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Heterosis for growth related traits in White Plymouth Rock and Single Comb White Leghorn reciprocal crosses reared under two crude protein regimens*

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ABSTRACT

Studies of dietary effects on heterosis for body weight gain (BWG) and feed conversion ratio (FCR) are few. In the present work, heterosis, heterosis due to sex chromosome, and maternal and line effects for BWG and FCR were compared in reciprocal crosses of White Plymouth Rock (WPR) and Single Comb White Leghorn (SCWL). These birds were reared on either 18 or 20% crude protein (CP) diets from hatch to 8 weeks. The WPR birds exhibited larger body weights and consumed more feed than the SCWL birds. Also WPR birds on 20% CP diet were larger than those on 18% CP diet. Although FCR of SCWL birds on 18% CP diet was lower than those on 20% CP diet at 1 and 3-6 weeks, FCR was lower in WPR than SCWL birds. Heterosis was higher at 18% CP diets and the average maternal and line effects for BWG were higher (P<0.05) for WPR than SCWL and at 18 than 20% CP diets. However, maternal effects for FCR of WPR progeny were higher at 20 than 18% CP diets. Average line effects were also higher for WPR than SCWL males and significant at 20% CP diets for both lines. Heterosis due to sex chromosome was significant (P<0.05) and positive for BWG but negative for FCR. This study indicates that SCWL males and WPR females exhibited higher combining ability at 18 than 20% CP diets. The significant heterosis for BWG and FCR due to sex chromosomes and maternal effects suggest that these two traits are also affected by genes on the sex chromosome.

KEY WORDS: heterosis, crude protein, chickens, performance

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INTRODUCTION

Heterosis, the average performance of progeny relative to their genetically distinct parents, has been extensively used in the poultry industry to measure performance and maximize production. There is, however, no other reliable method to predict the level of heterosis that will occur from the mating of individuals from two populations unless the traits are measured in the offspring. Likewise, there is no accurate method of estimating the optimum nutrient requirements of the offspring from these crosses since heterosis will vary with populations included in the cross and environmental changes, including dietary nutrient composition (Barlow, 1981).

Although varied and inconclusive, changes in heterosis have also been found with respect to nutritional treatment (Hull et al., 1963; Emsley et al., 1980). Thus, the relative feed conversion efficiency of individual birds or different strains of birds with different specific nutrient requirements may be affected by the nutrient composition of the diet used. According to Noble et al. (1993) and Pincard et al. (1993), fast-growing chickens are more sensitive to protein and amino acid concentration in diets. Similar observations involving dietary protein concentration were reported by Hruby et al. (1995) and Siegel et al. (1997). Thus, estimation of heterosis may also be influenced by dietary protein concentration.

This study was, therefore, designed to evaluate the effect of dietary crude protein level on heterosis and reciprocal effects for feed efficiency and body weight gain in crosses involving White Plymouth Rock and Single Comb White Leghorn. These two traits are commonly used in determining performance of both meat and egg-type birds. Further, these traits with an estimated correlation of +0.52 have been of both biological and economic significance towards genetic improvement through selection of faster growing and high producing birds (Chambers et al., 1984; Leenstra et al., 1986).

MATERIAL AND METHODS

Crosses

In two replicates, 100 each of Single Comb White Leghorn (SCWL) and White Plymouth Rock (WPR) progeny of either sex were reared separately on 18 and 20% CP diets (Table 1) from hatch to 8 weeks of age (WOA) after which they were fed commercial diets (NRC, 1994) through the growth and breeding periods. At 18 weeks of age, 10 cocks and 40 females were sampled from each line and dietary treatment and randomly placed in individual laying cages throughout the breeding period. The crosses were produced by pedigree mating (1 male: 4 fe-

