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Survey of line crosses in a Brown Leghorn flock

1. EGG PRODUCTION

BY J. S. S. BLYTH AND J. H. SANG

Agricultural Research Council's Poultry Research Centre, West Mains Road, Edinburgh, 9

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As a preliminary to more specific studies of certain aspects of hybrid vigour in the fowl, some indication was needed of the combining abilities of the various isolate strains of the Centre's Brown Leghorn flock. A number of individual crosses had been made earlier, but they were mainly from single-sire matings (e.g. Greenwood & Blyth, 1951; Blyth, 1952a), and the effect of intervear variations among them made comparisons unsatisfactory. On the other hand, accommodation was insufficient to allow of testing all eight lines together, so the plan adopted was to set up a series of cross-matings including as many lines as possible, having regard to the minimum number of pullets per cross that could be expected to yield useful information. The resultant test is based on a set of 6×6 strain matings, with an average of just under 18 pullets housed per reciprocal group. The immediate purpose of this initial survey was to determine how far the characteristics of the parental strains were expressed in the crosses, and if any particular cross showed an outstanding degree of heterosis which could be further analysed. Subsequent reports will deal with hatchability, growth and body weight in the same experimental material.

The flock from which the birds derive has been closed since 1931. It was built up in the preceding three years from five widely differing sources (three in England, one in Scotland, and one in Denmark). At various times prior to 1939, seven isolate strains were formed from pullets showing diverse outstanding phenotypes. The remaining stock then became the eighth of the lines, all of which are still extant. The latter, line B, selected for both egg size and numbers, is included in the present survey along with L, large egg, I, intensity of production, and N, reduced pausing between laying cycles (a feature which did not persist). These lines, chosen for productive traits, were in existence by 1935. Of the others used, R, increased red pigmentation in the plumage, was formed in 1939. Line W, 'white', was established in the same year from two N hens with white speckled plumage (a simple recessive mutant), but had a bird from line B introduced in 1944. The lines have been subject to mild selection in the direction of their basal traits but, apart from the initial matings, the various degrees of inbreeding which they have undergone are largely incidental to the space allotted to them. The largest line, B, has had annual replacement of about eighty pullets (three to five sires), while I has been maintained at not more than half that number (two to three sires). In the remaining lines only one to two sires have been used with an annual quota of twenty pullets or less. In the latter groups some mitigation of the consanguinity consequent on such small numbers has occurred through the use of hens of several generations to supply each season's stock. Estimates of the inbreeding coefficients of the lines and crosses are given in Table 1.

Table 1.	Coefficients	of i	nbreeding for	lines	and crosses	(%)*
Line	L	в	Ν	W	I	\mathbf{R}
\mathbf{L}	64	14	6	9	8	5
в		31	5	11	6	5
N			57	21	4	7
W				62	4	5
I					46	3
\mathbf{R}						74

* The line coefficients were estimated directly by Wright's method. We are indebted to Mr A. G. Cock for the figures for the crosses; they were obtained by calculating coefficients of inbreeding for hypothetical matings of sets of early line ancestors, and weighting them according to the product of the proportions in which each pair of ancestors now contribute to their respective lines.

Breeding was carried out by artificial insemination. Ideally each sire would have been mated to representatives of all six strains but, with low semen production in some, this was not always possible. The plan was operated as far as practicable and only two sires were used with single females. The total number of parents included in the survey were:

Lines	\mathbf{L}	\mathbf{B}	N	W	I	\mathbf{R}
Sires Dams	$\frac{5}{26}$	3 24	9 27	6 28	$\frac{4}{23}$	7 23

Chicks were hatched at 5-weekly intervals in February and March 1958. This was about a month earlier than usual, but designedly so, to give the pullets an opportunity of entering production before the season of rapidly decreasing daylength which introduces marked genotype-environment interactions into maturity variations. Up to 6 weeks of age they were reared in battery brooders in mixed batches but separated into three rough-size groups. Later the females were transferred to floor pens in an intensive house where they remained until the fastestdeveloping individuals were close to maturity. Half the population was then moved to individual cages in a battery house, and the remainder rearranged in twenty-bird pens. All the mating groups were divided as evenly as possible, full-sibs being allocated to each location, and pullets of each group distributed randomly over pen and cage positions.

