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Line and crossing effects in a diallel mating system with highly inbred lines of White Leghorn chickens

C. Hagger
Institute of Animal Production, Swiss Federal Institute of Technology, CH-8092 Zürich, Switzerland

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Summary. Seven highly inbred lines of White Leghorn chickens were used in a near complete diallel mating plan during eight years. The lines originated from three different base populations selected for egg weight. Average inbreeding coefficients of parents of chicks hatching in successive years were 0.75, 0.80, 0.84, 0.86, 0.89, 0.91, 0.93 and 0.94. The composition of line, specific combining ability and reciprocal effects and their estimated values are given. These effects were estimated for age at first egg (AFE), average weight of all eggs laid to 40 weeks (EW40), body weight at 40 weeks (BW40), number of eggs to 40 weeks (EP40) and number of eggs between 41 and 60 weeks (EP60). Records of 3247 hens surviving to 40 weeks and of 3133 birds to 60 weeks could be used. Large differences between line effects could be found in all traits. They were only partly due to the preceding selection in the base populations. All specific combining effects were in the expected direction, negative for AFE and positive for EW40, BW40, EP40 and EP60. Recovery of inbreeding depression inflated these effects rather substancially. Average heterosis, defined as the relative superiority of a line combination over the mid parent value, was −11.3%, 5.8%, 7.8%, 45.1% and 35.8% for AFE, EW40, BW40, EP40 and EP60 respectively. One line showed a relative superiority in AFE of −19.3% compared to about −7.9% for all other combinations. Reciprocal or sex-linked effects were generally smaller in all traits than specific combining effects, they were considerably smaller in AFE, EP40 and EP60. General reciprocal effects could be found for several lines in one or more traits. Offspring of two lines, when used as sire lines, showed a negative correlation between reciprocal effects of egg weight and body weight.

Key words: Inbred chickens – Diallel plan – Line effects – Specific and reciprocal effects

Introduction

Inbred lines and their crosses provide a means to investigate the importance of direct line and crossing effects in quantitative traits.

Different statistical models, including various genetic effects, have been proposed to analyse diallel tables, e.g. Henderson (1948); Griffing (1956) and Eisen et al. (1966). Crossing effects in production traits of poultry have been given by e.g. Cock and Morton (1963); Wearden et al (1965); Eisen et al. (1967) and recently Fairfull et al. (1983). The estimation of variance components is appropriate, if the lines or breeds used can be thought of as a random sample from a population of lines or breeds. If only a small number of lines is available or if highly inbred lines with repeatable performances are used, an analysis of fixed effects is appropriate (Griffing 1956).

It is known from theory (e.g. Falconer 1982, p. 241) that subdivision of a population through inbreeding increases the total genetic variance in the population, thus resulting in lines with very different genetic values. These differences as well as inbreeding depression and its recovery in crosses are well known. It is expected from theory (Falconer 1982, p. 233ff.), that, with the exception of wide crosses, fixed effects estimated from a diallel crossing system with inbred lines are a function of the inbreeding coefficient and the genetic variance in base populations. This may result in large line differences, even for lines from the same genetic origin. It seems useful to take these effects as an indication for the possible range of values which might be found in crosses of noninbreds.

Data for five traits, sexual maturity, egg weight, body weight and two production traits, of a diallel crossing experiment involving seven highly inbred lines of White Leghorns was used in this study. The lines originated from three differently selected populations out of a common base population (Fig. 1). Line effects, specific combining ability effects and reciprocal effects, all taken as fixed, are presented and their genetic composition is briefly outlined.