TABLE 1

Composition of experimental diets, %

Ingredients	CP, % 18	20
Maize, yellow (8% CP)	68.86	63.76
Soyabean meal (48% CP)	25.60	30.20
Lucerne meal (17% CP)	1.00	1.00
Poultry blended fat	0.46	0.96
Dicalcium phosphate (18.5% P, 24% Ca)	2.10	2.10
Limestone flour (37% Ca)	0.93	0.94
DL-Methionine	0.10	0.09
Salt	0.37	0.37
Vitamin premix[1]	0.25	0.25
Trace mineral premix[2]	0.25	0.25
Coban 60	0.08	0.08
Calculated levels		
CP	18	20
Kcal ME/kg	3.000	3.000
calcium	0.99	0.98
total P	0.67	0.67
availailable P	0.40	0.40
Met	0.30	0.30
Met + Cyst	0.56	0.56

[1] – provided per kg of diet: retinyl acetate, 3337 IU; cholecalciferol, 1000 ICU; dl-tocopheryl acetate, 3.6 IU; menadione sodium bisulfite complex, 2.8 mg; vitamin B_{12}, 6.1 mg; riboflavin, 2.5 mg; pantothenic acid, 5.9 mg; niacin, 16.4 mg; choline, 227 mg; folic acid, 230 µg; ethoxyquin, 56.7 mg

[2] – provided per kg of diet: Mn, 65; J, 1; Fe, 54.8; Cu, 6; Zn, 55; Se, 3

males) via artificial insemination. Both purebred and crossbred progeny were obtained in a single hatch from a 14-day egg collection. To ensure hatching ability, the eggs were stored in a cold room (13-15°C and 75-80% relative humidity) until incubated.

Design

In three replicates, a total of 1,178 F1 reciprocal crosses of SCWL and WPR parental populations were randomly assigned to isocaloric (3,000 Kcal ME/kg) diets containing 18 and 20% CP (Table 1) from hatch to 8 WOA. Chickens of each cross and the purelines were weighed at hatch and placed on the two dietary treatments for the eight weeks and raised using standard brooding techniques (North and Bell, 1990). The two diets were fed *ad libitum* in mash form. Body weight (BW) and feed consumption (FC), from which feed conversion ratios (FCR) were calculated, were measured weekly.

Statistical analysis

The statistical model used to represent the mean of a specific parental line or cross within sex and dietary crude protein levels adopted from Eisen et al. (1984) and modified by Barbato et al. (1991) was:

$$Y_{ij} = \hat{y}_a + (l_i + l_j)/2 + m_j + * \, h_{ij}$$

where:
Y_{ij} = the mean performance of sire line i crossed with dam line j (* = 0 for parental line progeny and * = 1 for crossbred progeny),
$\hat{y}_a$ = mean of the parental lines,
$m_j = \hat{y}_{.j} + \hat{y}_{j.}$,
$L_i = \hat{y}_{ii} - \hat{y}_a - m_j$,
$h_{ij} = \frac{1}{2} (\hat{y}_{ij} + \hat{y}_{ji} - \hat{y}_{ii} - \hat{y}_{jj})$

Specific reciprocal effects (independent of m_j) were assumed to be zero in this model.

According to Carbonell et al. (1984), heterosis in males (h^p_{ij}) and females (h^f_{ij}) has different expectations such that:

1. $h^p_{ij} = h^a ij + h^s ij + aa^h_{ij}$
2. $h^f_{ij} = h^a_{ij} + aa^h_{ij}$

where:
h^a_{ij} = specific heterosis of the autosomes
h^s_{ij} = specific heterosis of the sex chromosomes (only in males) and
aa^h_{ij} = specific additive-by-additive heterosis.

Solving for h^s_{ij} in the simultaneous equations 1 and 2:
$h^s_{ij} = h^p_{ij} - h^f_{ij}$; this equation was used to estimate heterotic effects due to heterozygosity of the sex chromosomes, which can only occur in the homogametic sex (Carbonell et al., 1984).

Significance of heterosis, line and maternal effects was evaluated by the Student's *t*-test with n-r degrees of freedom, with n being the total number of observations (1,178) and r the number of groups (8). The analyses were performed using the General Linear Model (GLM) procedure of SAS® (SAS Institute, 1990).

