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General and Specific Combining Abilities for Different Economic Traits in Broiler Chickens

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Summary. A complete diallel cross of four broiler breeds was made to investigate whether there are breed differences in the combining abilities for the traits, body weight, weight gain and feed efficiency, measured during the growing period from 4 to 12 weeks of age. Data collected from male and female birds were analysed separately. General combining ability (GCA) was found to be the largest and most significant source of variation contributing to differences between crosses for all the traits, in both male and female birds. Specific combining ability (SCA) was important for body weight in both sexes and for weight gain in females. Feed efficiency in both sexes did not appear to be influenced by SCA effects. Reciprocal effects (RE) were generally absent in both sexes for all the traits, except possibly for feed efficiency.

Introduction

Interpopulation selection, based on variability in the combining abilities of populations with one another, has been so extensively exploited to improve production that the modern layer or broiler chick is invariably a hybrid with a heterogeneous ancestry involving two or more populations. Crossing systems designed to analyse variability in crossing abilities and to estimate the responsible components usually involve the diallel cross or one of its modified forms. Various analytical methods, depending on the model of effects assumed, have been devised and, in most cases, the observed variability is described in terms of general and specific combining abilities and also reciprocal effects where appropriate.

Diallel crossings with poultry have been used to study combining abilities for egg production traits, while similar studies for broiler traits have been relatively few and limited to body weight measured for age (Eisen et al., 1967; Brunson et al., 1956; Yao, 1961). The present study was initiated to extend the limited literature on combining abilities for broiler traits in chickens. A diallel crossing system with four breeds of chicken was used and the traits investigated included body weight, weight gain and feed efficiency measured during the period of growth from 4 to 12 weeks of age.

Materials and Methods

Experimental stocks

Samples of four broiler breeds, namely Red Cornish, White Cornish, White Rock and New Hampshire, were obtained as day-old chicks from the Poultry Research and Development Station, Johore Bahru, West Malaysia. The chicks were raised to maturity in the poultry farm of the Faculty of Agriculture, University of Malaya, and were later used as parents in the diallel crossing.

Experimental Design

Initially it was decided that each of the mating types from the diallel mating system would be represented by twelve different families accommodated within a randomised block design, with separate blocks for the two sexes. However, with the facilities and space available, it was necessary to divide the whole experiment into four smaller but similar experiments, each conducted successively at intervals of five weeks. In each of the four experiments, each mating type was represented by three families so that at the end of the whole study, data would have been collected from a total of twelve families for each mating type. The progenies from the diallel crossing system were housed in the experimental growing cages at 4 weeks of age, with each cage housing a family of up to 3 chicks of the same sex.

Reproduction of Progeny for each Experiment

A set of diallel crosses was made to produce progeny for each of the four experiments. In each set, six matings were made for each mating type to ensure that three families of a sufficient size to supply 3 chicks of each sex would be available at 4 weeks of age to fill the cages in the experimental blocks. All matings were made by artificial insemination; semen from each cockerel was used to inseminate two females from different breeds to eliminate any relationship between families of the same crossing type. Eggs were collected and pedigreed for a period of two weeks before they were set for incubation.

Management

At hatching, chicks were wing banded and then vaccinated against Newcastle disease. All chicks of the same mating type were brooded together to four weeks of age before three families of each crossing combination were randomly selected to fill the experimental cages. At six weeks of age all chicks were vaccinated against Fowlpox. Throughout the whole study the same starter and same grower mashes were fed to all chicks. Similar management procedures were followed in each of the four experiments.

Traits studied

The traits studied were: (i) body weight (gm) measured at 8, 10 and 12 weeks; (ii) weight gain (gm) during the four periods of growth 4-8, 4-10 and 4-12 weeks of age; (iii) feed efficiency expressed as a percentage and measured as the ratio of the weight gain to the weight of the feed consumed during the periods 4-8, 4-10 and 4-12 weeks of age. Family means were used in the statistical analyses.