The pens were well lit by continuous roof lighting, but the battery house was considerably darker, daylight entering through small recessed windows in a flat roof. Extra winter lighting was supplied in both houses from October to March, the day being increased from $11\frac{1}{2}$ to 12 hours over the last three months of the year. Mash was fed *ad lib*. in the pens with a scratch feed of mixed grain in the

evening. The cage birds had the same total food formula as an all mash diet till the beginning of May when alterations in the Centre's feeding plans necessitated a change to pellet feeding.

Since the lines derive from the same foundation stock, they represent segregate samples of the same gene pool and, along with the crosses, they can be expected to give some idea of the level and variety of performance that can be obtained by reassortment of genotypes within a particular population of fowls. With all the line and F_1 samples treated alike, it should be possible to regard the group mean differences as mainly attributable to the line genotypes they contain. Thus, comparison of production traits in the contemporary samples of lines and crosses made it possible to examine the position with regard to heterosis in the stock, to see if it occurred in all strain crosses, or was mainly restricted to particular lines or specific matings.

In the descriptions and analyses which follow, the term cross refers to the combined samples from the reciprocal matings of two lines. Where individual reciprocals are mentioned the convention has been adhered to of putting the female line first, e.g. BN refers to the mating B $\mathfrak{p} \times N \mathfrak{s}$. In the tables giving mean performances of the progeny groups, the matings have been ranked in order of the egg size normally characterizing the lines; for two, N and W, which are very similar for the character, the line weights have changed ranking in the survey samples.

RESULTS

Sexual maturity

Despite the intention of bringing the pullets into lay before the season when marked interaction with environment was likely, the mean maturity ages for the separate progenies showed a wide dispersion, with a range of the order of 10 weeks for both lines and crosses. In pens, the line means run from 174 to 249 days, and those of the cross groups from 150 to 235 days (Table 2). The cage samples are only slightly less variable, so that the general hybrid advantage of 18 days earlier in pens and 13 in cages means little without some knowledge of its content.

Ages at sexual maturity are not very different in the two locations; means of all

				Pens	5						Cage	es		
Dam	Ĺ	в	N	w	I	R	Mean*	Ĺ	в	N	W	I	R	Mean*
Sire														
\mathbf{L}	178	166	174	175	159	167	168	188	160	189	186	179	157	174
\mathbf{B}	167	174	198	191	164	171	178	162	173	215	190	181	167	183
N	173	176	208	206	169	178	180	172	183	193	223	166	180	185
w	180	235	199	249	186	178	196	174	185	192	243	194	175	184
Ι	156	165	189	207	183	178	179	152	165	194	196	166	173	176
$\mathbf R$	150	170	167	199	162	184	170	153	160	160	189	155	181	163
Mean*	165	182	185	196	168	174	178	163	171	190	187	175	170	178
						* C	rosses or	ıly.						

Table 2. Mean age at sexual maturity in days

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cross groups show caged birds to be less than 1 day earlier. This is perhaps not surprising since they were not separated until the most advanced individuals were at point of lay. However, the hybrid progenies of B and R dams laid slightly earlier in cages, as did those of W, I and R sires. The B-dam and W-sire differences of 11 days are entirely due to one extreme cross in pens (BW) which matured 66 days later than the other offspring of B dams there, and 50 days later than its cage equivalent; other differences for sire and dam means did not exceed 1 week. Of the pure lines, L was 10 days later in cages while N and I were 15 and 17 days earlier respectively: even the largest of these three differences is below the 5% level of significance, so it is unnecessary to look beyond sampling error for their source; the last two lines are of small body size, and peck order in the pens may have contributed to the location difference.

