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ANALYSIS OF GENE ACTION IN THE CONTROL OF BODY CONFORMATION AND EGG WEIGHT IN THE CHICKEN

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Summary

The *CH* and *IA* inbred lines and crosses between them up to the S_3 and sibbed backcross generations are used to analyse the genetic control of shank length and body conformation (1500 cocks and 1626 pullets) and egg weight in the autumn (854 pullets) and spring (670 hens).

Hatch effects are demonstrated for shank lengths and autumn egg weight. After adjustment for hatch effects, the genes controlling shank lengths and autumn egg weight are found to be associated with the genes for large size in the *CH* line. But association is less complete for spring egg weight, and such genes as might control the two derived measures of body conformation, an allometric index of plumpness and the modular difference between right and left shanks, show almost complete dispersion.

In the main analyses, by least squares equation of generation means to parameters for various genetic and maternal effects, the modular difference between shank lengths is not demonstrably heritable. Autumn egg weight shows only additive and dominant effects, the latter appearing more important. The remaining characters are best fitted by a model including interaction between pairs of linked loci. Maternal and sex-linked effects are shown for shank lengths. But shank lengths and plumpness in females are controlled primarily by duplicate gene interaction. In the less satisfactory analyses of spring egg weight and male plumpness, complementary gene interaction is indicated.

1. Introduction

The application of the Mather-Hayman method of gene action analysis by the comparison of the means of generations from crosses between inbred lines (*e.g.* Mather, 1949; Hayman, 1958) to growth of the chicken to 20 weeks of age has recently been reported (Morton, 1973). At the completion of the growth period, the shanks of these chickens were measured to give various assessments of body conformation, and egg weights of a sample of the pullets were obtained. A similar analysis of these traits is presented here.

2. Materials and data

The parental stocks used were the *CH* and *IA* inbred lines of White Leghorns (Pease and Dudley, 1954; Gilmour, 1959). At the start of the experiment the *CH* line had been sib mated for 25 generations and the *IA* line for 20, so that each was theoretically more than 99 per cent homozygous; but both continued to segregate at a number of blood-group loci (Gilmour, 1959).

Pure lines, the eight possible backcrosses and sibbed backcrosses and the reciprocal S_1, S_2 and S_3 generations were bred over 3 years and 14 hatches. The distribution of generations over years, and the regime of hatching and

rearing the birds to 20 weeks post-hatching, are given in Morton (1973), and the same 1500 cocks and 1626 pullets with complete records of that paper form the data for the body conformation analyses presented here.

At 20 weeks of age, the shank lengths of the chickens were measured to the nearest 0·1 mm with parallel-jaw vernier calipers, following the technique of Cock (1963). The technique is liable to operator variation and therefore all measurements were made by the author. Occasions when accidentally the same chicken was measured twice show that although the technique was not accurate to the nearest 0·1 mm, it was more accurate than to the nearest millimetre. Two further measurements were derived from the shank lengths. The modular difference between the length of the right and left shanks was calculated as a possible measure of homeostasis of body form. And as an index of plumpness the allometric form of (body weight)/(mean shank length)$^{2\cdot5}$ was used (Cock and Morton, 1963).

TABLE 1

Largest and smallest generation class means, after adjustment for batch effects, of each of the traits analysed

		Largest		Smallest	
Trait		*Generation	Class mean	Generation	Class mean
Left shank length (mm)	males	I × C	115·9	I	103·1
	females	$(CI \times C)^2$	97·2	I	88·4
Right shank length (mm)	males	I × C	115·8	I	103·1
	females	$(CI \times C)^2$	97·2	I	88·5
Modular difference	males	C	0·90	$(I \times IC)^2$	0·52
between shanks (mm)	females	CI × C	1·21	$(I \times IC)^2$	0·37
Plumpness index	males	I × C	4·44	$(CI \times C)^2$	3·48
(g/cm$^{2\cdot5}$)	females	I × C	4·98	$(CI)^2 \times (CI)^2$	3·88
5-Egg weights (g)	autumn	C × I	275	I	233
	spring	C × I	290	$(I \times CI)^2$	252

* C used for *CH* line and I for *IA* line. The male parent is placed first in each cross. $(CI)^2$ etc. are used conventionally for $(C \times I) \times (C \times I)$ etc. Thus $(I \times IC)^2$ is the result of sibmating the (I × IC) backcross.