Material and methods

Seven highly inbred lines of White Leghorns, developed and kept on the experimental farm, "Chamau" of the Swiss Federal Institute of Technology (ETH Zürich), were crossed in an almost complete diallel breeding plan during eight years. The history of the lines is given in Fig. 1. Two lines, one for high (–) and one for low (- - -) egg weight were selected from a common base population (B). A third line was obtained after seven cycles of selection by crossing the two selected ones (Hilfiker and Lörtscher 1972 and Hagger 1977). The inbred lines were started from these three populations, lines 71 and 75 from the high, lines 77, 79 and 81 from the low egg weight population and lines 87 and 92 from the cross. Fullsib matings by artificial insemination were always made to propagate the inbred lines. Although, no distinct selection was practized, matings were preferably made with the best egg-producing hens. The average inbreeding coefficient, calculated from pedigrees according to Cruden (1949), for parents of chicks hatched in 1974 to 1981 was 0.75, 0.80, 0.84, 0.86, 0.89, 0.91, 0.93 and 0.94 relative to the common base population B (Fig. 1). There was not much variation in inbreeding coefficients between lines within a given year. The true homozygosity of the lines was investigated 1977 by typing several blood group systems (Abplanalp et al. 1981). The homozygosity found was somewhat lower than expected after ten cycles of full sib mating. Blood typing was repeated for mated birds in the following years to keep the lines pure.

Six lines 71, 75, 77, 81, 87 and 92 were originally chosen for the diallel mating plan. Line 81 died out after three years and was replaced by line 79 which had been derived from the same selected line (small egg weight). Each year three matings with different males were planned for each line combination and its reciprocal. First priority was given to the reproduction of the inbred lines and the number of cross matings had to be reduced in some instances due to poor reproduction of the inbreds (Hagger and Steiger-Stafl 1982). At least six matings were made for each inbred line.

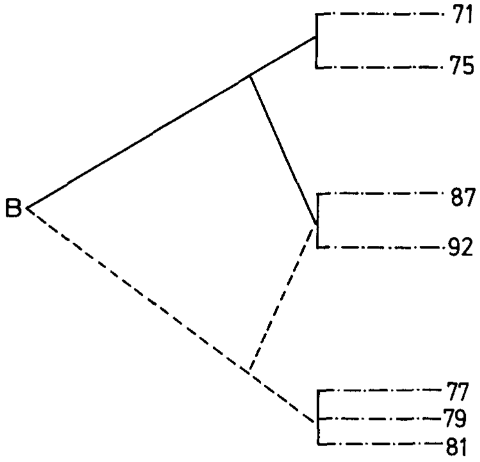

Fig. 1. Population structure. B: common base population; — : population selected for large egg weight; – – – : population selected for small egg weight; –· – ·–: inbred lines

The whole flock was reproduced by four weekly hatches every year in March–April. Chicks were reared intermingled on deep litter until 16 weeks of age and then transferred to single three floor battery cages. Twelve hours of light per day were given from hatch to about 40 weeks, and then increased gradually to 16 h. Individual egg production of all hens was recorded at seven days a week at the beginning of the laying period and at six days later on, including egg weight and the number of eggs adjusted for missing test days. Body weight was taken at 10, 20, 30, 40 and 60 weeks.

The following traits are considered in the analysis:

AFE: Age at first egg (days)
EW40: Average egg weight (g) of all eggs to 40 weeks
BW40: Body weight (g) at 40 weeks
EP40: Number of eggs to 40 weeks
EP60: Number of eggs between 41 and 60 weeks

To eliminate sick or irregularly behaving and moulting birds, retrictions on two traits were made as follows:

- for EP40, body weights at 20, 30 and 40, for EP60 also at 60 weeks had to be measured and only survivors data were used;
- for EP40, the difference between body weights at 40 and 30 weeks had to be greater than –150 g, for EP60, the difference between 60 and 40 weeks weight had to be greater than –200 g. Large negative weight changes were used as an indicator of moult.
- EP40 had to be greater than 9 and, independently, EP60 had to be greater than 9.

After thus screening the entire data set, 3247 birds remained for analysing AFE, EW40, BW40 and EP40 and 3133 birds for analysing EP60.