An analysis of variance of maturity ages of hybrids confirms that there are marked differences among them (Table 3). Interactions with location occur in

Table 3.	Sexual maturity: analyses of cross, reciprocal and location
	differences

		All data	Excluding B-W groups		
	d.f.	Mean square	d.f.	Mean square	
Locations	1	83	1	164	
Crosses	14	6753**	13	5765**	
Reciprocals	15	1555	14	1426**	
$Location \times Crosses$	14	639*	13	225	
$Location \times Reciprocals$	15	713*	14	379	
Error	398	314	366	286	

 $*P = \langle 0.05 \rangle$ $**P = \langle 0.01 \rangle$ throughout all Tables.

both crosses and reciprocals, and, tested against its discrepance, the variation due to reciprocal differences does not attain significance. Both location interactions depend on the presence of the atypically late BW pen sample, for they disappear when the progenies of the intermatings of lines B and W are excluded from the analysis. This allows the mean square for reciprocals to be compared with that for error; on this basis the F ratio becomes highly significant with, or without, the B-W groups. Apart from the latter, five of the other fourteen crosses appear to contribute individually to the inequality of reciprocal behaviour, but even so, the influence of the line characteristics is demonstrable when mean cross maturity ages are compared with the average of their parental means: for the combined pen and cage data there is a regression of 0.718 ± 0.15 of cross on mid-parent value, and a correlation of 0.793 between them. Although this accounts for some 60% of the cross variance, adjustment for this covariance is not sufficient to reduce the remainder mean square below a significant value when tested against error (Table 4). Exclusion of the B-W progenies does not alter the situation and yields slightly lower figures for b and r.

Table 4. Cross means. Sexual maturity: adjustment of mean square for covariance with mid-parent estimate. All data (b = 0.7181 r = 0.7926)

,	d.f.	Mean square
Regression	1	1956·8**
Remainder	13	89.1**
Error adjusted for		
analysis of means	398	10.3

The line mean differences in cross performance have been analysed by the reciprocal sums and differences method of Yates (1947), and the results are summarized in Table 8 along with the corresponding data for egg production. As was to be expected from the correlation with mid-parent values, average line differences in sexual maturity are highly significant. There is no indication that dams and sires of the same line are contributing unequally to the effect; the significant reciprocal differences exposed above fall in the remainder portion of their variance which is significantly greater than that for crosses within lines.

In addition to this divergence between reciprocals, the general hybrid advantage in sexual maturity covers a considerable amount of variation among individual groups. Nevertheless, all but two of the pen samples (NB and BW) showed some heterosis in that they matured earlier than the relevant mid-parent estimate. In cages, four were later than this, and the same number approximated to it.

Egg number

Production has been considered mainly on survivors' records. It is possible, and indeed demonstrable, that particular causes of mortality may affect the hybrids unequally. Location effects, however, have made it necessary to examine the pen and cage data separately and, with the initial small numbers in the samples, any chance incidence of non-specific mortality might materially distort the results. Accordingly all birds dying during the laying cycle, or obviously unhealthy, have been eliminated from the detailed analysis. This left a population of 558, of which 100 were purebreds. Comparable records for them are available up to 500 days of age.

The first pullets commenced to lay in July, and in the next few months the wide differences of maturity ages were strongly mirrored in the production records. At first, it seemed likely that the earliest laying crosses would retain their advantage over the whole cycle, but differences in inherent laying rate (clutch size) began to interact with the maturity effects to change the ranking: in pens, crosses of L and R, which along with those of L and I, and of B and I, had been among the top producers till the end of September, had only average records to 500 days; B and I crosses remained in the lead while the other pair of reciprocals finished intermediate between them.

Cross production to 500 days averages 50 eggs better than the parental lines in pens, but there are wide differences among the F_1 yields, which range from 186 to 274 eggs (Table 5); taken as a whole, the differences in mean performance are not

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				Pens							Cage	s		
Dam	Ĺ	в	N	W	I	R	Mean†	Ĺ	В	N	W	I	\mathbf{R}	Mean†
Sire														
\mathbf{L}	128	228	192	189	230	223	212	123	206	182	169	178	185	184
в	193	214	214	201	251	250	222	201	192	175	198	196	207	195
N	214	224	165	200	244	201	217	184	183	164	170	207	188	186
W	191	186	195	122	208	212	198	168	176	193	113	190	188	183
Ι	233	274	214	208	202	223	230	202	219	182	189	209	215	201
\mathbf{R}	215	227	220	206	243	168	222	213	214	208	186	220	153	208
$Mean^{\dagger}$	209	228	207	201	235	222	217	194	200	188	182	198	197	193

