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## Inbreeding Effects on Layer Performance at Two Levels of Protein Intake<sup>1</sup>

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ABSTRACT The growth and laying performance of two strains (6 and 8) after two generations of close inbreeding (44%) were compared with that of their reciprocal crosses ( $6 \times 8$  and  $8 \times 6$ ) under two levels (17% and 13%) of dietary protein and a corresponding 19% reduction in daily protein intake.

Inbreeding effects were large for most traits measured, including body weights, components of egg production, and egg quality.

Reduced dietary protein had adverse effects upon viability, egg mass, age at first egg, and body weight late in the laying period. However, this dietary modification improved egg mass produced per kilogram of protein intake and had no effects upon egg quality.

The tendency for inbreeding depression to be greater under the low (13%) protein diet for viability, sexual maturity, and egg production was too slight for statistical significance. Inbreeding did not change feed or protein conversion response to low protein because inbreds increased their intake of the low protein diet less than the crosses.

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#### INTRODUCTION

Several authors have investigated the effects of inbreeding upon laying house performance of egg-type chickens (Goodale, 1927; Jull, 1933; Shoffner, 1948; Duzgunes, 1950; Lerner, 1955; Schultz, 1953; Stephenson et al., 1953; Abplanalp, 1974). Others have investigated genotype × diet interaction (Hull and Gowe, 1962; Harms and Waldroup, 1962; Gowe et al., 1962; Hull et al., 1963; Moreng et al., 1964; Owings, 1964; Sharpe and Morris, 1965; Deaton and Quisenberry, 1965; Harms et al., 1966; Balloun and Speers, 1969; Krautmann. 1969; Marks et al., 1969; Aitken et al., 1972, 1973; Nesheim, 1975; Lagervall, 1977) but little attention has been given to possible effects of inbreeding (or heterosis) on response to dietary changes.

The use of inbred lines for genetic improvement of breeding stock has been controversial among geneticists because of the tendency for

inbreeding depression, extended generation interval, and reduced selection intensity to offset advantages of improved discrimination among genotypes. However, as indicated by Dickerson (1972), Abplanalp (1974), Dickerson and Lindhé (1977), and Kress (1977), there is continuing interest in the use of inbred lines to improve the effectiveness of selection. There is also considerable interest in the efficiency of dietary protein utilization by poultry and other animals. Is it possible that inbred pullets are more sensitive than outbreds or hybrids to marginal levels of dietary protein because of impaired biochemical pathways for utilizing certain amino acids, and hence have higher protein intake requirements for the same level of performance? Or do inbreds have lower protein/calorie dietary intake requirements because of inherently slower rates of synthesis of body tissue and of egg protein?

Objectives in the present study were 1) to evaluate the importance of interactions between level of dietary protein intake and the genotypic difference between inbreds and their crosses and 2) to estimate the direct effects of protein level and of inbreeding upon growth, egg production, and egg quality for two strains of egg-type chickens.

#### MATERIALS AND METHODS

Inbred sublines of two unrelated strains (6 and 8), their reciprocal crosses (6  $\times$  8 and 8  $\times$ 

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6) and a control strain (5) of Single-Comb White Leghorn chickens were hatched on June 17, 1966, and placed under two dietary regimes at the Central Experimental Farm facility of the Animal Research Institute. The numbers banded and housed are shown in Table 1.

Origin of the Inbred Lines. Strains 6 and 8 were derived from Ottawa strains 3 and 4, respectively. Strain 3 had been selected for high early egg production since 1951 and was derived from a relatively narrow genetic base. Strain 4 was derived from seven Canadian ROP strains beginning in 1951 and had been selected for high early egg production since 1952. Strain 5 was an unselected control population derived from the same base as strain 3. Details of the development of strains 3, 4, and 5 can be found elsewhere (Gowe et al., 1959, 1973). Matings of strain 3 males to their dams or full sisters in 1965 produced the first generation of 60 inbred sublines of strain 6. All breeders used had been selected earlier on 273-day performance to reproduce strain 3. The 60 strain 6 sublines were further reduced to 30 based on the full year (497 day) performances of the foundation strain 3 dams and their full sisters. Mating of strain 6 inbred males to their grand-dams or to inbred full sisters in 1966 produced the second generation of 30 inbred sublines of strain 6. The same procedure was used in 1965 and 1966 to produce 31 strain 8 inbred sublines from strain 4. The total cumulative pedigree inbreeding in 1966 from the origin of strain 3 in 1950 and of strain 4 in 1951 was 4.2% for strain 5, 44.2% for strain 6, and 44.6% for strain 8.

