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**GENETIC RESPONSE TO INDEX SELECTION FOR THE IMPROVEMENT
OF EGG PRODUCTION EFFICIENCY IN LAYER-TYPE CHICKENS**

Iowa State University

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Genetic response to index selection for the improvement
of egg production efficiency in layer-type chickens

by

Harpal Singh

A Dissertation Submitted to the
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TABLE OF CONTENTS

	<u>Page</u>
INTRODUCTION	1
REVIEW OF LITERATURE	3
Measure of Egg Production Efficiency	3
Selection Studies on Feed Efficiency	5
Egg-type chickens	5
Meat-type chickens	11
Beef cattle	13
Mice	14
Rats	15
MATERIALS AND METHODS	17
Origin of Flock	17
Management of the Flock	22
Record Collection	23
Selection Indexes and Statistical Methods	24
Responses to Selection	27
Heritability Estimates	29
Time Trends in the Control Lines	30
Drift Variance	30
Inbreeding	31
Analysis of Variance	31
RESULTS	33
Means	33
Genetic Responses	33
Body weight	42
Age at first egg	42

	<u>Page</u>
Rate of lay	59
Egg weight	59
Egg mass	59
Feed consumption	60
Feed efficiency	60
Feed Records	60
Selection Differentials	66
Regression of Response on Generation Number	70
Expected Genetic Response	72
Realized Heritabilities	72
Environmental Trends	75
Effective Population Size (N_e) and Drift Variance	78
Analysis of Variance	78
DISCUSSION	81
Selection Response	81
Variation in Selection Response	82
Expected Versus Realized Selection Responses	84
Feed Efficiency	87
SUMMARY	91
REFERENCES	92
ACKNOWLEDGMENTS	98
APPENDIX A: TABLES OF YEAR-GENERATION MEANS FOR VARIOUS TRAITS	99
APPENDIX B: SUPPLEMENT PAPER: SIGNIFICANCE OF BODY WEIGHT AS A PERFORMANCE PARAMETER	108
Abstract	110
Introduction	111

	<u>Page</u>
Results	113
Discussion	120
References	124

LIST OF TABLES

	<u>Page</u>
Table 1a. Mean body weight at 20 weeks (grams) for selected and control lines (pooled over replicates)	34
Table 1b. Mean body weight at 32 weeks (grams) for selected and control lines (pooled over replicates)	35
Table 1c. Mean age at first egg (days) for selected and control lines (pooled over replicates)	36
Table 1d. Mean rate of lay (percent) to 34 weeks of age for selected and control lines (pooled over replicates)	37
Table 1e. Mean egg weight (grams) at 32 weeks for selected and control lines (pooled over replicates)	38
Table 1f. Mean egg mass output (grams per day) during 30-34 weeks for selection and control lines (pooled over replicates)	39
Table 1g. Mean feed consumption (grams per day) during 30-34 weeks for selected and control lines (pooled over replicates)	40
Table 1h. Mean feed efficiency (egg mass/feed consumption) during 30-34 weeks for selected and control lines (pooled over replicates)	41
Table 2a. Cumulative genetic responses in 20-week body weight (grams)	43
Table 2b. Cumulative genetic responses 32-week body weight (grams)	44
Table 2c. Cumulative genetic responses for age at sexual maturity (days)	45
Table 2d. Cumulative genetic responses in rate of lay (percent)	46
Table 2e. Cumulative genetic response in egg weight (grams)	47
Table 2f. Cumulative genetic gain in egg mass (grams per day)	48

	<u>Page</u>
Table 2g. Cumulative genetic response in feed consumption (grams/day)	49
Table 2h. Cumulative genetic responses in feed efficiency (egg mass/feed consumption)	50
Table 3a. Genetic response in each generation for 20-week body weight (grams)	51
Table 3b. Genetic response in each generation for 32-week body weight (grams)	52
Table 3c. Genetic response in each generation for age at first egg (days)	53
Table 3d. Genetic responses in each generation for rate of lay (percent)	54
Table 3e. Genetic responses in each generation for egg weight (grams)	55
Table 3f. Genetic responses in each generation for egg mass (grams per day)	56
Table 3g. Genetic responses in each generation for feed consumption (grams per day)	57
Table 3h. Genetic responses in each generation for feed efficiency (egg mass/feed consumption)	58
Table 4a. Effect of feed record information (I_1-I_2) on body weight and age at first egg	62
Table 4b. Effect of feed record information (I_1-I_2) on rate of lay, egg weight and egg mass	63
Table 4c. Effect of feed record information (I_1-I_2) on feed consumption and feed efficiency	64
Table 5a. Selection differentials for body weight and age at first egg	67
Table 5b. Selection differentials for rate of lay, egg weight and egg mass	68

	<u>Page</u>
Table 5c. Selection differentials for feed consumption and feed efficiency	69
Table 6. Regression coefficients of cumulative selection responses for different traits on number of generations	71
Table 7. Expected genetic response per generation for individual traits based on population parameters	73
Table 8a. Regression coefficients (realized heritability) of cumulative response on cumulative selection differential	74
Table 8b. Estimates of heritability obtained from sire component of variance	76
Table 9. Regression coefficients of mean performance of control lines on number of generations	77
Table 10. Mean squares for various traits	79
Table A1. Mean body weight at 20 weeks of age (grams)	100
Table A2. Mean body weight at 32 weeks of age (grams)	101
Table A3. Mean age at first egg (days)	102
Table A4. Mean 32-week egg weight (grams)	103
Table A5. Mean rate of lay to 34 weeks of age (percent)	104
Table A6. Mean egg mass output at 32 weeks (grams per day)	105
Table A7. Mean feed consumption during 30-34 weeks of age (grams per day)	106
Table A8. Mean feed efficiency during 30-34 weeks of age (egg mass/feed consumption)	107
Table B1. Mean performance of body weight classes based on a phenotypic scale	114
Table B2. Mean performance of body weight classes based on a genetic scale	115
Table B3. Rate of lay for different body size classes averaged over two years in "winter" and "summer" records	118

	<u>Page</u>
Table B4. Phenotypic and genetic regression coefficients (pooled over populations) of different traits on body weight (unit = 100 g)	119

INTRODUCTION

Animal efficiency in biological terms is defined as feed input/product output (Dickerson, 1978). Input and output may also be expressed in protein and energy units. Efficiency of protein conversion is highly correlated with egg yield and had attained a level of about 20% in modern layer flocks producing 240 eggs per year per hen (Wilson, 1973). Higher total yields of egg mass could be obtained by: a) extending the laying period, b) increasing the intensity of laying, c) selecting for larger egg weight, and d) reducing age at first egg. Wilson (1973) suggested that efficiency of maximum protein conversion (about 36%) can be achieved the first year by hens coming into lay at four months of age and averaging 350 eggs in the first 365 days, and in the second laying year, producing 150 eggs after a short molt. At this production level, efficiency is nearly equal to that of a milking cow with first calving at two years and yielding 6800 kg milk in each of four lactations.

The measurement of biological efficiency has limited application because it ignores economic aspects of animal production. In a poultry enterprise, there is wide variation in costs of input and output as regards time and place. Therefore, the most useful measure of economic efficiency should include the cost of producing eggs or meat and the income derived from these products. In random sample egg laying tests, a popular measure of egg production efficiency has been "income over feed costs." Feed accounts for about two-thirds of the total cost of egg production in the United States. Thus, it seems logical to evaluate

feed record information in breeding experiments designated to genetically improve egg production efficiency.

The major objectives of this study are to 1) examine the efficacy of index selection to improve efficiency of egg production and 2) evaluate the significance of incorporating feed consumption data in a selection index.

REVIEW OF LITERATURE

Measure of Egg Production Efficiency

Nordskog et al. (1969) compared feed efficiency expressed in two ways: indirectly, from information on egg mass and body weight and directly, from information on egg mass, body weight, and feed consumption. Their results indicated that efficiency estimated indirectly is "statistically" more efficient.

Harris (1964) used the ratio egg mass/feed consumption for the improvement of feed efficiency in egg-type chickens. After two generations of selection, lines selected on this ratio showed statistically significant superiority in feed efficiency compared to a randombred control population.

Lee and Nordskog (1975) estimated the value of measuring feed consumption as a supplementary criterion of net performance. The study was based on data obtained from two sources: U.S. random sample test (USRST) and data from a test conducted by a private commercial Japanese company (GOTO Hatchery, Inc.). They computed a performance index (I6) with net income (NI) used as the dependent variable and taking egg rate, egg weight, body weight, mortality, maturity, and feed consumption as independent variables. A second performance index, I5, was computed in which feed consumption records were ignored. The correlations between NI and I6 were .820 and .824, respectively, and between NI and I5 were .818 and .822 in the USRST and GOTO data, respectively. They concluded that measuring feed consumption on individual birds did not

significantly improve the predictive value of a performance index if prior information is available on the other five variables. North (1980) suggested that egg mass output should be an adequate measure of efficiency and of income in a poultry enterprise.

Lin (1980) evaluated three selection criteria for the improvement of feed efficiency (i.e., body weight/feed intake) in mice. Selection criteria considered were: a linear approximation of the efficiency ratio, body weight gains, and a restricted selection index for increased body weight gain with feed intake constant. Direct selection on the linear approximation was 10 and 3% more efficient than selection on body weight gain and a restricted selection index, respectively.

In random sample tests, conducted in the U.S., income over feed and chick cost has been used to compare different commercial strains of chickens. This criterion corresponds to a performance index in which each trait is weighted according to its relative economic value.

For poultry breeding experiments, income over feed costs has been a useful measure of efficiency of egg production. It is expressed as a linear combination of income and cost-related traits. A selection index can be designed for genetic improvement but requires a priori information on phenotypic and genetic parameters for those traits included in the index.

Selection Studies on Feed Efficiency

Egg-type chickens

Reports on selection experiments on feed efficiency for egg production are few. No doubt, this is because of the labor cost of measuring feed consumption on individual birds. On the other hand, there seems little doubt that some improvement in feed efficiency has been brought about indirectly as a consequence of selection for more conventional production traits.

Selection for high rate of lay and small body size improves feed efficiency (Nordskog et al., 1972). Smaller sized hens, however, tend to lay smaller eggs, which is undesirable from a marketing standpoint.

Results of three generations of selection for feed conversion in egg-type chickens were reported by Lohman and Company (LSL Information, March, 1978). Responses were compared with selection on egg mass. Birds selected for feed conversion were lower in body weight, rate of lay, egg weight, daily egg mass, and feed consumption but higher in feed conversion. On the other hand, an income index expressed as the value of egg mass minus feed cost was better in the line selected on egg mass. Thus, even though feed conversion may be improved by selection for it, this may not lead to improvement in overall productivity in layer-type chickens.

Bordas and Merat (1981) reported on a selection experiment for a "residual" component of feed consumption. The latter was defined as

consumption adjusted for body weight, change in body weight and egg mass. For males, the residual component was defined as feed consumption adjusted for body weight and body weight change. Positive phenotypic correlations of the residual were found with wattle length, shank temperature, yolk to albumen ratio, broken eggs, and with shank length and width. For males, wattle length and shank temperature were also positively correlated with the residual. They suggested that selection for small appendages should improve the residual component of feed efficiency. In an earlier report (Bordas and Merat, 1974), hens consuming excessive amounts of water were less efficient.

Arboleda et al. (1976a,b) compared the relative efficiencies of four different selection indexes to improve income over feed costs. The indexes were: I_1 , containing information on body weight (BW), egg mass (EM), and feed consumption (FC); I_2 , containing information on BW and EM and supplemental information on the genetic correlation of FC with BW and EM; I_3 , using information on the partial phenotypic regressions of FC on BW and on EM; I_4 , maximizing net income on information only on BW and EM. A total of 1838 White Leghorn pullets were individually fed for two, 4-week periods separated by an 8-week interval. Parameters required for the selection indexes were estimated from the data. The theoretical expected gain in income over feed costs for the four different indexes, based on the values of heritability and correlations between BW, EM, and FC, were reported. The estimated heritabilities of the residual components of feed efficiency were .01 and .29 based on sire

and dam variance components, respectively. The residual was defined as feed consumption statistically adjusted for deviations in body weight and egg-mass output. They concluded that using either genetic correlations of feed consumption with body weight and egg mass (I_2) or phenotypic partial regression coefficients of feed consumption on body weight and egg mass (I_3) increased expected gain in income over feed costs by 3%, compared to I_4 , which used information only on body weight and egg mass. Using information on feed consumption, egg mass, and body weight in I_1 improved expected gains in income over feed costs by 9% compared to I_4 . Unfortunately, the experimental flock used for the study suffered an outbreak of Merek's disease and, because of this, the authors felt that the experiment should be repeated.

Wing and Nordskog (1982a,b) reported the results of an essentially replicated study to that reported by Arboleda et al. (1976a,b). Their estimate of the heritability of the residual component of feed efficiency was $.25 \pm .04$. They concluded that individual feed consumption records should enhance selection for efficiency of egg production. A comparison of the four selection indexes to improve income over feed costs was made and relative efficiencies of the different indexes in Leghorn populations, Q and R, is presented below:

Index	% Gain Relative to I_1		
	Q Population	R Population	Pooled
$I_1 = \text{NI:BW,EM}$	100	100	100
$I_2 = \text{IF:BW,EM,FC}$	115	128	117
$I_3 = \text{IF:BW,EM},r_G$	111	123	117
$I_4 = \text{IF:BW,EM,FC},\Delta\text{FC}=0$	89	125	115

where NI = net income, IF = income over feed cost, r_G = genetic correlation of FC with BW and EM, and ΔFC = genetic change in feed consumption.

I_1 included information only on BW and EM to improve net income. I_2 , I_3 , and I_4 were designed to improve income over feed costs. I_2 required information on all three traits. I_4 is similar to I_2 except that feed intake is restricted to zero change. I_3 required information on BW, EM, and genetic correlations of FC with BW and EM. The pooled results indicated that including feed consumption records or estimates of the genetic correlation of FC with BW and EM is expected to improve efficiency by 17%, compared to an index including only BW and EM (I_1). A restricted selection index, I_4 ($\Delta\text{FC} = 0$), was estimated to be 15% more efficient than I_1 , although the results in the two populations studied were not in good agreement.

Fairfull and Gowe (1979) examined feed consumption and feed efficiency in selected and control strains developed under long-term selection using "retrospective" indexes. They found that selection of rate of

egg production and egg numbers effectively improved the ratios of feed consumed to egg mass. The selected strains were also superior to controls in feed efficiency corrected for initial body weight and gain. A large portion of the variation in feed consumption was accounted for by initial body weight, weight gain (growth), and egg yield.

Harris (1964) reported the results of two generations of selection on the ratio of egg mass to feed consumption (EM/FC) in layer-type chickens. The selected line was significantly more efficient compared to the unselected control line. Selection on this ratio reduced body size which would enhance the ratio, but egg number and size were not reduced from selection.

Recent reports present some evidence that single genes influence efficiency of egg production. French and Nordskog (1973) produced reciprocal crosses of a large body line (B) and a small body line (C) segregating for the sex-linked dwarf-gene (*dw*). Their results showed that *dw* reduced body size about 30%, decreased egg weight by 8%, delayed sexual maturity by 7 days, and lowered egg production by about 5%. From their data it was possible to match cross line pullets of approximately the same body weights (i.e., 1.7 kg vs. 1.5 kg) but with one group carrying *dw* and the other carrying the normal allele. The dwarf pullets laid 11% fewer eggs and produced 12% less egg-mass per unit of feed consumed than did the normals. The feed conversion ratios of egg mass produced per gram of feed consumed were .38 g for the dwarfs and .43 g for the normals. They concluded that "mini-chickens," produced by

conventional selection, would be at least equal to and probably superior to the dwarf mini. However, about 7 generations of selection would be required to reduce body size to the equivalent of a dwarf mini-pullet.

Merat et al. (1979) studied the effect of color genes on egg mass and feed intake. They measured individual feed consumption records from 8 to 11 months of age for three, 28-day periods on 103 and 87 pairs of sibs differing in genotypes at the dominant white (I) and silver (S) plumage loci, respectively. Hens having genotype i^+i^+ (colored plumage) had significantly higher egg mass, feed intake, and feed intake statistically adjusted for body weight, body weight change, and egg mass compared to Ii^+ (absence of color) control hens. Females carrying the S gene produced greater egg mass, feed intake, and residual feed intake over the control hens.

Merat and Bordas (1979) reported on the influence of the pea-comb gene on feed efficiency. At normal temperature (mean 20°C), feed efficiency adjusted was significantly higher and egg size was significantly smaller in hens that lacked the pea comb gene. At the high temperature (27°C during 10 hours dark and 34°C during 14 hours light periods), feed consumption and feed efficiency were significantly higher for the single comb (non-pea) hens. The pea-comb gene modifies comb morphology as well as reduces comb size and decreases wattle size. The reduction of surface area of these appendages evidently reduced heat loss and, in turn, reduced the energy required to maintain body temperature.

Meat-type chickens

Pym and Nicholls (1979) reported the results of five generations of a selection study in meat-type chickens. The selection criteria used in four lines of chickens were: line W, selected for high body weight; line F, selected for high feed consumption (5 to 9 weeks); line E, selected for low feed conversion ratio; and line C, a randombred control. Weight-gain was increased in all selected lines with the largest in W followed by F and E. Feed consumption was also higher in F and W. Line E showed no change in feed consumption but feed conversion improved. Line F was consistently lower in conversion and line W was higher than the control. Realized heritability estimates of weight gain, feed consumption, and feed conversion were $.37 \pm .04$, $.44 \pm .05$, and $.21 \pm .04$, respectively. They concluded that body weight alone is not a wholly sufficient criterion to improve feed efficiency. Body weight is expected to increase only slightly from selection for improved feed conversion. They recommended that selection on an index, based on body weight and feed efficiency, should improve income.

Wilson (1969) selected on feed efficiency (feed consumption/weight gain) and on high daily gain from 5 to 10 weeks of age in two lines. His results indicated that direct selection was approximately three times more efficient than indirect selection, as a correlated response to feed efficiency, in increasing daily gain. Feed consumption increased by 133 g per bird in the line selected for daily gain but no change was found in the line selected for feed efficiency.

Guill and Washburn (1974) presented the results of three generations of selection for feed efficiency in a population of chickens selected previously for growth rate. Two lines were selected for high feed conversion (HL) and two were selected for low feed conversion (LL). One line pair (HLWK, LLWK) was selected so that body weight was held constant over generations, while in the other pair (HLWV, LLWV) body weight was allowed to vary. In three generations of selection, the units of feed required for a unit of gain increased by .12 g in HLWV and .08 g in the HLWK line. In the low feed conversion lines, the units of feed required for a unit of gain decreased .11 in LLWK and .07 in LLWV. In the randombred population, with no previous selection for growth, as much progress from selection in lowering the feed conversion ratio was made in one generation of selection as was made in three generations of the growth-selected populations. They also observed that one generation of selection for improved feed conversion in the randombred population reduced feed consumption and improved feed conversion ratio significantly.

