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Long-term selection for 8-week body weight in chickens – direct and correlated responses

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Summary. A bidirectional selection experiment for 8-week body weight in chickens was conducted. In addition to 27 generations of selection, random samples were chosen from each selected line in generations 6, 13, 19 and 26 to initiate lines in which selection was relaxed. Genetic change was evident in the selected high-weight line through the first 75% of the study after which response in the direction opposing selection occurred. Selection for low body weight resulted in considerable reduction in body size, particularly in the last quarter of the study. Correlated responses evaluated were body weight at several ages, conformation, age at onset of lay, various reproductive and egg quality traits and ratio (female : male) of some traits. Data from lines where selection was relaxed indicated that natural selection opposed artificial selection with the effects greater in later generations.

Key words: Long-term selection – Chickens – Body weight – Relaxed selection – Correlated responses – Reproduction

Introduction

Genetic factors influencing long-term artificial selection for a quantitative trait are difficult to evaluate, both in their occurrence and their effects. Although response to truncation selection for a single trait is a function of additive genetic variation and selection intensity, other factors are involved when artificial selection is carried on for many generations (Eisen 1980).

For example, rate of fixation of alleles (Robertson 1960), mutation (Frankham 1980), genetic drift (Hill 1971), changes in fitness (Verghese and Nordskog 1968), inbreeding depression (Nordskog and Hardiman 1980), change in variance of selected trait (Clayton and Robertson 1957), and approach of genetic and/or physiological limits (Lerner 1954; Robertson 1960) can influence responses observed in a long-term selection experiment. Some or all of these factors may be operating at any particular time, and their effects can alter other influences, resulting in a dynamic system that is difficult to assess. Bidirectional selection can further complicate interpretations – a topic discussed in detail by several authors (see Falconer 1981).

Artificial selection in conjunction with maintenance in a laboratory environment protects animals from environmental influences which may involve natural selection (e.g., predation, pathogens, parental care, shortage of food, severe climatic fluctuations). Also, rapid changes in gene frequencies contribute to inbreeding depression and homeostasis. In chickens, selection for increased or decreased body weight can reduce general fitness, which is often manifested in lowered reproductive performance (Dunnington et al. 1984; Siegel and Dunnington 1985).

Body weight, a trait generally considered as having moderate heritability, has often been used as the criterion of selection in experiments designed to examine both direct and correlated genetic changes in populations undergoing artificial selection. In chickens, with a generation interval of approximately one year, few single trait selection experiments have been carried out as far as the one reported herein. In addition to 27 generations of bidirectional, individual pedigreed selection for high and low body weight at eight weeks of age, relaxation of selection at various points in the experiment was evaluated. Data concerning the crossing of selected lines will be presented in a subsequent paper.

Materials and methods

Stocks and husbandry

The base population for this study was obtained by crossing seven inbred lines of White Plymouth Rocks which had been developed at Virginia Tech (Siegel 1978). Every generation, chicks were hatched on the first and third Tuesdays in March and wingbanded to uniquely identify their pedigree. Other than routine husbandry, the only disease preventatives were addition of a coccidiostat to the diet and vaccination for Marek's disease which commenced after the 17th generation of selection. Through generation 13, birds were maintained in littered floor pens. Thereafter, they were reared on litter to 126 days of age, and then housed individually in wire cages. Throughout the study, feed and water were provided ad libitum and the same feed formulations were used – chick starter until 8 weeks of age, chick developer from 8–20 weeks of age and breeder diet after 20 weeks. Percentages of protein were 20, 16 and 16 and levels of metabolizable energy were 2,685, 2,761 and 2,772 kcal/kg in the starter, developer and breeder diets, respectively.

Selection

Parents were chosen solely on the basis of 8-week body weight to develop lines selected for high (HWS) and low (LWS) juvenile body weight. The number of parents selected per generation to reproduce each line are given in Table 1. As a genetic control, a sample of at least 360 eggs from the Athens-Canadian Randombred population (Marks and Siegel 1971) was incubated with those from the selected lines. Chicks of all lines were hatched and maintained as contemporaries. This procedure was followed each generation except for the parental and 27th generations, when control-line chicks were not hatched.