Management and Pullet Assignment to Treatments. The birds were brooded in colony

 TABLE 1. Number of sire and dam families and of pullets banded and housed at Ottawa in 1966, by strain and cross

Genotypes	Sires	Dams	Progeny banded	Progeny housed
6	30	123	356	264
8	31	120	395	264
6 X 8	(30) <sup>a</sup>	98	297	264
8 × 6	(31) <sup>a</sup>	98	300	264
5	80	240	395	264
Total	141	679	1743	1320

<sup>a</sup>Same sires were used for inbred and linecross matings.

houses until 60 days of age, reared on range until 123 days of age, and housed in single-bird cages. The daily lighting schedule was 12 hr until 50% average production, 13 hr for the next week, and then 14 hr until 71 weeks of age.

The pullets within each sire progeny group of the five genotypes (5, 6, 8,  $6 \times 8$ ,  $8 \times 6$ ) were randomly divided between two feed treatments, Ottawa 18.6% CP and low protein 14% CP starters from 4 to 56 days of age. However, effects of starter diets on growth were negligible and separate rearing treatments were not feasible. All birds were fed Grower 1 from 56 to 84 days and then Grower 2 (Gowe *et al.*, 1960) until birds were laying at the rate of 1%. Thereafter, the primary feed treatment was either Ottawa (16.9% CP) or low protein (13.4% CP) laying ration until the end of test. Composition of the laying ration is shown in Table 2.

Within each sire progeny group and starter feed, alternate pullets were assigned to either the Ottawa or the low protein laying ration, until each laying house feed treatment had been assigned 132 pullets per genotype. Each group of 132 pullets was randomly divided into three replicate subgroups (blocks) of 44 birds each. One block of 44 cages from each of the five breeding groups was assigned randomly within each of three 220-cage rows in each feed treatment.

Components of Performance. Traits analyzed were block means: for age at first egg (omitting nonlayers) and total eggs per hen housed; for daily feed, calculated ME and crude protein intake, hen-day viability, and percent production by periods (one of 19 days plus 12 of 28 days); for body weight by ages at 40, 147 (housing), 350, and 497 days; for egg weights by ages during 5 days at 32 and 64 weeks and 1 day at 44 and 52 weeks; for egg mass per hen-day and per kilogram of feed and of protein intake in periods 2 to 5, 6 to 7, 8 to 10, and 11 to 13, corresponding to four ages of egg weights; and for egg quality during 5 days at 32 and 64 weeks of age, including specific gravity, albumen height, Haugh units (Nagai and Gowe, 1969), reflectometer shell color (Gowe et al., 1965), shell shape (100 length/width, and percent eggs with small («.33cm) and large (>.33 cm) blood spots.

Analysis. The general model for analysis of all traits measured at more than one age was as follows:

$$Y_{ijkl} = \mu + L_i + P_k + S_j + R_{l:i} +$$
$$LP_{ik} + LS_{ij} + PS_{kj} + PR_{kl:i} +$$
$$SR_{jl:i} + PSL_{kji} + PSR_{kjl:i}$$

where  $Y_{ijkl}$  = the mean of all observations on the i<sup>th</sup> dietary protein (L) level, the k<sup>th</sup> period (P) or age at which measurement taken, the j<sup>th</sup> genotype (S), and the l<sup>th</sup> row within feed i (R/L). Effects L, P, and S were considered fixed. Effects of R were considered random. The four degrees of freedom for genotypes were used to evaluate four single degree of freedom orthogonal contrasts as follows:

S1 - Crosses (6 × 8, 8 × 6) vs. inbreds (6, 8) S2 - 8 × 6 vs. 6 × 8 S3 - 6 vs. 8 S4 - Control strain 5 vs. all others

Furthermore, contrast S1 to S4 were interacted with levels, periods, and rows/feed. Error mean square were R/L for L; P × R/L for P and P × L; S × R/L for S and S × L; and P × S × R/L for P × S and P × S × L. Age at first egg and hen housed egg production were analyzed using a similar model without any period effect. Number of periods was 13, 4, 2, or 1, depending upon the trait.

