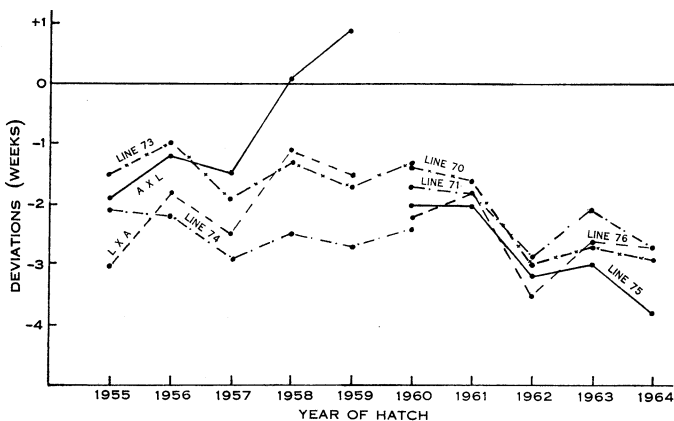


Fig. 4.—Age at first egg (in weeks) for the crossbreds and synthetic crosses—expressed as a deviation from the randomly mated non-selected control flock and based on the mean of two hatches.

On the other hand, the response in residual production seems to have been rather unsatisfactory. For further discussion of these observations we regard these two traits as typical of two particular kinds of traits: (1) the first kind, in which subsequent selection results in approaching, or even in surpassing, the performance of the F_1 generation, and (2) the second kind, where such an attempt seems to fail.

In the case of traits of the first kind, an optimistic model can be conjectured: a large component of the high performance in the F_1 generation—the "hybrid vigour"—was due to types of gene action accessible to conventional selection techniques: e.g. additive \times additive component of epistasis; pseudo-overdominance, due to the effects of partially or completely dominant "plus"-alleles (or both) present at complementary loci in the parental strains; and a special kind of "cubic" component of epistasis (optimum heterozygosis at "vigour" loci supporting maximum dosage of "plus"-alleles at "yield" loci). Recalling that there is no evidence that

TABLE 3
COMPARISONS OF VARIOUS TRAITS OF THE 1960 HATCHED GENERATION OF SYNTHETIC CROSSBREDS AND OF THEIR RECIPROCAL CROSSES

Line	Production Index			Survivor Production			Fertility (%)	Hatch-ability of Fertile Eggs (%)	Mortality (%)		Age at First Egg (weeks)	Mature Weight (g)	Egg Weight (g)	
	Part Period	Residual Period	72 Weeks	Part Period	Residual Period	72 Weeks			0-3 Weeks	Adult			May	Sept.
73*	86.1	112.1	198.2	89.3	121.2	208.3	90.0	66.4	9.9	12.1	24.3	1841	50.3	54.8
74†	87.4	110.0	197.4	89.5	126.2	217.1	78.7	72.9	6.9	17.1	23.1	1760	51.8	56.4
70*	85.3	106.7	192.0	87.6	122.4	211.8	83.1	75.3	8.0	16.5	24.0	1788	51.5	56.6
71	90.0	114.6	204.5	91.3	125.9	218.9	83.7	82.8	7.9	12.7	24.0	1813	52.0	57.3
75†	86.5	104.8	191.4	89.5	122.9	214.0	83.2	78.3	5.1	20.7	23.5	1812	52.1	57.3
76	92.2	113.4	205.6	93.9	123.6	218.3	84.9	81.0	5.6	12.5	23.3	1799	51.7	56.6

* Identical sires used for groups 73 and 70.

† Identical sires used for groups 74 and 75.

the parental lines, at the time of crossing, had reached the limit attainable by the selection techniques they were subjected to, an obvious objection can be raised against the abovementioned optimistic assumptions, viz. it could be asserted that the subsequent selection achieved little recapture of hybrid vigour or none at all; and that the observed progress was merely a "pseudo-recapture", achieved by drawing on the pool of additive genetic variation left unutilized in the parental lines prior to their being crossed. If this objection is valid, subsequent selection would not have been successful had both parent lines reached their plateaus prior to crossing. Moreover, the conjectured optimistic model may be regarded as supported (by analogy) by some findings in applied plant genetics: e.g. Gardner (1963), Aastveit (1964), and Moll, Lindsey, and Robinson (1964) report observations which tend to minimize the importance of the contribution of genuine (i.e. intra-locus) overdominance to hybrid vigour. Furthermore, the absence of heterosis of any importance in the subsequent crosses [see Section III(c)] suggests that conventional selection, prior to those subsequent crosses, had recaptured much of the lost hybrid vigour, leaving only limited scope for the action of the subsequent crossing. The value of this latter observation as supporting evidence for the optimistic conjecture is diminished by the likely genetic similarity of the lines entering into these crosses. Finally, genotype-environment interaction may be operative (cf. Comstock 1960); e.g. the kind of cubic component, indicated above, may be manifest only under certain environmental conditions which impose a moderate strain on the organism.

For traits of the second kind the failure, or relative failure, of subsequent selection could be accounted for by a model attributing most of the hybrid vigour, if not all, to the type of gene action inaccessible to conventional selection: e.g. genuine overdominance and the "quartic" component of epistasis. Against this model the objection can be raised that in the investigation reported here, subsequent selection was merely indirect for the very traits for which it was not successful (e.g. residual production). The observed non-recapture could be attributed not to genuine unaccessibility, but rather to the usual difficulties known to frustrate indirect selection (e.g. attenuation or even inversion of genetic correlation, possibly due to increasing disproportionality of demand on resources). If this objection is valid, subsequent selection, had it been direct, would have achieved for traits of the second kind progress comparable to that observed in traits of the first kind.

It may be noted that models of gene action, referred to above, are schematic rather than descriptive and merely serve to symbolize and indicate qualitative trends rather than form the basis of statistical analysis of quantitative data. Such models can be constructed by simplifying the conclusions of certain theoretical investigations, e.g. Rendel (1953), Comstock (1955, 1960), Van der Veen (1959), Latter (1964), and Aastveit (1964).

Statistical methods for the estimation of genetic parameters, postulated in the realistic biometrically oriented versions of such simple models are available in literature mostly relevant to plant rather than animal genetics. Relevant publications, additional to those already cited, are Hayman (1958, 1960), Comstock and Robinson (1952), and Jinks and Morley-Jones (1958). The conceptual interpretation of these descriptive models may, in some instances, require a sophisticated approach.

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