Beginning in generations 6, 13, 19 and 26, HWS and LWS individuals were randomly chosen before selecting parents for the subsequent generation, to begin lines in which selection was relaxed. Those lines originating from HWS were designated HWR1, HWR2, HWR3 and HWR4 and those from LWS were LWR1, LWR2, LWR3 and LWR4, respectively. Relaxed populations were maintained by random mating – pooled semen was used to inseminate females. Twenty dams were used to reproduce relaxed lines each generation. Five males were used for R1 and R2, and 10 for R3 and R4. Relaxed populations 1, 2 and 3 were maintained for seven or eight generations; HWR4 and LWR4 were in the second generation of relaxation at the time of this writing.

Unselected traits

Each generation, individual body weights were obtained for the entire population at 4 weeks of age and for all females at 24 and 38 weeks. Breast angle (Siegel 1962) was measured in degrees at 8 weeks of age in all chickens from lines HWS and LWS.

Age at first egg was determined when the first egg was laid, provided that a second egg was laid within the next 9 days. Egg production data from age at sexual maturity to a fixed date (240 or 300 days of age, depending on the specific generation) were obtained for all females that produced eggs during that period. In the later generations of selection, age at first egg in line LWS was biased downward because an increasing number of pullets did not begin to produce eggs by 240 days of age.

Table 1. Number of selected parents used to perpetuate lines HWS and LWS each generation

No. of selected parents		Generations	
Males	Females	HWS	LWS
8	48	1 – 4	1 – 4
12	48	5 – 8	5 – 25
14	56	9 – 27	26 – 27

During generations 0 through 13, egg production was calculated as the percentage of ovipositions per hen-day from sexual maturity to a fixed date. Since egg production data were obtained by trap-nesting, floor eggs reduced accuracy. Maintenance of pullets in individual cages in generations 14 through 27 enabled classification of each egg (Middelkoop and Siegel 1976) as normal, extra-calcified, compressed, broken, double yolked or otherwise defective (e.g., membranous, soft shelled, rough shelled). Percentage hen-day normal egg production was then used as the measure of production.

For three consecutive days at approximately 34 weeks of age, egg quality data were obtained for each pullet (Siegel 1963). Egg weight and albumen height were recorded and used to calculate Haugh units. Specific gravity was assessed by floating each egg in solutions of increasing salinity and designated by a score of 1–9 (1 having the lowest specific gravity). Blood and meat spots of each egg were scored from 1–6 according to the following classification:

1 – no spots
2 – small meat spot(s) – less than 0.6 cm
3 – large meat spot(s) – 0.6 cm or larger
4 – small blood spot(s) – less than 0.6 cm
5 – large blood spot(s) – 0.6 cm or larger
6 – meat and blood spots

For chickens selected to reproduce the populations each generation, percentages of fertility, hatch of fertile eggs and hatch of total eggs incubated were recorded. These data were based on natural mating through generation 13 and on artificial insemination thereafter.

Statistical analyses

Realized heritabilities were calculated as cumulative response regressed on cumulative effective selection differential (both in standard deviation units). Because this selection experiment did not conform to two of the assumptions necessary for calculation of standard errors of heritability (Hill 1972), namely, few generations of selection and little inbreeding, they were not calculated. Levels of significance based on standard errors obtained from regression analyses are biased downward (Hill 1972).

Regressions of 8-week body weight and correlated traits on generation were calculated in the selected lines from generation 0–27. Division of generations into overlapping intervals corresponding to the propagation of the relaxed lines (0–7, 6–14, 13–20 and 19–27) provided regressions where selected and relaxed lines could be compared.

Possible changes in degree of sexual dimorphism were evaluated by dividing the mean of traits in females by the corresponding mean in males and expressing the ratios in percentages.

Body weights and egg weights were transformed to common logarithms and percentages to arc sine square roots prior to analyses. Egg quality data were based on the average value for three days' collection of eggs.

Results

Inbreeding and genetic control line

Rate of change of inbreeding for lines HWS and LWS, calculated from the effective number of parents (Falconer 1981), averaged 1.5% per generation and accrued to 39.3 and 39.0, respectively, by the 27th generation of selection.

Regression of control flock means for 8-week body weight on generation were -0.81 ± 1.03 and -0.77 ± 1.13 g for females and males, respectively. These results showed that environmental trends did not appreciably alter 8-week body weight in unselected chickens.