Statistical Methods

Preliminary analyses of variance for phenotypic effects were carried out for all traits in each of the four diallel sets. Differences between crossing types were found to be highly significant and it was therefore decided to pool all the data from the four diallel sets to obtain a better estimate of the error variation. Before the pooling was made, the four error terms from the phenotypic analyses of the four diallel sets for each of the traits were tested for homogeneity using Bartlett's test of Homogeneity of Variances (Snedecor, 1956). The results (Table 1) showed that for most of the traits homogeneity was indicated.

Table 1. Bartlett's Test for homogeneity of the error variances in the four sets of diallel crosses

Economic Traits			Chi-Square Values: Male progeny	Chi-Square Values: Female progeny
	8	Weeks	1.36	6.32
Body	10	"	0.71	4.83
Weight	12	"	3.67	4.93
	4-8	Weeks	4.52	8.46*
Weight	4-10	"	4.04	4.10
Gain	4-12	"	1.10	2.46
	4-8	Weeks	3.42	12.98*
Feed	4-10	"	1.13	7.30
Efficiency	4-12	"	0.68	2.80

Note: *, ** denote significant departure from homogeneity at P = 0.05 and P = 0.01 respectively.

The materials used in this study were suitable for genotypic analysis by the methods presented by Griffing (1956) for the model of fixed effects. Since it was also required to estimate RE, Methods I and III (Griffing 1956) were applicable. However it was noted that in the case where the number of lines used was four, analysis by Method III would lead to the following relation for the fixed SCA effects in the crosses: $s_{ij} = s_{kl}$, being the SCA effect for the crosses between the lines i and j, the two remaining lines being k and l. Thus it would not be possible to determine which of the two different crosses showed the higher SCA effect. Consequently Method I was used for analysing all the traits.

Results and Discussion

Analysis of variance carried out on the pooled data for each of the traits in both sexes indicated that differences between the sixteen mating types or genotypes were highly significant. These differences were then analysed to determine the importance and relative magnitude of the genetic components involved. Results of these analyses are presented in Tables 2 and 3.

Differences due to GCA Effects

The results obtained indicate that GCA differences (P < 0.01; Table 2) form the major sources of genetic variation (Table 3) for body weight, weight gain and feed efficiency traits in both males and females. Large and significant estimates of GCA differences have been reported previously for 9-week body weight by Eisen et al. (1967) and for 10-week body weight by Brunson et al. (1956) and Yao (1961). Since the GCA differences are largely due to additive genetic variance, the estimates of GCA differences should be comparable with the estimates for heritability. Reports on estimates of heritability confirm this. Siegel (1962), summarizing his review of 176 published estimates of heritability for body weight at ages between 6 and 12 weeks, concluded that heritability for body weight at these ages ranges from moderate to high.

Estimates of GCA differences for weight gain and feed efficiency traits are not available in the literature. However, additive genetic variation for these traits has been found to be higher than nonadditive genetic variation in the heritability studies of Thomas et al. (1958) and in the diallel studies of Kan et al. (1959). The present study also shows that the relative magnitudes (bracketed values in Table 3) of the GCA component for the feed efficiency traits are much smaller than those for the body weight and weight gain traits. The smaller values for the feed efficiency traits are probably due to the large error components, whose relative magnitudes are much larger than those for body weight and weight gain traits. The large error component for feed efficiency traits demonstrates the fact that feed efficiency is a very complicated trait influenced by many physiological, environmental as well as individual differences.

Thomas et al. (1958), estimating heritabilities of feed efficiency traits from data obtained on a family basis, reported rather variable estimates which ranged from 0.05 to 0.32 in males and from -0.05 to 0.48 in females. In contrast, their estimates of heritability for body weight and weight gain traits were more uniform and very high, much higher than those generally reported in the literature. They attributed their much larger values to their system of raising the birds in batteries which, they contended, allowed more effective standardization of the environment, thereby reducing the error variance. If the latter were to be the case, then the large variability noted for their heritability estimates of feed efficiency could only mean variability of the error estimates caused by additional nongenetic sources of varia-

Table 2. Mean squares for the genotypic effects in male and female progeny for the economic traits