Singh (1976) reported the results of two generations of selection on eight-week body weight and feed conversion ratio (feed consumed/gain in weight) during an interval from 5 to 10 weeks in two lines, G and FE, respectively. A randombred line C served as a control. Average genetic responses per generation of 29.1 and 22.5 g were observed for eight-week body weight in G and FE, respectively. Corresponding changes in feed efficiency were -.034 and -.061 in G and FE, respectively. He

predicted that index selection (a linear combination of body weight and feed efficiency) should yield the best results in improving income over feed cost, although selection on feed efficiency alone would only be 4% less. Selection on eight-week body weight alone was predicted to be only 34% efficient as index selection.

Beef cattle

Swiger et al. (1965) used different selection indexes based on a combination of traits or on single traits for the improvement of total net merit. They concluded that feed consumption could be omitted from an index containing measures of growth rate with no loss of efficiency of selection. Selecting for final weight alone was expected to be 90% as effective as an index combining preweaning and postweaning gain with feed consumption and an accurate measure of fat thickness for selection for net merit.

Koch et al. (1963) studied three measures of feed efficiency in beef cattle: feed consumption adjusted for differences in gain; gain adjusted for differences in feed consumption; and the ratio of gain to feed consumed. Efficiency expressed as gain adjusted for differences in feed consumption (i.e., deviations from the regression of gain on consumption) was judged the most accurate and the heritability was highest of the three measures studied. Their results indicated selecting for gain should lead to an increase in both efficiency and feed consumption. Feed efficiency and weight gains were expected to improve with selection on feed efficiency without changing feed consumption.

Selection for feed consumption should increase feed intake and daily gain, but would lead to no improvement in feed efficiency.

Mice

Sutherland et al. (1970) developed four lines of mice from F_2 's of highly inbred lines. After nine generations of selecting these lines for rate of gain between 4 and 11 weeks, the selection criterion was modified. For the next 12 generations, line 1 was selected for feed efficiency, line 2 for feed consumption and line 3 for rate of gain. After 12 generations on the modified selection scheme, rate of gain continued to increase in all three lines. Gains were most rapid in the line selected for feed efficiency. The regressions of gain on generation number were $.75 \pm .11$, $.40 \pm .10$, and $.38 \pm .11$ g in the lines selected for feed efficiency, feed consumption, and rate of gain, respectively. Feed consumption continued to increase in all lines, the regression on generation number were $1.99 \pm .94$, $3.11 \pm .71$, and $1.50 \pm .92$ g in the feed efficiency, feed consumption, and rate of gain lines, respectively. Feed efficiency (gain in weight/feed consumed), likewise, improved; the regressions in the corresponding lines were $.003 \pm .007$, $.0006 \pm .0006$, $.0013 \pm .0005$, respectively.

Roberts et al. (1979) selected for feed efficiency (weight gain/feed intake) in the mouse over two test periods and two feeding regimes. Test periods were between 3 to 5 weeks and 5 to 7 weeks of age; feeding regimes included ad libitum and a fixed amount of feed fed for a two-day interval. After 8 generations of selection, feed efficiency improved

by almost 20%. Improvement in lines selected at a later age was smaller. Although feed intake did not change under either feeding regime, an increase in weight gain was observed.

Roberts (1981) reported the results of selection for large and small size in mice. Selection for large size increased both intake and efficiency and selection for small size decreased both. This held true for comparisons made at the same age or at the same weight. Feed intake and efficiency contributed almost equally to the selection response in growth rate. Even though mice ate the same amount after suspending feed restriction as nonrestricted controls, feed was converted more efficiently than mice which had been full-fed throughout.

Rats

Morris et al. (1933) selected two lines of rats, divergently, for efficiency of feed utilization. The low efficiency line was about 40% less efficient than the high efficiency line and was more variable. They also observed that sexes differed in efficiency. Females consumed more dry matter per unit of gain than males. Chemical analysis of the carcass showed that females were higher in dry matter, ash, and fat, but lower in nitrogen and fat-free dry matter. No relationship was found between dry matter consumed and length of the intestines in growing rats.

Wang et al. (1979) conducted 14 generations of family selection for growth and feed conversion in rats. In generation 15, the litter was divided and assigned to two environments, bulk (B) and tube (T)

cages. Growth and feed conversion were compared with control lines under the two feeding environments. The selected lines were 20 and 15% higher in daily gain under environment B and 27 and 18% higher under environment T. In feed efficiency, the selected lines were 13 and 11% better than the controls.

MATERIALS AND METHODS

Origin of Flock

Two populations of Single Comb White Leghorns used in this study are designated as Q and R. Population Q is derived originally from three Leghorn lines, A, D, and G, which have undergone long-term selection for various production traits (Nordskog *et al.*, 1974). Line A was selected for high rate of lay to 32 weeks of age for 11 generations based on an index including records on individuals, full sibs and half sibs (Osborne, 1957). Line D had also been selected for 11 generations for high egg weight. As egg production and egg size are sex limited traits, males in the corresponding lines were selected by the sib test. In 1960, line G was formed by crossing line C (selected for low body weight) and line D. Line G underwent seven generations of selection for high egg weight (EW) and low body weight (BW) using the index, $I = 10BW - EW$, where BW is in pounds and EW in grams. The foundation matings for population Q consisted of lines D x A and G x A. Lines S1 and S2, obtained from Hyline Incorporated, Des Moines, Iowa, were used to constitute population R (Nordskog *et al.*, 1973). Population R is segregating for the B blood group alleles B^2 , B^{13} , B^{14} , B^{19} , and B^{21} .

In 1969, population Q was subdivided into three lines, Q1, Q2, and Q3. Similarly, population R was subdivided into four sublines, R1, R2, R3, and R4. Sublines were subjected to different selection criteria as follows:

Selection criteria	Q lines	R lines
EP	Q1	R1
$EW^{1.50}/BW^{.75}$	Q2	R2
$EP*EW^{1.50}/BW^{.75}$	Q3	R3
Control	RCC	R4

where EP = rate of egg production and RCC = randombred Cornell control.

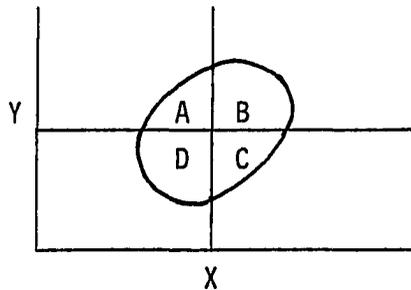
In each of the six selected lines, selection was based on the Osborne index, which included information from half-sibs, full-sibs, and on individual performance. Males were selected by the sib test; i.e., from those families having the largest number of selected pullets. Each sire was mated to two full-sibs, two half-sibs, and four non-sibs. This greatly increased the variance in inbreeding within generations, which made it possible to study the effect of inbreeding in addition to selection studies. This experiment was terminated in 1976, after having completed 7 and 6 generations of selection in populations Q and R, respectively. Populations Q and R had mean inbreeding coefficients of 13.8 and 6.4%, respectively (Nordskog and Hardiman, 1979).

Birds from the 1976 hatch were used in the foundation matings. The following two measurements (X and Y) were made on each bird:

$$X = \frac{EP \cdot EW^{1.50}}{BW^{.75}} \approx \frac{EM}{BW} \qquad Y = \frac{EM}{FC}$$

where EM and FC represent egg mass and individual feed consumption, respectively; symbols other than EM and FC have already been defined.

A bivariate distribution formed on the X and Y scales, was then truncated on both axes giving four doubly truncated segments, A, B, C, and D, as follows:



The foundation population for the lines to be used for indirect selection (X) consisted of C + 1/2 B and for direct selection (Y) consisted of A + 1/2 B. Birds in quadrant D were discarded. The foundation matings consisted of 20 males and 120 females selected equally from types X and Y. Thus, the total foundation breeding population consisted of 80 males and 480 females. In 1977, two new lines, A and B, were formed within the population Q and two lines, C and D, were formed within the population R. In 1977, lines A and C were selected on the ratio EM/BW and lines B and D were selected on the ratio EM/FC, both at 32 weeks of age.

In 1978, six sublimes were formed from the A and B lines and, likewise, six sublimes were formed from the C and D lines. At this point in time, a selection experiment was designed for the direct and

indirect measures of feed efficiency using two indexes:

$$I_1 = .42 \text{ BW} + 2 \text{ EM} - \text{FC}$$

$$I_2 = .42 \text{ BW} + \text{EM}$$

where BW = body weight in grams at 32 weeks, EM = daily egg mass output in grams over an interval of 30 to 34 weeks of age, and FC = daily feed consumption in grams during the 30 to 34 week age period.

I_1 contains information on BW, EM, and FC; FC information is omitted in I_2 . This was intended to measure the importance of adding actual feed records to information on BW and EM for the improvement of egg production efficiency. Phenotypic and genetic parameters, used to solve the indexes for the weighing coefficients, were taken from the literature. I_1 and I_2 , in the different lines, are:

Population	Line	Sub-lines	Selection criteria
Q	$\left\{ \begin{array}{l} \text{A} \\ \text{B} \end{array} \right.$	A ₁ , A ₂ A ₃	I ₁ Control
		B ₁ , B ₂ B ₃	I ₂ Control
R	$\left\{ \begin{array}{l} \text{C} \\ \text{D} \end{array} \right.$	C ₁ , C ₂ C ₃	I ₁ Control
		D ₁ , D ₂ D ₃	I ₂ Control

Each line was thus subdivided into two selected lines (replicates) and a control line. The control line permitted the measurement of response in the selected populations. The purpose of the replicated subline was to permit the measurement of random genetic drift. Each selected, as well as each control line, has been carried by 8 sires each mated to 6 dams, with the restriction that matings between full-sibs and half-sibs are avoided. Parents in each line were selected on the sire family means.

The selection indexes were revised in 1980, as it was felt that body weight had been overemphasized in the original indexes. The revised economic values and parameters of BW, EM, and FC were used to solve the normal equations for the weighting coefficients. The revised economic values used for BW, EM, and FC are .022, 23.0, and 4.32, respectively (Wing and Nordskog, 1982b). These were calculated by assuming a 60 g egg is worth 5¢; revenue from a spent hen is worth 10¢/lb, and feed costs are 7¢/lb. An egg production cycle of 280 days was used in the calculations. The revised indexes, thus obtained, had a lower weighting coefficient for BW as indicated below:

$$I_1 = .0297 \text{ BW} + 2.7698 \text{ EM} - .9596 \text{ FC}$$

$$I_2 = .0778 \text{ BW} + 2.1231 \text{ EM}$$

The populations for the present study have undergone 4 generations of selection on the indexes.

Management of the Flock

Chicks were handled in two separate hatches, separated by an interval of four weeks. This facilitated the work load specifically for measuring and recording the individual feed consumption. Each sire was mated to 6 dams in each line by artificial insemination. Hatching eggs were collected over a two-week period and were stored at 65⁰F (19⁰C) and 60 to 65% relative humidity. Eggs were then set in a Jamesway 252 incubator for hatching. After 18 days of incubation, the eggs were tested for fertility and transferred to the hatcher compartment of the incubator. The incubators were disinfected regularly between hatches.

All day-old chicks were pedigreed, wing banded, and vaccinated against Marek's disease. In each hatch, pullets and one male chick from each dam family were saved and transferred to the brooder house at the Poultry Research Center. Brooding pens were provided with infrared lamp brooders for supplemental heat. At eight weeks of age, chicks were debeaked and vaccinated for Fowl Pox. Vaccine for New Castle disease and Infectious Bronchitis was administered in the drinking water at four days, four weeks, and four months of age. Birds were dewormed at four weeks, ten weeks, and sixteen weeks of age by adding Piperazine to the drinking water. Chicks were provided with 8 hours of light per day until 20 weeks of age. All the pullets were housed randomly at 20 weeks in the individual cages (measuring 10 x 18 x 14 inches; .254 x .457 x .356 m) in the laying house. A layer ration and

water were provided ad libitum throughout the laying period. Twelve hours of light, including day light, were provided from 20 weeks until peak egg production was reached. An additional hour of light was added each month until 16 hours of light per day was attained. Dusting the birds with Sevin or Malathion was practiced to control Northern Fowl Mites at the time of housing and as required during the laying cycle.

Record Collection

Body weight of individual birds was recorded at 20 weeks of age. Part-time trapnesting, four days (Monday through Thursday) in each week, was practiced. Age at first egg, in days, was recorded on each pullet. All birds were fed individually for four weeks, starting at about 30 weeks of age. Body weight measurements were made at the mid-point of the feeding period; i.e., at about 32 weeks. Eggs laid during the third week of the feeding period were weighed and recorded for each pullet. Rate of lay was computed for each pullet from first egg to the end of the feeding period; i.e., to 34 weeks of age. Daily egg mass output was determined on each pullet as the product of rate of lay and average egg weight. Feed consumption per day was determined as the average of feed consumed over the four week feeding period. Feed efficiency was expressed as the ratio of egg mass to feed consumption.

During the feeding test, birds were fed in individual hoppers converted from two cardboard, half-gallon milk cartons (Arboleda et al., 1976a). Feeders were placed adjacent to each other in the metal trough, such that birds could not reach neighboring feeders. Feed wastage

seemed not to be a serious problem in this system (Wing, 1981). Feed not consumed, including feed spilled into the metal feed trough, was weighed back to calculate actual feed consumed.

Selection Indexes and Statistical Methods

Smith (1936) and Hazel (1943) have developed the theory of selection indexes designed to improve, simultaneously, several traits based on their relative importance. In chickens, net returns depend on several traits. In this study, BW, EM, and FC were used in the indexes. Revenue in the commercial poultry business is derived from the sale of eggs and spent hens. Feed constitutes approximately 70% of the total cost of production in a poultry enterprise. Thus, FC records were also included in the index. The indexes used in the two experimental populations were:

$$I_1 = b_1BW + b_2EM + b_3FC$$

$$I_2 = b'_1BW + b'_2EM$$

where b_1 , b_2 , and b_3 are the weighting coefficients (b values) for BW, EM, and FC, respectively, in I_1 and b'_1 and b'_2 are weighting coefficients for I_2 .

The weighting coefficients in these indexes are calculated such that the correlation between the index and the respective aggregate genetic merit is maximized. The aggregate genetic merit for I_1 and I_2 are:

$$H_1 = a_1G_1 + a_2G_2 + a_3G_3$$

$$H_2 = a_1G_1 + a_2G_2$$

where a_1 , a_2 , and a_3 are the relative economic values for BW, EM, and FC, respectively and G_1 , G_2 , and G_3 refer to the "true breeding value" for BW, EM, and FC, respectively. Thus, I_1 is expected to improve income over feed cost and I_2 is expected to improve net income. The above equations, expressed in matrix form are:

$$I = b'P$$

$$H = a'G$$

where b and P represent column vectors of weighting coefficients and phenotypic values, respectively, of the traits in the index and a and G are the column vectors for economic values and breeding values of traits.

To maximize the correlation between the index (I) and the aggregate genetic merit (H) requires the normal equation:

$$Pb = Ga$$

where P is the matrix of phenotypic variances and covariances of traits in the index and G denotes the corresponding genetic variance-covariance matrix.

The vector b is then solved as:

$$b = P^{-1}Ga$$

where P^{-1} represents the inverse of phenotypic variance-covariance (P) matrix.

Thus, the normal equations for I_1 and I_2 are:

$$\begin{array}{l} \text{BW} \\ \text{EM} \\ \text{FC} \end{array} \begin{array}{c} \text{BW} \quad \text{EM} \quad \text{FC} \\ \left[\begin{array}{ccc} P_{11} & P_{12} & P_{13} \\ P_{21} & P_{22} & P_{23} \\ P_{31} & P_{32} & P_{33} \end{array} \right] \end{array} \begin{array}{c} \left[\begin{array}{c} b_1 \\ b_2 \\ b_3 \end{array} \right] \end{array} = \begin{array}{c} \left[\begin{array}{ccc} G_{11} & G_{12} & G_{13} \\ G_{21} & G_{22} & G_{23} \\ G_{31} & G_{32} & G_{33} \end{array} \right] \end{array} \begin{array}{c} \left[\begin{array}{c} a_1 \\ a_2 \\ a_3 \end{array} \right] \end{array}$$

$$\begin{array}{l} \text{BW} \\ \text{EM} \end{array} \begin{array}{c} \text{BW} \quad \text{EM} \\ \left[\begin{array}{cc} P_{11} & P_{12} \\ P_{21} & P_{22} \end{array} \right] \end{array} \begin{array}{c} \left[\begin{array}{c} b'_1 \\ b'_2 \end{array} \right] \end{array} = \begin{array}{c} \left[\begin{array}{cc} G_{11} & G_{12} \\ G_{21} & G_{22} \end{array} \right] \end{array} \begin{array}{c} \left[\begin{array}{c} a_1 \\ a_2 \end{array} \right] \end{array}$$

The genetic change expected in the i^{th} trait based on the population parameter is (Cunningham, 1969):

$$\Delta G_i = D \frac{b'G_i}{\sqrt{b'Pb}}$$

where D is the selection differential in standardized units and G_i is a column of the G matrix corresponding to the i^{th} trait.

The above equation is valid if selection is based on the individual index values. For family selection, the prediction equation is (Falconer, 1981):

$$\Delta G_i = D \frac{b'G_i}{\sqrt{b'Pb}} \cdot \frac{1 + (n-1)r}{\sqrt{n[1 + (n-1)rh^2]}}$$

where n is the number of individuals in the sire family and r is the correlation between family members. A sire family consists of full- and half-sibs, such that the value of r is between .5 and .25. It is calculated by using the expression:

$$.25 \left[1 + \frac{(k-1)}{(n-1)} \right]$$

where k and n are the average number of offspring per dam and per sire, respectively. For the present case, $r = .286$.