Direct responses

Separation of the divergently selected lines in generation 25 from the original base population is illustrated by frequency distributions (Fig. 1). Linear regressions of control-adjusted, 8-week body weight means on generation (Table 2) indicated that responses to selection were similar in males and females and symmetrical in both directions. Response, however, was non-linear in line HWS and linear in line LWS (Fig. 2). Control-adjusted means of 8-week body weight regressed upon generation were calculated for generation intervals which corresponded to the series of relaxed lines (Table 2). The general pattern was similar for both sexes. Although change in line HWS was realized from generation 0 through 20, approximately 43% of that change was lost during the last quarter of the selection experiment, perhaps due, in part, to inbreeding depression. Greatest response in line LWS occurred in the first and last quarters of the study, with less downward change also being obtained in generations 6 through 20. Comparisons of each incremental regression in the relaxed lines showed that cessation of artificial selection stopped response in the direction of selection (generations 6 through 20) and caused regression of means towards control levels (generations 19 through 27).

Table 2. Regressions of control-adjusted 8-week body weight (g) on generation

	Generation intervals				
	0–27	0–7	6–14	13–20	19–27
Females					
HWS	15**	30**	18**	23*	-14^{+}
HWR			3	−9	−26**
LWS	−16**	−21*	-11^{+}	-14^{+}	−24*
LWR			1	1	−13*
Males					
HWS	18**	45**	26*	25*	-20^{+}
HWR			6	-22^{+}	−32**
LWS	−20**	−20**	-13^{+}	-17^{+}	−32**
LWR			2	1	−18*

$^{+}$ ($P<0.10$); * ($P<0.05$); ** ($P<0.01$) indicate regressions which were significantly different from zero

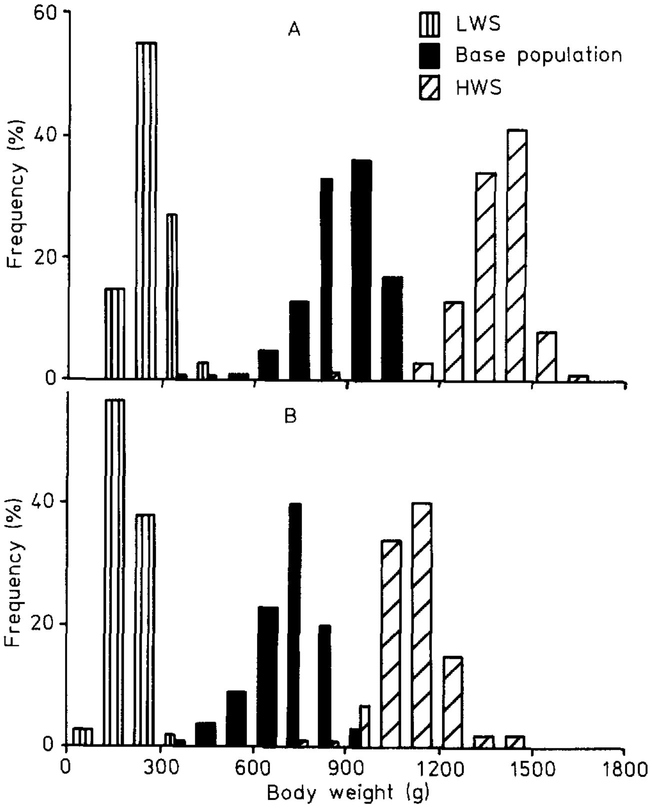

Fig. 1. Frequency distribution of 8-week body weight calculated in 100 g increments for males (**A**) and females (**B**) in the original base population and selected lines HWS and LWS in generation 25

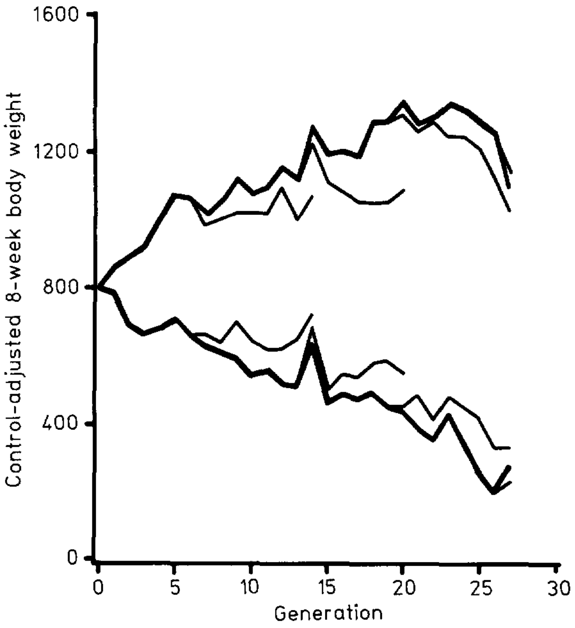

Fig. 2. Control-adjusted 8-week body weight (g) of chickens selected for high and low 8-week body weight (———) as well as samples in which selection was relaxed (———)