At 20 weeks of age pullets were selected to be placed in a battery house for the estimation of egg weights. The pullets were chosen in such a way as to equalise, as nearly as possible in each year, the numbers of each generation and hatch. The generation-hatch sub-groups were randomised through the battery blocks. For one year it was necessary to use an additional block of battery cages of different design to those used throughout the rest of the experiment. To eliminate any effects this may have had, the hens in this block were treated as of different hatches than those of their contemporaries in the standard cages in the Generation × Hatch analysis (see below). The pullets were fed *ad libitum* on a standard layers' ration.

In each laying year, egg collection was started in the last full week of November and again in the second full week of March. The eggs were numbered and stored on trays in a cool room. As soon as five eggs had been collected from a pullet, they were weighed together to the nearest 0·25 g. Mis-shapen, cracked, soft-shelled or otherwise clearly imperfect eggs were rejected. A total of 854 5-egg weights from 149 generation-hatch sub-groups were obtained in the autumn records, and 670 5-egg weights from 145 sub-groups in those of the spring.

TABLE 2

Analysis of variance of direct measurements by generations and hatches

Measurement	Shank length (mm)												5-Egg weights (g)					
	Male left			Male right			Female left			Female right			Autumn			Spring		
Source of variation	d.f.	MS	VR	d.f.	MS	VR	d.f.	MS	VR	d.f.	MS	VR	d.f.	MS	VR	d.f.	MS	VR
Generations (G)	23	215·75	18·42***	23	212·71	18·19***	23	158·90	21·27***	23	157·60	21·72***	23	2390	12·02***	23	2406	7·96***
Hatches (H)	13	120·23	10·27***	13	130·94	11·20***	13	69·20	9·26***	13	78·01	10·75***	18	3503	17·62***	18	160	<1
Interaction (G×H)	98	11·50	<1	98	11·70	1·00	107	7·74	1·04	107	7·65	1·06	107	206	1·04	103	314	1·04
Error (within cell)	1365	11·73		1365	11·69		1480	7·45		1480	7·23		705	199		525	302	

*** $P < 0{\cdot}001$.

To give some idea of the values of the traits analysed, the largest and smallest generation class means (after adjustment for hatch effects—see later) are listed in table 1. In the case of the plumpness indices, although there was some overlap between the sexes as shown, the great majority of females had indices greater than, and of males indices less than, 4 g per $cm^{2 \cdot 5}$.

3. Preliminary analyses

(i) *Hatch effects*

There were five hatches in each of the years 1959 and 1960 and four in 1961. These were analysed as 14 hatches without regard to year in the case of the shank lengths. For the 5-egg weights, there were 19 " hatches " because of the use of two types of battery cage in 1960. Analyses of variance were made by the generalised inverse method of generation and hatch effects, and the interaction of generations × hatches estimated from the residual between cells variance. As seen from table 2, the hatch effects on the direct measures are large, except in spring 5-egg weights, and particularly large in the autumn egg-weight data. The difference between the results for the two seasons is not surprising, since eggs for weighing were collected at a specific time of year when in the autumn the pullets varied between 7 and 9 months of age, whereas by the spring all were fully mature.

However, there are no signs of genotype × hatch interaction in any of the analyses. Therefore the generation class means and standard errors derived from these analyses were used as data for the main analysis for the direct measurements. For the derived measurements, hatch corrections were obtained from these analyses and applied to the individual values of each bird, from which the generation class means and standard errors and the overall error variances were newly calculated.

(ii) *Association and dispersion*

The approximate method of estimation of degree of genetic dispersion described in Morton (1970), whereby the extent to which the distribution of the more variable F_2 lies outside those of the inbred population, was used for the present characters. The method, although approximate, is conservative in that it can overestimate dispersion while complete association is the ideal. The results are given in table 3.

Table 3

Approximate estimates of degree of genetic dispersion per cent

	Shank length				5-Egg weights	
Character	Left	Right	Modular difference between shanks	Plumpness index*	Autumn	Spring
Sex						
females	5	6	91	87	0	21
males	0	1	60	88	—	—

* Of the two inbred lines, the smaller *IA* line had the larger plumpness index.