Source df	Mean Squares for Traits in Males				Mean Squares for Traits in Females			
	GCA 3	SCA 6	RE 6	Error 128	GCA 3	SCA 6	RE 6	Error 128
Traits								
Body Weight								
8 Weeks	74804.74**	1549.03*	564.15	641.21	46453.87**	1621.74**	527.12	369.32
10 Weeks	144902.05**	2300.06*	1148.57	1023.98	88187.68**	2686.23**	1153.62*	485.53
12 Weeks	214077.56**	4374.71**	2166.92	1122.69	125574.90**	3448.96**	946.70*	500.13
Weight Gain								
4- 8 Weeks	28609.42**	532.75	810.27	740.47	20657.30**	1294.74*	572.96	515.48
4-10 Weeks	72403.78**	1504.35	1590.47	1419.50	54289.36**	2168.19*	611.24	796.35
4-12 Weeks	127892.19**	2819.16	3215.79	1825.49	88036.28**	3029.27**	1322.74	918.83
Feed Efficiency								
4- 8 Weeks	4.11**	0.83	1.82*	0.69	6.27**	0.79	1.23	0.59
4-10 Weeks	3.96**	0.58	0.95	0.45	4.10**	0.22	0.70	0.35
4-12 Weeks	2.87**	0.35	0.67*	0.27	2.62**	0.33	0.57*	0.21

Note: *, ** Denote significance at P = 0.05 and P = 0.01 respectively.

Table 3. Estimates of the genotypic components of variation from the mean square expectations (Values in brackets are the magnitudes of the components expressed as percentages of the total variation)

Traits		Genotypic component of Variation in Male progeny				Genotypic component of Variation in Female progeny			
		GCA	SCA	RE	Error	GCA	SCA	RE	Error
		$\frac{1}{3}\sum_i \hat{g}_i^2$	$\frac{1}{6}\sum_i\sum_j \hat{s}_{ij}^2$	$\frac{1}{6}\sum_i\sum_j \hat{r}_{ij}^2$	$\hat{\sigma}^2$	$\frac{1}{3}\sum_i \hat{g}_i^2$	$\frac{1}{6}\sum_i\sum_j \hat{s}_{ij}^2$	$\frac{1}{6}\sum_i\sum_j \hat{r}_{ij}^2$	$\hat{\sigma}^2$
Body Weight	8 Weeks	9270.44	907.81	-38.53	641.21	5760.57	1252.40	78.90	369.32
		(85.7)*	(8.4)	(0.0)	(5.9)	(77.2)	(16.8)	(1.1)	(5.0)
	10 Weeks	17984.76	1276.09	62.30	1023.98	10962.77	2200.70	334.04	485.53
		(88.4)	(6.3)	(0.3)	(5.0)	(78.4)	(15.7)	(2.4)	(3.5)
	12 Weeks	26619.36	3252.02	522.11	1122.69	15634.30	2948.84	223.30	500.13
		(84.5)	(10.3)	(1.7)	(3.6)	(81.0)	(15.3)	(1.2)	(2.6)
Weight Gain	4- 8 Weeks	3483.62	-207.73	34.89	740.48	2517.22	779.27	28.74	515.48
		(81.8)	(0.0)	(0.8)	(17.4)	(65.6)	(20.3)	(0.8)	(13.4)
	4-10 Weeks	8873.04	84.85	85.48	1919.50	6686.63	1371.84	-92.56	796.36
		(84.8)	(0.8)	(0.8)	(13.6)	(75.5)	(15.5)	(0.0)	(9.0)
	4-12 Weeks	15758.34	993.68	695.15	1825.49	10889.68	2110.44	201.95	918.83
		(81.8)	(5.2)	(3.6)	(9.5)	(77.1)	(15.0)	(1.4)	(6.5)
Feed Efficiency	4- 8 Weeks	0.43	0.14	0.56	0.69	0.71	0.20	0.32	0.59
		(23.5)	(7.5)	(30.9)	(38.1)	(39.0)	(10.9)	(17.5)	(32.5)
	4-10 Weeks	0.44	0.12	0.25	0.45	0.47	-0.13	0.17	0.35
		(34.5)	(9.8)	(19.7)	(35.8)	(47.0)	(0.0)	(17.5)	(35.5)
	4-12 Weeks	0.32	0.08	0.20	0.27	0.30	0.12	0.18	0.21
		(37.3)	(8.7)	(23.2)	(30.9)	(37.1)	(14.9)	(22.2)	(25.8)

tion other than the environment. The present study also involved the battery system and the results obtained were in general agreement with the above.

