

LONG-TERM DIVERGENT SELECTION FOR 8-WEEK BODY WEIGHT IN CHICKENS – A REVIEW OF EXPERIMENTS

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ABSTRACT

In order to study the effects of long-term selection on genetic parameters, the effect of selection on selected and correlated traits and to develop lines for various physiological, biochemical and molecular genetic studies a comprehensive selection study for body weight in chickens has been conducted at the Biotechnical Faculty of University in Ljubljana. Long-term divergent selection in chickens for 8-week body weight for 31 generations produced a high weight (D+) and low weight (D-) line. Body weight at 8 weeks of age was the exclusive selection criterion. Selection lines were compared for body weight and for unselected traits including carcass traits, feed conversion, egg and meat quality traits, reproduction traits, muscle characteristics, nutritional and physiological traits. This paper describes the most important results of different experiments that were performed on animals from both lines in various generations of selection.

Key words: poultry / chickens / divergent selection / growth / correlated traits

REZULTATI POSKUSOV IZ DVOSMERNE SELEKCIJE NA TELESNO MASO PIŠČANCEV PRI 8. TEDNIH STAROSTI

IZVLEČEK

Z namenom ocenjevanja učinkov dolgotrajne selekcije na genetske parametre, selekcionirane in korelirane lastnosti ter za potrebe izvajanja raziskav s področij fiziologije, biokemije in molekularne genetike je bil na Biotehniški fakulteti Univerze v Ljubljani izpeljan obsežen dvosmerni selekcijski poskus na telesno maso piščancev. Enaintrideset generacij smo odbirali piščance na večjo (D+ linija) in manjšo (D- linija) telesno maso pri osmih tednih starosti, ki je bila vseskozi edini selekcijski kriterij. V posameznih generacijah smo proučevali direktne (telesna masa) in korelirane učinke selekcije (klavne lastnosti, izkoriščanje krme, kakovost jajc in mesa, reprodukcijske lastnosti, lastnosti mišičnih vlaken, prehranske in fiziološke lastnosti). V članku so zbrani najpomembnejši rezultati omenjenih raziskav.

Ključne besede: perutnina / piščanci / dvosmerna selekcija / rast / korelirane lastnosti

INTRODUCTION

Farmers have been implementing artificial selection in chickens for thousands of years. However, in the last century artificial selection has become a complex scientific business. A limited number of artificial selection effects can be deduced from the selection theory but many can only be demonstrated by conducting experiments. Long-term (exceeding ten generations) selection experiments can provide a substantial amount of information and have a practical value

for chicken improvement. By affecting many regions of the genome simultaneously, they can reveal relationships among interacting genetic pathways. Because correlated responses may have economic consequences, the impact of selection for actual target(s) of selection on total economic merit of chickens should be monitored. Long-term divergently selected lines are also a unique resource for dissecting the genetic basis underlying line divergence. Understanding the genetic architecture of traits such as growth and body composition has become a primary focus for biomedical and agricultural research.

At the University of Ljubljana we conducted a selection experiment over a period of 28-years (31 generations of selection) to measure long-term response to selection. Divergent selection on 8-week body weight produced a high weight (D+) and a low weight (D-) line. The work on the experiment is still in progress. Many other long-term selection experiments have also been conducted in chickens and other domestic poultry species for a range of traits (e.g. Dunnington and Siegel, 1996; Marks, 1996; Nestor *et al.*, 1996). Our investigation differs from earlier studies on responses to body weight selection by the duration of selection and by monitoring correlated effects in traits which differ from the traits used in other studies. The aim of this review is to describe the most general findings that have emerged from the long-term bidirectional mass selection for 8-week body weight.