Griffing (1956) has outlined criteria for deciding if lines, as used in our experiment, should be treated as fixed or random and what type of conclusions can be drawn. As natural selection acts quite severely during the formation of inbred lines of chickens, as the lines used were from differently selected populations and as only very few lines could be used, it seemed logical to take lines as fixed effects in the statistical analysis of our data. The genetic model proposed by Eisen et al. (1966) was used. It estimates not only additive genetic and specific combining ability effects but also maternal and sex-linked effects. For female offsping of homogametic males, the situation in our data, Eisen et al. (1966) gave the following model:

$$Y_{ijk} = \mu + G_i + G_j + S_{ij} + M_j + P_i + e_{ijk}.$$

where:

y_{ijk}: specific trait of the k-th offspring from mating a male of line i and a female of line j
μ: common constant to all individuals
G_i: additive effect of autosomal genes for line i
S_{ij}: genetic effect specific to the cross of line i and line j ("specific combining ability")
M_j: maternal effect of line j
P_i: additive effect of sex-linked genes for line i
e_{ijk}: individual deviation assumed to be random with $E(e) = 0$ and $Var(e) = \sigma_e^2$.

Due to the relatively large Z chromosome in the chicken, the term for sex-linked or paternal effects should be included in the model, as suggested by Waerden et al. (1967). It can be seen, that it is impossible to estimate all these parameters from a complete diallel table (too many parameters). This was also shown by Eisen et al. (1966) for the incomplete (without pure line information) diallel. An obvious assumption for this model is that $S_{ii} = 0$. The model of Griffing (1956) for the complete diallel table of a fixed set of lines can be found through rearranging the given terms in the following way:

$$2G_i^* = 2G_i + M_i + P_i\,,$$

$$\left.\begin{aligned} R_{ij} &= 1/2\,(M_j - M_i) + 1/2\,(P_i - P_j) \\ R_{ji} &= 1/2\,(M_i - M_j) + 1/2\,(P_j - P_i) \end{aligned}\right\}\ R_{ij} = -R_{ji}\,,$$

and setting $R_{ij} = 0$ for $i = j$.

The R-terms are know called reciprocal effects. If $2G_1^* = 0$ is introduced and if no further systematic influences, e.g. year effects have to be considered, the remaining parameters can be estimated simply from cell means, as is shown below:

$$\begin{aligned} 2G_i^* &= E(\bar{y}_{ii.} - \bar{y}_{11.}) = 2G_i + M_i + P_i\,, \\ S_{ij} &= 1/2\,E(\bar{y}_{ij.} + \bar{y}_{ji.} - \bar{y}_{ii.} - \bar{y}_{jj.})\,, \\ R_{ij}^* &= E(\bar{y}_{ij.} - \bar{y}_{ji.}) = R_{ij} - R_{ji} = M_j - M_i + P_i - P_j\,. \end{aligned}$$

In this model, the line effects, G_i^*, only, are dependent on the choice of the reference line, which is given through the assumption $2G_1^* = 0$.

In our data a year effect had to be included in the model to account for differences between year of hatch. For convinience an overall mean μ^* was also included. The estimation of the parameters was thus done by an ordinary least squares procedure, i.e. $\hat{b} = (X'X)^{-1}X'y$. It should be noted that in the design matrix X of the linear model not only the familiar 0's and 1's but also 2's appear. Most of the published results from diallel plans with chickens are based on cell means. Our analysis was based on the individual records. Therefore another error variance could be estimated and thus the F-tests and the standard errors of the estimates are also different. The development of the model used here, clearly shows the genetic composition of the estimated parameters:

- the line effects, G_i^*, contain the additive genetic part but also a portion of maternal and sex-linked effects;
- the reciprocal effects, R_{ij}^*, are a mixture of maternal and sex-linked effects;
- the specific combining ability, S_{ij}, is the same as the one in the model proposed by Eisen et al. (1966).

Genetic effects estimated from a complete diallel with inbred lines are expected to be a function of the inbreeding coefficients as mentioned above. This would probably result in larger than expected effects than found in crossings of non inbreds.

Results and discussion

The number of birds in each cell of the diallel which could be used to analyse the four traits AFE, EW40, BW40 and EP40 are given in Table 1. The diagonals, containing the number of pure line birds, are on average somewhat larger than the off diagonals. This is the result of the larger number of matings of this type as described above. The smallest number, 27, in the diagonal belongs to line 81, the line that was lost. There was also no cross between line 81 and line 79 which replaced it.