RESULTS AND DISCUSSION

Body weight gain, feed consumption, and feed conversion ratio

The body weight gains (BWG), feed consumption (FCR) and feed conversion ratio (FCR) are presented in Table 2. Since there were no significant diet x sex

TABLE 2

Average weekly feed consumption and body weight gain (g/bird/week) and feed conversion ratio (g feed/g BWG) of White Plymouth Rock (WPR) and Single Comb White Leghorn (SCWL) birds fed 18 and 20% crude protein diets

AGE, weeks	1		2		3		4		5		6		7		8	
CP, %	18	20	18	20	18	20	18	20	18	20	18	20	18	20	18	20
Feed consumption																
WPR	69^{b}	65^{b}	128^{a}	133	169^{ay}	187^{x}	253^{ay}	266^{ax}	311^{ay}	337^{ax}	378^{a}	374^{a}	438^{y}	459^{ax}	406^{ax}	333^{by}
SCWL	79^{ax}	69^{ay}	120^{by}	127^{x}	158^{by}	188^{x}	240^{by}	251^{bx}	282^{by}	316^{bx}	314^{by}	355^{bx}	436^{y}	452^{bx}	333^{by}	343^{ax}
Pooled SEM[1]	0.8	0.6	0.8	0.4	0.2	1.1	2.8	1.8	2.2	1.2	4.0	2.0	1.0	0.7	2.2	1.8
Body weight gain																
WPR	37	36	64^{a}	61	79^{a}	83^{a}	98	93	119^{a}	119^{a}	129^{a}	123^{a}	131^{y}	140^{ax}	147^{ax}	138^{ay}
SCWL	35	35	53^{b}	57	65^{b}	68^{b}	92	89	95^{b}	96^{b}	89^{b}	93^{b}	126	127^{b}	99^{b}	99^{b}
Pooled SEM[1]	1.1	1.2	1.4	1.5	1.8	2.1	2.4	2.4	2.8	3.0	3.0	3.2	3.5	3.0	3.9	3.6
Feed conversion																
WPR	1.95^{b}	1.87^{b}	2.05^{b}	2.15^{b}	2.25	2.36^{b}	2.75	2.99	2.79^{b}	2.95^{b}	3.03^{b}	3.10^{b}	3.49^{x}	3.34^{y}	2.91^{by}	3.24^{bx}
SCWL	2.33^{ax}	2.05^{ay}	2.31^{a}	2.24^{a}	2.53^{y}	2.86^{ax}	2.67^{y}	2.87^{x}	3.03^{ay}	3.36^{ax}	3.55^{ay}	3.87^{ax}	3.51	3.60	3.52^{a}	3.59^{a}
SEM[1]	0.04	0.05	0.05	0.04	0.06	0.08	0.07	0.06	0.07	0.09	0.08	0.07	0.09	0.12	0.09	0.11

a, b – means within columns with no common superscript differ significantly ($P \leq 0.05$)

x,y – means within rows of two consecutive columns representing 18 and 20% CP with no common superscript differ significantly ($P \leq 0.05$)

[1] – pooled means for males and females

interactions on BWG, FC and FCR, data for both sexes were pooled prior to comparison of means. As expected, WPR birds exhibited larger body weights and consumed more feed than the SCWL birds. The higher feed consumption of WPR birds is justified by their rapid growth rate and supported by reports of Pesti (1982) and Leeson et al. (1993) that birds adjust feed intake to meet their energy requirement for both growth and maintenance. Since these birds were fed isocaloric diets (3,000 Kcal ME/kg), its expected that the lean birds (SCWL) show less response to dietary fat than WPR birds (Karen-Zvi et al., 1990). It is also probably true that faster growing birds deposit more fat than their slow-growing counterparts (Pesternak and Slalev, 1983). Although differences in BWG of birds on 18 and 20% CP diets were not significant for most of the study period, birds on 20% CP diet consumed more feed than those on 18% CP diet. These observations were consistent with previous reports (Sengar, 1987; Leeson and Summers, 1989; Skinner et al., 1992) that birds on diets with relatively higher levels of CP consume more feed. The FCR was lower for SCWL birds on 18% than 20% CP diets at 1 and 3-6 weeks and also lower in WPR than SCWL birds. These results are consistent with those reviewed by Pym (1990), where birds with higher growth rate utilised nutrients more efficiently. Similarly, observations by Sabri et al. (1991) of genetic differences in feed efficiency were reported to be due to differences in energy requirements for growth for the genetic lines evaluated. Consistent with this rationale of the biological relationship between FCR and BWG were high phenotypic and genetic correlation estimates reported by Chambers et al. (1984).