From these it is clear that no estimates can be obtained for additive effects or additive interactions (Jinks and Jones, 1958) in the plumpness indices or the modular differences between shank lengths, and that some

caution will be necessary in the interpretation of these estimates for spring 5-egg weight. But it was decided to continue the analyses for these characters as interesting results had been obtained in the body weight analyses (Morton, 1973) concerning dominance and dominance interaction estimates, which are unaffected by genetic dispersion. The association of the genes for largeness in the *CH* line is most satisfactory for the shank lengths and the autumn 5-egg weights. Since 20-week body weight (Morton, 1973) and 20-week shank length are both highly associated, it is not surprising that the plumpness indices should be dispersed. The contrast between the autumn and spring egg weights is confirmed in table 1, for, despite obvious positive heterosis, the smallest spring egg weight is found in a segregating generation, while for the trait in the autumn the *IA* line has the smallest egg weight as would be expected for complete association.

4. Main analyses

(i) *Models and method*

Following Jinks and Perkins (1969), models of increasing complexity are fitted to the data until a satisfactory one is found. Models fitted include the additive-dominance, digenic interaction and linked digenics, combined with parameters for sex-linked and maternal effects, and in some cases interaction between the Z chromosome and the autosomes.

The expected value of the autosomal parameters to each generation mean in the absence of linkage may be found in Van der Veen (1959), and, with the exception of the S_3 generations, those for the presence of linkage are given in Jinks and Perkins (1969). The missing S_3 expectations together with the definitions of maternal and sex-linked effects are listed in Morton (1973). The parameters thus far defined are, then, m = notional mean, and deviations from this mean as follows:

d = additive	r = *IA* dam maternal
h = dominance	s = ($CH♀ \times IA♂$) S_1 dam maternal
i = additive × additive	q = ($IA♀ \times CH♂$) S_1 dam maternal
j = additive × dominance	z = Z chromosomal
l = dominance × dominance	zh = homogametic heterotic
n = *CH* dam maternal	w = W chromosomal

together with p, the recombination fraction. To these are added parameters for interactions between the Z chromosomes and the autosomes, with coefficients in the expectations of the generation means equal to the product of the coefficients of the appropriate autosomal and Z chromosomal parameters. Thus, in both sexes, iz is used for the interactions between the additive effects of the autosomes and of the Z chromosomes and takes as coefficient the product of the coefficients of d and z. Similarly, jz is the autosomal dominance × Z additive interaction with coefficient the product of those of h and z. For the male sex we need to add jzh ($d \times zh$) and lzh ($h \times zh$).

As explained by Morton (1973), the data available are insufficient to allow separate estimation of the linked digenics parameters, pi, pl, p^2i, p^3l and p^4l, and these are replaced by three joint parameters ($pi+pl$), (p^2i-p^3l) and (p^4l-2p^3l). Similarly, s and q can no longer be separately estimated in the linkage model, so that q is omitted whereupon s estimates ($s-q$).

TABLE 4

χ^2 tests for goodness of fit of models

Uncombined data

Model	Sex	d.f.	5-Egg weights		Shank lengths		Plumpness index
			Autumn	Spring	Left	Right	
Additive-dominance	females	15	*19·66*	41·00***	38·81***	39·63***	569·56***
	males	15			41·81***	37·11***	111·44***
Digenic interactions	females	12	—	32·89**	30·25**	31·88**	421·79***
	males	12			35·80***	32·35**	66·61***
Digenic + Z chromosome × autosome interactions	females	10	—	27·24**	23·71**	21·48*	
	males	8			29·14***	25·83**	55·55***
Linked digenics	females	10	*10·24*	*19·84**			

Combined data†

Model	Sex	d.f.	5-Egg weights		Shank lengths		Plumpness index
			Autumn	Spring	Left	Right	
Digenic interactions	females	10	—	32·77***	22·93*	25·90**	
	males	10			30·30***	*27·80***	63·69***
Digenic + Z chromosome × autosome interactions	females	8	—	27·12***	16·43*	*14·69*	301·40***
	males	6			23·64***	21·27**	52·64***
Linked digenics	females	8	—	19·71*	*10·10*	*10·72*	*19·63**
	males	8			*14·54*	*13·93*	32·70***
Linked digenics + Z chromosomes × autosome interaction	females	6	—	—			19·18**
	males	4					20·90***

* $P<0·05$; ** $P<0·01$; *** $P<0·001$.

† See text, p. 210.

Sexes are analysed separately, the equations of the parameters expected on each model to the generation means were solved by weighted least squares, and the goodness of fit of each model tested by χ^2 (Cavalli, 1952).