Line effects, $2\hat{G}_i^*$

Estimates of line effects have to be regarded as differences from line 71 as $2G_1^* = 0$. Table 2 contains the overall mean ($\hat{\mu}^*$) and the estimated line effects for the five traits. Lines differ statistically significantly ($P < 0.01$) in all traits. AFE exhibits very large differences between lines. The most striking one is the difference of 56 days between lines 77 and 81. Both originated from the small egg weight population, as is still indicated by their line effects for EW40. The third line with the same origin, 79, is intermediate. EW40 shows very clearly the selection history of the three base populations. This could be expected as egg weight is a trait strongly influenced by additive gene effects. The differences in egg weight between the lines are not reflected in body weight (BW40) as might have been expected from a positive genetic correlation between these traits. BW40 of lines 77, 79 and 81 are not clearly distinguishable from BW40 of lines 87 and 92 in spite of the different selection applied to their populations of origin (Table 2). A distinct difference in BW40 exists between lines 72, 75 and the five other lines. Number of eggs in the first period, EP40, is strongly influenced by AFE. Lines 81 and 87, with the earliest sexual maturity, produced the most eggs, lines 75 and 77 the fewest. Egg number in the second period, EP60, should not be related directly to AFE. Line 87 with highest production in the first had also the highest production in the second

Table 1. Distribution of birds in the diallel female line

Male line	71	75	77	81	87	92	79
71	147	49	85	34	89	60	57
75	88	81	77	31	107	45	55
77	105	56	119	27	97	72	55
81	52	52	55	27	39	43	0
87	124	66	84	15	128	68	48
92	98	63	86	28	100	122	56
79	37	14	48	0	61	24	173

Table 2. $\hat{\mu}^*$ and estimated line effects, $2G_i^*$

		AFE d	EW40 g	BW40 g	EP40 no	EP60 no
line	$\hat{\mu}^*$	180.3	54.2	2023	62.0	82.6
71		0	0	0	0	0
75		4.3	3.1	201	−5.4	− 8.8
77		17.3	−14.0	−400	−8.4	0.4
81		−38.7	−11.1	−447	25.4	−26.8
87		−23.1	− 6.9	−370	29.6	6.7
92		− 7.3	− 6.8	−427	12.8	−10.1
79		−15.9	−17.2	−583	19.3	−18.7
F-test		**	**	**	**	**

** $P < 0.01$

period. The reverse is true for line 81, where a high production in the first coincides with a low production in the second period.

Inbreeding over many generations has established quite different lines (genotypes) even from the same genetic origin as demonstrated by lines 77, 79 and 81. Sexual maturity and egg production were affected most heavily. This would be in line with the common observation, e.g. Falconer (1982, p. 224), that traits connected with reproduction or physiological efficiency are influenced strongly through inbreeding. The differentiation of the populations due to selection of egg weigth was still clearly visible between the lines.

Specific combining ability effects, $\hat{S}_{ij}$

The estimated specific combining ability effects, $\hat{S}_{ij}$, are in Table 3. These effects are also highly significant ($P < 0.01$) as was shown by the F-test from the analysis of variance. The classical definition of heterosis, i.e. the relative superiority of a line or strain combination over the mid-parent value, taken from $\hat{S}_{ij}/(\hat{\mu}^* + \hat{G}_i^* + \hat{G}_j^*)$ was used to demonstrate the relative importance of specific combining ability in different traits. The average superiority of crosses was −11.3%, 5.8%, 7.8%, 45.1% and 35.8% for AFE, EW40, BW40, EP40 and EP60 respectively (Table 3). All single estimates were in the expected direction in the five traits, i.e. negative for AFE and positive for the others. The average relative effects were smallest for EW40 and BW40, as could be expected since these two traits are controlled mostly by additive genetic effects. The reverse is true for egg production traits, which usually have only a small to moderate heritability. EP40 is influenced strongly by AFE as is evident from Table 3. Abplanalp (1974) found similar figures for the relative superiority of two way crosses compared to the inbreds, e.g. 2.6% for egg weight, 5.3% for body weight and 42.9% for EP40. The importance of specific combining ability effects for most traits of economic relevance in chicken breeding is described in the majority of published experiments, e.g. Eisen et al. (1967), Wearden et al. (1967), Cole and Hutt (1973) and Fairfull et al. (1983). These last authors reported much smaller relative superiorities but from non inbred lines and their crosses. It is evident that the recovery of inbreeding depressions increased the specific combining effects for crosses of inbred lines substancially.

