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Long Term Selection for Four-Week Body Weight in Japanese Quail under Different Nutritional Environments

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Summary. Individual phenotypic selection for high 4-week body weight was conducted for 40 generations in two lines of Japanese quail under two protein environments. Line P was selected on an adequate 28% protein diet, and line T was selected on a 20% protein diet containing 0.2% thiouracil (TU). In generation 20, a subline R was established by subjecting progeny from the T line to a 20% protein diet; in generation 27, a subline S was developed by subjecting progeny from the T line to a 28% protein diet containing 0.2% TU. Progeny from a non-selected control line (C) were reared with selected lines and sublines in all generations.

Quail in the P line continued to respond to selection for 40 generations; body weights increased from 90 to approximately 200 g. Mean body weights of T line quail peaked in generation 22 and did not appear to show any definite gains thereafter. Body weight responses of sublines R and S were greater than those in the T line and indicate that changing the selection environment following long-term selection may be an effective technique to maximize total selection responses for 4-week body weight in quail. Realized heritability estimates for 4-week body weight were larger in the P line than in the T line in all comparisons. Realized estimates were high (30-45%) for the ten generations 1-10; moderate (15-20%) for generations 11-30, and small (5-10%) for generations 31-40.

Key words: Phenotypic selection – Body weights – Japanese Quail

Introduction

Clayton and Robertson (1957) reported that short-term effects of selection for abdominal bristles in populations of *Drosophila melanogaster* were in fair agreement with theoretical expectation, however, the long-term behavior of these lines were bewilderingly complex. Siegel (1962) and Jaap (1963) found that short term selection responses for 8-week body weight in chickens agreed with expected gains. They observed realized heritabilities of 0.30 to 0.40 for 8-week body weight following four to five generations of selection. There is also evidence that selection responses for early growth in chickens follow predicted patterns for longer periods (Dev et al. 1969; Maloney et al. 1963, 1967). Robertson (1960) proposed a theory of limits in artificial selection, suggesting that the expected limit of individual selection in any population is a function only of N*i*, where N is the effective population size and *i* the selection differential in standard deviation units. Lerner (1954) proposed that self-regulation of populations (genetic homeostasis) is dependent on natural selection favoring intermediate rather than extreme phenotypes. Because responses in early generations of selection are expected to be greater than those in later generations, the nature of selection limits or plateau for early growth becomes an important consideration for future genetic improvement of poultry. The cessation of selection responses may result from either a ceiling or limit (when all relevant loci have become homozygous) or a plateau (Lawrence 1964). The primary difference between these two conditions is that a ceiling is static and final whereas a plateau, being transitory, has a dynamic quality. Response patterns of long-term studies in which selected lines fail to respond to selection for a number of generations and then for no explainable reason again respond to selection (Roberts 1966) suggest that plateaus rather than selection limits may be the most common of the two conditions.

There is no generally accepted theory concerning the cause of plateaus. Lerner (1958) proposed that genetic variability for the trait in question exists in the selected line, but that it is not expressed in the environment in which selection is being practiced. This hypothesis would appear plausable since a fundamental concept of quantitative genetics is that the phenotype of an individual is a function of both its genotype and environment. Contrariwise, Mather and Harrison (1949) also proposed that genetic variability exists in the line, but that it is not available to selection because of disadvantageous linkages which have accumulated between genes determining the trait in question and those determining fitness.

Although hypotheses have been advanced regarding causes of selection plateaus, there has been little investigation into possible ways of breaking or circumventing them. The purposes of this report are to: (1) provide information on long-term selection responses for 4-week body weight in Japanese quail when selection is practiced under different nutritional environments; and (2) explore the concept of changing environments to maximize genetic gains in long-term selection studies.