Table 5. Egg production to 500 days*

* Differences of 28 eggs for pens and 26 eggs for cages are significant at P = 0.05. † Crosses only.

random but show a noticeable parallelism with mid-parent estimates. In cage samples, which average 24 eggs fewer, the situation is somewhat different: there the variability of means is not so great, and the association with parental ranking less evident. The hybrid advantage is reduced to 34 eggs, and in the individual groups it appears to diminish with increases in mid-parent value. The lines themselves appear less affected by the cage environment and averaged only 8 eggs

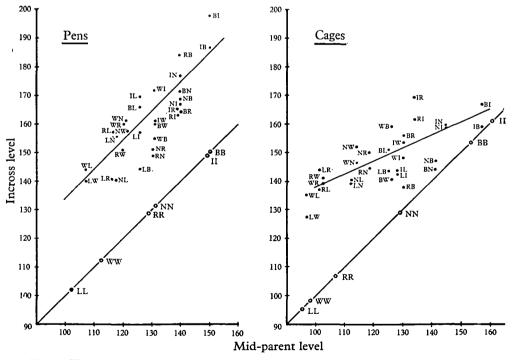


Fig. 1. November through June production of survivors in pens (left) and in cages (right) plotted against the mid-parent value. The production level of the parent strains themselves are joined by the heavy line and the regressions of cross on mid-parent is shown by the light line.

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fewer there. The contrast in behaviour in the two locations is particularly evident when the mean cross records for the months November to June are plotted against the corresponding figures for mid-parents; that is, for that part of the laying cycle from which the sexual maturity effects are excluded (Fig. 1). For the combined reciprocal means (d.f. 13) the regression slopes illustrated are 0.988 for pens, and 0.447 for cages, both significant but also significantly different. For each location removal of this covariance is sufficient to reduce the remainder cross mean square below the 5% level of significance, when tested against that for error (Table 6). For the full 500-day production the association with parental performance, though still marked, does not account for all the variation in cross means.

 Table 6. Egg production cross means: adjustment of mean square for covariance with

 mid-parent estimate

		November t	To 500 days			
b:		Pens 88 ± 0·13 Mean square	0.447	$\underbrace{\begin{array}{c} \text{ges} \\ \pm 0.10 \\ \\ \text{Lean square} \end{array}}_{\text{Iean square}}$	$\begin{array}{c} \hline Pens \\ 0.700 \pm 0.14 \\ Mean \\ square \end{array}$	Cages 0·365 ± 0·13 Mean square
Regression Remainder Error (adjusted)	1 13 199	1816 32 24	1 13 199	782 36 21	3446 139** 43	936 113** 41

Since it seemed to be the variation in sexual maturity that was reducing the relationship of total production and mid-parent level, a general analysis of variance is presented for the November to June period, which excludes it, as well as for the full cycle (Table 7). The cross and location mean squares show variation for both classifications, but the reciprocal differences are only significant in the 500-day one, indicating the effect on the latter of sexual maturity variations. The only significant location interation, that for 500-day crosses, also seems to be a carryover from the same source: removal of the B-W groups, with the atypically latematuring BW reciprocal in pens, is sufficient to reduce the F ratio below the 5%level.

Table 7. Egg production: analyses of cross, reciprocal and location differences

		November–June	0-500 days age
	d.f.	Mean square	Mean square
Locations	1	18950**	67643**
Crosses	14	3220*	7399**
Reciprocals	15	411	1657**
$Location \times crosses$	14	408	1183*
$\mathbf{Location} \times \mathbf{reciprocals}$	15	277	402
Error	398	336	636

The influence of age at first laying is also brought out in Table 8, where the line differences for all three criteria are analysed. There the parallel behaviour of the

sexual maturity and 500-day data is in contrast to that of the less variable November to June records. In all three cases there are definite line effects on the hybrids, but none that are consistent for sex of parents. Within lines, however, the reciprocal differences already noted for sexual maturity are also present in the 500-day analysis though their mean square is not significantly greater than that for the cross remainder.