#### RESULTS

Strain averages and results of F-tests for each level of protein are shown in Tables 3, 4 and 5. In general, there were large differences in performance between inbreds and crosses and, for some traits, between the two inbred strains themselves. Furthermore, these differences were consistent for both feeds in almost every case.

Although differences in the calorie/protein ratio did not affect total feed consumption (Table 3), birds on the low protein ration did consume 28 kcal more metabolizable energy (353 vs. 325) and 3.9 g less protein per day (16.5 vs. 20.4). Crosses consumed significantly more feed (129 vs. 115 g), energy (361 vs. 320 kcal), and protein (19.6 vs. 17.4 g) daily than the inbreds, and these breeding group differences in feed consumption were consistent across diets.

Body weight gain and egg production are two major products of the laying hen which TABLE 2. Percent composition of laying rations

	Laying	rations
Ingredient	Ottawa	Low protein
Corn	10	8
Wheat	37	29.6
Oats	20	16
Barley	10	8
Stabilized tallow	2	1.6
Fish meal (65% CP)	2	1.6
Meat meal (50% CP)	2	1.6
Soybean meal (44% CP)	5	4
Skim milk powder	1.5	1.2
Dehydrated cereal grass	1.5	1.2
Dehydrated alfalfa meal	1.5	1.2
Steamed bone meal	1.25	1.0
Sucrose	0	17.6 <sup>a</sup>
Dicalcium phosphate	0	.505
Ground limestone	5.75	6.365
Iodized salt	.375	.405
Micronutrients	.125 <sup>b</sup>	.125 <sup>a</sup>
Approximate composition <sup>b</sup>		
Crude protein	16.9	13.4
Calcium	3.8	3.8
Total phosphorus	.75	.70
Metabolizable energy (kcal/g)	2.71	2.87
Calorie/protein ratio	73	97

<sup>a</sup>Prepared by diluting Ottawa laying ration with sucrose before adding minerals and micronutrients (per kilogram of feed) to Ottawa and low protein rations, respectively, 1247 and 1373 IU vitamin A, 1499 and 1649 IU of  $D_3$ , 3.31 and 3.75 mg of riboflavin; and 123 and 137 mg of manganese sulphate.

<sup>b</sup>Composition was that expected from ingredients used and from batch analysis for protein and mineral content of laying rations.

were expected to be affected by level of dietary protein and of inbreeding.

Inbreds were 29 g lighter than crosses at 40 days of age and 174 g lighter during the laying period, based on three weights taken at and after housing. These differences were consistent across diets and across ages at which weights were taken. Body weight was greater for strain 8 than for strain 6 only at 497 days (1961 vs. 1909 g). In the three earlier weighings, strain 8 was lighter than strain 6 (299 vs. 323, 1551 vs. 1603, and 1937 vs. 1973 g, respectively). Birds on the low protein diet averaged 8 g heavier than those on normal diet at 147 days, but became 17 g lighter at 350 days and 43 g lighter at 497 days of age (P < .001).