Materials and Methods

Individual phenotypic selection for high 4-week body weight was conducted for 40 generations in two lines of Japanese quail (*Coturnix coturnix japonica*) under two protein environments. Line P was selected on an adequate 28% protein diet, whereas line T was selected on a 20% protein diet containing 0.2% thiouracil (TU). Details regarding the establishment of these lines and early responses have been reported (Marks and Lepore 1968; Marks 1971). Briefly, both lines originated from a common control population (Marks 1967) and consisted of approximately 400 straight run chicks/line/generation. Random bred control quail were raised intermingled with each population in each of the first 26 generations. Starting in generation 27 and continuing thereafter, controls were reared in the same battery but in separate decks from the selected lines. Within each population and generation, 24 males and 72 females were selected as breeders to produce the first 10 generations. Generations 11-40 were reproduced with 60 paired matings/line.

Two sublines were developed from the T line. Selection for high 4-week body weight was continued in these sublines to investigate the influence of changing the selection environment on ultimate response levels. In generation 20, a subline (R) was established by creating a new nutritional environment consisting of a 20% protein diet. This resulted in the removal of the 0.2% TU stress but the retention of the 20% protein stress in this subline. This line was discarded after six generations of selection under a 20% protein environment. In generation 27 a second subline (S) was established by subjecting chicks from the T line to a 28% protein diet containing 0.2% TU. This subline therefore, had the low protein stress (20% protein diet) removed but retained the TU stress. After establishment, both sublines were maintained and selected in a manner similar to the P and T lines. Nonselected controls were also reared with the sublines to measure environmental variations in these lines across generations.

Realized heritabilities (h^2 = R/S) of the selected trait (4-week body weight) were obtained for each generation by use of controls to correct for environmental variation. Realized heritabilities were also estimated by calculating the regression of mean 4-week body weights on the cumulative selection differentials and from regression of offspring on midparent. Body weight gains across generations were estimated by regressing population means on generation number across the 40 generations and also by 10-generation intervals. Regressions of the deviation of the selected population means from the control means on generation number were also calculated.

Results

The mean 4-week body weights of the controls (PC) reared with the P line remained fairly constant across 40 generations (Fig. 1). The regression of mean weights on generation yielded a small negative regression coefficient of –0.03 g. (Table 1). The regressions by 10-generation intervals were similar, except for the significant ($P \leqslant .05$) value (1.36) observed for generations 21-30. This may be due to the gradual decline in body weights of PC line controls from generations 1-20 (–0.12 and –0.25), apparently as a result of competition for feeder space by the smaller control bird. Starting in generation 27, controls were reared in a separate deck of the brooder to eliminate this factor from possibly influencing the body weights of control birds. A comparative study in generation 26 indicated that the control birds reared in separate decks were 6 to 8 g. heavier than controls reared intermingled with the heavier birds of the selected lines. The improvement in body weights of controls following this management change in generation 27 is evident in fig. 1.

The regression of mean body weights on generation for generations 1-40 in the TC line was –0.46 which was significant at the $P \leqslant .01$ level (Table 1). It appears that the greatest reduction in weights of the TC line occurred during the first 35 generations (Fig. 2). The regression coefficient for this line was 1.70 g. for generations 31-40 (Table 1).

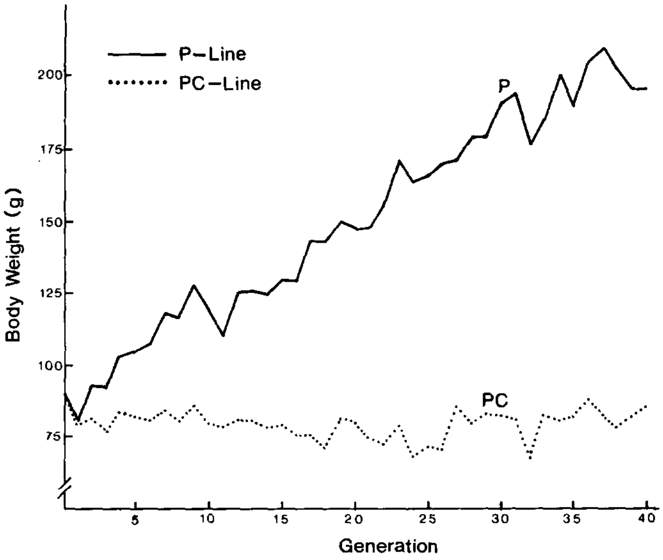

Fig. 1. Four-week body weights of P line and control line (PC) quail by generation following individual phenotypic selection