Responses to Selection

The mean performance for any trait in the selected line (\bar{S}_i) in the i^{th} generation is represented as the combined effect of selection and environment:

$$\bar{S}_i = R_i + E_i$$

where R_i is cumulative genetic response to selection over i generations and E_i is the cumulative environmental effect over i generations. Control lines were assumed to be genetically constant if no selection is practiced. Differences between control generation means would reflect purely environmental effects. Therefore, the mean of the control line (\bar{C}_i) in the i^{th} generation is assumed to be the cumulative effect

of environmental changes:

$$\bar{C}_i = E_i$$

The difference between the selected and unselected lines estimates the cumulative effect of selection:

$$\hat{R}_i = \bar{S}_i - \bar{C}_i$$

The cumulative effect of selection in the $(i-1)^{\text{th}}$ generation is the difference between the selected and control lines:

$$\hat{R}_{i-1} = \bar{S}_{(i-1)} - \bar{C}_{(i-1)}$$

The difference between the cumulative effects of selection between the i^{th} and $(i-1)^{\text{th}}$ generations is the expected genetic response observed in the i^{th} selected generation:

$$\Delta \hat{R}_i = \hat{R}_i - \hat{R}_{i-1}$$

where $\Delta \hat{R}_i$ represents the selection response gained in the i^{th} generation.

Mean values of genetic response by generation can be estimated as the regression of cumulative response (R_i) on generations:

$$R_i = b_0 + bX_i + e_i$$

where b_0 is the intercept, b refers to regression of cumulative response on the number of generations (X_i), and e is random error component. The

regression coefficient (b) represents the effect of selection per generation.

Heritability Estimates

Realized heritability (h_R^2) is estimated from a selection experiment as:

$$h_R^2 = \frac{R}{D}$$

where R and D denote the selection response and the selection differential, respectively. The latter is the difference between the mean of the selected parents and the population mean. A least square value of h_R^2 is obtained by the regression of the cumulative response on the cumulative selection differential.

Heritability estimates were also calculated by sib analysis using the following model:

$$Y_{ijkl} = \mu + LY_i + S_{ij} + D_{ijk} + e_{ijkl}$$

where Y_{ijkl} is the value of a trait for the l^{th} progeny from the k^{th} dam mated to the j^{th} sire from the i^{th} line-year subclass, μ is overall mean of the trait, LY_i is fixed effect of the i^{th} line-year subclass, S_{ij} is random effect of the j^{th} sire within the i^{th} subclass, D_{ijk} is random effect of the k^{th} dam mated to the j^{th} sire within the i^{th} subclass and e_{ijkl} is random error component. Sire component of variance was used to estimate the heritability for various traits.

Time Trends in the Control Lines

Genetic x environment interactions may be an important source of variance in response (Hill, 1972a,b) when control lines are measured along with the selected lines. A control line is assumed to be genetically constant over generations. Thus, the regression of the mean performance of control lines on number of generations would reflect environmental trends. It is estimated as:

$$\bar{C}_i = b_0 + bX_i + e_i$$

where \bar{C}_i is the mean of the control line, b_0 is the intercept, b is the regression of the control line performance on number of generation (X_i), and e_i is a random error component.

Drift Variance

Hill (1971; 1972a,b,c,d) showed that random drift may be a source of variance of response which accumulates over generations. He derived a formula to estimate drift variance (σ_D^2) and sampling error variance (σ_e^2) from a priori information on population parameters:

$$\sigma_D^2 = \frac{h^2(1 - h^2)}{N_e} \cdot \sigma^2$$

$$\sigma_e^2 = \frac{h^2(1 - h^2)}{M} \cdot \sigma^2$$

where h^2 is heritability of the trait, σ^2 is the phenotypic variance, N_e is the effective population size, and M is average size of the tested population per generation.

The ratio of σ_D^2/σ_e^2 measures the relative magnitude of drift variance and is estimated by M/Ne .

Inbreeding

Although full-sib and half-sib matings were avoided, closed flock breeding populations undergo some inbreeding which can be estimated from the effective population size (Ne) as:

$$\frac{1}{Ne} = \frac{1}{4M} + \frac{1}{4F}$$

where M and F denote the average number of males and females used as parents per generation. The rate of inbreeding (ΔF) per generation is:

$$\Delta F = \frac{1}{2Ne}$$

Analysis of Variance

The data from the four selected generations were subjected to analysis of variance using the following model:

$$Y_{ijkl} = \mu + G_i + P_j + SC_k + (GP)_{ij} + (GSC)_{ik} + (PSC)_{jk} \\ + (GPSC)_{ijk} + e_{ijkl}$$

where Y_{ijkl} is l^{th} observation belonging to k^{th} selection criteria, j^{th} population, and i^{th} generation; μ is overall mean; G_i is effect associated with i^{th} generation; P_j is effect peculiar to j^{th} population; SC_k is effect due to k^{th} selection criteria; $(GP)_{ij}$, $(GSC)_{ik}$, and

$(PSC)_{jk}$ are the two-way interactions involving generations, populations, and selection criteria; $(GPSC)_{ijk}$ is the three-way interaction; $e_{ijk\ell}$ is random error component.

RESULTS

Means

Year-generation means for traits and their standard errors (Tables A1 through A8) are presented in Appendix A. The mean performance of the selected lines, pooled over replicates, and their corresponding control is given in Tables 1a through 1h. Differences between generations reflect both selection and yearly environmental effects. The selection differential in the control line was set near zero. Generation differences in the control group should reflect only environmental error effects. Moreover, because the selected and control groups have common origins, the selection effect should be free of bias due to genetic and environment interaction. Birds of both the selected and control groups, being reared in a contemporary environment, permitted the estimation of genetic gains as the deviation of the selected from the control lines. Performance of the different groups would also have been subjected to random drift and inbreeding effects. Because effective population size was intentionally kept the same in both the selected and unselected lines, any bias due to inbreeding, other than random drift, would be eliminated. The later, however, can be reduced by averaging over replications and populations.

Genetic Responses

Genetic response was estimated as the difference between the selected line and its contemporary control. The estimates, however,

Table 1a. Mean body weight at 20 weeks (grams) for selected and control lines (pooled over replicates)

Population	Selected criteria	Generations				
		0	1	2	3	4
Q	I ₁	1207.0 ± 7.3	1190.2 ± 7.6	1343.3 ± 8.5	1269.0 ± 7.5	1270.2 ± 7.9
	Control		1102.2 ± 8.9	1239.1 ± 11.1	1192.7 ± 9.7	1127.4 ± 10.4
	I ₂	1231.8 ± 9.0	1161.9 ± 7.9	1333.2 ± 9.3	1277.0 ± 9.8	1325.3 ± 8.9
	Control		1138.2 ± 9.8	1249.7 ± 10.9	1223.4 ± 12.0	1199.1 ± 10.4
R	I ₁	1183.5 ± 5.7	1100.9 ± 6.5	1228.9 ± 9.1	1208.0 ± 7.8	1218.6 ± 8.2
	Control		1059.0 ± 7.7	1213.6 ± 12.1	1135.0 ± 9.6	1195.0 ± 11.5
	I ₂	1181.9 ± 6.0	1088.3 ± 6.8	1211.0 ± 7.7	1160.6 ± 7.0	1197.6 ± 7.4
	Control		1062.1 ± 7.6	1140.5 ± 8.7	1091.4 ± 8.4	1100.4 ± 8.1
Pooled	I ₁	1195.2 ± 6.5	1144.5 ± 5.3	1282.8 ± 6.8	1240.4 ± 5.6	1248.5 ± 5.9
	Control		1081.5 ± 6.1	1226.8 ± 7.9	1164.7 ± 7.0	1160.0 ± 8.0
	I ₂	1206.8 ± 7.6	1127.6 ± 5.5	1271.8 ± 6.6	1215.2 ± 6.5	1261.0 ± 6.5
	Control		1096.4 ± 6.5	1200.0 ± 7.8	1154.5 ± 8.3	1152.8 ± 7.4

Table 1b. Mean body weight at 32 weeks (grams) for selected and control lines (pooled over replicates)

Population	Selection criteria	Generations				
		0	1	2	3	4
Q	I ₁	1642.2 ± 11.0	1608.0 ± 12.0	1699.7 ± 13.4	1585.8 ± 10.0	1613.2 ± 10.9
	Control		1443.9 ± 15.9	1518.8 ± 15.0	1462.2 ± 12.7	1443.0 ± 17.5
	I ₂	1703.2 ± 14.7	1566.0 ± 13.1	1731.0 ± 13.1	1682.1 ± 13.6	1811.5 ± 13.9
	Control		1483.2 ± 14.5	1570.8 ± 15.2	1523.4 ± 12.7	1549.3 ± 12.9
R	I ₁	1628.2 ± 11.1	1549.1 ± 11.6	1671.6 ± 13.2	1616.3 ± 14.5	1724.2 ± 16.2
	Control		1460.4 ± 13.5	1552.5 ± 15.1	1469.6 ± 17.1	1598.3 ± 18.3
	I ₂	1645.1 ± 10.5	1538.2 ± 12.2	1612.9 ± 12.0	1562.1 ± 12.0	1663.1 ± 13.3
	Control		1488.1 ± 11.6	1493.9 ± 15.2	1394.0 ± 13.7	1473.4 ± 13.2
Pooled	I ₁	1635.2 ± 11.0	1578.8 ± 8.4	1685.0 ± 9.4	1599.5 ± 8.5	1657.6 ± 9.6
	Control		1451.3 ± 10.6	1534.6 ± 10.7	1465.6 ± 10.4	1517.1 ± 13.8
	I ₂	1674.1 ± 12.8	1553.8 ± 9.1	1671.7 ± 9.2	1621.2 ± 9.5	1739.4 ± 10.3
	Control		1485.7 ± 9.2	1536.0 ± 11.0	1457.5 ± 10.2	1514.5 ± 9.6

Table 1c. Mean age at first egg (days) for selected and control lines (pooled over replicates)

Population	Selection criteria	Generations				
		0	1	2	3	4
Q	I ₁	165.8 ± 1.0	171.6 ± 1.1	173.4 ± 1.0	180.4 ± 0.9	179.0 ± 1.1
	Control		169.2 ± 1.5	169.5 ± 1.3	176.0 ± 1.3	168.1 ± 1.3
	I ₂	166.1 ± 1.2	170.5 ± 1.2	174.6 ± 0.9	184.0 ± 1.1	177.8 ± 1.3
	Control		169.9 ± 1.7	172.9 ± 1.3	181.0 ± 1.8	178.8 ± 1.8
R	I ₁	173.7 ± 0.9	188.9 ± 1.2	183.5 ± 1.0	189.2 ± 1.2	182.6 ± 1.3
	Control		180.7 ± 1.8	171.3 ± 1.3	176.0 ± 1.7	166.7 ± 1.3
	I ₂	177.4 ± 1.2	183.3 ± 1.4	177.0 ± 1.0	184.2 ± 1.1	176.2 ± 1.1
	Control		185.9 ± 1.8	178.4 ± 1.5	186.6 ± 1.5	177.9 ± 1.9
Pooled	I ₁	170.0 ± 0.9	180.2 ± 0.9	178.7 ± 0.7	184.3 ± 0.7	180.4 ± 0.8
	Control		174.3 ± 1.2	170.4 ± 0.9	176.0 ± 1.0	167.4 ± 0.9
	I ₂	171.7 ± 1.2	176.1 ± 1.0	175.8 ± 0.7	184.1 ± 0.7	177.0 ± 0.8
	Control		178.5 ± 1.3	175.4 ± 1.0	183.9 ± 1.2	178.4 ± 1.3

Table 1d. Mean rate of lay (percent) to 34 weeks of age for selected and control lines (pooled over replicates)

Population	Selection criteria	Generations				
		0	1	2	3	4
Q	I ₁	75.5 ± 0.8	78.7 ± 0.9	78.8 ± 0.9	78.7 ± 0.7	78.7 ± 0.9
	Control		79.4 ± 1.1	82.7 ± 0.7	80.4 ± 1.0	76.7 ± 1.4
	I ₂	74.3 ± 1.0	78.0 ± 0.9	78.5 ± 0.7	77.6 ± 1.0	78.7 ± 0.8
	Control		77.9 ± 1.4	77.8 ± 1.0	78.0 ± 0.9	76.4 ± 1.4
R	I ₁	77.9 ± 0.8	78.0 ± 0.9	76.4 ± 1.0	74.7 ± 1.2	76.4 ± 1.4
	Control		74.8 ± 1.8	81.1 ± 1.1	76.7 ± 1.7	80.4 ± 1.8
	I ₂	78.9 ± 0.8	79.5 ± 1.1	80.6 ± 0.9	74.5 ± 1.3	79.0 ± 0.9
	Control		77.9 ± 1.3	80.1 ± 1.2	70.6 ± 1.7	80.4 ± 1.6
Pooled	I ₁	76.7 ± 0.8	78.4 ± 0.6	77.6 ± 0.7	76.9 ± 0.7	77.8 ± 0.7
	Control		77.4 ± 1.0	81.9 ± 0.6	78.7 ± 0.9	78.5 ± 1.1
	I ₂	76.6 ± 0.9	78.6 ± 0.8	79.5 ± 0.6	76.0 ± 0.8	78.9 ± 0.6
	Control		77.9 ± 0.9	78.9 ± 0.8	74.2 ± 1.0	78.3 ± 1.1

Table 1e. Mean egg weight (grams) at 32 weeks for selected and control lines (pooled over replicates)

Population	Selection criteria	Generations				
		0	1	2	3	4
Q	I ₁	52.7 ± 0.2	53.3 ± 0.2	55.0 ± 0.3	54.7 ± 0.2	55.0 ± 0.2
	Control		52.4 ± 0.4	52.3 ± 0.3	52.5 ± 0.4	51.8 ± 0.4
	I ₂	53.6 ± 0.3	54.8 ± 0.3	57.5 ± 0.3	56.9 ± 0.3	58.7 ± 0.3
	Control		54.4 ± 0.4	55.6 ± 0.4	55.4 ± 0.4	53.2 ± 0.4
R	I ₁	52.1 ± 0.2	51.9 ± 0.3	54.0 ± 0.2	53.2 ± 0.3	54.7 ± 0.4
	Control		50.9 ± 0.4	53.3 ± 0.4	51.3 ± 0.3	51.8 ± 0.4
	I ₂	53.1 ± 0.2	52.7 ± 0.2	53.3 ± 0.2	52.4 ± 0.3	53.6 ± 0.3
	Control		53.1 ± 0.3	54.1 ± 0.3	51.7 ± 0.4	53.0 ± 0.3
Pooled	I ₁	52.4 ± 0.2	52.6 ± 0.2	54.5 ± 0.2	54.0 ± 0.2	54.9 ± 0.2
	Control		51.8 ± 0.3	52.8 ± 0.2	52.0 ± 0.3	51.8 ± 0.3
	I ₂	53.3 ± 0.2	53.9 ± 0.2	55.5 ± 0.2	54.6 ± 0.2	56.2 ± 0.2
	Control		53.7 ± 0.2	55.0 ± 0.3	53.6 ± 0.3	53.1 ± 0.2

Table 1f. Mean egg mass output (grams per day) during 30-34 weeks for selection and control lines (pooled over replicates)

Population	Selection criteria	Generations				
		0	1	2	3	4
Q	I ₁	40.6 ± 0.4	40.6 ± 0.5	46.7 ± 0.5	42.4 ± 0.5	44.7 ± 0.4
	Control		40.4 ± 0.6	45.0 ± 0.6	40.5 ± 0.8	40.4 ± 0.6
	I ₂	40.2 ± 0.5	41.4 ± 0.5	47.3 ± 0.5	44.2 ± 0.6	46.7 ± 0.5
	Control		41.8 ± 0.7	46.0 ± 0.6	42.5 ± 0.7	42.2 ± 0.8
R	I ₁	42.2 ± 0.4	41.3 ± 0.5	43.2 ± 0.5	41.3 ± 0.7	43.9 ± 0.7
	Control		40.4 ± 0.7	43.5 ± 0.7	40.3 ± 0.8	42.7 ± 0.8
	I ₂	43.6 ± 0.4	43.3 ± 0.4	44.1 ± 0.5	41.2 ± 0.7	43.4 ± 0.5
	Control		42.5 ± 0.6	45.5 ± 0.6	38.7 ± 1.1	43.4 ± 0.8
Pooled	I ₁	41.4 ± 0.4	41.0 ± 0.3	45.0 ± 0.4	41.9 ± 0.4	44.4 ± 0.3
	Control		40.4 ± 0.5	44.3 ± 0.5	40.4 ± 0.6	41.5 ± 0.5
	I ₂	41.9 ± 0.4	42.3 ± 0.3	45.8 ± 0.3	42.7 ± 0.5	45.1 ± 0.4
	Control		42.2 ± 0.5	45.8 ± 0.4	40.6 ± 0.7	42.8 ± 0.6

Table 1g. Mean feed consumption (grams per day) during 30-34 weeks for selected and control lines (pooled over replicates)

Population	Selection criteria	Generations				
		0	1	2	3	4
Q	I ₁	87.5 ± 0.9	90.9 ± 1.0	97.7 ± 0.9	91.6 ± 0.7	98.5 ± 0.8
	Control		88.5 ± 1.1	92.9 ± 1.1	86.7 ± 1.0	93.8 ± 1.3
	I ₂	88.6 ± 1.1	90.9 ± 1.1	99.5 ± 0.8	94.1 ± 0.9	108.6 ± 1.0
	Control		87.8 ± 1.4	95.0 ± 0.9	89.8 ± 1.1	96.9 ± 1.4
R	I ₁	93.0 ± 0.8	91.8 ± 1.0	100.1 ± 1.1	89.8 ± 1.4	96.2 ± 1.4
	Control		86.2 ± 1.5	100.2 ± 1.2	87.2 ± 1.8	98.8 ± 1.4
	I ₂	95.3 ± 0.9	93.8 ± 1.2	101.4 ± 1.2	94.1 ± 1.2	103.6 ± 1.0
	Control		94.1 ± 1.1	99.1 ± 1.4	84.3 ± 1.8	92.6 ± 1.7
Pooled	I ₁	90.2 ± 0.8	91.3 ± 0.7	99.0 ± 0.7	90.8 ± 0.7	97.6 ± 0.7
	Control		87.4 ± 0.9	96.3 ± 0.8	86.9 ± 0.9	96.2 ± 1.0
	I ₂	91.9 ± 1.0	92.2 ± 0.3	100.4 ± 0.7	94.1 ± 0.8	106.1 ± 0.7
	Control		91.1 ± 0.9	96.9 ± 0.8	87.0 ± 1.1	94.9 ± 1.1

Table 1h. Mean feed efficiency (egg mass/feed consumption) during 30-34 weeks for selected and control lines (pooled over replicates)

Population	Selection criteria	Generations				
		0	1	2	3	4
Q	I ₁	0.451 ± 0.004	0.436 ± 0.005	0.475 ± 0.005	0.461 ± 0.005	0.452 ± 0.004
	Control		0.457 ± 0.007	0.481 ± 0.005	0.463 ± 0.008	0.428 ± 0.007
	I ₂	0.443 ± 0.006	0.446 ± 0.005	0.475 ± 0.004	0.463 ± 0.005	0.425 ± 0.005
	Control		0.461 ± 0.007	0.482 ± 0.006	0.469 ± 0.008	0.422 ± 0.007
R	I ₁	0.445 ± 0.004	0.438 ± 0.004	0.414 ± 0.004	0.437 ± 0.007	0.433 ± 0.006
	Control		0.444 ± 0.006	0.428 ± 0.008	0.437 ± 0.009	0.423 ± 0.007
	I ₂	0.439 ± 0.004	0.445 ± 0.004	0.416 ± 0.004	0.420 ± 0.006	0.416 ± 0.004
	Control		0.446 ± 0.005	0.448 ± 0.006	0.430 ± 0.010	0.445 ± 0.007
Pooled	I ₁	0.448 ± 0.003	0.437 ± 0.003	0.445 ± 0.004	0.451 ± 0.004	0.445 ± 0.004
	Control		0.452 ± 0.005	0.457 ± 0.005	0.451 ± 0.006	0.425 ± 0.005
	I ₂	0.441 ± 0.004	0.445 ± 0.003	0.447 ± 0.003	0.441 ± 0.004	0.420 ± 0.003
	Control		0.453 ± 0.004	0.467 ± 0.004	0.450 ± 0.007	0.432 ± 0.005

are subject to sampling error. The total gains for I_1 and I_2 in populations Q and R are presented in Tables 2a through 2h. The results show cumulative gains made in the selected lines for each generation. The estimated genetic gain realized for a given generation is the difference in cumulative gains between successive generations. Individual generation gains are given in Tables 3a through 3h. The cumulative and individual generation gains, by traits, lines, indexes, and populations are described below.