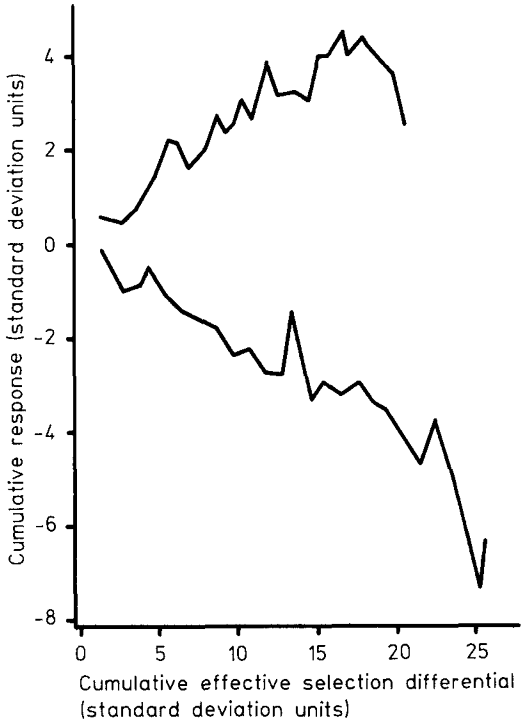

Fig. 3. Cumulative responses versus cumulative effective selection differentials (both in standard deviation units) of chickens (data for males and females combined) selected for high and low 8-week body weight

Table 3. Regressions of cumulative response on cumulative effective selection differential (in standard deviation units)

Line	Generation intervals				
	0-27	0-7	6-14	13-20	19-27
HWS	0.18**	0.31**	0.29**	0.24**	-0.28**
LWS[a]	-0.22**	-0.18**	-0.14**	-0.18**	-0.49**

** Indicates regressions which were significantly different ($P<0.01$) from zero

[a] The negative sign indicates a positive heritability in this line

Within-line realized heritabilities of 8-week body weight, were combined for males and females within each selected line. Cumulative response and selection differential were greater in the low than in the high line (Fig. 3), with overall heritabilities similar in the high and low directions (Table 3). Change due to additive genetic variation in the direction of selection occurred through 20 generations of selection with heritabilities greater in magnitude occurring in line HWS. From generations 19–27, however, realized heritabilities in line HWS were negative due to responses opposing the direction of selection. In contrast, the largest responses in line LWS occurred during generations 19 through 27.

Correlated responses

Body weights at 4, 24 and 38 weeks of age. Overall regressions (0 through 27 generations) of 4-week body weights on generation were symmetrical in the HWS and LWS lines and similar for males and females (Table 4, Fig. 4). Most of the changes in 4-week weight occurred during the first quarter of selection in line HWS and in the last quarter in line LWS. Body weights of HWS females at 24 and 38 weeks of age, assessed by a second order regression over 27 generations of selection in line HWS, followed a non-linear ($R^2=0.58$) rather than linear ($R^2=0.04$) course. Large increases in adult body weights during the first quarter of selection for high 8-week body weight were counteracted by linear decreases later in the experiment. In line LWS, 24- and 38-week body weights in females decreased considerably and at a rather consistent rate throughout selection.

Relaxation of selection generally resulted in 4-, 24- and 38-week body weights deviating toward control levels. These deviations occurred at greater rates when selection was relaxed in the later than earlier generations of selection.