MATERIAL AND METHODS

The base population for this experiment was stock from a commercial heavy sire line of the Slovenian provenance Prelux-bro. Two lines were established by selecting from the base population 10 males and 50 females that were the heaviest at 8 weeks of age and those that were the lightest. Within each line, the high-weight males and females were mated at random to establish a high-weight (D+) line, and the low-weight males and females used similarly to establish a low-weight (D-) line. After formation in the first generation of selection, the lines were closed, with parents for subsequent generations chosen as the extreme weighing males and females from each of the lines. A control line was not propagated. Progeny of each generation was obtained from two or even three hatches. The total number of animals per generation varied between 324 animals in the 30th generation and 1283 animals in the 18th generation. The proportion kept for breeding ranged from 22.7% to 56.5% per generation (Fig. 1).

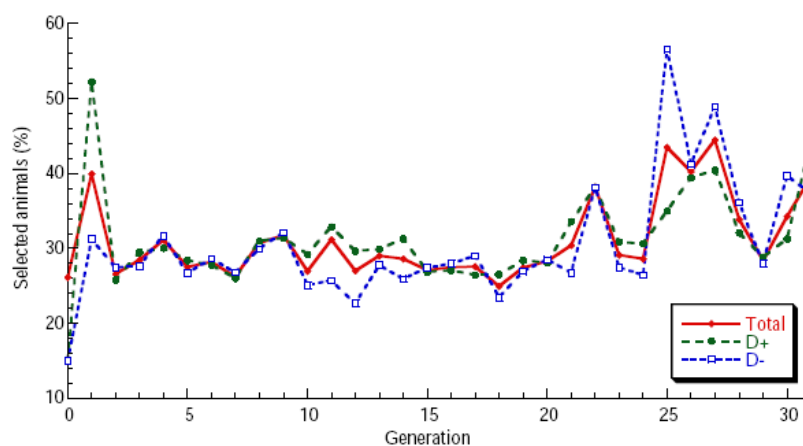


Figure 1. The proportion of animals selected to be parents of the next generation (D+ = high weight line; D- = low weight line; Total = both lines together).

Slika 1. Delež odbranih živali za starše naslednje generacije (D+ = linija selekcionirana na večjo telesno maso; D- = linija selekcionirana na manjšo telesno maso; Total = obe liniji skupaj).

Up to the age of 8 weeks growing chickens were reared together in a windowless house with a deep litter system. Afterwards selected parents of each line were reared in separate pens within the same poultry house. Pens were supplied with hanging bell waterers and feeders to provide *ad libitum* access to water and feed. Environmental factors were controlled so as to provide conditions that were as similar as possible across generations and hatches. Animals were exposed to a set-up lighting program. This program started from a constant short (8 hour) day length. At the age of 18 weeks the day length was increased by increments of 1 hour per week until day length reached 15 hours.

RESULTS AND DISCUSSION

After conducting divergent individual mass selection for 8-week body weight for seven generations, Holcman (1986) evaluated the direct (body weight) and correlated (age at maturity, egg number, egg weight, weight of one day old chicks, hatchability) selection responses. At each generation, the cumulated response to selection was computed as the difference between the phenotypic mean in the downward line and the phenotypic mean in the upward line. The mean realized heritability for body weight at 8 weeks was estimated as the regression of response to selection on accumulated selection differential. The rate of inbreeding per generation was calculated as $\Delta F = (1/8N_m) + (1/8N_f)$ where N_m is the number of males and N_f is the number of females. For calculating the cumulative inbreeding in generation t the following formula was used: $F_t = \Delta F + (1-\Delta F)F_{t-1}$. The total effect of divergent selection in seven generations was 752 g (783 g for males and 720 g for females). The realized heritability for 8-week body weight after 7 generations of selection was 0.26 (0.27 for males and 0.25 for females). The average rates of inbreeding per generation were 3.2% and 2.0% for lines D(+) and D(-), respectively. There was an increase in the cumulative inbreeding on successive years up to the mean of 20.9% in D(+) and 13.4% in D(-) line. Selection for high 8-week body weight resulted in a delay in age at sexual maturity and in an increase in egg weight. Thus, indirect selection for higher body weight had a positive effect on the weight of one day old chicks. According to the Witt and Schwalbach (2004) there is a strong positive correlation between egg weight and hatching weight. A negative relationship has been observed between high body weight and hatchability. In the seventh generation of divergent selection the average ages at sexual maturity were 27 and 22 weeks, the average egg weights were 65.0 and 55.0 g and the average percentages of hatchability were 52.3 and 68.1 for lines D(+) and D(-), respectively.