As in the body weight analysis (Morton, 1973), the weights used for the direct measures, 5-egg weights and shank lengths, are derived from the standard errors of the means taken from the generation × hatch analysis; and for the indirect measures, the modular differences between shank lengths and the plumpness index, from the larger of the variance within the relevant generation and within all generations. This avoids the finding of false significant results from over-large weights based on too few individuals within the generation.

Estimates of the standard errors of the parameters were initially calculated from the appropriate combination of the error variances of generation means. Where, however, the χ^2 for goodness of fit remained significant, they were corrected by multiplication by $\frac{\chi^2}{\nu}$, where ν is the number of degrees of freedom of the χ^2 and hence of the t-test for significance of the parameters.

(ii) *Fit of models*

The modular difference between right and left shanks was satisfactorily fitted by the parameter for the mean alone, in both sexes; that is, there was no evidence for genetic control of this character. The fit of models to the other traits is shown in table 4. The additive-dominance model provided a satisfactory fit to the autumn 5-egg weights, but to none of the remaining characters. For these, the digenic interaction model produced some improvement of fit to spring 5-egg weight and shank lengths, although the χ^2s remained clearly significant, but the fit to the plumpness indices remained very poor, particularly in the female. It was decided to drop this last trait from the analyses, until a satisfactory fit to female shank length had been obtained.

Inspection of the contribution of the individual generations to the overall χ^2s in the shank-length data showed that much of the failure to fit was found among the backcross and sibbed-backcross generations. It seemed then most profitable to investigate the effects of interaction between the sex chromosomes and the autosomes. Since in the analyses thus far made and throughout the previous body-weight analyses (Morton, 1973), there had been no indication of any effect of the W chromosome, the interactions fitted were limited to the Z chromosome. The fitting of this model (third pair of rows in table 4) improved the fit significantly only for the right shank lengths of females, and further, one pair of backcrosses and the pair of sibbed backcrosses derived from them still showed large contributions to the overall χ^2s.

The means and standard errors of shank lengths in these four generations are given in table 5. In the backcrosses, it can be seen that the right shank lengths of the two generations are more alike than the left, which partly accounts for the better fit of the models to right than to left shank-length data. But the important point to this table is that, if it is recalled that in the chicken the male is the homogametic sex, there is no model that can account for differences among these pairs of generations. Thus the marked differences between the sibbed backcross generations must be due to a sampling effect in the selection of their parents, that is to genetic drift. It was therefore

decided to combine the data from these pairs of generations whose expectations on any model must be the same, and the result of this combination is shown in the lower half of table 4, under the heading " combined data ".

The digenic interaction models with and without interaction between the Z chromosome and the autosomes were refitted to the combined data. There was little improvement of fit to the spring 5-egg weights, which in fact did not show the genetic drift effect, nor to the male plumpness index data. But the improvement of fit to the shank-length data was marked, and the fit to female right shanks of the digenic + Z chromosome × autosome interaction model was now satisfactory. It was thus decided to reinstate the female plumpness data, but the χ^2 remained extremely large at 301·4 for 8 degrees of freedom.

The failure to fit of the remaining characters could now be seen to stem primarily from the S_3 generation, indicative of the effects of linkage. The linked digenics model was therefore fitted and proved satisfactory for all the

TABLE 5

Means and standard errors in mm. of shank lengths of certain backcross and sibbed backcross generations

Generation† Shank		Backcross CI × C	Backcross IC × C	(CI × C)²	(IC × C)²
Female	left	97·01 ± 0·88	96·18 ± 0·66	97·16 ± 0·47	95·50 ± 0·43
Female	right	96·02 ± 0·87	96·10 ± 0·65	97·22 ± 0·46	95·58 ± 0·43
Male	left	114·03 ± 0·92	112·84 ± 1·07	115·48 ± 0·90	113·17 ± 0·57
Male	right	113·57 ± 0·92	113·41 ± 1·07	115·53 ± 0·89	113·28 ± 0·53

† CI × C = $(CH\sigma \times IA\varphi)\sigma \times CH\varphi$, (CI × C)² is the result of sib-mating CI × C birds, etc.

shank-length data and a fair fit to the spring 5-egg weight and female plumpness data. Since there had been evidence of improvement of fit to the male plumpness index by the addition of the parameters for Z chromosome interaction, these were added to the linked digenics model and fitted to the plumpness index data, but the fit was if anything worse.

Finally, since there was no evidence of the effect of genetic drift on the spring 5-egg weights, the linked digenics model was fitted to their original uncombined data and to those of the autumn 5-egg weights for the purpose of comparison.