Table 1. Regression of four-week body weights of selected and control quail lines on generation

	Line				Deviation from control	
	Selected		Control			
Generation	P (g.)	T (g.)	PC (g.)	TC (g.)	P-PC (g.)	T-TC (g.)
1-40	3.01**	1.32**	-0.03	-0.46**	3.00**	1.72**
1-10	4.22**	4.26**	-0.12	0.09	4.29**	4.24**
11-20	3.96**	3.18**	-0.25	0.48	4.21**	2.69**
21-30	3.58**	-0.53	1.36*	-1.34**	2.22*	0.80
31-40	1.83**	2.58*	0.78	1.70*	1.09	0.86

* $P \leq .05$
** $P \leq .01$

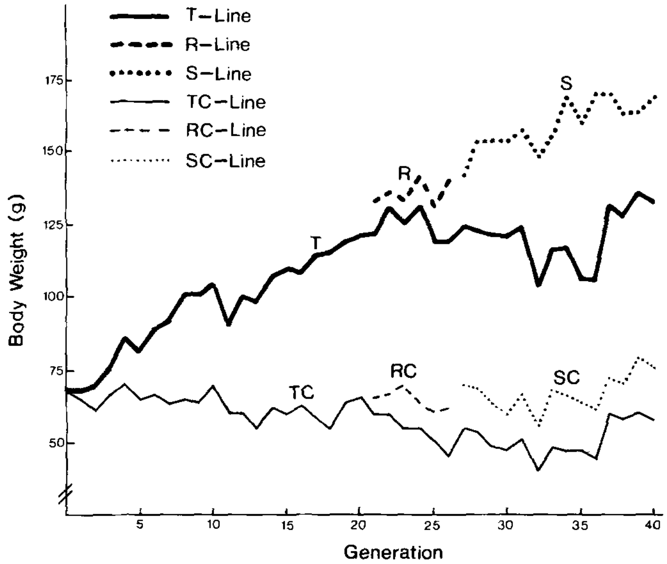

Fig. 2. Four-week body weights of T and TC lines, R and S sublines and control line (RC and SC) quail by generation following individual phenotypic selection

Response to Selection

The 4-week body weights of quail in the P line (selected under a 28% protein environment) continued to respond to selection for 40 generations (Fig. 1); body weights increased from 90.5 g. to approximately 200 g. There is, however, some indication that little progress has been obtained beyond generation 37. The regression coefficient (b) of body weights on generations was 3.01 ± .09 g. (Table 1). This mean gain of 3.01 g./generation for generations 1-40 is similar to the 2.97 g./generation observed during the first 15 generations of selection in this line (Marks 1971). The response of 4-week body weight in the T quail line, where selection occurred under a 20% protein diet containing 0.2% TU was not as great as the response observed in the P line (Fig. 2). The regression coefficient of 4-week body weights on generations 1-40 was 1.32 ± .14 g. (Table 1). This value is considerably less than the 2.78 g. increase/generation observed in the T line during the initial 15 generations of selection (Marks 1971). Regression coefficients of mean body weights on generations for the first 10 generations of selection were similar for the P and T lines (Table 1). Gains declined during each of the subsequent 10-generation intervals in the P line. In the T line, however, fluctuations occurred with the mean gain/generation being 3.18 g. for generations 11-20, –0.53 g. for generations 21-30, and 2.58 g. for generations 31-40.

To eliminate the environmental variation as measured by the controls, regression coefficients were calculated as deviations from the control. Although the regression coefficients (generations 1-40) were not appreciably different from those obtained from the uncorrected P and T line means, the use of controls allowed for a more accurate view of responses by 10-generation intervals (Table 1). There is evidence of a 10-generation lag in the T line compared to the P line with regard to the overall reduction in mean gain across generations (Table 1).