Table 8.	Analyses of line	differences in	age at s	sexual maturity,	egg production
	November to	o June, and to	500 days.	. Mean squares	

			Production			
		Age at	~			
	d.f.	Sexual maturity	Nov.–June	500 days		
Crosses				·		
Between lines	5	1174**	559**	1166**		
Within lines	9	40	29	58		
Reciprocals						
Between lines	5	87	17	37		
Within lines	10	133**	29	142**		
Error (adjusted)	398	21	22	42		

In general, the variations in the full hybrid production to 500 days appear to have three main sources: (1) parental genotype, as evidenced by correlation with mid-parent levels; (2) reciprocal differences originating from variations in sexual maturity, and (3) an additional hybrid gain. With the exception of the aberrant BW pen sample, the behaviour of the crosses in the two locations was reasonably consistent despite the lower level of production in cages.

Egg weight

There is a wide range of egg size in the parent lines, from 46 to 69g., but the hybrid means remain consistently close to the mid-parent values, averaging less than a gram above the latter (Fig. 2). The largest deviations from mid-parent levels are increases of 3.4 and 3.5 g. in WR and RI crosses respectively. Plotted against egg number, group mean egg weights showed the expected negative trend but there was some irregularity at the lower end of the size scale, and it was noticeable that the groups with the highest yields were near the mean for egg size. In examining the relations between the two characters statistically, the data for crosses were analysed in three ways: (1) as a whole, and then in two subclasses for groups with means, (2) of 55g. and over, and (3) or less than this. Correlations were computed using March egg weight with October to March production, as well as with estimates of inherent production rate (January to March per cent production with gaps of more than 1 day excluded). Both sets showed the same general picture for all three classifications, although, as was to be expected from previous experience (Blyth, 1952b), the significant associations were higher for the rate comparisons: for pens, the total correlation with egg weight for all cross individuals was -0.186 (d.f. 234) for October to March records, but -0.399 (d.f. 228)

for inherent production rate. (The difference in degrees of freedom results from inability to compute rate satisfactorily in a few irregular layers.) For classifications 1 and 2, the cross products for total and group variation were negative in sign; in the third class, they were consistently positive but non-significant. Only in the

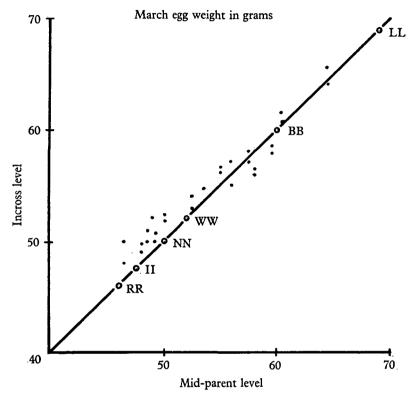


Fig. 2. The March egg weights of birds kept in pens plotted against their midparent values.

complete data, and the subclass containing the larger egg-size means, were significant correlations obtained in either pen or cage material. The correlations were slightly higher for the pen birds.

Attempts to split the data in other ways did not suggest any other rational arrangements of relationships. Thus the inference is that there is a limited range of egg size over which weight and numbers are negatively interdependent, and that outside this the association breaks down, or at least alters. The best producers are at the smaller-size end of the covariant range.

Mortality

No reliable picture of pullet mortality was to be expected from this survey: the overall percentages for lines and crosses do not differ greatly, being 13% and 9% respectively for 12 months to the end of June. The figure for lines was almost twice as high in pens (16%) as in cages; the incidence for crosses was the same in

both locations but of different composition: there were more deaths due to fowl paralysis in pens (3% of the cross population there), and cage layer fatigue occurred only in the batteries (3.5%). Most cases of the latter were among progeny of I dams which had 18% deaths in cages but only 8% in pens. N dams, with 25% deaths in both locations, spread very evenly over their cross progenies, had the highest incidence, while only a single pullet died among the offspring of W females.