The results for which the parameter estimates will be presented in the following section have been italicised in table 4. They are those for the uncombined data for the 5-egg weights, on the additive-dominance model for the autumn data and the linked digenics model for both periods. The linked digenics model fitted to the combined data will be presented for all the body conformation data, and in addition the best fits by an unlinked model to the shank lengths will be discussed, both because in the case of female right shanks a satisfactory fit is possible without invoking linkage and to aid interpretation of the combined parameters in the linkage results.

(iii) *Estimates of the parameters*

Solutions for the least square equations in unlinked models are given in table 6. In the case of autumn 5-egg weight, the additive-dominance model provided a satisfactory fit, and indeed only additive (d) and dominance (h) effects are detected, there being no evidence of sex-linked or maternal effects. By contrast, the fit of the digenic model with Z-chromosome × autosome

interaction to the right shank of pullets shows a multiplicity of effects. The largest is a positive value for dominance (h) but which is opposed by a significantly negative l, or dominance × dominance interaction deviation. On the other hand d, the additive effect, and i, the additive × additive interaction are both significantly positive. The maternal effects of *CH*, *IA* and *IA*♀ × *CH*♂ dams are all to suppress growth of the shank as are the effects of the *CH* W chromosome (w) and the interaction of the *CH* Z-chromosome with *CH* autosomes (iz) or with *CH* × *IA* heterozygotes (jz). The fit of the digenic interaction model to the right shanks of cocks was unsatisfactory with the result that none of the effects is significant when tested against its standard error adjustment by the significant χ^2. This set of parameter estimates is shown mainly for comparison with that of the pullets, to which it is apparently similar.

TABLE 6

Estimates of the parameters for unlinked models

		Female	Male
Trait	Autumn 5-Egg weight (grams)	Right Shank length (mm)	Right shank length (mm)
Model	Additive-dominance	Digenic with Z chromosome × autosome interaction	Digenic interactions
m	246	90·4	108·3
d	+14*	+3·2*	+1·9
h	+28***	+12·4***	+9·3
i	—	+5·5**	−0·6
j	—	+0·9	+0·1
l	—	−3·7*	−3·7
n	−1	−2·0**	−0·3
r	+2	−1·6**	−1·4
s	+5	+0·3	+0·2
q	+1	−1·1**	−1·0
z	−2	+0·4	+0·7
zh	—	—	+1·6
w	−2	−1·3*	—
iz	—	−2·2*	—
jz	—	−2·0*	—

*P<0·05; **P<0·01; ***P<0·001.

Table 7 gives the estimates of parameters for the linked digenics model. For spring 5-egg weight, the failure to achieve a wholly satisfactory fit has meant that none of the parameters other than those containing the mean (m) is significant. Yet some of the parameters containing p, the recombination fraction, must explain the marked improvement of fit over the additive-dominance model compared to the autumn 5-egg weights. The autumn data were fitted to the linked digenics model for this reason, and comparison of the autumn and spring results shows that parameters containing p and l, the dominance × dominance interaction, must have contributed primarily to the improved fit to the spring data.

The shank length data were satisfactorily fitted by the linked digenics model. As one would expect, there was close agreement between the parameter estimates for left and right shanks within sexes, except in the significance of $p^4l - 2p^3l$, which however can be seen to be on the border line of significance and negative throughout. In most respects there is also

agreement between the sexes. The estimates of $m+h+l$ are consistently considerably larger than those of $m+i$: since the standard errors of these estimates are about 0·5 mm in pullets and 0·8-0·9 mm in cocks, there seems no doubt that these differences are real. The estimates of $pi+pl$ and of p^2j are significantly negative and of p^2i-p^3l significantly positive throughout the shank length data. The depressive effect of p^2l and the enhancing effect of n, the *CH* line maternal effect, are significant in the female results, but smaller and non-significant in the males. By contrast the relative effect of the *CH* to the *IA* Z chromosome (z) although similarly positive throughout, only reaches statistical significance in males. Homogametic heterosis (zh) is highly significantly positive.

The fit of the model to the plumpness indices was unsatisfactory, particularly for the cocks. None the less, enough parameters remained significant when tested against adjusted standard errors to suggest different forms of inheritance in the two sexes. The significantly positive value of $pi+pl$ in males is clearly not seen in the females, while a similar effect of p^2i-p^3l in females is certainly absent in males. Although a negative value was found in males for the parameter p^4l-2p^3l, it clearly did not approach the highly significant value for females.