Breast angle. Although breast angle increased during selection in line HWS, it decreased to a much greater

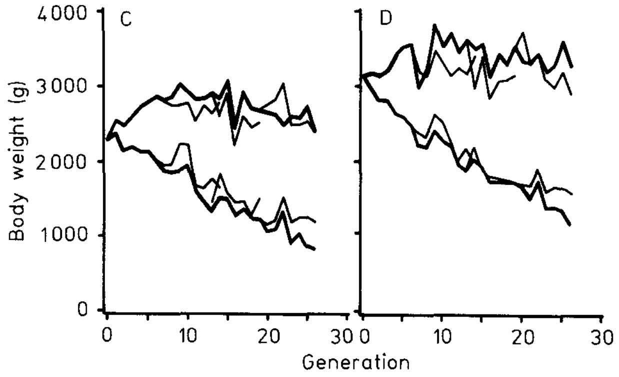

Fig. 4. Means (g) of 4-week body weight in females (**A**), 4-week body weight in males (**B**), 24-week body weight in females (**C**) and 38-week body weight in females (**D**) during 27 generations of selection for high and low 8-week body weight (———) and during relaxation of selection (———)

Table 4. Regressions of 4-, 24- and 38-week body weights (g) and breast angles (degrees) on generation

	Generation intervals				
	0 – 27	0 – 7	6 – 14	13 – 20	19 – 27
4-week Weight (Males)					
HWS	6**	17*	6	3	3*
HWR			4	–6	–5
LWS	–6**	–6	–6	–6^{+}	–10*
LWR			–2	0	–3
4-week Weight (Females)					
HWS	5**	14*	4	3	3
HWR			1	–5	–3
LWS	–5**	–5	–7^{+}	–5	–8*
LWR			–4	1	–2
24-week Weight (Females)					
HWS	–2	78**	–2	–35	–22
HWR			–16	–67	–55^{+}
LWS	–58**	–55**	–81**	–45*	–53*
LWR			–55^{+}	–41	–3
38-week Weight (Females)					
HWS	4	28	34	–28	–10
HWR			–12	–54	–99**
LWS	–65**	–114**	–59**	–43**	–73**
LWR			–61*	–60*	–20
Breast Angle (Males)					
HWS	0.17*	0.15	0.90**	–0.27	–0.57
HWR			0.73**	–0.46	0.04
LWS	–1.05**	–0.71	–0.18	–1.85**	–2.21**
LWR			0.25	–0.46	–0.61
Breast Angle (Females)					
HWS	0.15^{+}	–0.06	0.85**	–0.29	–0.42
HWR			0.50^{+}	–0.43	–0.11
LWS	–1.13**	–0.67	–0.55	–1.61*	–2.10**
LWR			–0.07	–1.06	–0.79

$^{+}$ ($P<0.10$); * ($P<0.05$); ** ($P<0.01$) indicate regressions which were significantly different from zero

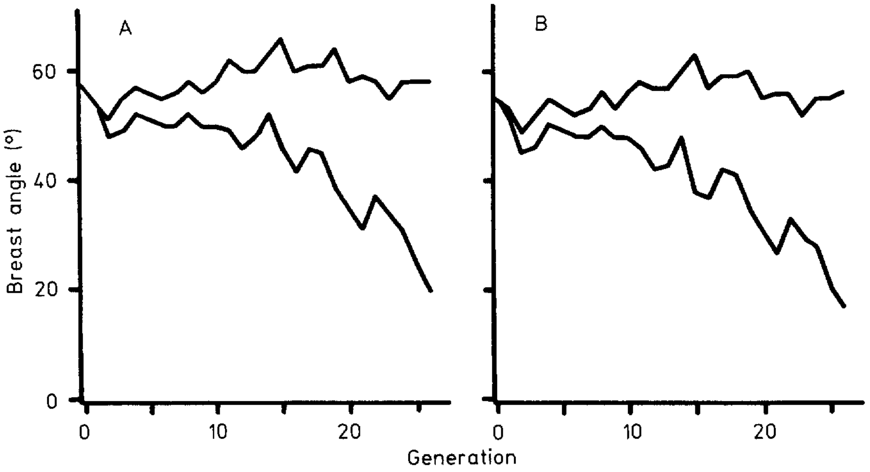

Fig. 5. Mean breast angle (degrees) in males (**A**) and females (**B**) during 27 generations of selection for high and low 8-week body weight

extent in line LWS, with responses being similar for males and females (Table 4, Fig. 5). In line HWS, a large increase occurred from generations 6 through 14, which was a lag of several generations behind the increases in body weights. In the second half of the selection experiment, however, reductions in breast angle occurred. In line LWS, greatest decreases in breast angle were during the second half of the experiment, again occurring after those for body weights.

Relaxation of selection was accompanied by regression of breast angle toward control levels in all cases in low-weight chickens and through generation 20 in high-weight chickens.