Table 3. Specific combining ability effects, $\hat{S}_{ij}$ and average heterosis %

Cross	AFE d	EW40 g	BW40 g	EP40 no	EP60 no
71×75	− 9.2	3.0	80	13.2	10.2
71×77	−33.9	3.7	77	43.2	25.2
71×81	−14.9	3.2	98	38.3	39.5
71×87	−11.4	2.9	54	21.5	20.0
71×92	− 9.6	3.4	67	20.9	26.3
71×79	−14.7	4.4	123	24.2	21.6
75×77	−44.6	1.2	20	51.7	26.8
75×81	−17.0	1.6	145	37.7	37.7
75×87	−13.7	1.1	74	25.4	24.0
75×92	−17.8	1.2	73	26.7	24.6
75×79	−20.6	1.6	99	34.3	35.0
77×81	−31.8	3.0	244	39.8	24.2
77×87	−32.9	2.9	167	42.7	27.4
77×92	−34.3	2.5	49	45.8	30.8
77×79	−34.1	2.6	177	39.5	26.8
81×87	−10.1	1.5	256	26.1	18.7
81×92	−10.4	3.1	195	25.4	29.1
87×92	− 7.7	2.6	130	19.4	26.6
87×79	−13.9	2.8	250	24.4	24.2
92×79	−15.4	5.0	218	26.2	29.4
F-test	**	**	**	**	**
Average heterosis %	−11.3	5.8	7.8	45.1	35.8

** $P < 0.01$

All combinations with line 77 showed large specific combining effects in AFE and thus also in EP40, as can be seen in Table 3. The relative superiority of these crosses for the two traits was −19.3% and 69.0% respectively. In EW40 the specific combining efect of line combination 79×92 with 5.0 g or 11.8% relative superiority was exceptionally large. Crosses with lines 81 and 79 had a relative superiority in BW40 of 11.1% compared to only 4.4% in the remaining crosses.

These differences indicate clearly, that there are genotypes which produce large specific combining effects with several other genotypes. A possible explanation would be, that these genotypes are homozygous for several recessive genes influencing a trait in a particular direction.

The linear regression of cross means on mid-parent values was used by Blyth and Sang (1960); Abplanalp (1974) and Fairfull et al. (1983) to investigate the degree of additive inheritance of quantitative traits. The method was applied for estimated cross means and parent values in our material. The strongest linear relationship was found for EW40 with a regression coefficient of 0.93 and $R^2 = 0.94$. Blyth and Sang (1960) also found a strong linear relationship in this trait but Fairfull et al. (1983) did not observe this relationship. A medium linear regression of 0.69 could further be found for BW40 and lower values of 0.32, 0.48 and 0.53 for AFE, EP40 and EP60 respectively. For body weight, a significant regression was reported by Fairfull et al. (1983). For egg production, the same authors found a significant linear relationship in multiple bird cages but not in single cages. Strong linear relationships in egg production were found by Blyth and Sang (1960) and Abplanalp (1974). Compared to experience from many investigations, this regression method seems not consistently lead to the same conclusions. This may also be a consequence of the different populations, concerning selection history and inbreds vs. noninbreds, used in different investigations.

Reciprocal effects, $\hat{R}^*_{ij}$

In case of a complete diallel, the reciprocal effects as defined here, contain mostly maternal and sex-linked effects as shown above. Gowe and Fairfull (1982) pointed out, that the greatest part of the reciprocal effects is likely due to the large sex chromosome of the chicken, with the exception of early growth rate and the effect of vertically transmitted diseases like lymphoid leucosis. Only small or no maternal effects in quantitative traits of chickens have been published, e.g. Wearden et al. (1965). A test for lymphoid leucosis in our inbred lines revealed no contamination with this diseas in 1980. It seems reasonable therefore to assume that the estimated values of R^*_{ij} from our material are useful indications for sex-linked effects.