These data suggest that the gain in mean body weights of the P line across generation continues to respond to selection (Fig. 1) even though the control-corrected regression of 1.09 g. for generations 31-40 was not significant, indicating that the response has slowed. Contrariwise, the gain in body weights of the T line appears to have plateaued during the last 20 generations (Fig. 2). The overall downward trend of control body weights (TC), however, precludes any definite comments on the true status of the T line.

The responses of the P and T lines expressed as a percentage of deviation from their respective controls were surprisingly similar (Fig. 3). The rapid response of both lines during the first 25 generations became erratic there-

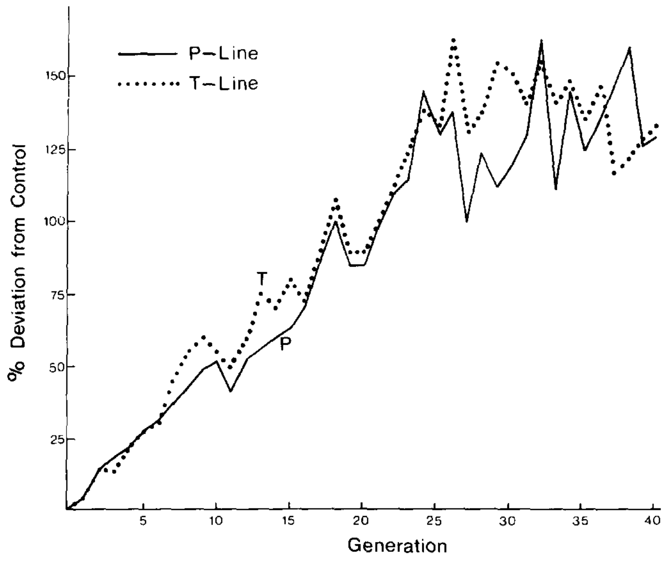

Fig. 3. Percentage deviation from control in P and T line quail by generation

Table 2. Regression of four-week body weight of line T and sublines R and S quail on generation

	Line			Deviation from control		
Generation	T (g.)	R (g.)	S (g.)	T-TC (g.)	R-RC (g.)	S-SC (g.)
21-26	–1.69	0.84	–	1.38	2.28	–
27-40	0.56	–	1.89**	–0.02	–	1.14*

* P ⩽ .05
** P ⩽ .01

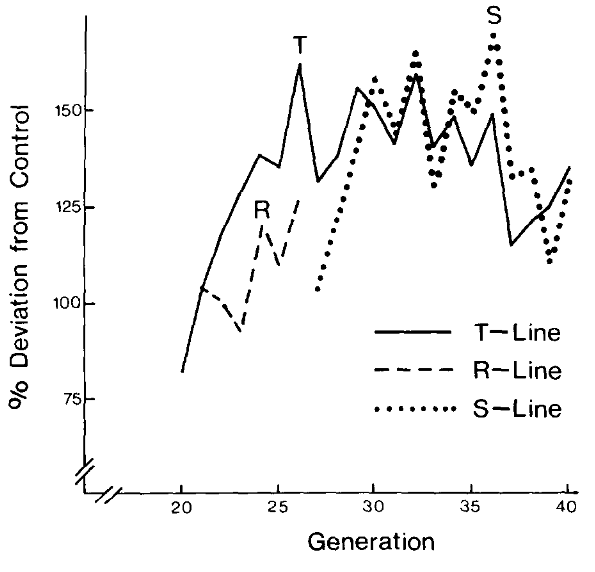

Fig. 4. Percentage deviation from control in the T line and the R and S subline quail for generations 20-40

after. A positive trend in the P line curve after generation 27 appears to be evident, while the corresponding curve for the T line appears to level off or even decline. These data support the hypothesis that P line birds are continuing to show limited responses to selection, while T line birds have perhaps reached a plateau.

Responses of Sublines

Subline R did not show a dramatic response to selection for generations 21-26 (Fig. 2). The mean gain (0.84 g.) per generation was larger, however, than the mean gain observed in the T line (–1.69 g.) for the corresponding generations (Table 2). The regressions of body weights on the deviations from controls also demonstrated greater gains in the subline R than in the T line (2.28 vs. 1.38 g.). When plotted as a percentage deviation from the control (Fig. 4), both lines showed a positive trend across six generations. This positive trend in the T line is present only because of the large negative decline in the control (TC) means.