Body weight

Line means, combined over indexes, were heavier than their controls in all generations, at both 20 and 32 weeks of age at generation 4. The selected lines were 83 and 112 g heavier, respectively, at 20 weeks and 148 and 225 g heavier, respectively, at 32 weeks. The increased body weight very likely is a consequence of the indirect selection for body weight imposed by the indexes. The gain in generation 1 on I_1 was unexpectedly higher than on I_2 . Moreover, the body weights of the selected groups, initially, were heavier at generation zero, which is carried forward to generation 4 (Tables 3a and 3b). Except for generation 1, gains made on I_1 were mostly smaller on I_2 . Populations Q and R also showed some disparity over generations.

Age at first egg

Age at first egg is the criterion used to estimate age at sexual maturity. This trait increased more on I_1 than on I_2 over all

Table 2a. Cumulative genetic responses in 20-week body weight (grams)

Selection criteria	Population	Generations			
		1	2	3	4
I ₁	Q	88	104	76	143
	R	42	15	73	24
	Pooled	65	60	75	83
I ₂	Q	24	83	54	126
	R	26	71	69	97
	Pooled	25	77	62	112

Table 2b. Cumulative genetic responses 32-week body weight (grams)

Selection criteria	Population	Generations			
		1	2	3	4
I ₁	Q	164	181	123	170
	R	89	119	147	126
	Pooled	127	150	135	148
I ₂	Q	83	160	159	262
	R	50	119	168	188
	Pooled	67	140	164	225

Table 2c. Cumulative genetic responses for age at sexual maturity (days)

Selection criteria	Population	Generations			
		1	2	3	4
I ₁	Q	2.4	3.9	4.4	10.9
	R	8.2	12.2	13.2	15.9
	Pooled	5.3	8.0	8.8	13.4
I ₂	Q	0.6	1.7	3.0	-1.0
	R	-2.6	-1.4	-2.4	-1.7
	Pooled	-1.0	0.2	0.3	-1.4

Table 2d. Cumulative genetic responses in rate of lay (percent)

Selection criteria	Population	Generations			
		1	2	3	4
I ₁	Q	-0.7	-3.9	-1.7	2.0
	R	3.2	-4.7	-2.0	-4.0
	Pooled	1.2	-4.3	-1.9	-1.0
I ₂	Q	0.1	0.7	-0.4	2.3
	R	1.6	0.5	3.9	-1.4
	Pooled	0.8	0.6	1.7	0.5

Table 2e. Cumulative genetic responses in egg weight (grams)

Selection criteria	Population	Generations			
		1	2	3	4
I ₁	Q	0.9	2.7	2.2	3.2
	R	1.0	0.7	1.9	2.9
	Pooled	0.9	1.7	2.0	3.1
I ₂	Q	0.4	1.9	1.5	5.5
	R	-0.4	-0.8	0.7	0.6
	Pooled	0	0.5	1.1	3.0

Table 2f. Cumulative genetic gain in egg mass (grams per day)

Selection criteria	Population	Generations			
		1	2	3	4
I ₁	Q	0.2	1.7	1.9	4.3
	R	0.9	-0.3	1.0	1.2
	Pooled	0.6	0.7	1.4	2.7
I ₂	Q	-0.4	1.3	1.7	4.5
	R	0.8	-1.4	2.5	0.0
	Pooled	0.2	-0.1	2.1	2.3

Table 2g. Cumulative genetic responses in feed consumption (grams/day)

Selection criteria	Population	Generations			
		1	2	3	4
I ₁	Q	2.4	4.8	4.9	4.7
	R	5.6	-0.1	2.6	-2.6
	Pooled	4.0	2.4	3.7	1.0
I ₂	Q	3.1	4.5	4.3	11.7
	R	-0.3	2.3	9.8	11.0
	Pooled	1.4	3.4	7.0	11.3

Table 2h. Cumulative genetic responses in feed efficiency (egg mass/
feed consumption)

Selection criteria	Population	Generations			
		1	2	3	4
I ₁	Q	-0.021	-0.006	-0.002	0.024
	R	-0.006	-0.014	0.000	0.010
	Pooled	-0.014	-0.010	-0.001	0.017
I ₂	Q	-0.015	-0.007	-0.006	0.003
	R	-0.001	-0.032	-0.010	-0.029
	Pooled	-0.008	-0.019	-0.008	-0.013

Table 3a. Genetic response in each generation for 20-week body weight (grams)

Selection criteria	Population	Generations			
		1	2	3	4
I ₁	Q	88	16	-28	67
	R	42	-27	58	-49
	Pooled	65	- 6	15	9
I ₂	Q	24	59	-29	72
	R	26	45	- 2	28
	Pooled	25	52	-15	50

Table 3b. Genetic response in each generation for 32-week body weight (grams)

Selection criteria	Population	Generations			
		1	2	3	4
I ₁	Q	164	17	-58	47
	R	89	30	28	-21
	Pooled	127	24	-15	13
I ₂	Q	83	77	- 1	103
	R	50	69	49	20
	Pooled	67	73	24	62

Table 3c. Genetic response in each generation for age at first egg (days)

Selection criteria	Population	Generations			
		1	2	3	4
I ₁	Q	2.4	1.5	0.5	6.5
	R	8.2	4.0	1.0	2.7
	Pooled	5.3	2.8	0.7	4.6
I ₂	Q	0.6	1.1	1.3	-4.0
	R	-2.6	1.2	-1.0	0.7
	Pooled	-1.0	1.1	0.1	-1.6

Table 3d. Genetic responses in each generation for rate of lay (percent)

Selection criteria	Population	Generations			
		1	2	3	4
I ₁	Q	-0.7	-3.2	2.2	3.7
	R	3.2	-7.9	2.7	-2.0
	Pooled	1.2	-5.6	2.4	0.9
I ₂	Q	0.1	0.6	-1.1	2.7
	R	1.6	-1.1	3.4	-5.3
	Pooled	0.9	-0.3	1.2	-1.3

Table 3e. Genetic responses in each generation for egg weight (grams)

Selection criteria	Population	Generations			
		1	2	3	4
I ₁	Q	0.9	1.8	-0.5	1.0
	R	1.0	-0.3	1.2	1.0
	Pooled	0.9	0.8	0.3	1.0
I ₂	Q	0.4	1.5	-0.4	4.0
	R	-0.4	-0.4	1.5	-0.1
	Pooled	0	0.5	0.5	2.0

Table 3f. Genetic responses in each generation for egg mass (grams per day)

Selection criteria	Population	Generations			
		1	2	3	4
I ₁	Q	0.2	1.5	0.2	2.4
	R	0.9	-1.2	1.3	0.2
	Pooled	0.6	0.1	0.7	1.3
I ₂	Q	-0.4	1.7	0.4	2.9
	R	0.8	-2.2	3.9	-2.5
	Pooled	0.2	-0.3	2.1	0.2

Table 3g. Genetic responses in each generation for feed consumption (grams per day)

Selection criteria	Population	Generations			
		1	2	3	4
I ₁	Q	2.4	2.6	0.1	-0.2
	R	5.6	-5.7	2.7	-5.2
	Pooled	4.0	-1.6	1.4	-2.7
I ₂	Q	3.1	1.4	-0.2	7.4
	R	-0.3	2.6	7.5	1.2
	Pooled	1.4	2.0	3.6	4.3

Table 3h. Genetic responses in each generation for feed efficiency
(egg mass/feed consumption)

Selection criteria	Population	Generations			
		1	2	3	4
I ₁	Q	-0.021	0.015	0.004	0.026
	R	-0.006	-0.008	0.014	0.010
	Pooled	-0.014	0.004	0.009	0.018
I ₂	Q	-0.015	0.008	0.001	0.008
	R	-0.001	-0.031	0.022	-0.019
	Pooled	-0.008	-0.011	0.011	-0.006

generations (Table 2c). The average decrease in age at first egg was 1.4 days for populations Q and R combined. Thus, selection on I_1 , but not on I_2 , delayed sexual maturity.

Rate of lay

Rate of lay was lower in the lines selected on I_1 in all except generation 1 than on I_2 (Table 3c). The former had positive gains in all generations except in generation 2 (Table 3d). The gains on I_2 failed to show a clear trend over generations. The lower rate of lay in I_1 seems to be due to the marked negative response in generation 2.

Egg weight

Egg weight increased in the lines selected on I_1 (Table 2e) and at generation 4 were 3.1 g heavier than the unselected controls. Both populations were in good agreement for I_1 , but for I_2 populations were in poor agreement. In general, selection on both indexes increased egg weight.

Egg mass

Daily egg mass output is the product of rate of lay and egg weight. The combined results over indexes showed an increase in generation 4. Selections on I_1 increased egg mass by 2.7 g and selections on I_2 increased egg mass by 2.3 g. However, the results between populations Q and R differed particularly in the initial two generations. Population Q, but not population R, was consistent for both indexes. In general, selections on either index increased egg mass as expected because this trait is included in each index.

Feed consumption

Records on daily feed intake were included in I_1 in an attempt to genetically improve egg production efficiency. This information was intentionally excluded in I_2 to permit an evaluation of the impact of feed records in I_1 when contrasted with I_2 . Agreement, however, between populations was not good. In generation 4 of population Q, feed consumption increased by 4.7 g and declined by 2.6 g in population R in I_1 . On the other hand, feed consumption increased for the lines selected on I_2 in both populations Q and R. The average increase was 1.3 g. Thus, the overall results show that selection on I_2 , but not on I_1 , increased feed intake.

Feed efficiency

Feed efficiency (egg mass/feed consumption) showed small differences between selected lines and their corresponding control lines. Generation means did not show any consistent trend. At generation 4, selection on I_1 showed increased feed efficiency by .024 and .011 units in populations Q and R, respectively. On the other hand, feed efficiency was inconsistent in populations Q and R selected on I_2 . In general, the results indicate a slight increase in feed efficiency for I_1 . The response on I_2 was inconsistent.

Feed Records

A primary objective of this study was to evaluate feed records for use in a selection index to improve egg production efficiency in layer-type chickens. The differences between the mean performance of lines

selected on I_1 and I_2 should reflect the impact of feed record input in the selection index. The mean deviations, $I_1 - I_2$, for each of the performance traits over populations Q and R, separately and pooled, are given in Tables 4a through 4c. Positive values favor I_1 and negative values favor I_2 .

Body weight at 20 weeks was higher in the lines selected on I_1 than on I_2 , except in generations 1 and 4. I_2 birds, however, were heavier in generation 4. I_1 birds were lighter at 32 weeks, except in generations 2 and 3. Overall, the results fail to show an increased body weight on a consequence of adding feed records in the index. A delay in sexual maturity from incorporating feed records in I_1 is indicated, but some discrepancy is noted between populations. Body weight in population R was considerably higher than in population Q. Overall, it seems that inclusion of feed records in the index increases age at first egg. At generation 4, I_1 selected lines were 3 to 8 days later in age at first egg.

The overall results indicate a lower rate of lay for I_1 . Population differences showed some disagreement in the first two generations. At generation 4, I_1 birds were lower in rate of lay by 1.3%. Rate of lay seems not to be improved by adding feed consumption records to the selection index.

Egg weight was also lower in I_1 lines. Egg size was larger in population Q than in population R. The mean difference of $I_1 - I_2$, in generation 4, was positive in R but negative in Q. Apparently,

Table 4a. Effect of feed record information (I_1 - I_2) on body weight and age at first egg

Trait	Unit	Population	Generations				
			0	1	2	3	4
Body weight 20 weeks	g	Q	-25	28	10	-4	-55
		R	2	13	18	47	21
		Pooled	-11	20	14	21	-17
Body weight 32 weeks	g	Q	-61	42	-31	-96	-198
		R	-17	11	59	54	61
		Pooled	-39	27	14	-21	-69
Age at first egg	days	Q	-0.3	1.1	-1.2	-3.6	1.2
		R	-3.7	5.6	6.5	5.0	6.4
		Pooled	-20.	3.4	2.6	0.7	3.8

Table 4b. Effect of feed record information (I_1 - I_2) on rate of lay, egg weight and egg mass

Trait	Unit	Population	Generations				
			0	1	2	3	4
Rate of lay	Percent	Q	-1.2	0.7	0.3	1.1	0.0
		R	-1.0	-1.5	-4.2	0.2	-2.6
		Pooled	-1.1	-0.4	-1.9	0.6	-1.3
Egg weight	g	Q	-0.9	-1.5	-2.5	-2.2	-3.7
		R	-1.0	-0.8	0.7	0.8	1.1
		Pooled	-1.0	-1.2	-0.9	-0.7	-1.3
Egg mass	g/day	Q	0.4	-0.8	-0.6	-1.8	-2.0
		R	-1.4	-2.0	-0.9	0.1	0.5
		Pooled	-0.5	-1.4	-0.7	-0.9	-0.7

Table 4c. Effect of feed record information (I_1 - I_2) on feed consumption and feed efficiency

Trait	Unit	Population	Generations				
			0	1	2	3	4
Feed consumption	g/day	Q	-1.1	0.0	-1.8	-2.5	-10.1
		R	-2.3	-2.0	-1.3	-4.3	- 7.4
		Pooled	-1.7	-1.0	-1.6	-3.4	- 8.8
Feed efficiency (egg mass/feed consumption)	g/g	Q	0.008	-0.010	-0.000	-0.002	0.027
		R	0.006	-0.007	-0.002	0.017	0.017
		Pooled	0.007	-0.008	-0.001	0.006	0.022

including feed records in the index adversely affected egg weight. The mean difference, $I_1 - I_2$, also was negative over all generations. Thus, the I_1 selected lines were lower than I_2 lines in daily egg mass production, but some discrepancy was noted between populations and generations 3 and 4. Egg mass production per day seems not to be improved by the addition of feed consumption records in the index. Because egg mass is the product of rate of lay and egg weight, the trends observed in both rate of lay and egg weight should be correlated with daily egg mass output.

The purpose for including feed consumption in the index was to maximize the economy of feed for the egg production efficiency. I_1 selected birds were considerably lower in daily feed intake. Feed consumption was lower in the I_1 birds; at generation 4, these birds consumed 8.8 g less feed than I_2 birds.

Feed efficiency, taken as the ratio of daily egg mass to the daily feed consumption, was slightly better for I_2 in generations 3 and 4, although population differences were somewhat discordant. The negative mean differences observed in generation 1 were small and likely were sampling effects. Adding feed consumption records to the index improved feed efficiency only slightly at best.

Summarizing the results of four generations of selection, the addition of feed information to the selection index, on the average, decreased 32 week body weight by 69 g, increased age at first egg by 3.8 days, lowered egg mass output by .7 g per day, lowered feed

consumption by 8.8 g, and increased feed efficiency (egg mass/feed consumption) by 2.2%.

Selection Differentials

Selection differentials for the different traits, computed by subtracting the overall mean from the mean of selected birds used as parents (Tables 5a through 5c), were positive for body weights, both at 20 and at 32 weeks. Values over generations were consistent for both populations and for each index. However, marked discrepancies were observed between populations for age at first egg. I_1 had negative values in population Q, but with no clear pattern. For I_2 , except for generation 3 (population Q), the selection differentials were positive in population Q but negative in R. Thus, it seems that selection on both indexes favored the heavier parents. Values for age at first egg were not consistent.

The selected birds were higher in rate of lay than the overall average. Selection differentials were consistent within indexes and populations. The selected breeders were also higher in egg weight in all generations. Results for both indexes and populations were in fair agreement. For daily egg mass output, birds selected as parents also were superior. Thus, the selected parents, on either index, exceeded the overall generation mean in rate of lay, egg weight, and daily egg mass output.

The selection differentials were positive for feed consumption for each generation. Both indexes were in good agreement on both

Table 5a. Selection differentials for body weight and age at first egg

Trait	Unit	Population	Index 1				Index 2			
			Generations				Generations			
			0	1	2	3	0	1	2	3
Body weight 20 weeks	g	Q	107	37	3	23	55	40	21	109
		R	60	70	15	15	70	53	35	42
		Pooled	84	54	9	19	62	47	28	76
Body weight 32 weeks	g	Q	185	65	5	26	162	120	88	71
		R	195	128	38	40	172	52	80	78
		Pooled	190	97	21	33	167	86	84	74
Age at first egg	days	Q	-0.3	-0.3	-2.0	-2.1	2.6	3.1	2.3	-2.1
		R	3.5	-0.3	2.3	-2.7	-2.1	-2.0	-2.1	0.1
		Pooled	1.6	-0.3	0.1	-2.4	0.2	0.6	0.1	-1.0

Table 5b. Selection differentials for rate of lay, egg weight and egg mass

Trait	Unit	Population	Index 1				Index 2			
			Generations				Generations			
			0	1	2	3	0	1	2	3
Rate of lay	Percent	Q	3.1	5.4	5.4	4.0	4.1	2.9	2.1	4.6
		R	5.3	4.1	6.9	7.0	2.3	2.9	6.3	9.2
		Pooled	4.2	4.8	6.2	5.5	3.2	2.9	4.2	6.9
Egg weight	g	Q	1.1	-0.6	0.7	0.5	1.4	1.3	1.8	1.3
		R	1.4	1.5	0.8	0.3	1.3	0.0	0.8	1.1
		Pooled	1.2	0.5	0.7	0.4	1.4	0.6	1.3	1.2
Egg mass	g/day	Q	1.3	1.4	4.5	4.0	2.1	1.5	2.7	4.4
		R	2.2	2.9	3.8	3.5	2.0	-0.4	3.4	4.9
		Pooled	1.7	2.1	4.1	3.7	2.0	0.5	3.0	4.7

Table 5c. Selection differentials for feed consumption and feed efficiency

Trait	Unit	Population	Index 1				Index 2			
			Generations				Generations			
			0	1	2	3	0	1	2	3
Feed consumption	g/day	Q	7.7	5.2	2.6	1.6	9.5	9.2	4.3	6.4
		R	8.4	7.6	5.4	5.0	7.4	3.8	8.3	8.1
		Pooled	8.1	6.4	4.0	3.3	8.5	6.5	6.3	7.2
Feed efficiency (egg mass/feed consumption)	g/g	Q	-0.016	0.004	0.036	0.042	-0.011	0.015	0.010	0.023
		R	-0.004	0.007	0.003	0.043	0.001	0.007	0.020	0.032
		Pooled	-0.010	0.005	0.035	0.042	-0.005	0.011	0.015	0.027

populations, except in generation 1; the birds selected as breeders also had better feed efficiency (egg mass/feed consumption) within both indexes and populations. Thus, the birds selected as parents consumed more feed but had better feed efficiency.