Sexual dimorphism. The ratio of means for a trait (female : male) was used to assess changes in sexual dimorphism during selection. In line HWS, sexual dimorphism ratios for 4- and 8-week weights and breast angles were not altered during selection (Table 5). In LWS birds, however, significant reductions in ratios occurred, particularly during generations 6 through 14. These negative regressions were contrary to what was expected. Males should have decreased in weight faster than females due to the greater selection intensity practiced in males. Since means and variances were correlated for body weight, scaling might have influenced the analyses. Results were essentially the same whether untransformed or logarithm-transformed data were analyzed suggesting that scaling was not influential. Relaxed lines closely followed trends of corresponding increments in selected populations.

Changes in correlations. Product-moment correlations between 8-week weight (selected trait) and other weight and conformation traits were calculated each generation. The regressions of these correlations on generation (Table 6) indicated that, in line HWS, no significant changes in correlations occurred over time. In line LWS, breast angle, 4-week weight of males and 38-week weight of females became more closely associated with 8-week weight during the course of selection.

Changes in reproductive performance. Age at first egg increased in both selected lines, with a relatively greater increase in LWS than HWS pullets (Table 7). A decrease in age at first egg in line HWS during the first quarter of selection was followed by trends towards increased age at first egg and then a plateauing during the last fourth of the experiment. In line LWS the opposite occurred – a large delay in age at sexual maturity (generations 6–14) was followed by modest changes during the remainder of the study. This observation may have been an artifact because means were based on those individuals which commenced lay by a fixed age.

Extremely low-weight chickens are often unable to commence egg production (Dunnington et al. 1984). In generations 10 through 23, approximately 85% of females in line LWS matured by 240 days of age. In generations 24 and 25, percentage of females maturing dropped to 49 and 39%, respectively. As a result, parents of generation 27 had a greater mean body weight than the entire generation 26 population from which they were selected (i.e., selection pressure was negative). This reversal of selection resulted in 73% of LWS females maturing by 240 days of age in generation 27. When Zelenka (unpublished data) increased amounts of ingested food by gavage in immature pullets over 240 days of age, they commenced lay sooner than in those fed ad

Table 5. Regressions of ratio of female to male 4- and 8-week body weights and 8-week breast angles on generation

	Generation intervals				
	0 – 27	0 – 7	6 – 14	13 – 20	19 – 27
Four-week Weight					
HWS	–0.08	–0.26	–0.38	0.08	0.05
HWR			–0.71	0.01	0.34
LWS	–0.16*	0.38	–1.08^{+}	0.01	–0.16
LWR			–1.25^{+}	0.35	0.04
Eight-week Weight					
HWS	–0.04	–0.21	–0.30	0.08	0.24^{+}
HWR			–0.23	0.62	0.09
LWS	–0.19**	–0.02	–0.21	0.16	–0.46
LWR			–0.38	0.39	–0.30
Eight-week Breast Angle					
HWS	–0.03	–0.38^{+}	–0.01	–0.04	0.21
HWR			–0.34	0.02	–0.25
LWS	–0.42**	0.03	–0.76**	0.10	–0.56
LWR			–0.59*	–1.21	–0.87

$^{+}$ ($P<0.10$); * ($P<0.05$); ** ($P<0.01$) indicate regressions which were significantly different from zero

Table 6. Regression of correlations between 8-week body weight and correlated traits on generation

	HWS	LWS
Females		
4-week weight	0.0055	0.0049
8-week breast angle	0.0011	0.0076*
24-week weight	–0.0038	0.0041
38-week weight	–0.0026	0.0084*
Males		
4-week weight	0.0015	0.0062*
8-week breast angle	–0.0010	0.0094**

* ($P<0.05$); ** ($P<0.01$) indicate regressions which were significantly different from zero

Table 7. Regressions of age at first egg (d), percent egg production and percent normal egg production on generation

	Generation intervals				
	0–27[a]	0–7	6–14	13–20	19–27
Age at first egg					
HWS	0.63*	−2.52*	1.28^{+}	2.60	−0.04
HWR			0.93	1.07	−0.31
LWS	1.76**	−0.03	4.48*	−1.51	−1.09
LWR			−0.33	−0.15	−6.11**
Percent production					
HWS	−0.73	−2.87**	2.36^{+}		
HWR			1.62		
LWS	−0.28	−0.71^{+}	0.87*		
LWR			2.40^{+}		
Percent normal production					
HWS	−0.88			2.31	2.57
HWR				−1.24	3.12**
LWS	−0.93**			−0.33	0.24
LWR				−0.74	1.27