Heterosis

The mean heterotic effect, percent heterosis and heterosis for sex-linked effects for body weight gain are presented in Table 3. Significant and negative average heterosis, ranging from −19 to 20 and −48 to −9 in male and female progeny, respectively, was observed for BWG except at 2 WOA. Although with a great deal of variation, heterosis was highly negative at 1 WOA and increased with age of birds. These observations were, in part, consistent with previous reports of Verma and Chaudhary (1980). Fairfull (1990) also reported a great deal of variation in heterosis between crosses of pairs of strains and this heterosis depended on the nature and degree of the genetic difference between strains. Even though the average heterosis for females was also significant throughout the studied period, males exhibited higher heterosis than females in most part of the study except at 4 and 6 WOA. The higher heterosis for male than female progeny suggest that there was positive heterosis for body weight gain due to the sex chromosome among the male progeny. Average heterosis for sex chromosome was also significant throughout the study period. In most part, the average heterosis for males and heterosis for sex chromosome was 186 and 14% higher at 18 than 20% CP diets, respectively.

TABLE 3

Heterosis (h_{ij}), percent heterosis (%h_{ij}) and heterosis for sex linked effects (h^s_i) for body weight gain of White Plymouth Rock (WPR) and Single Comb White Leghorn (SCWL) reciprocal crosses on 18 and 20% crude protein diets

		Age, weeks	1		2		3		4		5		6		7		8	
Sex	Effect	CP,%	18	20	18	20	18	20	18	20	18	20	18	20	18	20	18	20
Male	h_{ij}		-13	-13	NS	NS	NS	NS	-8	NS	NS	-9	20	16	-13	-19	8	NS
	%h_{ij}		-32	-36	NS	NS	NS	-8	-8	NS	NS	-9	18	15	-10	-14	NS	NS
	h^s_i		NS	NS	8	9	11	10	15	15	20	20	27	22	29	29	32	16
	%h^s_i		5.5	10	6	15	12	13	NS	17	8	18	21	21	NS	22	16	24
Female	h_i		NS	-13	-9	-10	NS	NS	-13	-15	-24	-29	NS	NS	-42	-48	-24	-35
	%h_{ij}		-23	-46	-8	-17	NS	8	-12	-17	-11	-27	NS	NS	-17	-36	-10	-29
								SE[1] = 1.2 – 8.1										

* – significant heterosis (P<0.05)

[1] – standard error of mean

NS – non significant

TABLE 4

Heterosis (h_{ij}), percent heterosis (%h_{ij}) and heterosis for sex linked effects (h^s_i) for feed conversion ratios of White Plymouth Rock (WPR) and Single Comb White Leghorn (SCWL) reciprocal crosses on 18 and 20% crude protein diets

		Age, weeks	1		2		3		4		5		6		7		8	
Sex	Effect	CP, %	18	20	18	20	18	20	18	20	18	20	18	20	18	20	18	20
Male	h_{ij}		0.34	0.21	NS	NS	NS	NS	NS	-0.37	-0.27	-0.47	-0.46	-0.7	NS	-0.26	NS	0.25
	%h_{ij}		16	11	NS	NS	NS	NS	NS	-13	-9.4	-15	-14	-20	NS	NS	NS	7
	h^s_i		-0.52	-0.31	-0.5	-0.43	-0.37	-0.58	-0.51	-0.65	-0.54	-0.75	-0.58	-0.91	-1	-1	-1.4	
	%h^s_i		-4.2	-20	-9	-21	-7	-14	-11	-18	-16	-17	-19	-17	-16	-30	-14	-40
Female	h_{ij}		0.81	0.61	0.22	0.27	0.51	0.23	0.56	NS	0.37	NS	0.29	NS	0.71	0.79	1.2	1.6
	%h_{ij}		-20	31	NS	12	11	8.8	10	NS	6.4	NS	NS	NS	10	22	19	47
								SE[1] = 0.04 – 0.3										