Regression of Response on Generation Number

Table 6 presents regression coefficients of cumulative response of various traits on generation number. These are least squares estimates of the change in a trait per generation resulting from selection. The change in body weight for lines selected on I_2 but not on I_1 was statistically significant. Most of the regression coefficients for body weight on generation number for I_2 were statistically significant. Age at first egg increased by 2.5 days per generation in I_1 , but no change was evident in I_2 .

Rate of lay for both indexes showed little change. An increase of .7 and 1 g per generation for egg weight was observed in the lines selected on I_1 and I_2 , respectively. Daily feed intake showed no change in I_1 , but a significant increase of 3.35 g per day per generation was noted for the I_2 selected lines. Feed efficiency improved significantly by .01 units per generation in I_1 but for I_2 some improvement is noted in population Q but not in R.

In general, selection on I_1 had only a slight effect on body weight, rate of lay, and feed consumption. However, age at first egg increased by 2.5 days, egg weight increased by .66 g, daily egg mass increased by .73 g, and feed efficiency increased by .01 units. On the other hand,

Table 6. Regression coefficients of cumulative selection responses for different traits on number of generations

Trait	Unit	Index 1			Index 2		
		Population Q	Population R	Pooled	Population Q	Population R	Pooled
Body weight: 20 wks.	g	13.7	0.4	7.0	27.7	21.1*	24.4**
32 wks.	g	-4.0	13.9	5.0	53.6**	46.3**	50.0**
Age at first egg	days	2.6*	2.4**	2.5	-0.4	0.2	-0.1
Rate of lay	Percent	1.0	-1.9	-0.4	0.6	-0.6	-0.01
Egg weight	g	0.64	0.69*	0.66**	1.49	0.45	1.0
Egg mass	g/day	1.25**	0.22	0.73*	1.51**	0.15	0.83
Feed consumption	g/day	0.70	-2.19	-0.74	2.56	4.14**	3.35**
Feed efficiency (egg mass/feed cons.)	g/g	0.014**	0.006	0.010**	0.006**	-0.006	-0.001

*P < .05.

**P < .01.

the lines selected on I_2 increased significantly in body weight, egg weight, egg mass, and feed consumption. Age at first egg, rate of lay, and feed efficiency, however, seemed not to have been affected by selection on I_2 .

Expected Genetic Response

The genetic response per generation expected from population parameters estimates for individual traits is given in Table 7. The corresponding realized responses have already been presented (Table 6). Body weight in I_1 was not in good agreement between realized gains and that predicted from parameter estimates. For I_2 realized gains were in good agreement with predicted gains in population R but not in population Q. For age at first egg and rate of lay, both the indexes were markedly discrepant between the observed and expected gains. Realized genetic gains, compared to predicted gains, were consistent for egg weight and daily egg-mass output. Realized genetic response in feed consumption, for I_2 was then the expected response, but with some discrepancies. Feed efficiency for I_1 was lower in observed than in expected gains.

Realized Heritabilities

The regression coefficients of cumulative responses on cumulative selection differentials, presented in Table 8a, are estimators of realized heritability. Several were inconsistent or negative. Moderately high estimates were obtained for body weight in I_2 and for

Table 7. Expected genetic response per generation for individual traits based on population parameters.

Trait	Unit	Index 1			Index 2		
		Population Q	Population R	Pooled	Population Q	Population R	Pooled
Body weight 32 wks.	g	-35.6	10.8	-12.4	-3.9	50.3	23.2
Age at first egg	days	- 0.67	-1.87	-1.27	-0.59	-1.34	-0.96
Rate of lay	Percent	0.67	1.17	0.92	0.76	0.97	0.86
Egg weight	g	0.55	0.70	0.62	0.76	0.73	0.74
Egg mass	g/day	0.96	1.40	1.18	1.02	1.28	1.15
Feed cons./day	g/day	- 0.22	1.98	0.88	1.04	2.47	1.76
Feed efficiency (egg mass/feed cons.)	g/g	0.045	0.005	0.025	0.035	0.002	0.018

Table 8a. Regression coefficients (realized heritability) of cumulative response on cumulative selection differential

Trait	Unit	Index 1			Index 2		
		Population Q	Population R	Pooled	Population Q	Population R	Pooled
Body weight: 20 wks.	g	0.82	-0.03	0.40	0.54	0.51*	0.52**
32 wks.	g	-0.03	0.23	-0.02	0.57	0.63*	0.60**
Age at first egg	days	-1.72	-0.18	-0.95	0.37	-0.09	-.30**
Rate of lay	Percent	0.19	-0.27	-0.09	0.21	-0.12	0.05
Egg weight	g	0.40	0.63	0.51	0.96	0.67	1.05**
Egg mass	g/day	0.35	0.07	0.17	0.52*	0.07	0.32
Feed consumption	g/day	0.26	-0.37	-0.30	0.39	0.59*	0.47**
Feed efficiency (egg mass/feed cons.)	g/g	0.46*	0.24	0.34**	0.36**	-0.25	-0.11

*p < .05.

**p < .01.

egg weight in both the populations and indexes. For egg mass, estimates of .17 and .32 were noted in I_1 and I_2 , respectively, but with higher values in population Q than in R. For I_2 the estimate of daily feed consumption was .47 but for I_1 the estimate was negative. For feed efficiency, the estimate of realized heritability was .34 in the I_1 data but the estimates between populations were inconsistent in the I_2 data.

Estimates of heritabilities obtained from sib analysis using sire component of variance are given in Table 8b. Realized heritabilities have fairly good agreement with the estimated heritabilities from the data for body weight (I_2), age at first egg (I_2), rate of lay (population Q), egg weight, egg mass and feed consumption (population Q). Feed efficiency had higher realized heritability than estimated in population Q. However, indexes showed some disagreement in the population R.

Environmental Trends

If the control lines used in a selection experiment are genetically stable, the variation in mean performance between generations would reflect time trends in environmental changes. The regression coefficients of control line means on generation number by individual traits are given in Table 9. No traits showed statistical significance. Thus, no environmental trends could be demonstrated over the span of four generation-years. It is concluded, therefore, that the estimates of genetic responses over generations in the selected lines are valid and unbiased.

Table 8b. Estimates of heritability obtained from sire component of variance

Trait	Populations		
	Q	R	Pooled
Body weight	0.48 ± 0.08	0.66 ± 0.10	0.56 ± 0.06
Age at first egg	0.48 ± 0.08	0.36 ± 0.08	0.42 ± 0.06
Rate of lay	0.25 ± 0.06	0.14 ± 0.06	0.19 ± 0.04
Egg weight	0.89 ± 0.11	0.57 ± 0.10	0.77 ± 0.07
Egg mass	0.22 ± 0.06	0.26 ± 0.07	0.24 ± 0.05
Feed consumption	0.34 ± 0.07	0.29 ± 0.08	0.32 ± 0.05
Feed efficiency (egg mass/feed cons.)	0.22 ± 0.06	0.13 ± 0.06	0.18 ± 0.04

Table 9. Regression coefficients^a of mean performance of control lines on number of generations

Trait	Unit	Population Q lines		Population R lines		Combined
		A ₃	B ₃	C ₃	D ₃	
Body weight: 20 wks.	g	2.9	15.6	32.9	32.9	21.1
32 wks.	g	-6.0	15.3	32.2	-14.5	7.0
Age at first egg	days	0.4	3.4	-3.8	-1.6	-0.4
Rate of lay	Percent	-1.0	-0.3	1.2	-0.2	-0.1
Egg weight	g	-0.2	-0.4	0.1	-0.3	-0.2
Egg mass	g/day	-0.4	-0.2	0.4	-0.4	-0.2
Feed consumption	g/day	1.0	2.2	2.5	-1.9	0.9
Feed efficiency (egg mass/feed cons.)	g/g	-0.010	-0.010	-0.005	-0.002	-0.008

^aNone are statistically significant.

Effective Population Size (N_e) and Drift Variance

Each line was carried by 8 sires and 48 dams per generation in both the selected and unselected lines. Thus, effective population number was the same in both groups. Even though matings between full-sibs and half-sibs were strictly avoided, only the effective population size governs the rate of inbreeding in a closed flock (Nordskog and Hardiman, 1979). Thus, the inbreeding depression effects should be the same in both selected and control lines. The average N_e was 27.4 per line which represents an increase of 1.8% inbreeding per generation. Over five generations this would amount to approximately 9% of inbreeding.

Variance in response to genetic drift (σ_D^2) is the major source of variance in response compared to the variance due to sampling errors of measurement (σ_e^2). In each line about 125 individuals are tested. Thus, the ratio σ_D^2/σ_e^2 would be 4.6 with $N_e = 27.4$. Therefore, it seems that for this selection experiment drift variance was 4.6 times larger than the sampling variance among individuals tested per generation.

Analysis of Variance

Total variance was partitioned into effects associated with generations, populations, selection criteria, in addition to the two- and three-way interactions. Significance of effects, tested against appropriate error terms, are presented in Table 10. Significant generation differences for all traits imply large environmental effects between generations. Because the populations Q and R were produced in

Table 10. Mean squares for various traits

Source of variation	Degrees of freedom	Body weight at		Age at first egg	Rate of lay	Egg weight	Egg mass	Feed cons.	Feed effic. x 10 ⁻⁴
		20 wks	32 wks						
Generations (G)	3	39,351**	32,600**	123**	16.6*	6.1*	38.1**	338.3**	8.6**
Populations (P)	1	79.462**	11,347	448**	12.0	47.2	13.4**	15.5	73.3
Selection criteria (SC)	2	25,781**	111,079**	119**	2.5	17.3**	12.0**	161.0**	3.5*
G*P	3	897	2,180	109**	14.3	0.9	7.5**	16.7	17.1**
G*SC	6	1,049	4,042	5	3.2	1.6	1.6	20.6	2.5
P*SC	2	2,397	14,962**	51	6.7	11.4**	2.6	3.1	0.7
G*P*SC	6	886	4,111	1	4.4	1.2	2.3	9.1	1.5
Error	24	1,776	3,382	16	5.4	1.6	1.2	14.1	0.8

* P < .05.

** P < .01.

different hatches four weeks apart, the effects due to populations and hatches are confounded. This component was statistically significant for body weight at 20 weeks, age at first egg, and daily egg mass. Except for rate of lay, the variation associated with the selection criteria was statistically significant for all traits. With few exceptions, the two-way interactions were nonsignificant. None of the three-way interactions were significant.

DISCUSSION

Selection Response

The primary objective of commercial breeders is to improve total performance. The latter depends on many traits. Smith (1936) and Hazel (1943) developed selection index theory for the improvement of several traits simultaneously. Hazel and Lush (1942) concluded that a selection index for multiple traits is expected to be more efficient than independent culling levels or tandem selection. Similar conclusions were reached also by Young (1961) and Finney (1962) who pointed out that effectiveness of index selection is dependent also on the precision of the parameter estimates used in the index equations.

Because the determination of relative economic values of traits is frequently a difficult problem in the application of selection indexes, economic weight-free indexes have been proposed (Yamada et al. (1975). In a discussion of the frequently observed lack of agreement between predicted and realized genetic responses from the index selection, Berger (1976) cited biased parameter estimates and failure to account for important correlated traits as possible causes.

In the present study, body weight seemed to be changed only slightly by selection on I_1 , but selection on I_2 markedly increased body weight. However, considerable variation between populations and generations were evident. The lower response to change in body weight by selection on I_1 may be the result of the feed records added to

the index. This may also have been the reason for delayed sexual maturity.

Selection on either index seemed not to influence the response in rate of lay. Although the two populations were in poor agreement, selection on the indexes clearly increased egg weight and daily egg mass output. In fact, increased egg mass output mainly resulted from increased egg weight. I_1 seemed to make more effective use of feed by restricting daily feed intake, but feed intake increased considerably by selection on I_2 . Feed efficiency was significantly improved by selection on I_1 , but not on I_2 .

These observations lead to the conclusion that selection on I_1 was more effective in improving egg production efficiency than selection on I_2 . Most of the improvement seemed to result from restricting body weight increase accompanied by lower feed intake but yet permitting some increase in egg size.

Variation in Selection Response

The causes of variable responses from selection were discussed in a series of excellent papers by Hill (1971, 1972a, 1972b, 1972c, 1972d, 1976). These are genetic drift, sampling variance, genetic X environment interaction, environmental time trends and natural selection. In general, Nicholas (1980) and Hill's studies indicated that variance due to random genetic drift (σ_d^2) is the major source of variation in response to selection. The errors of genetic drift

accumulate with each generation of selection (Foster and Thompson, 1980), but variance of sampling error, σ_e^2 does not. Rather, the latter diminishes over generations; the ratio of σ_d^2/σ_e^2 , estimable as M/N_e (number of individuals tested (M) divided by the effective population size, N_e), represents the variance associated with random drift variance relative to sampling variance. In this study, it was estimated that drift variance, on the average, was 4.6 times greater than the sampling variance within lines.

The bias of genetic X environment interaction, as a source of error in selection response, is especially important when a control line is maintained in parallel with the selected lines. In the present study, this should not have been a major source of variation because the pairs of selected lines and their respective controls were of the same origin. Because the control lines showed no consistent evidence of linear time trends for any of the traits in the present study, they seemed to have adequately served their purpose in providing an unbiased and valid measure of genetic response in the selection lines. Moreover, the observed responses in the selection lines did not require adjustment for inbreeding because the effective population size (N_e) was intentionally kept the same in the selected and the control lines. An N_e of 27.4 per line is expected to increase the inbreeding coefficient by 1.8 percent. Thus, at the fifth generation of selection, the total increase in inbreeding per line is expected to be approximately 9 percent in both the selected and control lines.

Expected Versus Realized Selection Responses

The problem of realized response to selection for certain performance traits is generally less than that theoretically expected. Nordskog (1976a, 1976b) pointed out that response to selection for medium to highly heritable nonreproductive traits agrees well with the theoretical predictions in the short term. On the other hand, the response to selection for reproductive traits is usually less than that expected using population parameter estimates. He further concluded that the predictive value of the theory is lower in the case of multitrait selection. According to his views, genetic improvement in the level of egg production for most of the highly selected commercial strains seems to have leveled off, while progress in broiler production is steadily increasing. These views are also supported by an early study on a commercial breeding flock (Dickerson, 1964). Possible limitations of the quantitative genetic theory in poultry breeding has also been discussed by Harris (1976a, 1976b). Kempthorne (1976) concluded that blending of natural selection with directed selection for metric traits is the major theoretical and experimental problem. Gowe (1976), in his comments on International Conference on Quantitative Genetics, concluded that the Smith-Hazel index may not lead to optimal response in the complex of traits required. In a recent appraisal of the effectiveness of selection in the fowl, Sheldon (1980) was of the opinion that quantitative genetic theory would continue to play a vital role in commercial poultry breeding. He

suggested, however, that a more realistic biological basis should embrace the theory such that the efficiency of breeding methods can be increased within the framework of the statistical model.

The application of selection index theory requires several assumptions. Relative economic values for each trait should be known without error and should not change over time. Also, the economic values, ideally, should be linearly related to the traits. Further, an important assumption is that the index values and true breeding values are normally distributed. This assumption may be violated in the populations subjected to intense selection. Phenotypic and genetic parameters are also assumed to be known without error. Williams (1962) and Harris (1964) suggested that unless a considerable amount of data is available for estimating parameters, it is preferable to use a 'base index' in which the economic values are used directly as weighting coefficients. Harris (1964) further reported that in a two-trait selection index, with heritabilities of 0.2 for each trait, at least 1,000 observations are needed to reliably estimate variances and covariances from paternal half-sib analysis. Williams (1962) and Harris (1964) showed that even if all the assumptions are met, the total genetic gains from index selection are over-estimated.

The theoretically expected responses based on population parameters and realized responses (Tables 6 and 7) indicate that the change in body weight in the I_1 was over-estimated. In I_2 , the expected and realized responses agreed well in the population R, but not in Q. For

age at first egg and rate of lay, the realized responses were in poor agreement with the expected. On the other hand, egg weight and daily egg mass output were in good agreement for the expected and realized responses. For feed consumption, realized responses agreed well with the expected responses in the I_2 , but not in I_1 . For feed efficiency, gain expected in both the indexes seem to have been over estimated. These observations point to the considerable discrepancy between observed and expected responses. It should be noted that parameters used in the solution of index equations were initially taken from the literature. On the other hand, these may differ greatly from the real populations under study. Thus, the data of the last five generations of this study might be used to derive new parameter estimates and these, in turn, to revise the indexes. As pointed out in the materials section, body weight was given unintentional excessively high economic values in the first two generations; thus, some of the discrepant results of this study may be explained by this. Certain small discrepancies may be due to small sampling error effects. Bohren et al. (1966) concluded that the validity of the existing theory for the prediction of correlated responses is much poorer than for prediction of direct responses. Bohren (1975) deduced that to evaluate the effect of one or more criteria of selection for the same trait, only two or three generations would be needed.

Feed Efficiency

Efficient utilization of feedstuffs for maximum productivity is a highly important objective in animal improvement. This is especially critical in countries facing food shortages and where animal feeds compete with human food. In this case, efforts should be made to develop animals with better feed utilization. The genetic improvement of poultry stocks in their ability to convert low quality and high fibre rations would not only make the poultry industry economically stronger, but would help in reserving high quality foods exclusively for human consumption. Therefore, it follows that breeding projects aimed on maximizing feed use by animals would be especially desirable in developing countries.