$^{+}$ ($P<0.10$); * ($P<0.05$); ** ($P<0.01$) indicate regressions which were significantly different from zero

[a] Generations 0–13 for percent production and generations 14–27 for % normal production

Table 8. Regressions of egg quality measurements on generations

	Generation intervals				
	0–27	0–7	6–14	13–20	19–27
Egg weight (g)					
HWS	−0.06^{+}	−0.03	0.04	0.09	0.58
HWR			0.04	−0.86^{+}	0.54^{+}
LWS	−0.42**	−0.79**	−0.27^{+}	−0.37	0.13
LWR			−0.47**	−0.91	0.19
Specific gravity					
HWS	−0.01	−0.04	0.10	−0.31	−0.07
HWR			0.04	−0.32	−0.14
LWS	0.04**	−0.01	0.19^{+}	−0.16	−0.06
LWR			0.23^{+}	−0.26	−0.23*
Spots					
HWS	−0.02**	−0.03	−0.01	−0.02	0.04
HWR			−0.03	−0.06	0.02
LWS	−0.01	−0.04^{+}	0.01	−0.06^{+}	0.04
LWR			−0.02	0.03	0.05
Haugh units					
HWS	0.04	−0.53	0.04	0.47*	0.68^{+}
HWR			1.06*	1.01	−0.47
LWS	0.09	−0.75^{+}	0.57**	−1.07	1.08*
LWR			0.12	1.18	0.76^{+}

$^{+}$ ($P<0.10$); * ($P<0.05$); ** ($P<0.01$) indicate regressions which were significantly different from zero

Table 9. Average number of offspring per dam in HWS and LWS lines from generations 1–27

Generation	HWS	LWS
01[a]	9.49	10.44
02	10.41	7.94
03	11.61	12.71
04	9.00	10.95
05	9.00	11.25
06	6.68	10.00
07	7.62	11.61
08	7.30	11.90
09	6.46	8.24
10	5.67	7.28
11	6.38	9.69
12	7.69	10.87
13	8.93	9.26
14	6.58	10.45
15	7.86	8.28
16	9.76	11.82
17	8.87	8.38
18	6.32	6.68
19	6.57	5.61
20	6.26	5.24
21	6.12	7.36
22	5.04	7.59
23	8.39	7.89
24	6.07	7.05
25	6.74	7.97
26	6.25	6.46
27	7.54	6.00
Regression of average offspring on generation	−0.11±0.04**	−0.19±0.04**

[a] Offspring of parents of the first selected generation

** ($P<0.01$)

Table 10. Regressions of fertility measurements on generation

	Generation intervals				
	0–27	0–7	6–14	13–20	19–27
Percent fertility[a]					
HWS	0.27	−5.62**	2.88^{+}	2.66	1.48
HWR			4.18^{+}	2.77	
LWS	0.62^{+}	−2.48	2.40^{+}	0.32	2.32
LWR			5.52*	−1.10	
Percent hatch of fertile eggs					
HWS	−0.69*	−2.42*	1.13	1.43	−1.26
HWR			0.96	−3.76*	
LWS	0.32	−2.40^{+}	1.99^{+}	0.13	0.61
LWR			1.37	−2.44	
Percent hatch of total eggs					
HWS	−0.32	−4.17**	1.88	2.85	0.24
HWR			3.38^{+}	−0.42	
LWS	0.57*	−2.32	2.78^{+}	0.08	2.08
LWR			3.84^{+}	−2.56	

$^{+}$ ($P<0.10$), * ($P<0.05$); ** ($P<0.01$) indicate regressions which were significantly different from zero

[a] Natural mating was through generation 13 and artificial insemination thereafter

libitum. Thus, failure to achieve sexual maturity in line LWS females may be attributed to their low levels of feed intake described by Barbato et al. (1984), since it was remedied by reversing selection or increasing feed intake.

Percent hen-day egg production (generations 0–13) and percent normal egg production (generations 14–27) decreased consistently but regressions were statistically different from zero ($P < 0.05$) only for percent normal production in line LWS. Percent production decreased significantly in generations 0 through 7 and increased in generations 6 through 14 in both selected lines. No significant changes in percent normal egg production occurred in either selected line for the remainder of the selection experiment. Relaxation of selection caused a considerable decrease in age at first egg in LWR females and an increase in percent normal egg production in HWR females.