The average number of eggs per hen housed

			Intake/hen day			Body	Body weight (g)	
Protein level (L)	Genotypes (S)	Feed (g)	ME (kcal)	Protein (g)	40 days	147 days	350 days	497 days
16.9%	5	118	320	19.9	349	1695	2273	2168
	6	116	315	19.6	327	1611	1980	1924
	8	112	304	18.9	297	1536	1958	1985
	$6 \times 8$	128	347	21.6	346	1741	2125	2155
	$8 \times 6$	126	342	21.3	338	1731	2149	2158
	Inbreds	114	309	19.3	312	1573	1969	1954
	Crosses	127	344	21.5	342	1736	2137	2157
13.4%	5	120	344	16.1	343	1712	2291	2170
	9	117	335	15.7	319	1595	1966	1894
	×	113	324	15.1	300	1565	1916	1938
	$6 \times 8$	133	381	17.8	338	1732	2101	2059
	8 X 6	130	372	17.4	340	1751	2132	2115
	Inbreds	115	330	15.4	310	1580	1941	1916
	Crosses	132	376	17.7	339	1742	2116	2087
SE for genotype/feed <sup>a</sup> SE for protein levels <sup>a</sup>		1.7	(4.6, 4.9) (2.7, 2.9)	(.29, .23) (.17, .13)	8	30		
F values (d.f.)								
Protein levels (L)	1/4	4.61 <sup>†</sup>	6.47†	17.94*	2.57		1.27	
Periods (P) (k-1)/4(k-1)	14	194.4***	* * *	* * *			6154***	
$P \times L (k-1)/4(k-1)$	14	1.58					18.3***	
Crosses vs. inbreds (S <sub>1</sub> )	1/4	258.4***	***	* * *	28.4**		69.9***	
S, X L	14	3.13			$\stackrel{\sim}{\sim}$		₽	
$S_{1} \times P (k-1)/4(k-1)$	1/4	9.45***	***	* * *			₽	
$S_1 \times P \times L (k-1)/4(k-1)$	1/4	7					√	
$6 \times 8 vs. 8 \times 6 (S_2)$	1/4	2.26			√1		5	
$S, \times L$	1/4	$\sim$			1.03		₽	
$S_{2} \times P (k-1)/4(k-1)$	14	1.36					√	
$S_{c} \times P \times L (k-1)/4(k-1)$	14	v					~	

TABLE 3. Means by genotypes and protein levels with F-tests for feed intake and body weights

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was much lower for inbreds than for crosses (178 vs. 248), but the 10-egg advantage for the high protein diet was not statistically significant (Table 4). Inbreeding affected all components of hen-housed egg production: age at first egg, laying house viability, and eggs per hen-day. Age at first egg was later for the inbreds than crosses by 7 days. Reducing protein level delayed age at first egg by nearly 2 days and that of strain 6 more than strain 8 (3.3 vs. .6 days).

Laying-house viability was poorer for inbreds than for crosses (86.1 vs. 94.3%) and for the low protein diet than for the high (88.0 vs. 92.4%). However, among the crosses, high protein feed increased viability only in  $6 \times$ 8 (98.2 vs. 91.7%). The markedly greater cumulative mortality (100 - viability) over the 13 periods for strains 5, 6 and 8 (15%) than for crosses  $6 \times 8$  and  $8 \times 6$  (6%) is shown in Figure 1.

Hen-day rate of egg production also was 19% lower for inbreds than crosses on both diets and slightly lower for the low protein diet, primarily during the first one-third of the laying period. Inbreds started to lay later but peaked only 13% lower in hen-day rate in period 3 than the crosses (Figure 2). In other respects, the shapes of the curves were very similar. Strain 5 controls began laying a few days later than lines 6 and 8 but laid slightly better in periods 5 to 8.

Average egg weight was 2.9 g smaller for inbreds than for crosses and .8 g less for the low dietary protein level in both inbreds and crosses. Egg mass per hen-day for inbreds averaged about 70% of that for crosses (29.4 vs. 42.2 g) on both diets and the small effect of low dietary protein was slightly greater for inbreds (-1.9 vs. -1.2 g) than for crosses. Inbreds were only about 79% as efficient as crosses in terms of either feed (254 vs. 320 g/kg) or protein (1688 vs. 2135 g/kg) conversion into egg mass on both diets. Both inbreds and crosses on the low protein diet produced 7% less egg mass per kilogram of feed consumed (276 vs 298 g), but 17% more per kilogram of protein consumed (2064 vs. 1760 g). The decline from first to fourth quarter was much greater for inbreds than for crosses in egg mass per hen day (32 vs. 14%) and per kilogram feed or protein intake (22 vs. 8%).

Egg quality traits were not significantly affected by protein level (Table 5). Only specific gravity and albumen height were influenced by inbreeding. In general, inbreds

	<1 11.0** 1.34		<1 17.7*** <1		
10.3*	₽	5.58 <sup>†</sup>	₽		
			* * *	et.	
3.22	<1 1.10 1 <	3.67	<1 9.90*** <1	for 16.9%, second for 13.4% diet.	
₩	* * *	14	7 7 7 7	is for 16.99	
6 vs. 8 (S <sub>3</sub> )	$\begin{array}{l} S_{3} \times L \\ S_{3} \times P \ (k\text{-}1)/4(k\text{-}1) \\ S_{3} \times P \times L \ (k\text{-}1)/4(k\text{-}1) \end{array}$	5 $vs.$ other $(S_4)$	$\begin{array}{l} S_4 \times L \\ S_4 \times P \ (k-1)/4(k-1) \\ S_4 \times P \times L \ (k-1)/4(k-1) \end{array}$	<sup>a</sup> For <i>t</i> -tests, first value in ( ) is <sup>†</sup> P<.10.	*P<.05. **P<.01.