In a subsequent report Terčič *et al.* (2006) presented data for 24 additional generations of selection for high and low 8-week body weight. In the 30th generation of selection, the D(+) males and females weighed 2304 and 1679 grams more, respectively, compared with D(-) males and females. These differences represent a 7.5-fold increase in body weight at 8 weeks of age for the D+ compared to the D- line. Selection responses for generations 0 to 31 in the D(+) and D(-) line are shown in Fig. 2. It can be seen that patterns of responses are unpredictable. Substantial responses that were observed in both lines were followed with periods of little or no response to selection (Fig. 2). Dunnington and Siegel (1996) suggested two possible explanations for the phenomenon of irregular response: a) after many generations of selection, genotypes are more sensitive to microenvironmental factors that facilitate irregular responses or b) spontaneous mutations may have occurred periodically. Regressions of mean body weights on generation across the 30 generation period yielded respective regression coefficients of 25.46 g and -36.07 g per generation in the D(+) and D(-) line. The differences in selection intensity values within lines represent plausible reason for asymmetry between upward and downward selection responses. The realized heritability of body weight (mean \pm s.e.) was 0.12 ± 0.014 in the D(+) and 0.22 ± 0.015 in the D(-) line. The realized heritability was computed as the slope of the

linear regression of the generation means, measured as deviations from founder population, on the cumulated selection differential. Realized heritability estimates for generations 1-7 were relatively high, however, after 30 generations of selection, heritability estimates were reduced. Because of the variation in the genetic constitution of the founder populations and/or effects of population size it is difficult to compare the current estimates for realized heritability with published estimates obtained in different experiments.

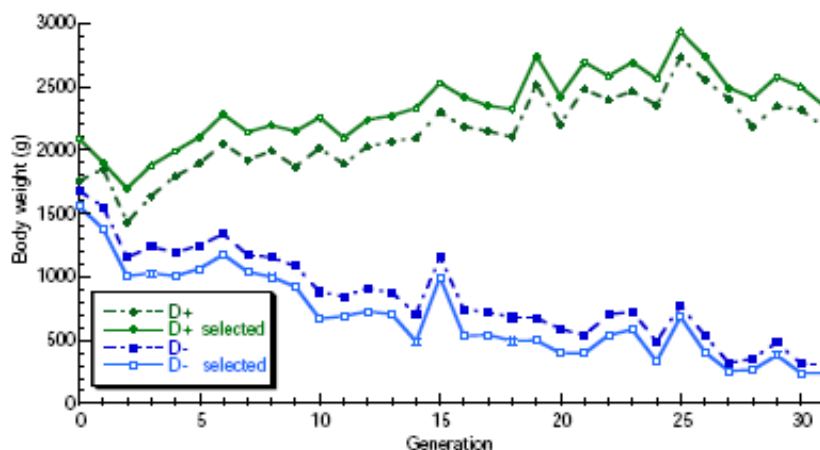


Figure 2. Mean 8-week body weights of D(-) and D(+) line from generations 0 to 31.

Slika 2. Srednje vrednosti za telesne mase piščancev D(-) in D(+) linij iz generacij 0 do 31.