The gain in mean body weights of birds in the subline S increased steadily from generations 27 to 40 (Fig. 2). The overall trend of the control (SC) also improved and resulted in only a moderate corrected regression coefficient (1.14 g.). Nevertheless, this regression coefficient was significant ($P \leqslant .05$) and much larger than the corresponding value (–0.02) in the T line (Table 2). The responses of sublines R and S indicate that changing the selection environment following long-term selection may maximize total selection responses for 4-week body weight in quail.

Selection Differentials

Differences between the expected (unweighted) and effective (weighted) selection differentials across generations were small and not significant in either the P or T lines (Table 3). Therefore, natural selection has apparently exerted little influence on the reproductive fitness of these lines. The magnitude of the T line selection differentials (generation 0-39) were only slightly greater than corresponding P line values. Selection differentials for generations 0-9, however, were significantly greater in the T line than in the P line. Mean selection differentials for 10 generation intervals thereafter were similar for the P and T lines (Table 3). The size of the selection differentials increased across generations in both lines. This increase was evident for all periods in the P line; however, it did not become visible in the T line until after generation 20. Regression of effective selection differentials on generation yielded significant ($P \leqslant .01$) regression coefficients of

Table 3. Mean selection differentials by 10 generation intervals

	P-line			T-line		
Generation	Expected (g.)	Effective (g.)	*i*	Expected (g.)	Effective (g.)	*i*
0-39	12.38	12.11	0.85	12.57	12.78	0.96
0- 9	9.42	9.26	1.08	11.38	11.39	1.20
10-19	11.15	11.19	0.89	11.12	11.31	0.88
20-29	14.42	13.95	0.76	13.76	13.88	0.95
30-39	14.53	14.04	0.66	14.02	14.52	0.81

$i = \frac{\text{Sel. Diff.}}{\sigma_p}$

0.16 ± .03 and 0.12 ± .02 for the P and T lines, respectively. Expected and effective selection differentials were similar in sublines R and S. The selection differentials of sublines R and S tended to be smaller than corresponding values in the T line. In generations 21-26 the mean selection differential was 11.9 g. in subline R and 12.8 g. in the T line. The difference between the T line and S subline in generations 27-39 was 14.7 g. in the T line and only 10.6 g. in the S line.

The intensity of selection (*i*) obtained by dividing the selection differential by the phenotypic standard deviation (σ_p) of the population (Falconer 1960), decreased across generations in both lines (Table 3). This pattern may in part be due to scaling effects. Significant regression coefficients of –0.014 ± .002 and –0.007 ± .002 were observed in the P and T lines, respectively. Although the increase in the size of the selection differentials was due to increased variation accompanying an increasing population mean, decreasing (*i*) values suggest that the σ_p of these populations increased at a faster rate than the selection differentials. The trends of the (*i*) values, therefore, more accurately reflect the expected trend in actual genetic gain in the selected lines. The (*i*) values were smaller in the R and S sublines than in the parental T line. This difference was approximately 10% less in subline R and 20% less in the subline S. Marks and Lepore (1968) and Marks (1971) noted that the environmental restrictions utilized to formulate the T line environment resulted in greater variability in body weight and larger selection differentials than in the P line during the first 15 generations of selection. Results obtained from this long-term selection study indicate that this situation may occur only during the initial stages of selection because selection differentials in the T line were not different from those in the P line after the initial 20 generations of selection (Table 3).