Estimats of reciprocal effects, $\hat{R}^*_{ij}$, in Table 4 are statistically highly significantly ($P < 0.01$) different from zero for all traits. They are considerably smaller than the specific combining effects for AFE, EP40 and EP60 but of similar magnitude in some line combinations for EW40 and BW40. Evidence for important sex-linked effects in age at sexual maturity, egg production and viability were given earlier by Goto and Nordskog (1959) and Wearden et al. (1967) and recently by Fairfull et al. (1983). Eisen et al. (1967) also found reciprocal effects in other traits, including egg and body weight. Distinct reciprocal effects of a line would suggest that such a line could be used as a male or a female line, depending on the sign and the magnitude of the effect and on the trait. Some of our lines produced distinct sexlinked effects in one or more traits with all other lines. Offspring of sires from lines 77 and 81 had a somewhat higher egg production in both periods than their reciprocals. In the same traits, offspring from sires of line 87 were below the reciprocals. When used as sire line, this line also had offpsring with later sexual maturity ranging from 1–6.5 days. Sires from lines 79 and 81 gave rise to such an effect for BW40. Both lines originated from the small egg weight population and were the smallest birds of the lines used (Table 1). The sex-linked dwarf gene seemed not to be present in any of the inbred lines used. Relatively large reciprocal effects resulted in line combinations 71×87 and 81×87 for egg number in both periods. A larger effect in the second laying period after a forced moult was reported also by Gowe and Fairfull (1982) in crosses with selected, non inbred lines. As a whole, the conclusion reached by these authors, that it is important to test all crosses from available lines to find the best combination is confirmed from our data.

Table 4. Reciprocal effects, $\hat{R}^*_{ij}$ ($\hat{R}^*_{ij} = -\hat{R}^*_{ij}$)

Cross ♂ ♀	AFE d	EW40 g	BW40 g	EP40 No	EP60 No
71×75	−5.0	−0.2	6	3.5	−0.2
71×77	−2.1	1.0	− 56	1.2	−6.2
71×81	3.5	3.0	−153	−4.0	−4.7
71×87	−6.6	1.4	− 56	11.5	14.5
71×92	4.7	2.2	− 32	−6.2	−2.6
71×79	4.1	1.1	− 80	−5.8	2.3
75×77	2.4	−0.1	30	−4.0	−3.7
75×81	2.4	1.6	−151	−5.9	−3.3
75×87	−4.2	−0.4	− 61	5.4	4.6
75×92	−6.0	1.4	− 6	5.5	−7.7
75×79	1.6	1.2	− 36	−3.7	−2.7
77×81	−2.4	−0.1	−145	3.1	3.0
77×87	−2.3	0.3	− 50	3.7	5.6
77×92	−6.1	−0.4	− 28	7.6	1.2
77×79	−1.3	0.5	− 80	3.0	2.3
81×87	−3.9	−2.1	25	14.7	23.5
81×92	−4.9	−1.5	33	4.9	6.8
87×92	0.9	1.4	137	−3.1	−5.2
87×79	5.0	0.9	− 31	−3.5	−1.1
92×79	10.0	−0.6	−254	−4.1	7.0
F-test	**	**	**	**	**

** $P < 0.01$

An intersting situation between egg weight and body weight can be seen in offspring of males from line 71 and of males from line 81. Positive reciprocal effects in EW40 are associated with negative reciprocal effects in BW40 or vice versa. The correlation between the sex-linked effects of the traits within these two groups would be negative, thus being in the opposite direction of what was often found for the relationship between egg and body weight in chickens, e.g. Emsley et al. (1977). This observation would be explainable if the sensitivity of genetic correlations to gene frequency changes (Bohren et al. 1966) is taken into account. Such a change of sign of the correlation coefficient seems to be found easier in crosses of highly inbred lines than in crosses between non inbreds because changes in gene frequency would expected to be more pronounced through inbreeding than through selection. If a quantitative trait is determined heavily through a major gene, selection also would result in different genotypes rather quickly.

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