Growth performance, feed conversion, nutrient digestibility, carcass traits and blood serum parameters were explored on the male chickens from the tenth generation of divergent selection for 8-week body weight (Mužic, 1990). Thirty-two birds from each line were placed in individual cages. Nutritionally complete diets were formulated for starter and finisher periods. Time of feeding the diets was adjusted to 0 to 3 weeks for starter, and 4 to 7 weeks for finisher. Feed and water were provided for *ad-libitum* consumption. Body weights and feed consumption were recorded at weekly intervals. The traditional method of total excreta collection was applied for all animals from 36 to 40 day of age to determine the digestibility coefficients for the dry matter, organic matter, crude protein, crude fibre, crude fat and nitrogen-free extract. Blood samples were collected from the wing (brachial vein) at 6 weeks of age, to obtain the total cholesterol, triglycerides, total protein and total fat concentration in the serum. All birds were slaughtered to determine dressing percentage and parts yield at 49 days of age. Differences were reflected in the performance of the lines. High weight males had higher ($P < 0.05$) body weights (1.94 vs 1.12 kg), lower (better) ($P < 0.05$) feed conversion rates (1.95 vs 2.16 kg), and higher ($P < 0.05$) carcass yields (66.99 vs 64.72%). The absolute weight of the abdominal fat pads as well as the weight of the abdominal fat pads expressed as a percentage of body weight were higher ($P < 0.05$) in D(+) males (48.11 g; 2.46%) compared to D(-) males (20.23 g; 1.78%). The nutrient digestibility studies showed a higher ($P < 0.05$) digestibility of crude fibre and crude fats in D(+) males. There was no difference ($P > 0.05$) between the digestibility coefficients for crude protein, nitrogen-free extract, organic matter and dry matter obtained in D(+) males and the values obtained in D(-) males. Blood serum total protein and total cholesterol concentrations were higher ($P < 0.05$) in D(+) males than in D(-) males, whereas total fat and trygliceride concentrations did not differ ($P > 0.05$) between the birds from the two lines.

To study the effects of divergent selection for 8-week body weight on growth and feed conversion Holcman (1992) designed an experiment with animals from fifteenth generation of selection. Two hundred and forty-one chickens [112 from line D(+) and 129 from line D(-)]

were reared in two separate pens in deep litter within the same poultry house. All birds were fed a common starter diet in mash form. Body weights were recorded individually, whereas feed conversion was recorded by line. All measurements were done at weekly intervals up to nine weeks of age. The increases in body weight per 1-wk periods were plotted as a percentage of values for body weight at the start of the week (relative increase in body weight). The relative increase in body weight of the D(+) line was superior to the relative increase in body weight of the D(-) line during the first two weeks after hatching and in the fourth and in the fifth week of age. At the age of three weeks and from the sixth week onwards the relative growth rate was higher in D(-) line. Differences among lines in weekly feed conversion ratios were most striking in the second week of the experiment. Birds from D(-) line had higher (poorer) weekly feed conversion ratios during the whole experiment. Cumulative feed conversion ratios of birds from the D(-) and D(+) line were 2.34 and 2.04 kg, respectively. Thus selection for high body weight in chickens, is positively associated with efficiency of feed utilization as already demonstrated the experiment of Mužic (1990). These findings are not in accordance with findings of Siegel and Wisman (1966) who demonstrated that under *ad libitum* feeding there was no difference between high weight and low weight lines in feed efficiency to a fixed age. But when the feed intake of high weight chickens was limited to that of the low weight line counterparts, they utilized feed more effectively, indicating that correlated response for feed consumption masked those for feed conversion. In subsequent generations this difference between lines has increased (O'Sullivan *et al.*, 1992).

The purpose of the investigation carried out by Holcman and Bevc (1992) in the fourteenth generation of selection was to determine differences in physical characteristics of eggs produced by two divergently selected lines of chickens at two different ages. External (shape index, egg weight, shell colour, shell weight, shell thickness) and internal (albumen height, Haugh units, yolk colour, blood & meat spots) quality traits were examined in fresh eggs obtained at the age of 39 weeks (group I) and at the age of 43 weeks (group II). At each age 300 eggs per line were collected and analyzed. A set of electronic instruments (Technical Services and Supplies, York, UK) was used to measure egg quality traits. Egg quality values showed differences ($P < 0.05$) in all analysed characteristics. Egg weight, albumen height, Haugh units, yolk colour, shell weight and shape index were better ($P < 0.05$) in D(+) line compared with D(-) line. Additionally, D(+) hens had higher ($P < 0.05$) percent of eggs with blood & meat spots. The D(-) hens have laid eggs with paler ($P < 0.05$) and thicker ($P < 0.05$) shells than did the hens from D(+) line. Internal and shell quality increased ($P < 0.05$) with age with increments in albumen height, Haugh units, yolk colour, shell weight and egg weight.