DISCUSSION

Before discussing the results it may be well to recall the nature of the experimental material used in this survey. The lines are descended from the same foundation stock, and so represent segregate samples of the same gene pool. The numbers in the individual groups are small, particularly where it has been necessary to examine location samples separately, and any deductions relating to specific crosses must remain tentative. Trends over the whole series, however, are likely to be more reliable; they lead to generalizations which may have wider application in similar closed flocks, or even in relation to strains or breed crosses, but authentication of this must await further experiments. Until this is obtained the conclusions reached must be regarded as relevant only to the stock under consideration.

Although the 500-day records of the hybrids tested vary greatly, most are superior to that of the better-parent line in pen samples, and it is striking how far the differences among them reflect parental characteristics rather than an expected diversity of heterotic effects. The relationship is particularly marked when variations deriving from age at sexual maturity are excluded: in the records for November to June, the variation among cross means is completely accounted for by the covariance with mid-parent levels, and the hybrid gain of 34 eggs appears to represent a similar improvement in all crosses. A comparable situation obtains for the less variable cage sample means over the same period, though the hybrid gain is less in the more productive groups.

These two major factors affecting F_1 production rate, parental constitution and hybrid gain, must clearly have been confounded in many previous comparisons. Yet the influence of the former had been suspected as early as 1938 by Knox and Olsen, who believed that better crosses came from better parent stock. Also Harada (1956), working with inbred lines of silkworms, reported regressions of F_1 cocoon weights and filament lengths on mid-parent values very similar to the ones obtained here for pen data. He did not consider the possibility, however, that the association might be complete, but concluded that the hybrid gains decreased proportionately with the increase in parental performance. The 500-day pen records might be interpreted in this way, and, taken alone, the figures for caged groups certainly give grounds for such an inference, for the increases in crosses involving the better parents become insignificant and sometimes negative.

The housing of the birds in two ways has brought in variation in an unexpected form. Lerner (1958) has discussed the general problem of production under different environments; earlier (1955) he expressed the opinion that cross genotypes may

be better 'buffered' than more homozygous ones, and so more resistent to the vagaries of their surroundings. Superficially, the reverse appears to be true here for the lines seem to have withstood the cage conditions somewhat better than the crosses; this applies even when mortality is taken into consideration. In pens, however, even the best of the lines did not reach the mean level of the cross groups, and it may be that they do not actually differ from the latter in their response to the cage environment; they may only appear less affected because they are low in the production series. This makes the virtual absence of location-cross interaction more comprehensible, for the picture for cages of a loss in production that falls most heavily on the higher producers, is partly conditioned by the lesser reduction in line performance. Since the obvious difference between locations. relates to the impaired lighting in the battery house, it may be that some relatively simple restriction is then operating, such as insufficient feeding time during the shorter days to allow of a food intake adequate for higher production potentialities. to be fully expressed. The change from mash to pellet feeding in May also caused a. temporary slackening in production.

Although differences in hybrid performance, once the birds were actually in lay, seemed a matter of 'general combining ability' and additive dependance on parental characteristics, the behaviour of sexual maturity brings in complications. which prevent accurate prediction of their relative capabilities. The effect of the single late-maturing BW sample in pens was particularly marked, but its caged homologue fitted quite well into the general patterns of behaviour. Further, the full-sib families in one were equally represented in the other, so there seems little doubt that it is a chance effect. Other reciprocal differences may be of more consequence, but the smallness of the groups makes them particularly subject to sampling errors, and repetitions of the relevant line matings are necessary to test. the validity of the differences. Again, in this latitude at least, sexual maturity is considerably affected by interactions between genotype and date of hatch (Osborne,. 1952). In the present study the pullets were hatched early, and most of the groups were well in production by the time the disadvantageous conditions of autumn became operative. The late-maturing ones, especially line W and the BW pen sample, however, may have been still further retarded by the rapidly shortening day-length as they approached maturity. This should have brought an error into the mid-parent values containing a W parent, yet the significance of the correlation between cross and parental maturity ages depended largely on these groups. Again, the autumnal environmental effect may have been reflected in pausing among the earlier laying groups, but if so, it did not greatly disturb the general trends brought out in annual production.