5. Discussion

The reliabilities of all the solutions for estimates of the parameters in tables 6 and 7 are not equal. For autumn 5-egg weight, there was complete association of the genes concerned (table 3), a good fit to the additive-dominance model, and no evidence of other effects when the linkage model was fitted; thus the additive-dominance model is reliable. Spring egg-weight showed some evidence of genetic dispersion, and was not perfectly fitted by any of the models tested. Further, the best fit, the linkage model for which the estimates are given in table 7 shows significance only in the two parameters containing the mean. Yet there must be something in this solution that is not found in the parallel solution for the autumn trait, which explains the great improvement of fit of this over the additive-dominance model (table 4). Thus this comparison will be used to discuss the results with spring egg weight.

The shank lengths were satisfactorily associated and fitted by the linkage model, whose parameter estimates are thus reliable, and is preferred for female right shank length which alone was fitted by a non-linkage model. This latter result is, however, of value in discussing the nature of the compound parameter estimates in the linkage model, and the unsatisfactory digenic interaction solution for male right shanks will be used for the same purpose. The plumpness indices were almost totally dispersed, so that only h and l of the genetic effects can be discussed. Also the fit of the models to these indices was poor, particularly for the males, so that any conclusions are further limited.

Maternal and sex-linked effects were demonstrated only for shank lengths. The *CH* line dams increased shank length, significantly in females, and the *CH* line Z chromosome increased shank length, significantly in males, in which there was also marked homogametic heterosis. The first two of these results confirm the findings of Cock and Morton (1963), whose data included the S_1 and S_2 generations of the present analysis, but without separate analysis of the two sexes.

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TABLE 7

Estimates of the parameters for the linked digenics model

Trait	5-Egg weights (g)		Shank lengths (mm)				Plumpness index (g/cm$^{2.5}$)	
			Left		Right			
	Autumn	Spring	Female	Male	Female	Male	Female	Male
d	+28**	+30	+0·8	+0·9	+0·4	+1·2	+0·20	−0·03
$m+h+l$	272***	292***	96·6***	112·6***	96·6***	112·9***	4·85***	4·38***
$m+i$	245***	277***	91·2***	106·4***	91·4***	106·5***	3·99***	3·67***
$pi+pl$	−4	+17	−1·7*	−2·3*	−1·6*	−2·0*	−0·10	+0·38*
p^2i-p^3l	−5	−33	+4·6***	+4·0*	+4·1***	+4·2**	+0·52*	−0·05
pj	−5	−5	0	−0·3	0	−0·4	−0·09	−0·05
p^2j	+7	+2	−4·0**	−4·7***	−4·5**	−4·4**	−0·16	+0·17
p^2l	0	+10	−1·1*	−0·8	−1·0*	−0·7	−0·04	+0·19
p^4l-2p^3l	+7	+27	−2·6*	−2·9	−2·2	−3·2*	−1·02***	−0·34
n	−4	−13	+1·6**	+1·2	+1·6**	+1·2	−0·03	+0·13
r	+9	+3	−1·3	−0·9	−1·6	−0·7	+0·07	+0·04
$s-q$	+7	0	+0·6	+1·2	+0·4	+1·2	+0·07	+0·05
z	−8	−6	+0·7	+0·7*	+0·9	+0·7*	−0·17	−0·02
zh	—	—	—	+1·8***	—	+1·5***	—	−0·04
w	−5	−2	−0·4	—	−0·2	—	−0·03	—

Not only did the additive-dominance model fit the autumn 5-egg weights, but only the additive (d) and dominance (h) parameters reached significance. The dominance parameter was highly significant and its estimate twice the value of d, but the difference between the two parameters could not be shown to differ significantly from zero. Thus the simple overdominance indicated in the control of autumn egg weight cannot be unequivocally demonstrated. As noted above, the control of spring egg weight can only be inferred from a comparison of the solutions of the linkage model for the two egg-weight characters, which shows relatively large values for spring egg weight of $pi+pl$, p^2l and p^2i-2p^3l. Since the first two are positive and the last negative this suggests a positive value for l. As further, the excess of the estimate of $m+h+l$ over that of $m+i$ is less in the spring result than the autumn, it is unlikely that the large value for h for the trait in the autumn is carried over to the spring. Thus the most likely explanation of the difference between the two characters is that the simple overdominance of the autumn is replaced by dominance × dominance interaction between linked loci in the spring.