In the thirty-first generation of divergent selection the actual egg cholesterol content was determined. Hens from both divergently selected lines were fed with a commercial diet for laying hens. Cholesterol level in the yolk was measured using the enzymatic-spectrophotometric method (Boehringer Mannheim, Germany). Ten eggs from each line were analysed when the hens were 49 weeks of age. The egg yolk and egg white were separated, and weighed. Each yolk sample was analysed in duplicate. The mean yolk cholesterol contents (mean \pm s.d.) expressed in mg per 100 g of egg yolk mass were 1605.00 ± 127.17 and 1373.39 ± 91.00 in the D(+) and D(-) line, respectively. The average contents of cholesterol per egg were 341.47 ± 32.72 mg in D(+) line and 212.37 ± 17.85 mg in D(-) line. The lines differed ($P < 0.001$) in cholesterol content per 100 gram of yolk and per egg. However most of the variation in cholesterol content per egg was attributable to line differences in egg weight. The D(+) line showed higher ($P < 0.001$) average egg weight (77.24 ± 4.91 g) than the D(-) line (48.42 ± 1.37 g). The average percentages of yolk per egg were 27.6% and 31.9% in the D(+) and D(-) lines, respectively. In comparison to D(-) line, hens from D(+) line produced eggs with higher cholesterol concentrations per 100 g of yolk, which was less pronounced when expressed per egg, due to the low yolk content of the eggs.

In the seventeenth generation of selection, a study was conducted to study the effects of divergent selection for 8-week body weight on body weight gain, dressing percentage, abdominal fatness and chemical composition of the meat (Holcman *et al.*, 1995). Chickens reared on *ad libitum* intake of conventional starter diet (first 14 days) and finisher diet (last 33 days) were placed into cages. Average body weight was determined at day 47 on 45 and 42 animals from lines D(+) and D(-), respectively. Samples from eight-animals per line (four males and four females) were taken to determine chemical composition. Dressing percentage was determined using either traditional carcass weight (carcass together with lungs, kidneys, head, neck, lower parts of legs, giblets and abdominal fat) or grill carcass weight (carcass with lungs and kidneys) as a proportion of body weight. Abdominal fat was used as an indicator of the fat content of the carcass and was calculated as a percentage of body weight. Chickens from the D(+) line had higher ($P < 0.01$) dressing percentages and also higher ($P < 0.001$) share of abdominal fat from live weight than the chickens from the D(-) line. The line difference in traditional dressing percentage was 2.99%, 4.25% in grill dressing percentage and 2.2% in abdominal fatness. These results are consistent with those from Dunnington and Siegel (1996) where high weight chickens had higher percentage of body fat than those from the low weight line. Calabotta *et al.* (1985) pointed out that regardless of feeding state (fasted/nonfasted chickens) lipogenic and lipolytic capacity was higher in low weight chickens than in high weight chickens indicating that fat deposition is more dependent upon lipid degradation than lipid synthesis. Referring to chemical composition of meat from breasts, thighs and drumsticks (with skin), meat from chickens that were selected for a higher body weight contained less moisture ($P < 0.01$) and more fat ($P < 0.01$) in comparison to meat from chickens that were selected for lower body weight. No differences ($P > 0.05$) were found in the content of protein and ash. Thigh and drumstick meat with skin was found to contain 69.9 vs 70.1% moisture, 17.2 vs 17.6% protein, 12.7 vs 10.9% fat and 0.7 vs 0.8% ash in D(+) and D(-) lines, respectively. The breast meat with skin in lines D(+) and D(-) contained 71.5 and 72.8% moisture, 22.0 and 21.5% protein, 4.5 and 4.1% fat, and 1.09 and 1.0% ash, respectively.