Animals store excess energy as fat. Thus, when body maintenance, growth and production requirements are met, the surplus energy of a diet will be stored as fat. Therefore, feed consumed above the requirements for production and maintenance would be wastage through fat deposition. In meat-type chickens, abdominal leaf fat is mostly discarded before cooking. Gyles et al. (1982) estimated a direct annual loss of \$250 million in the United States as leaf fat. Additional losses may occur through poor feed efficiency and production. A correlation of $-.30$ between number of eggs and abdominal fat (Gyles et al., 1982) infers that fat hens have lower egg production. They also reported a correlation of $.71$ between live body weight and abdominal fat. Therefore, increasing the growth rate

in broilers would be accompanied by excessive abdominal fat deposits. Greenberg (1976) suggested that a certain quantity of fat is desirable at sexual maturity in order to maximize production. At the onset of production, fat is metabolically activated and provides energy for egg production. Thus, the excessive fat deposited during the laying period may have an adverse effect on production.

Another factor which contributes to lower feed efficiency is the feed wasted by the birds from the hoppers. This is a frequent problem encountered by poultry producers. The tendency of individual hens to waste may have genetic basis. Therefore, it may be useful to measure feed wasted by individual birds in order to examine the role that genetics plays as regards wastage.

The digestibility of a feed is a major factor determining efficiency of feed utilization. The physical characteristics of the gastro-intestinal tract as well as levels of hormones or of digestive enzymes might also influence the digestibility of feed. Other factors which influence feed utilization include energy lost in urine, energy lost in maintaining body temperature and physical activity.

McDonald (1978) compared the different formulas proposed by different workers to predict daily metabolizable energy intake of laying hens. Factors affecting the accuracy of the prediction include genotype, management factors including ambient temperature, air velocity, housing systems and number of birds per cage.

In the present study, indexes I_1 and I_2 were used to improve efficiency of feed utilization. I_2 seems not to have improved feed efficiency, but the expected improvement by selection on I_1 seemed to have improved feed utilization by .01 unit per generation. Taking this estimate at face value, a hen producing 45 grams of daily egg mass output with a feed efficiency of .44 would conserve feed intake by .05 gram to produce one gram of egg mass. Thus, a flock of 1,000 hens would consume 2.25 kilograms less feed per day. Assuming a laying cycle of 280 days and an average response of .01 in feed efficiency throughout the laying period, one generation of selection on I_1 would reduce feed consumption of entire flock by 2.25 kilograms per day or 630 kilograms over the entire 280 days production period.

Realized and parameter-estimated heritabilities revealed some inconsistencies between populations and selection indexes. Part of these differences are most likely due to sampling error effects. Higher estimated realized heritability than the parameter-estimations for feed efficiency in I_1 suggests that selection on I_1 was more effective than that predicted. For I_2 , the realized heritability estimates were strongly discrepant in populations Q and R.

Because of the apparent discrepancies between populations and over generations, the question is whether this experiment should be continued in its present design in order to draw more definite conclusions regarding the original objectives of the project. Selection on I_1 was significantly superior to I_2 in improving feed utilization.

Yet, it would seem that this selection experiment should be continued for some additional generations to permit more reliable estimations of the value and use of feed records in a selection index. The exact number of generations to continue might best be answered sequentially. In an earlier study (Nordskog et al., 1974), selected two lines on part-record egg production over a span of 10 generations, definite improvement in egg rate was not observed until the last 3 generations of the experiment.

In a recent study by Birkmeyer et al. (1982), differences in body weight were associated with the B blood group locus and a locus controlling immune response to the amino acid polymer, glutamine-alanine-tyrosine. Thus, it might seem worthwhile to characterize the Q and R populations for B blood group alleles and perhaps immune response alleles to examine whether or not these loci have major effects on egg production and on efficiency traits.

SUMMARY

The primary objective of this study was to determine whether information on feed consumption is useful for the improvement of egg production efficiency. Selection based on two indexes, I_1 and I_2 , was conducted in two populations of Leghorn chickens. I_1 contained information on body weight, feed consumption and egg mass output, while I_2 contained information only on body weight and egg mass output, feed consumption information being intentionally omitted.

Results over four generations of selection indicated that I_2 increased body weight markedly. Delayed age at sexual maturity was observed in the I_1 lines. Rate of lay did not seem to change by selection on either I_1 or I_2 . Both indexes increased egg size and daily egg-mass output. These increases were accompanied by increased feed consumption in I_2 , but not in I_1 . Statistically, the I_1 selected lines were significantly improved in feed efficiency (egg mass/feed consumption), but I_2 failed to show any improvement in feed efficiency.

Inconsistencies in responses, however, were observed between populations and between generations. Part of the discrepancies can be explained by incorrect choice of an economic value constant for body weight in the initial two generations of selection. A second cause could be a poor choice of parameters used to solve the index equations. These estimates were from the literature. In order to increase the certainty of the apparent superiority of selection using feed consumption records as in the I_1 lines, it is recommended that the experiment be continued over additional generations.

REFERENCES

- Arboleda, C. R., D. L. Harris, and A. W. Nordskog. 1976a. Efficiency of selection in layer-type chickens by using supplementary information on feed consumption. I. Selection index theory. *Theoretical and Applied Genetics* 48:67-73.
- Arboleda, C. R., D. L. Harris, and A. W. Nordskog. 1976b. Efficiency of selection in layer-type chickens by using supplementary information on feed consumption. II. Application to net income. *Theoretical and Applied Genetics* 48:75-83.
- Baker, R. J. 1974. Selection indexes without economic weights for animal breeding. *Canadian Journal of Animal Science* 54:1-8.
- Berger, J. P. 1976. Multiple-trait selection experiments: Current status, problem areas and experimental approaches. *Proceedings of the International Conference on Quantitative Genetics*. Iowa State University Press, Ames, Iowa.
- Birkmeyer, R. C., Harpal Singh, and A. W. Nordskog. 1982. Effects of the Ea-B and immune response regions of the B complex on body weight and mortality in chickens (Manuscript in preparation).
- Bohren, B. B., W. G. Hill, and A. Robertson. 1966. Some observations on asymmetrical correlated responses to selection. *Genetical Research* 7:44-56.
- Bohren, B. B. 1975. Designing artificial selection experiments for specific objectives. *Genetics* 80:205-220.
- Bordas, A., and P. Merat. 1974. Variabilité génétique et corrélations phénotypiques caractérisant la consommation alimentaire de poule pondeuse après correction pour le poids corporel et la ponte. *Annales de Génétique et Sélection Animale* 6:363-379.
- Bordas, A., and P. Merat. 1981. Genetic variation and phenotypic correlations of food consumption of laying hens corrected for body weight and production. *British Poultry Science* 22:25-33.
- Cunningham, E. P. 1969. *Animal Breeding Theory*. Landbruks Landbruksbokhandelen Oslo. Universitet Forlaget Vollebakk.
- Dickerson, G. E. 1964. Experimental evaluation of a selection theory in poultry. *Genetics Today*. Pergamon Press, Macmillan Company, New York.
- Dickerson, G. E. 1978. Animal size and efficiency: Basic concepts. *Animal Production* 27:367-379.

- Falconer, D. S. 1981. Introduction to quantitative genetics. Longman Incorporated, New York.
- Fairfull, R. W., and R. S. Gowe. 1979. Feed consumption and feed efficiency in selected and control strains of egg stocks under long term selection for a complex of economic traits. Proceedings of Symposium on Selection Experiments in Laboratory and Domestic Animals held at Harrogate, UK on July 21-22, 1979.
- Finney, D. J. 1962. Genetic gains under three methods of selection. *Genetical Research* 3:417-423.
- Foster, W. H., and R. Thompson. 1980. Random genetic drift in an egg-laying strain of poultry. *Genetical Research* 35:231-239.
- French, H. L., and A. W. Nordskog. 1973. Performance of dwarf chickens compared with normal small-bodied chickens. *Poultry Science* 52:1313-1328.
- Greenberg, H. S. 1976. Relationship between body composition and reproductive performance in the laying hen. Ph.D. dissertation. Library, Iowa State University, Ames, Iowa. 98 pp.
- Gowe, R. S. 1976. Comments on the conference. Proceedings of the International Conference on Quantitative Genetics. Iowa State University Press, Ames, Iowa.
- Guill, R. A., and K. W. Washburn. 1974. Genetic changes in efficiency of feed utilization of chicks maintaining body weight constant. *Poultry Science* 53:1146-1154.
- Gyles, N. R., Ali Meeza, and T. L. Goodwin. 1982. Female breeder link to reduced fat in offspring. *Broiler Industry* 48:48.
- Harris, D. L. 1964. Expected and predicted progress from index selection involving estimates of population parameters. *Biometrics* 20:46-72.
- Harris, D. L. 1976a. Past, present and potential contributions of quantitative genetics to applied animal breeding. Proceedings of the International Conference on Quantitative Genetics. Iowa State University Press, Ames, Iowa.
- Harris, D. L. 1976b. What's different about chickens? Proceedings of the International Conference on Quantitative Genetics. Iowa State University Press, Ames, Iowa.
- Hazel, L. N. 1943. The genetic basis for constructing selection indexes. *Genetics* 28:476-490.

- Hazel, L. N., and J. L. Lush. 1942. The efficiency of three methods of selection. *Journal of Heredity* 33:393-399.
- Hill, W. G. 1971. Design and efficiency of selection experiments for estimating genetic parameters. *Biometrics* 27:293-311.
- Hill, W. G. 1972a. Estimation of realized heritabilities from selection experiments. I. Divergent selection. *Biometrics* 28:747-765.
- Hill, W. G. 1972b. Estimation of realized heritabilities from selection experiments. II. Selection in one direction. *Biometrics* 28:767-780.
- Hill, W. G. 1972c. Estimation of genetic change. I. General theory and design of control populations. *Animal Breeding Abstracts* 40:1-15.
- Hill, W. G. 1972d. Estimation of genetic change. II. Experimental evaluation of control populations. *Animal Breeding Abstracts* 40:193-213.
- Hill, W. G. 1976. Variation in response to selection. *Proceedings of the International Conference on Quantitative Genetics*. Iowa State University Press, Ames, Iowa.
- Kempthorne, O. 1976. Status of quantitative genetic theory. *Proceedings of the International Conference on Quantitative Genetics*. Iowa State University Press, Ames, Iowa.
- Koch, R. M., L. A. Swiger, D. Chambers, and K. E. Gregory. 1963. Efficiency of feed use in beef cattle. *Journal of Animal Science* 22:486-494.
- Lee, C. Y., and A. W. Nordskog. 1975. Value of feed consumption records to predict net income in layer-type chickens. *Poultry Science* 54:1912-1918.
- Lin, C. Y. 1980. Relative efficiency of selection methods for improvement of feed efficiency. *Journal of Dairy Science* 63:491-494.
- LSL Information. 1978. Feed conversion: A useful criterion for determining the efficiency of egg production. Lohmann and Company, Luxhaven, West Germany.
- McDonald, D. 1978. Feed intake of laying hens. *World's Poultry Science Journal* 34:209-221.
- Merat, P., A. Bördas, and G. Coquerelle. 1979. The relationship of several genes suppressing plumage colour with body weight, food intake and feather loss of laying hens. *British Poultry Science* 20:587-594.

- Merat, P., and A. Bordas. 1979. Effects associated with the pea-comb gene on chick weight, and body weight and food efficiency of adult hens. *British Poultry Science* 20:463-472.
- Morris, J. P., L. S. Palmer, and Cornelia Kennedy. 1933. Fundamental food requirements for the growth of the rat. VII. An experimental study of inheritance as a factor influencing food utilization in the rat. University of Minnesota Agricultural Experiment Station Technical Bulletin 92.
- Nicholas, F. W. 1980. Size of population required for artificial selection. *Genetical Research* 35:85-105.
- Nordskog, A. W. 1976a. Introductory Statement: Poultry. Proceedings of the International Conference on Quantitative Genetics. Iowa State University Press, Ames, Iowa.
- Nordskog, A. W. 1976b. Success and failure of quantitative genetic theory in poultry. Proceedings of the International Conference on Quantitative Genetics. Iowa State University Press, Ames, Iowa.
- Nordskog, A. W., H. L. French, Jr., C. R. Arboleda, and D. W. Casey. 1972. Breeding of efficiency of egg production. *World's Poultry Science Journal* 29:175-188.
- Nordskog, A. W., H. French, and S. L. Balloun. 1969. Direct versus indirect estimation of feed efficiency as a measure of performance. *Poultry Science* 48:1303-1310.
- Nordskog, A. W., and J. Hardiman. 1979. Inbreeding depression and natural selection as factors limiting progress from selection in poultry. Proceedings of Symposium on Selection Experiments in Laboratory and Domestic Animals, held at Harrogate, UK on July 21-22, 1979.
- Nordskog, A. W., W. A. Rishell, and D. M. Briggs. 1973. Influence of B locus blood groups on adult mortality and egg production in the White Leghorn chicken. *Genetics* 75:181-189.
- Nordskog, A. W., H. S. Tolman, D. W. Casey, and C. Y. Lin. 1974. Selection in small populations of chickens. *Poultry Science* 53:1188-1219.
- North, M. O. 1980. Egg mass: Your best production index. *Poultry Digest* 39:136-140.
- Osborne, R. 1957. The use of sire and dam family averages in increasing the efficiency of selective breeding under a hierarchical mating system. *Heredity* 11:93-116.

- Pym, R. A. E., and P. J. Nicholls. 1979. Selection for food conversion in broilers: Direct and correlated responses to selection for body-weight gain, food consumption and food conversion ratio. *British Poultry Science* 20:73-86.
- Roberts, R. C. 1981. The growth of mice selected for large and small size in relation to food intake and the efficiency of conversion. *Genetical Research* 38:9-24.
- Roberts, R. C., E. Yuksel, and W. G. Hill. 1979. Selection for efficiency of food conversion in the mouse. *Proceedings of Symposium on Selection Experiments in Laboratory and Domestic Animals held at Harrogate, UK, on July 21-22, 1979.*
- Sheldon, B. L. 1980. Prospectives for poultry genetics in the age of molecular biology. *World's Poultry Science Journal* 36:143-173.
- Smith, H. F. 1936. A discriminant function for plant selection. *Annals of Eugenics* 7:240-250.
- Singh, Harpal. 1976. Selection for feed efficiency in broilers. Ph.D. dissertation. Library, Punjab Agricultural University, Ludhiana, India. 97 pp.
- Sutherland, T. M., F. E. Biondini, L. H. Haverland, D. Pettus, and W. B. Owen. 1970. Selection for rate of gain, appetite and efficiency of feed utilization in mice. *Journal of Animal Science* 31:1049-1057.
- Swiger, L. A., K. E. Gregory, L. J. Susption, B. C. Breidenstein, and V. H. Arthand. 1965. Selection index for efficiency of beef production. *Journal of Animal Science* 24:418-424.
- Wang, C. T., G. E. Dickerson, S. E. Hadden, and R. D. Allrich. 1979. Physiological responses to selection for rate and efficiency of post weaning growth in rats. *Proceedings of Symposium on Selection Experiments in Laboratory and Domestic Animals held at Harrogate, UK, on July 21-22, 1979.*
- Williams, J. S. 1962. The evaluation of a selection index. *Biometrics* 18:375-393.
- Wilson, P. N. 1973. *The biological efficiency of protein.* Edited by J. G. W. Jones. Cambridge University Press (England).
- Wilson, S. P. 1969. Genetic aspects of feed efficiency in broilers. *Poultry Science* 48:487-495.

Wing, T. L. 1981. Importance of individual feed records in breeding for feed efficiency in layer-type chickens. Ph.D. dissertation. Library, Iowa State University, Ames, Iowa. 117 pp.

Wing, T. L., and A. W. Nordskog. 1982a. Use of individual feed records in a selection program for egg production efficiency. I. Heritability of the residual component of feed efficiency. Poultry Science 61:226-230.

Wing, T. L., and A. W. Nordskog. 1982b. Use of individual feed records in a selection program for egg production efficiency. II. Effectiveness of different selection indexes. Poultry Science 61:231-235.

Yamada, Y., Kunio Yokouchi, and Akira Nishida. 1975. Selection index when genetic gains of individual traits are of primary concern. Japanese Journal of Genetics 50:33-41.

Young, S. S. Y. 1961. A further examination of the relative efficiency of three methods of selection for genetic gains under less-restricted conditions. Genetical Research 2:106-121.