While such semi-fortuitous factors could have been responsible for the significant differences between reciprocals, both sex-linkage and maternal effects have been considered with regard to this kind of variation in earlier investigations (Hazel & Lamoreux, 1947). In the present case it is clear from Table 8 that they are not line attributes, and occur only in specific combinations. Their most likely congenital source appeared to be the great differences in line egg size (46 to 69 g.) which might.

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be producing maternal effects giving rise to interaction with the embryo genotype. No statistical evidence of such intervention could be obtained. Body weight, too, in which parental variations range from 1200 to over 2000 g., but do not entirely parallel those of egg weight, appeared to have no clear connexion with reciprocal behaviour until the set containing the atypical BW group was excluded. Then the differences in mean maturity ages between reciprocals for pen, and pooled location means (but not for cage figures alone), yielded significant correlations (0.62 and 0.52; d.f. 12) with the difference in adult body weights of the parent lines. The evidence is slight; it may be fortuitous, or relate only to variations within a particular gene pool. Nevertheless, the possibility that the way in which two strains of differing size are mated may affect the production of their progeny is a point worth further investigation.

Although the irregularities of variation in sexual maturity detract from the general parent-progeny association for the full records, two of the lines used were very late in maturing, and strains as retarded as line W are unlikely to be retained in commercial flocks. Further, the practice of controlling the time at which pullets enter production, by artificial means, would also tend to reduce these initial differences, and so make the parental production rate a better guide to cross behaviour. It should be emphasized, however, that the results of the present study depend on a comparison of cross production with the mean performance of the parent lines: comparison with the better parent would not lead to so consistent a picture.

The fact that the hybrid gain in pens appears to be a constant for all groups over the greater part of the laying year, is an unexpected phenomenon. It had been supposed that the lines were suffering from inbreeding degeneration, and that cross improvement would be related to the variable, though not extreme, amounts of inbreeding to which they had been subjected or to the consanguinity of the parents. If the hybrid gain represents restitution of inbred loss, why has it not reflected these differences? Is it that the degree of inbreeding is not different enough to create measureable variation, or that the methods of stock replacement used, involving a relatively slow increase in homozygosity over a long period, have resulted in genotypes which are different but yet subadequate to nearly the same extent? As far as the material will allow, this aspect of hybrid vigour will be taken up in a later report, but it is clear that similar analyses of the whole problem are needed using other stocks. The wide inter-line variation in production phenotypes has been advantageous in exposing the role of general factors participating in cross improvement, but their relative importance in more uniform, and genetically different, commercial stocks remains to be determined. The few experiments reported that are in any way comparable with the present survey do not suggest that our results are atypical. Warren (1942), Knox et al. (1949) and King & Bruckner (1952) did not get as much hybrid gain with breed crosses though the last-mentioned authors used larger numbers. Maw (1949), with six inter-matings of seven inbred lines, obtained about the same range of variation of cross increases. In Yao's (1959) report, it is not clear whether the 9 months production figures

given refer to birds actually in lay, but if so they provide an interesting comparison with the post-maturity records described here. Reduced to an 8-month value to bring them in line with the November to June figures quoted above, it appears that the parental inbred lines were more degenerate, and that the best of his F_1 groups laid at approximately the same level as the poorest crosses in the present series. Plotted against their mid-parent values, the scatter of his crosses suggested that the hybrid gain was greater for the better parents. When combined with the November to June data, however, a regression on mid-parent of 0.79 ± 0.05 (d.f. 19) was obtained which is within the limits of error of the value 0.99 ± 0.13 , calculated for the latter alone.

The importance of parental performance levels in relation to cross records raises the question of the attributes of a good line in this respect. Further investigation of the components of production may hold some clue. It was noted, for instance, that the negative interdependence of egg number and egg weight only extended over the upper half of the egg-weight range, and that the egg size in the best laying crosses was at the lower end of this covariant series, and so near the flock mean. These crosses were also roughly intermediate in adult body size. Whether this represents an optimum for the flock genotype seems a point worthy of investigation. In pens, IN and IR, with smaller egg size, both laid over 240 eggs in 500 days, but none of the groups with means of over 56 g. exceeded 230 eggs. It may be that, in some stocks, egg-size requirements constitute a limiting factor in the search for better egg production.