\*P<.001

								Egg mass (g) per	
Protein level	Genotypes	Eggs/hen housed	Hen-day viability	Eggs/ hen-day	Age 1st egg (days)	Egg weight <sup>a</sup>	Hen-day	Feed	Protein
			(%)	(%)		(g)		(kg)	(kg)
16.9%	5	180	85.5	52.3	173.3	56.6	31.6	264	1562
	6	177	87.2	51.8	162.9	55.6	29.8	254	1503
	8	190	90.4	54.6	159.2	55.6	31.0	273	1615
	$6 \times 8$	258	98.2	72.0	154.2	57.9	42.8	329	1947
	$8 \times 6$	247	93.6	71.1	154.6	59.0	42.8	335	1982
	Inbreds	184	88.8	53.2	161.0	55.6	30.4	263	1556
	Crosses	252	95.9	71.6	154.7	58.4	42.8	332	1964
13.4%	5	172	81.4	50.0	175.6	55.6	29.7	243	1813
	6	170	84.8	49.8	166.2	55.0	28.4	238	1776
	8	174	81.9	51.7	159.8	54.4	28.7	250	1865
	$6 \times 8$	244	91.7	70.1	155.3	57.2	41.5	305	2276
	$8 \times 6$	245	93.8	69.4	155.2	58.3	41.7	313	2335
	Inbreds	172	83.4	50.8	163.0	54.7	28.5	244	1821
	Crosses	244	92.7	69.8	155.2	57.7	41.6	309	2306
SE for genotype/feed <sup>b</sup> SE for protein levels <sup>b</sup>		6.2	۲.	1.6	1.0	ë	1.0	ø	(47, 60) (15, 19)
F values (d.f.)									
Protein levels (L)	14	3.40	9.80*	2.99	8.41*	36.1**	$5.04^{\ddagger}$	33.8**	*
Periods (P) (k-1)/4(k-1) P X L (k-1)/4(k-1)			5.27*** 1.52	969*** 1.90 <sup>†</sup>			271*** 3.67*	63.1*** 1.09	<b>물</b> 불 북
Crosses vs. inbreds $(S_1)$	1/4	170.0***	14.70*	152***	98.6***	66.6***	141***	69.4***	* *
$ \begin{array}{l} S_1 \times L \\ S_1 \times P \ (k\text{-}1)/4(k\text{-}1) \\ S_1 \times P \times L \ (k\text{-}1)/4(k\text{-}1) \end{array} \end{array} $	4	√1	<1 1.19 2.02	<1 3.76*** <1	$\vec{\nabla}$	₩	<1 7.55** <1	<1 12.63*** <1	* * *

TABLE 4. Means by genotypes (S) and protein levels (L) and F-tests for egg production and feed conversion

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$6 \times 8 vs. 8 \times 6 (S_2)$	1/4	1.84	1.31	1.88	$\stackrel{<}{\sim}$ 1	13.4*	$\sim$ 1	<2.49	
$\begin{array}{l} S_{2} \ \times L \\ S_{2} \ \times P \ (k\text{-}1)/4(k\text{-}1) \\ S_{2} \ \times P \ \times L \ (k\text{-}1)/4(k\text{-}1) \end{array}$	74	$\stackrel{<}{\sim} 1$	10.0* 2.63** 4.14***	<1 1.08 <1	$\nabla$	$\nabla$	$\overrightarrow{}\overrightarrow{}\overrightarrow{}\overrightarrow{}$	$\Box  \Delta  \Delta$	
6 vs. 8 (S <sub>3</sub> )	1/4	4.74†	√	2.57	1992***	19.3*	$\stackrel{\sim}{\sim}$	4.34	
$\begin{array}{c} S_{3} \times L \\ S_{3} \times P \ (k\text{-}1)/4(k\text{-}1) \\ S_{3} \times P \times L \ (k\text{-}1)/4(k\text{-}1) \end{array}$	14	5.47†	3.72 <1 1.11	<1 4.65*** <1	130.1***		<1 3.40* <1	<1 8.56** <1	*
5 $vs.$ other (S <sub>4</sub> )	1/4	40,0***	5.44 <sup>†</sup>	53.9***	134.5***	6.10†	35.6**	23.6**	*
$ \begin{array}{l} S_{4} \times L \\ S_{4} \times P \ (k-1)/4(k-1) \\ S_{4} \times P \times L \ (k-1)/4(k-1) \end{array} $	*	<1	<1 2.19 <1	<1 22.1*** <1	$\overrightarrow{}$		<1 16.8*** 1.30	<1 9.19** 1.07	*
<sup>a</sup> Unweighted mean of egg weights at 225	g weights at	225, 308, 365, and 450 days of age	50 days of age.						