Differences due to SCA Effects

The presence of significant SCA differences was detected for body weight traits in both sexes (Table 2). For the weight gain traits, significant SCA differences were obtained only among females while for the feed efficiency traits, neither sex showed any significant SCA differences (Table 2). Reports of SCA differences of nonadditive genetic differences have been made by previous workers for body weight in chickens. Hill and Nordskog (1958) and Eisen et al. (1964) found significant SCA effects for 8-week body weight and Yao (1959, 1961) found dominance effects of moderate significance for the same trait. The lower magnitude of the heritability estimates calculated from the sire component of variance, as compared with the similar estimates from the dam variance component, have been taken as evidence of non-additive genetic effects. Evidence of these effects was shown in the heritability studies of Lerner et al. (1947), Thomas et al. (1958) and Siegel (1962). Moreover, the numerous reports of heterosis, noted for body weight traits reviewed by Tindell (1961), are further indications that non-additive genetic effects are of considerable importance for these traits.

No reports of SCA effects for weight gain traits are available but Kan et al. (1959) have reported the possibility of a dominance effect for weight gain from 4 to 9 weeks of age, and general observations of the heritability studies of Thomas et al. (1958) also support this view. Reports of SCA effects for feed efficiency traits are also not available. However earlier studies appeared to indicate that nonadditive genetic effects have considerable influence on feed efficiency, for comparisons have shown crossbred chicks to be more efficient than their purebred siblings and inbreeding has been observed to have a depressive effect on feed efficiency. In the present study, the relative magnitudes of the SCA component for feed efficiency traits (Table 3) are quite appreciable and comparable in size to those for the body weight traits but the large error components for the feed efficiency traits probably prevented the detection of any significant SCA differences.

The relative magnitudes of the SCA components for the female traits (Table 3) were consistently much larger than those for the traits measured in males. The values for traits in females appear to follow a downward trend with time, while the relative magnitudes of the SCA component for traits in males appear to increase with time. These observations seem to indicate that there are differences in the genetic expression of traits between males and females at different periods. Comstock (1956), using data compiled from records from 25,000 New Hampshire birds, showed that the genetic correlation between the two sexes for growth rate was not equal to one and estimated its value to be 0.75. In addition he found 40 % greater genetic variance in males than in females for 8-week body weight. Thomas et al. (1958) also observed that the values of the heritabilities tended to decrease with time for traits measured in males and to increase for traits in females. A possible explanation for these results is that nonadditive effects are expressed earlier among females with a subsequently earlier decline, while among males these effects are probably expressed in a similar pattern but at a later age. A detailed study of traits measured at regular intervals from day-old up to maturity could provide more conclusive evidence, if any, of differences in the sequential expression of genetic effects in males and females.

Differences due to Reciprocal Effects

Reciprocal effects as estimated in the present study include both maternal and sexlinked effects, the latter being expressed only among individuals of the heterogametic sex. Table 2 shows that variances due to RE were not significant for body weight traits in both sexes except for 10-week body weight in females. Weight gain traits in both sexes are not influenced by RE (Table 2) and the relative magnitudes obtained are very small (Table 3). The relative magnitude of the RE component for feed efficiency traits were very much larger (Table 3) and significant RE differences were noted for 4-8 week and 4-12 week feed efficiency among males and for 4-12 week feed efficiency among females (Table 2). Since RE, if present, would most likely influence traits taken at earlier ages, and measured in the heterogametic sex, the present findings are not consistent enough to be conclusive. However, the indications are there that maternal effects but not sexlinkage are the probable causes of reciprocal differences between crosses for the feed efficiency traits.

Previous reports of RE or evidence of such effects for body weight traits are not in general agreement, and reports of these effects for weight gain and feed efficiency traits are lacking although evidence of sexlinkage has been presented for weight gain traits. Eisen et al. (1967) could not find RE differences for 8-week pullet weight and earlier workers have also shown or inferred RE to be absent or of minor importance for body weight. Wyatt (1953) regarded significant differences between female testers in his topcrosses as indications of maternal effects but was unable to demonstrate these effects for 8-week body weight. Likewise, Martin et al. (1953), found no evidence of maternal effects and sexlinkage at 3, 6, 9 and 12 weeks of age.