Egg weight decreased and specific gravity increased in line LWS during the first 14 generations of selection and then plateaued (Table 8). No consistent changes in incidence of blood and meat spots or Haugh units were apparent. In line HWS, an overall decrease in spotting was accompanied by initial reductions in egg weight and Haugh units followed by a plateau in egg weight and an increase in Haugh units. The plateaus in egg weight occurring in both selected lines might have signalled an intermediate optimum in egg size for the particular line, as hatchability is lower for larger and smaller eggs (Skoglund et al. 1948). Relaxed lines were not generally different from their selected counterparts for egg quality traits.

Number of progeny produced is a function of many traits. Of the chickens selected as parents for succeeding generations, number of offspring per dam declined in both selected lines (Table 9). Yet, the regression of percent fertility (generations 0 through 27) was generally positive in both selected lines. Interpretation should be cautious because the data are from a biased sample rather than a random sample or the entire population. Also, the mode of reproduction changed from natural mating to artificial insemination in generation 14 and line HWS had lower mating frequency than line LWS (Blohowiak et al. 1980). Both regressions of hatchability were negative in line HWS and positive in line LWS and may have reflected increases in chromosomal aberrations in line HWS (Reddy and Siegel 1977). Percent fertility, percent hatchability of fertile eggs and percent hatchability of total eggs initially decreased in both selected lines (generations 0–7) and then generally increased (Table 10). Although relaxation of selection was accompanied by increased reproductive capabilities in generations 6 through 14, negative trends occurred in generations 13 through 20.

Discussion

Bidirectional selection for body weight at eight weeks of age resulted in dramatic alterations in body size and conformation of White Rock chickens. Males originating from common stock, after 27 generations of selection in the high and low directions, weighed 1,212 and 299 g at 8 weeks of age, respectively. This 4-fold divergence spanned 12.8 genetic standard deviation units and demonstrated ability to successfully alter anatomical characteristics such as size of skeleton, muscle and fat depots as well as behavioral and physiological traits such as feed and oxygen consumption (Dunnington et al. 1985).

Body weight is a function of both chronological age, which was the same in both selected lines, and physiological age, which differed between the lines (Dunnington et al. 1983). Comparisons of HWS and LWS females in the 13th generation showed that the former were 2.3, 2.5, 2.2 and 1.9 times heavier than the latter at 4, 8, 24 and 38 weeks of age, respectively. When comparisons were made after 27 generations of selection, the respective values were 4.1, 4.4, 2.8 and 2.4. These data showed that selection for body weight at 8 weeks of age had a greater effect on body weight during the growing period than later in life. Differences in juvenile weight became accentuated during the latter half of the experiment, while changes in older birds steadily declined. This pattern may be attributable, in part, to inbreeding depression and, in part, to a physiological limit for food consumption. Burkhart et al. (1983) reported that hypothalamic lesioning resulted in hyperphagia in LWS but not HWS females, and concluded that HWS birds had been "genetically lesioned" through selection because intact and lesioned birds were both consuming food at near maximum capacity. On a relative basis, early growth involves more protein deposition while fat is deposited later in life and requires more energy to deposit than protein. This, coupled with the different calorie : protein ratios in the diets fed, may explain the proportionately greater weight of juvenile HWS birds, when compared to LWS birds, and lack of change in proportionate weight with age as selection was continued.

Although an effort was made in this experiment to maintain consistent macroenvironment over generations, external control was not complete and effects of natural selection were manifested in the selected chickens. One example was the precipitous drop in proportion of LWS females maturing by 240 days of age in generations 24 and 25, which indicated that a threshold had been crossed. Another example was the series of reproductive complications (fat content of body, erratic ovulations, chromosomal aberrations, reduction in libido, etc.) correlated with selection in HWS chickens

(Reddy and Siegel 1977; Siegel and Dunnington 1985). Because the high incidence of nonlayers and aberrations in reproductive fitness were ameliorated by relaxation of selection, it was apparent that they were caused by opposition between natural and artificial selection and demonstrate the delicate balance between those two forces. Disruption of reproductive competence and success, through artificial manipulation, is an important phenomenon to understand and anticipate in the present commercial climate of continually expecting more production from fewer animals.

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