<sup>b</sup> For t-tests, first value in ( ) is for 16.9%, second for 13.4% protein level

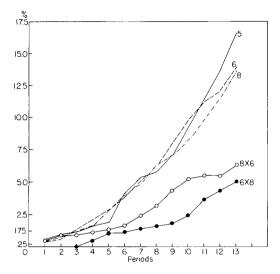


FIG. 1. Cumulative percent hen-day mortality over 13 periods for strains 5, 6, and 8 and crosses  $6 \times 8$  and  $8 \times 6$ .

had thinner shells than crosses (1.0838 vs. 1.0855 specific gravity) and strain 8 shells were thinner than those of strain 6 (1.0829 vs. 1.0847). Inbreds also had lower albumen heights than crosses (5.66 vs. 5.82 mm). At 32 weeks, average albumen height for strain 6 was smaller than that for strain 8 (5.87 vs. 6.13 mm), but at 64 weeks the values were almost identical (5.31 vs. 5.34 mm). Similarly, at 32 weeks, average albumen height for cross  $8 \times 6$ was smaller than that for cross  $6 \times 8$  (6.11 vs. 6.31 mm), but at 64 weeks values were almost identical (5.44 vs. 5.40 mm).

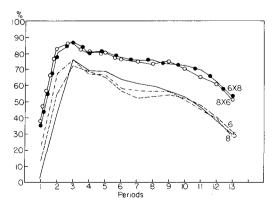


FIG 2. Percent hen-day production by periods for strains 5, 6, and 8 and crosses 6 × 8 and 8 X 6.

			and an address of a		contract and sea to fract			
Profein		Specific gravity	Albumen heiøht	Shell color	Hauøh	Shape	Blood	Blood spots
level	Genotypes	$(SG-1) \times 10^4$	$(mm) \times 10^{2}$	(100=white)	units	(100 L/W)	Small	Large
								(%)
16.9%	5	834	605	91.7	78.1	143.9	1.35	.97
	6	841	565	92.2	75.5	144.5	1.41	.85
	8	823	574	89.4	76.0	140.0	1.35	1.53
	$6 \times 8$	856	580	91.3	75.4	141.8	1.01	1.33
	$8 \times 6$	854	576	90.6	75.1	141.6	1.32	1.11
	Inbreds	832	570	90.8	75.7	142.2	1.38	1.19
	Crosses	855	578	90.9	75.3	141.7	1.16	1.22
13.4%	5	831	618	91.6	79.4	143.5	1.42	.64
	6	853	553	92.2	74.9	144.2	1.16	.87
	8	835	574	90.4	76.5	140.0	1.55	1.38
	$6 \times 8$	862	591	91.4	76.7	141.6	1.34	.70
	8 X 6	849	579	91.5	75.6	141.8	1.36	.87
	Inbreds	844	563	91.3	75.7	142.1	1.36	1.12
	Crosses	855	585	91.5	76.2	141.7	1.35	.78
SE for genotype/feed		4.9	5.4	.39	.35	.66	.22	.21
F values (d.f.)								
Protein levels (L)	14	3.38	√	2.10	2.30	5	₽	1.18
Periods (P)	14	4951***	1122***	418***	1966***	634***	$\sim$ 1	2.62
$P \times L$	<sup>1</sup> / <sub>1</sub>	12.0*	7.95*	3.50	6.96 <sup>†</sup>	₽	₽	5
Crosses vs. inbreds (S <sub>1</sub> )	1/4	16.6*	13.4*	₽	₽	1.94	<1	