[1] – standard error of mean

NS – non significant

Although changes in heterosis have been reported with respect to nutritional treatment (Hull et al., 1963; Emsley et al., 1980), differences for 8 week average heterosis for females on either 18 or 20% CP diets were not significant.

Average heterosis for FCR of male and female crossbred progeny are presented in Table 4. The high variation in FCR may be due to residual feed consumption (Byerly et al., 1980) which has a genetic basis (Schulman et al., 1994). The average heterosis for FCR of male progeny was negative and significant in most part of the study except at 2 and 4 WOA, whereas the average heterosis for females was positive and significant throughout the study period. The heterosis values for males and females on 18 and 20% CP diets ranged from –0.46 to 0.34 and 0.22 to 1.2, and –0.47 to 0.25 and 0.23 to 1.6, respectively. The lower average heterosis for males is due to the negative and significant heterosis due to the sex chromosome in males. On averaging means for the 8 weeks study period, heterosis was 260 and 48% higher at 18 than 20% CP diets for males and females, respectively. Percent heterosis for sex chromosome was also 4% higher at 18 than 20% CP diets.

Maternal and line effects

With the exception of females on 18% CP diet, maternal effects on body weight gain (Table 5) were positive and significant for WPR males and females at 6 and 8 WOA, whereas for the most part birds on 18% CP diet exhibited higher maternal effects (–19 to 24 and –18 to 11, respectively) than those on 20% CP diet (–27 to 18 and –19 to 11, respectively). The observed differences in patterns of heterosis due to maternal and line effects with age and CP levels is suggestive of the existence of line x diet interactions. Average line effects were positive, significant although greater for WPR than SCWL males. Average line effect for both WPR and SCWL females was in most part negative but significantly higher in WPR than SCWL progeny. Average line effects for WPR males and females were also 40 and 176% higher, respectively, at 20 than 18% CP diets.

Average maternal effects on feed conversion ratio were not significant for the most part of the study for progeny of both sexes (Table 6). Maternal effects of WPR males and females ranged from –0.85 to 0.61 and –0.61 to 0.81, respectively. Average maternal effects for WPR males and females was 116 and 271% higher at 20 than 18% CP diets.

Average line effects for WPR males were higher than SCWL and significant at 20% CP diets for both lines (Tables 5 and 6). The reverse trend was observed in females and especially from 6 to 8 WOA where line effects were significant for both WPR and SCWL progeny. However, SCWL progeny exhibited higher average line effects than WPR during this study period. Line effect in males and fe-

TABLE 5

Maternal (M_{ij}) and line (L_{ij}) effects for body weight gain of White Plymouth Rock (WPR) and Single Comb White Leghorn (SCWL) reciprocal crosses on 18 and 20% crude protein diets

		Age, weeks	1		2		3		4		5		6		7		8	
Sex	Effect	CP, %	18	20	18	20	18	20	18	20	18	20	18	20	18	20	18	20
Male	(M_{ij}) WPR		NS	NS	NS	NS	9	NS	NS	NS	NS	NS	24	15	-19	-27	13	18
	(L_{ij}) WPR		NS	NS	NS	NS	11	17	15	21	37	39	10	19	18	30	35	35
	SCWL		NS	NS	NS	7	NS	NS	NS	NS	NS	NS	18	11	NS	-20	NS	NS
Female	(M_{ij} WPR		NS	NS	NS	NS	NS	NS	-12	NS	NS	NS	NS	12	24	29	NS	-26
	SCWL		NS	NS	NS	NS	NS	-11	NS	-11	-31	-41	-23	-18	-36	-38	NS	-15