On the other hand, some evidence of sexlinked effects for body weight has been obtained by Brunson et al. (1956). The sire component of variance obtained for traits measured on female progenies includes half the total variation due to sexlinkage, so larger heritabilities estimated from the sire component than from the dam component would indicate considerable influence due to sexlinkage. This criterion was used by Thomas et al. (1958), whose studies showed important sex-linked ef-

Table 4a. Estimates of GCA effects in each breed for the economic traits in the male progeny and the graphical results of the DMRT for differences in GCA effects between the breeds

Traits	GCA Effects ($\hat{g}_i$) of the Breeds				Standard Errors		Graphical Results of the DMRT (P = 0.05)
	Red Cornish (RC)	White Cornish (WC)	White Rock (WR)	New Hampshire (NH)	($\hat{g}_i$)	($\hat{g}_i - \hat{g}_j$)	
Body Weight							
8 Weeks	82.34**	84.32**	-71.75**	-94.93**	7.75	12.66	WC RC WR NH
10 Weeks	116.66**	113.89**	-90.98**	-139.57**	9.80	16.00	RC WC WR NH
12 Weeks	146.25**	133.17**	-107.15**	-172.27**	10.26	16.75	RC WC WR NH
Weight Gain							
4- 8 Weeks	56.75**	46.33**	-46.68**	-56.40**	8.33	13.60	RC WC WR NH
4-10 Weeks	91.90**	70.69**	-65.61**	-96.97**	11.53	18.84	RC WC WR NH
4-12 Weeks	118.77**	96.79**	-82.73**	-132.82**	13.08	21.36	RC WC WR NH
Feed Efficiency							
4- 8 Weeks	0.8243*	0.3518	-0.4318	-0.7443*	0.2549	0.4161	RC WC WR NH
4-10 Weeks	0.7231*	0.2956	-0.0856	-0.9331**	0.2059	0.3363	RC WC WR NH
4-12 Weeks	0.6168**	0.1968	-0.0043	-0.8093**	0.1589	0.2596	RC WC WR NH

Note: *, ** Denote significance at P = 0.05 and P = 0.01 respectively; and in the DRMT results, GCA effects of breeds not bracketed together are asserted to be different.

Table 4b. Estimates of GCA effects in each breed for the economic traits in the female progeny and the graphical results of the DMRT for differences in GCA effects between the breeds

Traits	GCA Effects ($\hat{g}_i$) of the Breeds				Standard Errors		Graphical Results of the DMRT (P = 0.05)
	Red Cornish (RC)	White Cornish (WC)	White Rock (WR)	New Hampshire (NH)	($\hat{g}_i$)	($\hat{g}_i - \hat{g}_j$)	
Body Weight							
8 Weeks	71.96**	58.86**	-54.93**	-75.90**	5.88	9.61	RC WC WR NH
10 Weeks	100.67**	78.92**	-72.71**	-106.88**	6.75	11.02	RC WC WR NH
12 Weeks	119.38**	90.88**	-69.92**	-140.33**	6.85	11.18	RC WC WR NH
Weight Gain							
4- 8 Weeks	47.10**	38.42**	-28.70**	-56.82**	6.96	11.35	RC WC WR NH
4-10 Weeks	73.42**	65.02**	-45.17**	-93.27**	8.64	14.11	RC WC WR NH
4-12 Weeks	94.57**	78.01**	-46.97**	-125.61**	9.28	15.15	RC WC WR NH
Feed Efficiency							
4- 8 Weeks	0.9593**	0.3606	-0.1956	-1.1243**	0.2355	0.3844	RC WC WR NH
4-10 Weeks	0.6406*	0.4243	-0.0981	-0.9668**	0.1819	0.2970	RC WC WR NH
4-12 Weeks	0.5081*	0.1806	0.1318	-0.8206**	0.1398	0.2284	RC WC WR NH

fects to be apparent for 8 and 10 week body weight and for most of the weight gain traits investigated. Yao (1961), in his diallel crosses with inbred lines of chickens, found moderately significant maternal effects for 10-week pullet weight. In his comparisons of the magnitudes of heritability for 8-week body weight from the sire and from the dam components of variance, when data from both sexes were combined, Siegel (1962) obtained higher heritabilities from the dam component. He concluded that either dominance or maternal effects, or a combination of both, must be responsible for the larger heritabilities estimated from the dam component.