TABLE 5. Means by genotype and protein level with F-tests for egg quality traits

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1.35	₽	1.66	$\leq$ 1	2.05	4.43 <1	3.34	~	√	1.60	30.1**	√1	√	4
$\stackrel{\wedge}{\sim}$	1.0	5	1.18	1.0	⊽ ⊽	1.18	2.06	√	1.48	$\sim$	₽		~1
₽	~1	$\stackrel{<}{\sim}$	√1	<b>1</b>	⊽ ⊽	82.9***	₽	7	1.03	4.84 <sup>†</sup>	√	4.56	$\leq 1$
2.94	2.57	√	5.69†	1.64	3.27 < 1	6.62 <sup>†</sup>	1.95	15.7*	√	151***	3.16	2.24	<1
$\overrightarrow{}$	5	13.1*	2.43	4.17	7.82*	20.6*	1.0	2.58	<1	3.22	√	7	√
					8.55* <1							2.37	<1
2.12	~1	1.14	2.18	1.16	<1 1.57	14.6*	$\sim$ 1	₽	₽	23.0**	2.55	4.04	1.26
1/4	1/4	1/4	5% 5%	* 2	74 1/4	1/4	14	14	5/1	1/4	1/4	14	4
$S_1 \times L$	$S_1 \times P$	$S_1 \times P \times L$	$6 \times 8 vs. 8 \times 6 (S_1)$	$S_2 \times L$	$S_2 \times P \times L$ $S_2 \times P \times L$	6 vs. 8 (S <sub>3</sub> )	$S_3 \times L$	$S_3 \times P$	$S_3 \times P \times L$	$5 vs.$ other $(S_4)$	$S_4 \times L$	$S_4 \times P$	$S_4 \times P \times L$

#### DISCUSSION

Sugar dilution of the diet lowered daily protein consumption by 19% (3.9 g/bird) for both inbreds and crosses despite apparent efforts by the birds to compensate, as indicated by the 7 to 9% increase in energy intake. Krautmann (1969) also reported that some strains of birds attempted to compensate for protein shortage through additional feed consumption.

There were clear direct adverse effects of the low protein diet upon only five traits: 4% higher hen-day mortality, 1% later age at first egg, 1% smaller eggs, 2% lighter body weights during the laying period, and 7% poorer conversion of feed (and energy) intake to eggs. However, the lower protein intake was accompanied by 17% improvement in the conversion of dietary protein to egg mass, confirming that economically optimum protein intake depends upon relative costs of dietary protein and energy.

Inbreeding had adverse effects for almost all traits, assuming that the difference between inbreds and crosses reflects inbreeding depression since 1950 or 1951. Shell color, Haugh units, egg shape, and blood spots were the only exceptions. Shoffner (1948) and Stephenson et al. (1953) reported regression values of several traits on percent inbreeding. Changes expected (E) using these regression values are compared with the observed deviation (D) of inbreds from crosses in Table 6. Agreement of D with E is close for egg weight and percent production, but age at first egg was delayed less (7 vs. 26 days) and depression was greater for adult body weight (-179 vs. -80 g) and total eggs per hen housed (-70 vs. -41) because of the 8% depression in viability (Table 4). Results from 25% inbreeding reported by Abplanalp (1974) would predict, for 44% inbreeding, a decline of about 8% in adult viability and 188 g in final body weight but only 40 eggs per hen housed and no change in age at first egg or in egg size.

Since strains 3 and 4 came from unrelated base populations, crosses between them may exhibit heterosis in addition to that explainable as recovery from inbreeding depression associated with the 44% inbreeding from the base of each line. Another possible reason for the greater magnitude of inbreeding effects on egg production and body weight in the strains from which strains 6 and 8 were derived may be that selection has moved average performance to

Trait	(b)	(E)	(D)
Age at first egg (days)	.60 ± .11	26.5	7.2
Hen-day production (%)	43 ± .04	-19.1	-18.7
Egg production (number/hen housed)	$93 \pm .07$	41	-70
Adult body weight (g)	$-1.8 \pm 1.4$	-80	-179
Egg weight (g)	06 ± .23	-2.7	-2.8