Table 4. Heritability estimates by line for four-week body weight

	P-Line			T-Line		
Generation	Realized[1]	Realized[2]	b[3]	Realized[1]	Realized[2]	b[3]
1-10	.45	.49 ± .06	.35	.32	.38 ± .02	.32
1-20	.33	.29 ± .02	.31	.24	.21 ± .02	.27
1-30	.28	.28 ± .01	.29	.20	.16 ± .01	.28
1-40	.22	.24 ± .01	.25	.16	.09 ± .01	.24
11-20	.24	.34 ± .04	.27	.17	.28 ± .03	.22
21-30	.24	.24 ± .04	.22	.13	–.03 ± .04	.26
31-40	.09	.14 ± .07	.13	.04	.17 ± .06	.14

[1] Cumulative $h^2 = R/S$
[2] Regression
[3] Regression on mid-parent

Heritabilities

Realized heritability estimates were consistently 0.05 to 0.10 points greater in the P line (Table 4). Realized estimates calculated by two methods [(1) cumulative $h^2 = R/S$ and (2) regression of generation means on cumulative selection differentials] were remarkably similar for the various observation periods. The largest discrepancies occurred in estimates for generations 11-20 in both lines. Regression estimates were approximately 0.10 points greater than those derived by dividing the total response by the cumulative selection differentials (Table 4). In the T line, this discrepancy was probably related to the fact that subsequent estimates for generations 21-30 were negative (–0.03) and smaller than the corresponding realized estimate (0.13). Individual generation estimates ($h^2 = R/S$) yielded negative values as well as values larger than one and thus indicated considerable variation to selection pressures. Negative estimates tended to be followed by unusually large values in the subsequent generation and thereby compensate for negative heritabilities. The influence of duration of selection on the size of the heritability estimates is clearly visible. The realized heritability of 4-week weight in the P line for the first 10 generations of selection was approximately 0.45; estimates for generations 11-20, 21-30 and 31-40 were 0.24, 0.24, and 0.09, respectively. Estimates obtained in both lines appear to be markedly different, after generation 30, than earlier estimates in these lines (Marks and Lepore 1968; Marks 1971). These data indicate that the realized heritability for 4-week body weight was high (0.32-0.45) for generations 1.10 selection, moderate (0.15-0.24) for generations 11-30, and small (0.04-0.09) for generations 31-40. This pattern is in agreement with the general concept of expectation from selection, since it is assumed that the greatest progress will occur during the initial stages of selection to be followed by a gradual decline until selection becomes negligible (Lawrence 1964).

Heritability estimates for 4-week body weight obtained by regression of progeny on mid-parent were similar to realized estimates in the P line with only one exception. The regression of progeny on mid-parent values for generations 1-10 in the P line (Table 4) was 0.10 and 0.14 points smaller than the realized estimates for this period. The other comparisons of realized and mid-parent regression estimates were within a narrow range (0.02-0.06). With the exeption of similar estimates in generations 1-10, the mid-parent regression estimates in the T line were consistently larger than realized estimates (Table 4). Although these discrepancies were not large they tended to increase across generations; the largest differences were between estimates for generations 21-30 and 31-40. The mid-parent regression heritabilities in the T line appear to be an overestimate of heritability. The presence of additive genetic variance is not uncommon in studies in which selection progress has diminished or ceased (Falconer 1960; Lerner 1958).

Discussion

The long-term responses of the P and T lines to individual phenotypic selection support the hypothesis that there was considerable additive gene action for 4-week body weight at the beginning of this selection experiment. The increase in each of the selection environments was over 100% in less than 20 generations of selection (Fig. 3). Although the absolute body weights of P line birds continued to increase after generation 24 (Fig. 1), the increase in percentage deviation from controls after this generation was small and erratic. This response suggests that although a fair amount of residual additive genetic variance was still present in the line, its expression had been reduced. Contrariwise, the absolute body weights of T line birds did not appear to increase after generation 22 (Fig. 2). This response is related to the definite decline in body weights of the controls (TC) across generations under the 20% protein + 0.2% TU selection environment.

These data indicate that both the longest and greatest response to selection for body weight occurs under an adequate environment (28% protein) as opposed to a stress environment (20% protein + 0.2% TU). During the last 20 generations of this study, the P line continued to respond to selection pressures whereas the T line appeared to plateau; this suggests that an adequate environment may favor the fullest expression of the genotype. Therefore, although similar progress was obtained during the early phases of selection (first 20 generations) under both adequate and stress environments, greater progress was obtained under an adequate environment during the latter generations. If an adequate or optimum environment favors the fullest expression of the genotype, the hypothesis may be that major gene action (major genes) is similar under both adequate and stress environments (or all environments), whereas action of other genes(minor genes) is more fully expressed under an adequate environment than under a stress environment. This concept would also suggest that major genes are the first to be influenced by selection followed by the additive action of minor genes in latter stages of selection programs.