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APPENDIX A:
TABLES OF YEAR-GENERATION MEANS FOR VARIOUS TRAITS

Table A1. Mean body weight at 20 weeks of age (grams)

Selection criteria	Population	Line	Year-generation				
			1977-0	1978-1	1979-2	1980-3	1981-4
I ₁	Q	A ₁	1207.0 ± 7.3	1178.2 ± 9.7	1357.3 ± 12.3	1240.3 ± 10.6	1217.3 ± 11.0
		A ₂	1207.0 ± 7.3	1202.3 ± 12.7	1330.8 ± 11.6	1299.5 ± 10.0	1303.8 ± 10.2
	R	C ₁	1183.5 ± 5.7	1094.4 ± 8.4	1214.3 ± 12.7	1216.7 ± 10.9	1220.7 ± 11.1
		C ₂	1183.5 ± 5.7	1108.8 ± 10.0	1244.0 ± 13.0	1198.5 ± 11.2	1216.3 ± 12.1
	Pooled		1195.2 ± 6.5	1144.5 ± 5.3	1282.8 ± 6.8	1240.3 ± 5.6	1248.5 ± 5.9
I ₂	Q	B ₁	1231.8 ± 5.7	1146.7 ± 9.6	1263.6 ± 11.0	1223.2 ± 12.3	1272.1 ± 10.6
		B ₂	1231.8 ± 5.7	1176.0 ± 12.2	1392.8 ± 12.3	1326.5 ± 13.5	1381.0 ± 12.6
	R	D ₁	1181.9 ± 6.0	1096.1 ± 10.0	1225.2 ± 10.9	1174.0 ± 10.6	1237.0 ± 11.0
		D ₂	1181.9 ± 6.0	1081.7 ± 9.2	1196.9 ± 10.7	1146.6 ± 9.0	1163.3 ± 8.9
	Pooled		1206.8 ± 5.8	1127.6 ± 5.5	1271.8 ± 6.6	1215.2 ± 6.5	1261.0 ± 6.5
Control	Q	A ₃	1207.0 ± 7.3	1102.2 ± 8.9	1239.1 ± 11.1	1192.7 ± 9.7	1127.4 ± 10.4
		B ₃	1231.8 ± 5.7	1138.2 ± 9.8	1249.7 ± 10.9	1223.4 ± 12.0	1199.1 ± 10.4
	R	C ₃	1183.5 ± 5.7	1059.0 ± 7.7	1213.6 ± 11.2	1135.0 ± 9.6	1195.0 ± 11.5
		D ₃	1181.9 ± 6.2	1062.1 ± 7.6	1140.5 ± 8.7	1091.4 ± 8.4	1100.4 ± 8.1
	Pooled		1201.0 ± 6.2	1089.1 ± 4.5	1212.5 ± 5.6	1159.6 ± 5.4	1156.0 ± 5.4

Table A2. Mean body weight at 32 weeks of age (grams)

Selection criteria	Population Line	Year-generation					
		1977-0	1978-1	1979-2	1980-3	1981-4	
I ₁	Q	A ₁	1642.2 ± 10.9	1579.7 ± 15.1	1714.6 ± 19.8	1565.4 ± 13.8	1566.8 ± 15.4
		A ₂	1642.2 ± 10.9	1635.2 ± 18.3	1686.6 ± 18.1	1607.4 ± 14.4	1643.3 ± 14.5
	R	C ₁	1628.2 ± 11.1	1529.1 ± 13.9	1645.4 ± 19.3	1630.9 ± 20.1	1760.6 ± 24.2
		C ₂	1628.2 ± 11.1	1574.1 ± 19.2	1698.5 ± 17.7	1600.4 ± 20.8	1686.5 ± 20.8
	Pooled		1635.2 ± 11.0	1578.8 ± 8.4	1684.9 ± 9.4	1599.5 ± 8.5	1657.6 ± 9.6
I ₂	Q	B ₁	1703.2 ± 14.7	1557.7 ± 17.0	1645.0 ± 17.8	1622.6 ± 20.0	1742.4 ± 18.0
		B ₂	1703.2 ± 14.7	1573.7 ± 19.7	1802.0 ± 16.5	1734.4 ± 17.3	1885.1 ± 18.9
	R	D ₁	1645.1 ± 10.5	1551.1 ± 16.4	1653.4 ± 16.2	1583.3 ± 18.5	1753.4 ± 19.6
		D ₂	1645.1 ± 10.5	1526.2 ± 17.9	1573.1 ± 16.9	1539.1 ± 14.8	1585.0 ± 14.4
	Pooled		1674.2 ± 12.8	1553.9 ± 9.1	1671.7 ± 9.2	1621.2 ± 9.5	1739.4 ± 10.2
I ₃	Q	A ₃	1642.2 ± 10.9	1443.9 ± 15.9	1518.8 ± 15.0	1462.2 ± 12.7	1443.0 ± 17.5
		B ₃	1703.2 ± 14.7	1483.2 ± 14.5	1570.8 ± 15.2	1523.4 ± 12.7	1549.3 ± 12.9
	R	C ₃	1628.2 ± 11.1	1460.4 ± 13.5	1552.5 ± 15.1	1469.6 ± 17.1	1598.3 ± 18.3
		D ₃	1645.1 ± 10.5	1488.1 ± 11.6	1493.9 ± 15.2	1394.0 ± 13.7	1473.4 ± 13.2
	Pooled		1654.7 ± 11.9	1469.2 ± 7.0	1535.4 ± 7.7	1461.4 ± 7.3	1515.7 ± 8.1

Table A3. Mean age at first egg (days)

Selection criteria	Population	Line	Year-generation					
			1977-0	1978-1	1979-2	1980-3	1981-4	
I ₁	Q	A ₁	165.8 ± 0.9	173.5 ± 1.6	172.2 ± 1.3	179.3 ± 1.3	175.4 ± 1.6	
		A ₂	165.8 ± 0.9	169.7 ± 1.5	174.5 ± 1.5	181.4 ± 1.6	181.3 ± 1.4	
		R	173.7 ± 0.9	188.7 ± 1.7	183.1 ± 1.3	185.5 ± 1.5	182.8 ± 1.6	
	Pooled	C ₁	173.7 ± 0.9	189.2 ± 1.7	183.8 ± 1.4	193.3 ± 1.8	182.4 ± 2.1	
		C ₂	169.7 ± 0.8	180.2 ± 0.9	178.7 ± 0.7	184.3 ± 0.7	180.4 ± 0.8	
	I ₂	Q	B ₁	166.1 ± 1.2	169.9 ± 1.6	179.3 ± 1.4	186.6 ± 1.7	176.7 ± 1.8
			B ₂	166.1 ± 1.2	171.0 ± 1.7	170.6 ± 1.1	181.6 ± 1.3	179.0 ± 1.7
			R	177.4 ± 1.2	182.7 ± 2.1	175.6 ± 1.3	179.9 ± 1.4	176.3 ± 1.5
		Pooled	D ₁	177.4 ± 1.2	183.8 ± 1.9	178.4 ± 1.4	188.9 ± 1.8	176.2 ± 1.5
D ₂			171.7 ± 1.1	176.1 ± 0.9	175.8 ± 0.7	184.1 ± 0.8	177.0 ± 0.8	
I ₃	Q	A ₃	165.8 ± 0.9	169.2 ± 1.5	169.5 ± 1.3	176.0 ± 1.3	168.1 ± 1.3	
		B ₃	166.1 ± 1.2	169.9 ± 1.7	172.9 ± 1.3	181.0 ± 1.8	178.8 ± 1.8	
		R	173.7 ± 0.9	180.7 ± 1.8	171.3 ± 1.3	176.0 ± 1.7	166.7 ± 1.3	
	Pooled	C ₃	177.4 ± 1.2	185.9 ± 1.8	178.4 ± 1.5	186.6 ± 1.5	177.9 ± 1.9	
		D ₃	170.7 ± 1.1	176.5 ± 0.9	173.1 ± 0.7	179.9 ± 0.8	173.4 ± 0.9	

Table A4. Mean 32-week egg weight (grams)

Selection criteria	Population	Line	Year-generation				
			1977-0	1978-1	1979-2	1980-3	1981-4
I ₁	Q	A ₁	52.7 ± 0.2	52.8 ± 0.4	54.9 ± 0.4	54.7 ± 0.3	53.4 ± 0.4
		A ₂	52.7 ± 0.2	53.8 ± 0.3	55.0 ± 0.4	54.6 ± 0.3	56.1 ± 0.2
	R	C ₁	52.1 ± 0.2	51.5 ± 0.3	53.8 ± 0.3	53.4 ± 0.3	55.2 ± 0.4
		C ₂	52.1 ± 0.2	52.3 ± 0.4	54.2 ± 0.3	53.0 ± 0.5	54.2 ± 0.6
	Pooled		52.4 ± 0.2	52.6 ± 0.2	54.5 ± 0.2	54.0 ± 0.2	54.9 ± 0.2
I ₂	Q	B ₁	53.6 ± 0.3	54.6 ± 0.4	56.9 ± 0.5	57.7 ± 0.4	59.0 ± 0.4
		B ₂	53.6 ± 0.3	54.9 ± 0.4	58.0 ± 0.4	56.2 ± 0.4	58.5 ± 0.5
	R	D ₁	53.1 ± 0.2	53.6 ± 0.3	54.6 ± 0.3	54.0 ± 0.3	55.3 ± 0.4
		D ₂	53.1 ± 0.2	51.9 ± 0.3	52.0 ± 0.2	50.8 ± 0.4	52.1 ± 0.3
	Pooled		53.3 ± 0.2	53.9 ± 0.2	55.5 ± 0.2	54.6 ± 0.2	56.2 ± 0.2
Control	Q	A ₃	52.7 ± 0.2	52.4 ± 0.4	52.3 ± 0.3	52.5 ± 0.4	51.8 ± 0.4
		B ₃	53.6 ± 0.3	54.4 ± 0.4	55.6 ± 0.4	55.4 ± 0.4	53.2 ± 0.4
	R	C ₃	52.1 ± 0.2	50.9 ± 0.4	53.3 ± 0.4	51.3 ± 0.3	51.8 ± 0.4
		D ₃	53.1 ± 0.2	53.1 ± 0.3	54.1 ± 0.3	51.7 ± 0.4	53.0 ± 0.3
	Pooled		52.9 ± 0.2	52.8 ± 0.2	54.0 ± 0.2	52.8 ± 0.2	52.5 ± 0.2

Table A5. Mean rate of lay to 34 weeks of age (percent)

Selection criteria	Population	Line	Year-generation				
			1977-0	1978-1	1979-2	1980-3	1981-4
I ₁	Q	A ₁	75.5 ± 0.8	78.7 ± 1.4	77.9 ± 1.5	77.3 ± 1.2	78.8 ± 1.6
		A ₂	75.5 ± 0.8	78.7 ± 1.1	79.7 ± 1.1	80.1 ± 0.8	78.6 ± 1.1
	R	C ₁	77.9 ± 0.8	77.3 ± 1.2	76.2 ± 1.4	75.0 ± 1.4	71.7 ± 2.0
		C ₂	77.9 ± 0.8	78.8 ± 1.3	76.6 ± 1.4	74.3 ± 1.9	81.2 ± 1.7
	Pooled		76.7 ± 0.8	78.4 ± 0.6	77.6 ± 0.7	76.9 ± 0.7	77.8 ± 0.8
I ₂	Q	B ₁	74.3 ± 1.0	78.7 ± 1.1	76.4 ± 1.2	74.6 ± 1.4	76.9 ± 1.1
		B ₂	74.3 ± 1.0	77.3 ± 1.3	80.3 ± 0.8	80.4 ± 1.4	80.6 ± 1.3
	R	D ₁	78.9 ± 0.8	79.0 ± 1.6	79.3 ± 1.2	73.9 ± 1.9	79.2 ± 1.2
		D ₂	78.9 ± 0.8	80.0 ± 1.6	81.8 ± 1.2	75.1 ± 1.7	78.9 ± 1.3
	Pooled		76.6 ± 0.9	78.6 ± 0.7	79.5 ± 0.6	76.0 ± 0.8	78.9 ± 0.6
Control	Q	A ₃	75.5 ± 0.8	79.4 ± 1.1	82.7 ± 0.7	80.4 ± 1.0	76.7 ± 1.4
		B ₃	74.3 ± 1.0	77.9 ± 1.4	77.8 ± 1.0	78.0 ± 0.9	76.4 ± 1.4
	R	C ₃	77.9 ± 0.8	74.8 ± 1.8	81.1 ± 1.1	76.7 ± 1.7	80.4 ± 1.8
		D ₃	78.9 ± 0.8	77.9 ± 1.3	80.1 ± 1.2	70.6 ± 1.7	80.4 ± 1.6
	Pooled		76.6 ± 0.8	77.6 ± 0.7	80.3 ± 0.5	76.5 ± 0.7	78.3 ± 0.8

Table A6. Mean egg mass output at 32 weeks (grams per day).

Selection criteria	Population	Line	Year-generation				
			1977-0	1978-1	1979-2	1980-3	1981-4
I ₁	Q	A ₁	40.6 ± 0.4	40.5 ± 0.7	47.1 ± 0.8	41.9 ± 0.8	43.9 ± 0.7
		A ₂	40.6 ± 0.4	40.7 ± 0.6	46.3 ± 0.8	42.8 ± 0.6	45.2 ± 0.4
	R	C ₁	42.2 ± 0.4	40.7 ± 0.7	42.9 ± 0.8	41.5 ± 0.8	43.0 ± 0.7
		C ₂	42.2 ± 0.4	42.0 ± 0.7	43.6 ± 0.5	41.0 ± 1.05	44.8 ± 1.1
	Pooled		41.4 ± 0.3	41.0 ± 0.3	45.0 ± 0.4	41.9 ± 0.4	44.4 ± 0.3
I ₂	Q	B ₁	40.2 ± 0.5	41.6 ± 0.6	46.3 ± 0.7	43.5 ± 0.8	45.7 ± 0.7
		B ₂	40.2 ± 0.5	41.2 ± 0.7	48.2 ± 0.6	44.8 ± 0.8	47.8 ± 0.8
	R	D ₁	43.6 ± 0.4	43.7 ± 0.5	44.5 ± 0.7	42.7 ± 0.9	45.1 ± 0.6
		D ₂	43.6 ± 0.4	43.0 ± 0.6	43.7 ± 0.6	39.7 ± 1.0	42.0 ± 0.7
	Pooled		41.9 ± 0.3	42.3 ± 0.3	45.8 ± 0.3	42.7 ± 0.5	45.1 ± 0.4
Control	Q	A ₃	40.6 ± 0.4	40.4 ± 0.6	45.0 ± 0.6	40.5 ± 0.8	40.4 ± 0.6
		B ₃	40.2 ± 0.5	41.8 ± 0.7	46.0 ± 0.6	42.5 ± 0.7	42.2 ± 0.8
	R	C ₃	42.2 ± 0.4	40.4 ± 0.7	43.5 ± 0.7	40.3 ± 0.8	42.7 ± 0.8
		D ₃	43.6 ± 0.4	42.5 ± 0.6	45.5 ± 0.6	38.7 ± 1.1	43.4 ± 0.8
	Pooled		41.6 ± 0.3	41.4 ± 0.3	45.1 ± 0.3	40.5 ± 0.4	42.2 ± 0.4

Table A7. Mean feed consumption during 30-34 weeks of age (grams per day)

Selection criteria	Population	Line	Year-generation				
			1977-0	1978-1	1979-2	1980-3	1981-4
I ₁	Q	A ₁	87.5 ± 0.9	89.9 ± 1.3	98.4 ± 1.4	87.5 ± 1.0	95.9 ± 1.2
		A ₂	87.5 ± 0.9	91.8 ± 1.4	97.1 ± 1.1	80.1 ± 0.8	100.2 ± 1.0
	R	C ₁	93.0 ± 0.8	91.0 ± 1.2	99.2 ± 1.7	89.8 ± 2.0	94.6 ± 2.0
		C ₂	93.0 ± 0.8	92.7 ± 1.6	101.0 ± 1.5	89.7 ± 1.8	97.9 ± 2.1
	Pooled		90.2 ± 0.8	91.3 ± 0.7	99.0 ± 0.7	90.8 ± 0.7	97.6 ± 0.7
I ₂	Q	B ₁	88.6 ± 1.1	89.1 ± 1.5	95.1 ± 1.2	89.0 ± 1.3	103.2 ± 1.4
		B ₂	88.6 ± 1.1	92.5 ± 1.5	103.1 ± 0.9	98.5 ± 1.1	114.4 ± 1.4
	R	D ₁	95.3 ± 0.9	95.4 ± 1.5	104.6 ± 1.5	97.3 ± 1.9	107.7 ± 1.3
		D ₂	95.3 ± 0.9	92.3 ± 1.8	98.2 ± 1.7	90.6 ± 1.5	100.0 ± 1.4
	Pooled		91.9 ± 1.0	92.2 ± 0.8	100.4 ± 0.7	94.1 ± 0.8	106.2 ± 0.7
Control	Q	A ₃	87.5 ± 0.9	88.5 ± 1.1	92.9 ± 1.1	86.7 ± 1.0	93.8 ± 1.3
		B ₃	88.6 ± 1.1	87.8 ± 1.4	95.0 ± 0.9	89.8 ± 1.1	96.9 ± 1.4
	R	C ₃	93.0 ± 0.8	86.2 ± 1.5	100.2 ± 1.2	87.2 ± 1.8	98.8 ± 1.4
		D ₃	95.3 ± 0.9	94.1 ± 1.1	99.1 ± 1.4	84.3 ± 1.8	92.6 ± 1.7
	Pooled		91.1 ± 0.9	89.3 ± 0.7	96.6 ± 0.6	87.0 ± 0.7	95.5 ± 0.7

Table A8. Mean feed efficiency during 30-34 weeks of age (egg mass/feed consumption)

Selection criteria	Population	Line	Year-generation				
			1977-0	1978-1	1979-2	1980-3	1981-4
I ₁	Q	A ₁	0.451 ± 0.004	0.437 ± 0.007	0.478 ± 0.008	0.473 ± 0.009	0.456 ± 0.007
		A ₂	0.451 ± 0.004	0.436 ± 0.007	0.472 ± 0.006	0.449 ± 0.006	0.450 ± 0.006
	R	C ₁	0.445 ± 0.004	0.437 ± 0.006	0.411 ± 0.007	0.440 ± 0.010	0.432 ± 0.007
		C ₂	0.445 ± 0.004	0.439 ± 0.006	0.417 ± 0.005	0.433 ± 0.010	0.434 ± 0.010
	Pooled		0.448 ± 0.004	0.437 ± 0.003	0.445 ± 0.004	0.451 ± 0.004	0.445 ± 0.004
I ₂	Q	B ₁	0.443 ± 0.006	0.456 ± 0.008	0.484 ± 0.006	0.477 ± 0.007	0.435 ± 0.007
		B ₂	0.443 ± 0.006	0.436 ± 0.007	0.467 ± 0.006	0.450 ± 0.007	0.413 ± 0.007
	R	D ₁	0.439 ± 0.004	0.445 ± 0.005	0.411 ± 0.006	0.420 ± 0.008	0.415 ± 0.006
		D ₂	0.439 ± 0.004	0.445 ± 0.006	0.422 ± 0.006	0.420 ± 0.010	0.417 ± 0.006
	Pooled		0.441 ± 0.005	0.445 ± 0.003	0.447 ± 0.003	0.441 ± 0.004	0.420 ± 0.003
Control	Q	A ₃	0.451 ± 0.004	0.457 ± 0.007	0.481 ± 0.005	0.463 ± 0.008	0.428 ± 0.007
		B ₃	0.443 ± 0.006	0.461 ± 0.007	0.482 ± 0.006	0.469 ± 0.008	0.422 ± 0.007
	R	C ₃	0.445 ± 0.004	0.444 ± 0.006	0.428 ± 0.008	0.437 ± 0.009	0.423 ± 0.007
		D ₃	0.439 ± 0.004	0.446 ± 0.005	0.448 ± 0.006	0.430 ± 0.010	0.445 ± 0.007
	Pooled		0.444 ± 0.003	0.452 ± 0.003	0.463 ± 0.003	0.451 ± 0.004	0.429 ± 0.004

APPENDIX B:

SUPPLEMENT PAPER: SIGNIFICANCE OF BODY WEIGHT AS A
PERFORMANCE PARAMETER

SIGNIFICANCE OF BODY WEIGHT AS A
PERFORMANCE PARAMETER¹

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Abstract

The laying performance of different body weight classes, defined on both a genetic and phenotypic scale, was compared. The distribution of pedigreed Leghorn breeders of both sexes was truncated, on the basis of 30 week body weight, into two classes: light (L) or heavy (H). The progeny then were classified according to parental mating types as either L x L, L x H, or H x H. Differences among these progeny groups defined the genetic scale. The phenotypic scale was derived separately by phenotypic truncation of the progeny distribution into light (L), medium (M), and heavy (H) body weight classes at 30 weeks.