While the limitations of the present material preclude any accurate assessment of the part played by mortality in contributing to the variations in hybrid production, the general distribution of deaths among the cross groups suggests that it may be not unimportant. Though its effect may be less serious under practical conditions, the situation with regard to sexual maturity also requires further elucidation. Yet, however much these variables contribute to the level of egg production in crosses, it is clear that one essential requirement for successful hybrids is parent stock which are themselves good layers.

SUMMARY

Six isolate lines of long standing, from the Centre's Brown Leghorn flock, were intermated in all possible directions, providing thirty cross and six pure line samples. Half the birds from each line and reciprocal cross were kept in floor pens and the rest caged in an adjacent battery house.

Sexual maturity, survivors' production to 500 days of age, and November through June egg numbers, all showed two main factors contributing to variations in cross performance: (1) a significant association with parental production levels as measured by mid-parent averages, and (2) an additional hybrid gain. For November to June production in pens, this hybrid gain appeared to approach a constant for the cross groups. Additional sources of variation were present in age at sexual maturity.

The 500-day records for the penned hybrids exceeded the line average by 50

420

eggs. Caged samples did less well and showed an advantage of only 34 eggs. In this location the hybrid gain for individual groups decreased with increases in mid-parent level.

Egg weight varied negatively with egg numbers only in the upper half of the wide egg-size range. The best layers fell at the lower end of the covariant range for egg size.

The importance of improving closed strains may not have been lessened by the expansion of the hybrid side of the poultry industry, for the pattern of relationships of line and cross production in this flock is consistent enough to justify the inference that the best hybrids come from the best-producing parents.

REFERENCES

- BLYTH, J. S. S. (1952a). Degenerate inbred lines of Brown Leghorns and their first crosses. Emp. J. exp. Agric. 20, 133-141.
- BLYTH, J. S. S. (1952b). Longtime trends in egg production in a closed line of fowls. Proc. roy. Soc. Edinb. B, 65, 52-65.
- GREENWOOD, A. W. & BLYTH, J. S. S. (1951). A repeated cross between inbred lines of poultry. J. agric. Sci. 41, 367-370.
- HARADA, C. (1956). On the relation between commercial characters of parents and their F_1 hybrids in the Bombyx silkworm. Proc. int. Genet. Symp., Tokyo and Kyoto, pp. 352-356.
- HAZEL, L. N. & LAMOREUX, W. F. (1947). Heritability, maternal effects and nicking in relation to sexual maturity and body weight in White Leghorns. *Poult. Sci.* 26, 508-514.
- KING, S. C. & BRUCKNER, J. H. (1952). A comparative analysis of purebred and crossbred poultry. *Poult. Sci.* **31**, 1030–1036.

KNOX, C. W. & OLSEN, M. W. (1938). A test of crossbred chickens, Single Comb White Leghorns and Rhode Island Reds. *Poult. Sci.* 17, 193–199.

- KNOX, C. W., GORDON, C. D. & MEHRHOF, N. R. (1949). Performance of Rhode Island Reds and Light Sussex as compared with that of their F_1 and three-way crossbreds. *Poult. Sci.* 28, 415–419.
- LERNER, I. M. (1955). Buffered genotypes and improvement in egg production. Amer. Nat. 89, 29-34.
- LERNER, I. M. (1958). The Genetic Basis of Selection. Wiley.
- MAW, A. J. G. (1949). Performance of crosses of certain inbred lines. Poult. Sci. 28, 499-503.
- OSBORNE, R. (1952). Sexual maturity in Brown Leghorns. The interactions of genotype and environment. Proc. roy. Soc. Edinb. B, 64, 445-455.
- WARREN, D. C. (1942). The crossbreeding of poultry. Tech. Bull. Kans. agric. Exp. Sta. No. 52.
- YAO. T. S. (1959). Additive and dominance effects of genes in egg production and 10-week body weight of crossbred chickens. *Poult. Sci.* 38, 284–287.
- YATES, F. (1947). Analysis of data from all possible reciprocal crosses between a set of parental lines. *Heredity*, 1, 287-301.