SE[1] (M_{ij}) = 1.3-5.9 SE[1] (L_{ij}) = 1.2-6.0

[1] – standard error of mean

NS – non significant

TABLE 6

Maternal (M_{ij}) and line (L_{ij}) effects for feed conversion ratios of White Plymouth Rock (WPR) and Single Comb White Leghorn (SCWL) reciprocal crosses on 18 and 20% crude protein diets

		Age, weeks	1		2		3		4		5		6		7		8	
Sex	Effect	CP, %	18	20	18	20	18	20	18	20	18	20	18	20	18	20	18	20
Male	(M_{ij}) WPR		-0.85	NS	NS	NS	NS	NS	NS	NS	NS	NS	-0.68	NS	NS	0.61	NS	-0.61
	(L_{ij}) WPR		NS	NS	NS	NS	NS	-0.53^{-}	NS	-0.45	NS	NS	0.36^{-}	NS	NS	-0.16	NS	41
	SCWL		-1.1	NS	NS	NS	NS	0.50	NS	NS	NS	NS	-0.39	NS	0.56	1.0	NS	NS
Female	(M_{ij}) WPR		NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	-0.54	NS	1.5	0.81	NS	-0.61
	(L_{ij}) WPR		0.59^{+}	NS	NS	NS	NS	NS	NS	NS	NS	NS	0.47^{+}	-0.51	-1.9	-1.4	-0.36	0.47
	SCWL		-0.42	NS	NS	NS	NS	NS	NS	NS	NS	NS	-0.44	NS	1.4	0.58	0.82	-0.85

SE[1] (M_{ij}) = 0.08-0.38 SE[1] (L_{ij}) = 0.10-0.35

$^{+}$ – significant line x diet interaction ($P<0.05$); [1] – standard error of mean

NS – non significant

male progeny were higher for WPR at 18 than 20% CP diets by 148 and 104%, respectively, and for SCWL at 20 than 18% CP diet by 248 and 46%, respectively.

CONCLUSIONS

This study indicates that SCWL males and WPR females exhibited higher combining ability at 18 than 20% CP diets. The significant heterosis for BWG and FCR due to sex chromosomes and maternal effects suggests that these two traits are also affected by genes on the sex chromosome for the crosses included in this study.

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STRESZCZENIE

Heterozja przyrostów i wykorzystania paszy u mieszańców White Plymouth Rock i Single Comb White Leghorn odchowywanych na dietach o zróżnocowanym poziomie białka

Porównano heterozję, spowodowaną chromosomem płciowym, oraz efekty matczyne i linii u mieszańców odwrotnych wzajemnych White Plymouth Rock (WPR) i Single Comb White Leghorn (SCWL). Ptaki od wylęgu do wieku 8 tyg. żywiono dietami zawierającymi 18 lub 20% białka ogólnego (CP). Ptaki WPR miały większe przyrosty i zjadały więcej paszy niż SCWL, a ptaki WPR żywione dietą zawierającą 20% CP były większe niż na diecie 18% CP. Mimo, że FCR u ptaków SCWL na diecie 18% CP było niższe niż na diecie 20% CP w 1 i 3-6 tygodniach, było ono wyższe niż u ptaków WPR. Heterozja był większa u ptaków na diecie 18% CP, a średni wpływ matczyny i wpływ linii na BWG były większe ($P<0,05$) u WPR niż SCWL i na diecie 18 niż 20% CP. Efekt matczyny na FCR u potomstwa WPR był jednak większy na diecie 20 niż 18% CP. Średni wpływ linii był również większy u samców WPR niż SCWL i istotny u obu linii żywionych dietą 20% CP.

Heterozja spowodowana chromosonem płciowym była istotna ($P<0,05$) i dodatnia w przypadku BWG, a ujemna dla FCR. Przeprowadzone badania świadczą o tym, że samce SCWL i samice WPR wykazują większą zdolność kombinacyjną na diecie 18 niż 20% CP. Istotna heterozja BWG i FCR spowodowana chromosonem płciowym oraz efekty matczyne pozwalają sądzić, że na obie te cechy mają wpływ geny na chromosomie płciowym.