Differences in rate of lay and in egg mass output between classes were in poor agreement with respect to the two scales. Light birds were poorest egg producers on the phenotypic scale but were the best egg producers on the genetic scale. Superior egg production by the heavy-bird class during the late spring and early summer months of the year could not be demonstrated. Deviations in body weight sharply reflected poorer performance on the phenotypic scale, but not the genetic scale. This emphasizes the dominant role of management, feeding, and disease control over the genetic influence in maintaining optimum size for satisfactory productivity.

Introduction

Commercial breeders and producers have recognized the importance of body weight in egg-type chickens, although its functional relationship to production traits is not well-understood. Body weight, per se, is an important indicator of general health. Also, a minimum body size is required for the production of satisfactory egg size for the commercial market. The maintenance of satisfactory body weight requires careful attention to nutrition, management practices, and disease control. Body weight can easily be changed through breeding because it is highly heritable and, hence, is highly responsive to selection.

The unique aspect of the present study is the contrast of two scales of measurement, one "phenotypic" and one "genetic," to measure the influence of body weight on performance. Additionally, some data are presented which bear on the question of optimum body size as related to seasonal performance.

Materials and Methods

Each of two White Leghorn populations, Q and R, maintained as a set of 6 sublines, are currently undergoing selection using different indexes (Wing and Nordskog, 1982). The indexes were designed to study the relationship of feed efficiency to egg production. For each population, 48 sires and 288 dams were used per generation. The observations taken on individual birds include age at first egg, body weight, rate of lay, egg weight, daily egg mass, daily feed consumption, and feed conversion (feed consumption/egg mass). Observations were recorded in

period 1 and 30 to 34 weeks of age and in period 2 at 50 to 54 weeks of age. Rate of lay was measured from first egg to 34 weeks of age (P34) and to 66 weeks of age (P66).

The data on body weights at 30 weeks of age for the parents of the last two generations, consisted of 1458 and 1366 birds in populations Q and R, respectively. These were truncated into a light group (L) and a heavy group (H), below and above the mean, respectively. In this way, the chance-determined assortative mating effects of body weight among the parents, measured as differences between the progeny of three mating classes, L•L, (L•H + H•L)/2, and H•H, served as estimates of genetic effects of body weight. The first and second letters of each class represent the phenotypic size class of the male and female parents, respectively. The genetic body size classes generated in the progeny were light (L•L), intermediate (L•H and H•L combined), and heavy (H•H).

Birds of the same generation also were assigned to three classes, light (L), medium (M), and heavy (H), based on their 30-week body weight, which served as a conventional phenotypic scale. The points of truncation for forming the three classes were chosen such that the number of birds in each of the phenotypic classes was the same as those in each genetically-determined class. The same generation of birds served as the basis for both the genetic and phenotypic analyses.

Rates of lay of the different body weight classes for the winter and summer months were also contrasted. For population Q, the "winter" and "summer" records spanned from December through March and from April

through June, respectively. Correspondingly, in population R, the winter and summer records spanned from January through April and from May through July, respectively. However, the temperature in the hen houses was controlled to 60°F (15.6°C) in winter and to about 85°F (29.4°C) in the summer; houses were ventilated with electric fans. It should be understood that the terms, "winter" and "summer," are used in the context defined here.

In addition to the above analysis, the data of the last four generation-years were subjected to a conventional regression analysis with 30-week body weight as the independent variable. Phenotypic and genetic regression coefficients were each computed within lines and years. The latter were estimated from the sire components of variance using Harvey's (1977) mixed-model computer program.

Results

Truncation analysis

The comparative performances of the different body weight classes, averaged over both generations and periods and derived both phenotypically and genetically as defined in the Methods section, are presented in Tables B1 and B2. No consistent trend for age at sexual maturity, with respect to either phenotypic or genetic body weight classes, was observed.

On the phenotypic scale (Table B1), a significant trend is noted in egg weight, egg mass, and feed consumption reflecting a strong positive association of these traits with body weight. Feed conversion in

Table B1. Mean performance of body weight classes based on a phenotypic scale

Trait	Unit	Population Q			Population R			Combined		
		Light	Medium	Heavy	Light	Medium	Heavy	Light	Medium	Heavy
Body weight at 32 weeks	g	1378.0 ^a	1602.3 ^b	1859.6 ^c	1336.1 ^a	1548.4 ^b	1782.8 ^c	1357.0 ^a	1575.4 ^b	1821.2 ^c
Age at first egg	days	169.6 ^a	173.6 ^b	171.7 ^{a,b}	182.5 ^a	181.4 ^a	183.3 ^a	176.0 ^a	177.5 ^a	177.5 ^a
Rate of lay	%	71.4 ^a	71.9 ^a	69.5 ^b	71.0 ^a	74.1 ^b	72.6 ^c	71.2 ^a	73.0 ^b	71.0 ^a
Egg weight	g	55.4 ^a	57.0 ^b	59.3 ^c	54.4 ^a	56.1 ^b	57.6 ^c	54.9 ^a	56.6 ^b	58.4 ^c
Egg mass	g/day	40.4 ^a	42.5 ^b	43.4 ^c	39.9 ^a	43.1 ^b	43.8 ^c	40.2 ^a	42.8 ^b	43.6 ^c
Feed consumed	g/day	87.3 ^a	95.7 ^b	102.1 ^c	86.5 ^a	97.2 ^b	103.6 ^c	86.9 ^a	96.5 ^b	102.8 ^c
Feed conversion ^d	g/g	2.29 ^a	2.40 ^b	2.53 ^c	2.44 ^a	2.39 ^a	2.56 ^b	2.34 ^a	2.40 ^a	2.54 ^b

^{a,b,c} Means on the same line for Light, Medium, and Heavy classes of each population, with different superscripts, are significantly different from one another.

^d Feed consumed/egg mass.

Table B2. Mean performance of body weight classes based on a genetic scale

Trait	Unit	Population Q			Population R			Pooled		
		Light	Medium	Heavy	Light	Medium	Heavy	Light	Medium	Heavy
Body weight at 32 weeks	g	1506.7 ^a	1611.8 ^b	1699.8 ^c	1465.5 ^a	1573.4 ^b	1657.4 ^c	1486.1 ^a	1592.6 ^b	1678.6 ^c
Age at first egg	days	172.0 ^a	171.8 ^a	171.4 ^a	181.2 ^a	181.9 ^a	183.6 ^a	176.6 ^a	176.8 ^a	177.5 ^a
Rate of lay	%	71.7 ^a	70.6 ^b	70.8 ^{a,b}	73.3 ^a	73.1 ^a	73.4 ^a	72.5 ^a	71.8 ^b	72.1 ^{a,b}
Egg weight	g	56.3 ^a	57.3 ^b	58.0 ^c	55.4 ^a	56.1 ^b	56.7 ^c	55.8 ^a	56.7 ^b	57.4 ^c
Egg mass	g/day	42.0 ^a	42.0 ^a	42.3 ^a	42.1 ^a	42.6 ^a	43.4 ^b	42.0 ^a	42.3 ^a	42.8 ^b
Feed consumed	g/day	92.6 ^a	95.1 ^b	96.7 ^c	93.7 ^a	96.4 ^b	99.7 ^c	93.2 ^a	95.8 ^b	98.2 ^c
Feed conversion ^d	g/g	2.31 ^a	2.42 ^b	2.47 ^b	2.37 ^a	2.45 ^b	2.46 ^b	2.34 ^a	2.44 ^b	2.46 ^b

^{a,b,c}Means on the same line for Light, Medium, and Heavy classes of each population, with different superscripts, are significantly different from one another.

^dFeed consumed/egg mass.

the heavy class was significantly the lowest in both populations which reflects the higher body maintenance requirement. The medium weight class was the highest in rate of lay in both populations.

On the genetic scale (Table B2), differences in egg weight, egg mass, and feed consumption followed the same trend as on the phenotypic scale (Table B1). On the other hand, feed conversion was consistently lowest, in both populations, for the light weight class. The difference between the medium and heavy classes in feed conversion favored the latter in both populations but not significantly so. For the rate of lay, the light class was highest in population Q and in the combined data, although differences between classes were small and not consistent.

Undoubtedly, the poorer rate of lay of the light class reflects morbidity on the phenotypic scale, but this would not be reflected on the genetic scale; smaller birds lay smaller eggs at a faster rate, as expected. This probably accounts for the apparent discrepancy among phenotypic classes in egg-mass output and in feed conversion. Phenotypically, lighter birds, on the average, produce the lowest egg mass because this class would include more unhealthy birds than the heavier classes. This "morbidity" bias is responsible for the so-called body weight egg production paradox discussed by Nordskog and Briggs (1968). Evidently, the maintenance of optimum body weight is dependent more on proper nutrition, management, and disease control than on genetically-determined body size.

Seasonal effects

Rates of lay for body weight classes, as observed from "winter" and "summer" seasonal records, are presented in Table B3. Even though the R population was hatched one month later than Q, differences between season means should not be confounded by age differences. On a phenotypic scale, the medium class had the highest egg rate in both the "summer" and "winter" tests. On the genetic scale, body size class differences were not significantly different by populations or seasons. Thus, our data fail to demonstrate that heavy birds, on either a phenotypic or on a genetic scale, are superior in egg production over smaller sized birds.

Regression analysis

The phenotypic, $b(P)$, and genetic, $b(G)$, regression coefficients for the different traits on body weight are presented in Table B4. For age at first egg, $b(P)$ is negative and nonsignificant, but $b(G)$ is positive and statistically significant. For rate of lay, the $b(P)$ are positive and highly significant and the $b(G)$ are small and nonsignificant. For the remaining traits, egg weight, egg mass, feed consumption, and feed conversion, the $b(P)$ and $b(G)$ were in fair agreement. The regressions for feed conversion were positive and, except for the first feeding period, P30-34, were nonsignificant.

In general, the regression analysis predicts that, for a 100 g body weight increase on the phenotypic scale, age at first egg is expected to decrease by .13 days. At the same time, the following increases are

Table B3. Rate of lay for different body size classes averaged over two years in "winter" and "summer" records

Season	Population	Phenotypic class			Genetic class		
		Light	Medium	Heavy	Light	Medium	Heavy
Winter	Q	70.6 ^a	71.1 ^a	67.7 ^b	71.2 ^a	69.7 ^a	69.4 ^a
	R	71.4 ^a	76.2 ^b	75.5 ^b	74.5 ^a	75.3 ^a	74.4 ^a
	Combined	71.0 ^a	73.6 ^b	71.6 ^a	72.8 ^a	72.5 ^a	71.9 ^a
Summer	Q	63.4 ^a	64.4 ^a	61.6 ^a	64.4 ^a	62.8 ^a	62.9 ^a
	R	63.4 ^a	64.4 ^b	61.6 ^c	64.4 ^a	62.8 ^a	64.8 ^a
	Combined	63.6 ^a	67.0 ^b	62.1 ^a	64.8 ^a	63.5 ^a	63.8 ^a

a,b,c, Means having different superscripts for body weight classes (Light, Medium, and Heavy), within seasons and populations, are significantly different from one another.

Table B4. Phenotypic and genetic regression coefficients (pooled over populations) of different traits on body weight (unit = 100 g)

Trait	Unit	Period ^a	Phenotypic, b(P)	Genetic, b(G)
Age at first egg	days		-0.13	0.43**
Rate of lay	%	P34	1.12**	0.30
	%	P66	1.14**	-0.02
Egg weight	g	P32	0.86**	0.57**
	g	P52	0.62**	0.25**
Egg mass	g/day	P30-34	1.25**	0.59**
	g/day	P50-54	0.89**	0.36**
Feed consumed	g/day	P30-34	4.11**	3.39**
	g/day	P50-54	3.94**	3.58**
Feed conversion ^b	g/g	P30-34	0.03**	0.05
	g/g	P50-54	0.04	0.08

^aPeriods: P34 = first egg to 34 wks
P66 = first egg to 66 wks
P32 = at 32 wks
P52 = at 52 wks
P30-34 = 30 to 34 wks
P50-54 = 50 to 54 wks.

^bFeed consumed/egg mass.

**P < .01.

predicted: rate of lay, 1%; egg weight, .62 to .86 g; egg mass output, .9 to 1.2 g; daily feed consumption, 4 g; and feed conversion, .03 to .04 units. On the genetic scale, a 100 g increase in body weight is expected to increase age at first egg by .43 days, change rate of lay by -.02 to .3%, increase egg weight by .25 to .57 g, increase egg mass by .36 to .59 g, increase feed consumption by 3.4 to 3.6 g per day, and increase feed efficiency by .05 to .08 units. Thus, the predicted changes in the production traits, associated with body weight differences, are less, as might be expected, on the genetic than on the phenotypic scale.

Discussion

The problem to determine optimum body weight for a given set of environmental conditions remains. It has been hypothesized that small-sized strains, with concomitant lower feed intake in hot climates, are more prone to early nutritional deficiencies than are large-bodied birds; they are, therefore, at a disadvantage in hot environments. This hypothesis suggests that an optimum body weight that maximizes performance exists for each unique environment.

The study demonstrates that the influence of body weight on layer performance generally is greater on a phenotypic than on a genetic scale. This is a consequence of the difference in composition of the genetic vs. environmental components of body weight. Critical roles played by genetics in determining bone framework and that of environment on fleshing (condition) has been demonstrated by Tierce (1973). An

attempt to more fully understand the significance of optimum body weight in a given environment is illustrated in Figure B1. Different strains may have different optimum weights on the genetic scale on which is superimposed an environmental scale. Birds deviating phenotypically from this optimum body size would lead to poorer layer performance. A loss in body weight may be caused by morbidity or malnourishment; excessive weight may result from overfeeding or improperly balanced diets. Deviations from optimum body weight, caused genetically, may not seriously reduce production performance because the genetic curve is flat-topped.

This study does not lend support to the hypothesis that heavier birds, because of their increased feed intake, perform better in hot climates. In the present study, the large-bodied class of hens laid eggs at the lowest rate in the summer. Similar observations have also been reported by Horst and Petersen (1975). They compared layer performance at normal (20°C) and high (34°C) ambient temperatures of different body weight classes formed by assortative mating based on the body weight of parents. The large-bodied hens did not excel in performance over the small and medium size classes.

Huston et al. (1957) compared the performance of a light breed (White Leghorn) and two heavy breeds (White Plymouth Rock and New Hampshire) under variable temperatures (42.6°F to 61.5°F) and high temperature (90°F). A significant decline in egg production was observed for the heavy breeds maintained at the high temperature but not for the Leghorns.

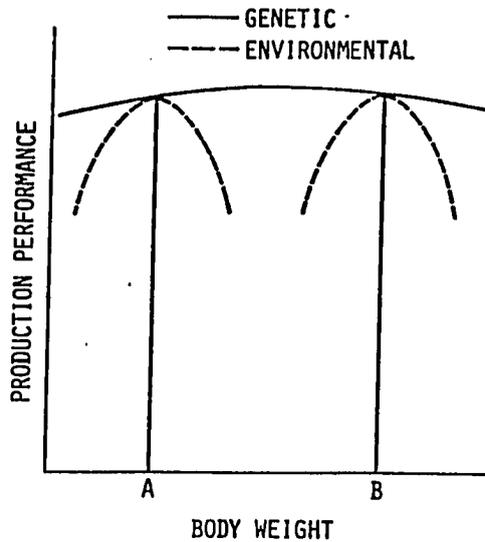


Figure B1. The influence of body weight on egg production looked at hypothetically from both a genetic and environmental point of view. The genetic curve (solid line) is considered the maximal limit of egg production if total environment (i.e., management, feeding, and disease control) is ideal. However, because of genetic differences between strain A and strain B in body weight and other performance traits, their total performance may differ. On the other hand, any suboptimal treatment of total management, such as underfeeding or overfeeding, will lower performance (dotted line).

Emmans and Chalres (1977) compared the performance of Shaver 288 and Warren SSL layer strains at 16, 20, 22, and 25°C. Egg production declined with a temperature increase for Shaver 288 birds, but not for the Warren SSL. They attributed the poorer performance of Shaver 288 to limiting nutrients caused by less feed intake. The possibility of genotype x environment interaction, however, cannot be ruled out. For example, the Warren SSL strain may be genetically more capable to withstand the effects of high temperature. Evidence of genetic differences in heat tolerance have been reported by Huston et al. (1957) and Ahmad et al. (1967).

Havenstein (1977) reported no significant difference in egg production between two strain crosses differing in body weight. He acknowledged the possibility of strain x environment interaction for rate of lay and recognized that small-bodied layers were efficient egg producers per unit of feed consumed.

The hypothesis that genetically heavier birds are superior in hot environments or under stress conditions merits further experimental testing. Genetic differences between strains to withstand stress would be confounded with strain differences in body size. Ideally, populations should differ in body size, but otherwise, should have a common genetic background.

References

- Ahmad, N. M., R. E. Moreng, and H. D. Muller. 1967. Breed responses in body temperature to elevated environmental temperature and ascorbic acid. *Poultry Sci.* 46:6-15.
- Emmans, G. L., and D. R. Chalres. 1977. Climatic environment and poultry feeding in practice: Nutrition and the climatic environment. Butterworth Groups (Publishers), Inc., Boston, MA.
- Harvey, W. R. 1977. User's guide for LSML76 mixed model least-squares and maximum likelihood computer program. Ohio State University, Columbus, OH.
- Havenstein, G. B. 1977. Comparisons of genetically related Leghorn strains differing in body weight. Proceedings 19th British Poultry Breeder's Roundtable, Edinburgh, Scotland.
- Horst, P., and J. Petersen. 1975. Untersuchungen zur Auswirkung hoher Umwelttemperaturen auf die Leistungsreaktion von Legehennen unterschiedlichen Körpergewichtes. *Arch. Geflügelkd.* 39:225-321.
- Huston, T. M., W. P. Joiner, and J. L. Carmon. 1957. Breed differences in egg production of domestic fowl held at high environmental temperature. *Poultry Sci.* 36:1247-1254.
- Nordskog, A. W., and D. M. Briggs. 1968. The body weight egg production paradox. *Poultry Sci.* 47:498-504.
- Tierce, J. F. 1973. Genetic aspects of body weight and growth parameters as related to reproductive performance in the fowl. Ph.D. Dissertation, Iowa State University, Ames, IA. Univ. Microfilm 74-583, Ann Arbor, MI.
- Wing, T. L., and A. W. Nordskog. 1982. Use of individual feed records in a selection program for egg production efficiency. I. Heritability of the residual component of feed efficiency. *Poultry Sci.* 61:226-230.