The procedure of changing or altering the environment under which selection is practiced appears to offer promise in maximizing long-term genetic improvement of traits that are influenced by additive gene action. Assuming that the T line had reached a plateau following approximately 20 generations of selection (Fig. 2), the greater responses of the R and S sublines than the T line following a change in the selection environment indicates that this procedure may have potential in dealing with plateaued populations. The greater improvement obtained in the R and S sublines than in the parental T line following the removal of environmental selection restrictions also tends to support the hypothesis that minor genes may be more fully expressed under more favorable environments. It is possible therefore that plateaus may represent the cessation and/or fixation of major gene action. The progress observed in some situations after a plateau has been reached could be due to the utilization of the residual additive genetic variation of minor genes brought into action by a favorable change either by chance or design in the selection environment. Similar weighted and unweighted selection differentials (Table 3) suggest that the plateau of the T line was not due to natural selection for fitness operating in the opposite direction from artifical selection as discussed by Lerner (1958).

Although selection progress may have diminished to some degree for body weight in broilers, there appears to have been continued progress following an extended number of generations of selection. This continued progress is due partly to the extreme selection pressures that can be applied to such a trait. Continued improvement in nutrition, housing and management may provide a changing environment that allows for maximum expression and utilization of residual additive genetic variation and thus result in continued genetic improvement of broiler body weights.

Literature

Clayton, G.A.; Robertson, A.: An experimental check on quantitative genetical theory. II. The long-term effects of selection. J. Genet. **55**, 152-170 (1957)

Dev, D.S.; Jaap, R.G.; Harvey, W.R.: Results of selection for eight week body weight in three broiler populations of chickens. Poultry Sci. **48**, 1336-1348 (1969)

Falconer, D.S.: Introduction to Quantitative Genetics. New York: Ronald Press Co. 1960

Jaap, R.G.: Selection for rapid growth rate in chickens. Poultry Sci. **42**, 1393-1397 (1963)

Lawrence, M.J.: Environment and selection in *Drosphila melanogaster*. Heredity **19**, 105-124 (1964)

Lerner, I.M.: Genetic Homeostasis. New York: John Wiley & Sons, Inc. 1954

Lerner, I.M.: The Genetic Basis of Selection. New York: John Wiley & Sons, Inc. 1958

Maloney, M.A.; Gilbreath, J.C.; Morrison, R.D.: Two-way selection for body weight in chickens. Oklahoma Agricult. Exper. Sta. Tech. Bull. T-99 (1963)

Maloney, M.A.; Gilbreath, J.C.; Tierce, J.F.; Morrison, R.D.: Divergent selection for twelve-week body weight in the domestic fowl. Poultry Sci. **46**, 1116-1127 (1967)

Marks, H.L.: A Japanese quail control population. Quail Quarterly, **4**(1), 2-4 (1967)

Marks, H.L.: Selection for four-week body weight in Japanese quail under two nutritional environments. Poultry Sci. **50**, 931-937 (1971)

Marks, H.L.; Lepore, P.D.: Growth rate inheritance in Japanese quail 2. Early responses to selection under different nutritional environments. Poultry Sci. **47** 1540-1546 (1968)

Mather, K.; Harrison, 'B.J.: The manifold effect of selection. Heredity **3** 1-52; 131-162 (1949)

Roberts, R.C.; The limits to artificial selection for body weight in the mouse I. The limits attained in earlier experiments. Genet. Res. **8** 347-360. (1966)

Robertson, A.: A theory of limits in artificial selection. Proc. Roy. Soc. (Lond.) **153**, 234-249 (1960)

Siegel, P.B.: Selection for body weight at eight weeks of age 1. Short term response and heritabilities. Poultry Sci. **41**, 954-962 (1962)

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