For female shank length p^2l and $pi+pl$ are significantly negative and p^2i-p^3l significantly positive, clearly indicating a negative value for l. The pattern is the same for the males except that the value of p^2l is smaller and not significant. Also $pi+pl$ is more negative in males than in females suggesting that i may be negative in males or positive in females. In the estimates from unlinked models (table 6), i was clearly significantly positive in pullets and effectively zero in cocks, so that the latter alternative is confirmed. Since l is negative in both sexes and i positive in females, the considerably larger estimate of $m+h+l$ compared to $m+i$ must indicate a large positive value for h, particularly in females, and this again is confirmed in the solutions for unlinked models. This pattern of a positive value of h partly balanced by negative l is described as duplicate interaction (Jinks and Jones, 1958) which we have previously argued (Morton, 1970, 1973) is a method of homeostatic control. This homeostasis could be one reason for the failure to demonstrate any inheritance of the modular difference between shank lengths, although the inaccuracy of measurement compared to the differences found was probably a more important reason. The duplicate interaction was more clear-cut in females, as was the excess of the positive value of h over the negative of l. Hence the positive additive × additive interaction (i) found in the females may be the result of natural selection against the depression of shank length which must have occurred during the inbreeding of the *CH* and *IA* lines.

Fit of the models to the plumpness indices was not good, yet some of the parameter estimates were found significant even after adjustment of their standard errors to allow for the lack of fit. In males $pi+pl$ is significantly positive. Since p^2l is positive and p^2i-p^3l marginally negative, the major effect must be of positive l, although a smaller positive value for i cannot be excluded. In females p^2i-p^3l is significantly positive. As $pi+pl$ is negative and p^2l negative although small, l must be negative but again some positive value for i cannot be excluded. With l positive in males and negative in females and no evidence that i is more positive in the former than the latter, the fact that $m+h+l$ exceeds $m+i$ by a greater amount in females than in males argues for a considerably greater positive value of h in the pullets. Any values ascribed to i are vitiated by the marked dispersion that was demonstrated for the plumpness indices, but h and l are unaffected by

dispersion. Thus the contrast is real between the female data, in which the duplicate interaction shown in the shank length is continued in the plumpness indices, and the male data, in which an opposing positive value of l is demonstrated. This result links with the previous analysis of body weights (Morton, 1973), where it was shown that homeostatic control by duplicate interaction was maintained to 20 weeks of age in females but had disappeared by this age in males. Thus in cocks the homeostatic control which was demonstrated at earlier ages is apparently maintained in the basic skeleton and the decontrol on weight as they reach maturity, which is postulated to be related to the need for a dominant male to be chosen (Morton, 1973), is mediated through positive dominance × dominance interaction in the degree of plumpness, presumably musculature, developed. The highly heterozygous cock will come to rule the roost.

The estimates of the compound parameter p^4l-2p^3l are generally in disagreement with the pattern of estimates of the remainder of the linkage parameters, as described above. This may be seen particularly clearly in the case of the female left shanks, in which p^4l-2p^3l is significantly negative but the other three terms in p and l agree well that l itself is significantly negative. The values of p^4l-2p^3l derive primarily from differences between the S_2 and S_3 generations although they are also estimated from the sibbed backcrosses. Specifically, a fall in mean values from the S_2 to the S_3 greater than could be accounted for by the other parameters could yield a negative value of p^4l-2p^3l. The most likely explanation for such a fall is the effect of the remaining segregation in the highly inbred *CH* and *IA* lines which had been shown to exist for blood groups by Gilmour (1959), as was suggested for the body weight results (Morton, 1973). The possibility exists that the highly significant negative estimates of p^2j in the shank length analyses have the same origin. For the estimates of pj are essentially zero, as was the estimate of j in the non-linkage model for males, while that for females j is non-significantly positive. But from the values of p^4l-2p^3l above, the shank lengths, the female plumpness index and probably male plumpness index and spring egg weight, all show evidence that they are inherited to an important extent via the small proportion of the genomes of the inbred lines which continues to segregate. Since this proportion includes blood group loci of known linkage relationships (Gilmour, 1960), the results of this and the previous paper on body weight extends the hypotheses to polygenes of the conclusion for major genes of Hutt (1964) that " it may be that most of the fowl's genes belong in its seven longer chromosomes ".

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