 TABLE 6. Predicted<sup>a</sup> effect of 44% inbreeding (E) and observed deviation of inbreds from crosses (D) in the present study

<sup>a</sup>From regressions (b) on percentage inbreeding reported by Shoffner (1948) and Stephenson et al. (1953).

much higher levels than those in 1950 and 1951 (Gowe *et al.*, 1973). Strain 5 has been maintained without directional selection and with minimum inbreeding (4%) since 1950 and is very similar in overall performance to the 44% inbred strain 6 derived by long-term selection and intense inbreeding from the same base population. Thus, the marked superiority of the linecross over the strain 5 birds is generally indicative of selection response without inbreeding. Such selection might be expected to increase the relative importance of nonadditive gene effects, including dominance effects.

Although the crosses were slightly heavier and consumed considerably more nutrients than the inbreds, they produced even greater egg mass per hen-day and their efficiency of egg production was better than that of inbreds, whether calculated per unit of feed or per unit of protein consumed. Comparison of feed consumption per hen-day with values reported by Aitken et al. (1972) and Lagervall (1977) indicates that crosses in this study tended to consume at a relatively high rate. Consumption by the inbreds in our study was closer to that reported by these authors for commercial crosses. Average shell thickness as indicated by specific gravity was greater for crosses but albumen height differences disappeared when they were adjusted for egg size (i.e., converted to Haugh units). Although important differences between the two inbred lines were evident for age at first egg, egg weight, early body weight, specific gravity, shell color, and shell shape, no differences were found between reciprocal crosses, suggesting an absence of appreciable sex-linked or maternal effects for these traits, at least when the background genotype is heterozygous.

Despite clear differences among genotypes

and moderate effects of protein level per se, virtually no sure evidence of genotype  $\times$ protein level interaction was found. In the two instances in which interactions were significant, they involved differences between either reciprocal crosses (hen-day viability) or inbreds (age at first egg) and did not involve the more extreme genotypic differences between inbreds and crosses.

The absence of any major genotype-protein level interaction in this study is in agreement with recent results of Hamilton (1978) but in contrast to results published by Deaton and Quisenberry (1965) for 14% to 17% protein rations and four egg production stocks; by Moreng et al. (1964) for 13 to 17% protein and four commercial egg stocks; and by Harms et al. (1966) for 11% to 17% protein and six stocks. In the last study, the interaction involved either the one meat line or ration protein levels outside the range of the present study. The results of Deaton and Quisenberry (1965) are difficult to compare with those of the present study because the two rations they used each involved changes in protein level during the laying period. The lack of strain × protein level interaction in Hamilton's (1978) report may be explained by the small direct effects of either strain or protein levels on performance.

Moreng *et al.* (1964) concluded that their interaction was probably due to the failure of one strain to assimilate sufficient quantities of at least one amino acid. The lack of interaction in our study suggests that the different genotypes evaluated were similar in their requirements for limiting amino acids.

Although not statistically significant, the greater *proportional* effect of the low protein diet for inbreds was consistent for eggs per hen housed  $(-7 \ vs. \ -3\%)$ , hen-day viability  $(-6 \ vs. \ -3\%)$ 

-3%), eggs per hen-day (-5 vs. -3%), age at first egg (1.2 vs. .3%), egg weight (-1.6 vs. -1.4%), and egg mass per hen-day (-6 vs. -3%). However, inbreds compensated less than crosses for the low protein diet in daily feed (1 vs. 4%) and in energy (7 vs. 9%) intake. For this reason, daily protein intake was reduced slightly more for inbreds than crosses (-20 vs.)-18%) by the low protein diet, in line with the greater decline in egg output for inbreds. Thus, the proportional effect of the low protein diet on feed (-7%) and protein (17%) conversion to eggs was the same for inbreds and crosses. If the crosses had not been able to increase feed and energy intake more and thus reduce protein intake less than the inbreds, reduction in egg production of crosses presumably would have been more nearly the same as for the inbreds, but still with little difference in effect of low protein diet on feed and protein conversion.

In retrospect, it appears that a diet still lower in protein (10%) or direct control of protein intake, would have produced larger and more readily interpretable effects on performance. Because of their higher genetic level of egg output, the crosses might well be more sensitive than inbreds to reductions in protein intake below their requirements for potential synthesis of egg protein.

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