Estimates of Combining Ability Effects

The present study assumes the model of fixed effects in the analyses so that estimates of these fixed effects for combining abilities for each breed and cross could be obtained. Table 4 presents the estimates of GCA for each

Table 5. Estimates of SCA effects and standard errors associated with these effects for the economic traits in male and female progeny

Traits		SCA Effect ($\hat{S}ij$) for the Crosses						Standard Errors		
		RC×WC	RC×WR	RC×NH	WC×WR	WC×NH	WR×NH	$\hat{S}ij$	$\hat{S}ij - \hat{S}ik$	$\hat{S}rj - \hat{S}kl$
Males										
	8	19.48	35.55	-8.48	-4.42	18.43	7.13	14.16	21.92	17.91
Body	10	6.57	57.81*	-16.74	-16.80	29.00	-2.34	17.72	27.71	22.63
Weight	12	21.84	71.99**	-33.52	-19.31	34.31	11.76	18.73	29.02	23.70
	4-8	8.41	27.12	-16.30	-8.69	5.80	-1.88	15.57	23.57	19.25
Weight	4-10	-1.52	46.16	-31.79	-15.17	23.29	-10.07	21.06	32.62	26.65
Gain	4-12	4.89	64.57	-41.02	-20.17	27.01	-9.02	23.88	37.01	30.21
	4-8	0.41	0.96	-0.57	-0.54	0.55	0.02	0.47	0.72	0.59
Feed	4-10	0.25	0.75	-0.71	-0.38	0.49	-0.17	0.38	0.58	0.48
Efficiency	4-12	0.12	0.72	0.36	-0.40	0.19	0.01	0.29	0.45	0.37
Females										
	8	-8.33	33.13*	-11.28	1.89	45.60**	-13.52	10.74	16.64	13.59
Body	10	-5.60	45.48**	-23.19	6.52	48.60**	-0.31	12.32	19.08	15.58
Weight	12	-2.14	47.62*	-32.14	18.12	47.11*	1.70	15.50	19.36	15.81
	4-8	11.52	26.82	-6.25	12.12	22.83	-3.39	12.69	19.67	16.05
Weight	4-10	4.62	31.58	-8.08	23.85	31.93	-2.82	15.78	24.44	16.95
Gain	4-12	7.62	29.38	-5.85	43.87	23.10	-5.32	16.94	26.25	21.42
	4-8	0.62	-0.26	0.29	0.57	0.26	0.08	0.43	0.67	0.54
Feed	4-10	-0.14	-0.24	0.45	0.42	0.05	0.01	0.33	0.51	0.42
Efficiency	4-12	-0.19	-0.14	0.53	0.67	-0.22	-0.17	0.26	0.40	0.32

breed for each trait and also the comparison between breeds for their GCA. All estimates are found to be significant when compared with the mean GCA for all breeds (zero in this case for all traits), with the exception of the GCA estimates for the White Cornish and White Rock breeds for feed efficiency traits in both sexes. The results of the Duncan's Multiple Range test show that the Red Cornish and the White Cornish are not significantly different in GCA for all traits but their GCA are generally significantly better than the GCA of both the White Rock and New Hampshire Breeds.

The estimates of SCA for the six possible crossbred combinations (reciprocals have similar SCA) are shown in Table 5. Each estimate is tested to determine whether it is significantly different from zero (the mean SCA for the whole diallel cross for each trait). Significant SCA estimates are noted among the male crossbreds only for the Red Cornish-White Rock crosses for body weight at 10 and 12 weeks. Among female crossbreds, significant estimates are obtained only for body weight traits and these are for the Red Cornish-White Rock and for the White Cornish-New Hampshire crosses. Comparisons among the crossbreds for differences in SCA are not made because of the scarcity of significant estimates.

Since RE are not conclusively shown to be of importance in the variation among reciprocal crosses, the RE estimates for each of the crosses for each of the traits were not computed.

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