In the fifteenth generation of selection an experiment was carried out to evaluate the cock's semen from both selection lines (Holcman *et al.*, 1993). Sperm quality (expressed as progressive motility, percentage of fertility, percentage of hatchability and percentage of morphologically normal/abnormal/dead sperm cells) and sperm quantity (expressed as sperm concentration and semen volume) were the parameters evaluated in each cock. The results showed that ejaculate volume, sperm concentration, mobility, percentage of fertility and percentage of hatchability were higher in the D(-) line than in the D(+) line, values being (mean \pm s.d.) 0.27 ± 0.02 vs 0.23 ± 0.08 ml, $1.81 \times 10^9 \pm 0.41 \times 10^9$ vs $1.69 \times 10^9 \pm 0.69 \times 10^9$ spermatozoa/ml, 4.75 ± 0.50 vs 4.0 ± 1.15 , 86.19 ± 4.86 vs $80.15 \pm 8.57\%$ and 76.56 ± 10.02 vs $62.10 \pm 9.20\%$. High weight cocks were superior to the low weight cocks in percentage of abnormal and dead spermatozoa, values being 11.57 ± 2.15 vs $12.25 \pm 3.30\%$ and 8.14 ± 3.08 vs $8.25 \pm 1.50\%$. The results revealed that percentage of hatchability was the only variable ($P < 0.05$) affected by the line. All other variables did not change ($P > 0.05$) in the lines.

Dahmane *et al.* (1995a,b) analysed structural and histochemical characteristics of the muscles *biceps femoris* (BF) and *pectoralis profundus* (PP) in cockerels from the sixteenth generation of divergent selection for 8-week body weight. Seven samples of each line D(+) and D(-) were collected at 3, 6, 9 and 12 weeks of age, respectively. Transverse sections of 10 μ m were cut from both muscles and placed onto coverslips for immediate histochemical assay. Quantitative histochemical determination of succinic dehydrogenase activity (SDH) and menadion-linked α -glycerol phosphate dehydrogenase activity (GPDH) were used as estimates of oxidative and glycolytic energy supply, respectively. SDH and GPDH activities were determined by using the histophotometer linked to a personal computer with special software for measuring absorbtion

within muscle fibres. Within each of four age groups fifty muscle fibres per slice were investigated and for each muscle and line under investigation informations about mean SDH and GPDH activities as well mean fibre diameter were obtained. Selection for body weight had no effect on energy metabolism, but it induced an increase in cross sectional areas of muscle fibres. Cockerels from the D(+) line had ($P < 0.05$) larger mean diameter than those from the D(-) line. From comparisons of two chicken lines, one selected for high juvenile (8 week) and high adult (36 week) body weight and the other selected for low juvenile (8 week) and adult (36 week) body weight Remignon *et al.* (1995) concluded that the change in muscle size appears to be in number and size of fibers rather than in myosin isoform profiles. In the D(+) line giant cells were observed which are the sign of morphologic alteration. The SDH and GPDH showed high activity in the third and sixth week of age, whereupon a slight ($P = 0.065$) decrease occurred. These changes in enzyme activities were in accordance with animal growth rates which initially (third, sixth week of age) steadily increased and then (ninth, twelfth week of age) declined as the birds moved to their mature live weight. At all four ages the mean fibre diameters were larger ($P < 0.05$) in the *m. pectoralis profundus* compared to the *m. biceps femoris*.

In the eighteenth generation of selection two divergently selected lines of chickens were analysed by DNA profiling using random amplification of genomic DNA (RAPD) pooled from 10 individuals of each line with 200 different 10-base primers (Terčič, 1997). Only one primer was used per reaction. Amplification products obtained with primers UBC-563 (5' - CGCCGCTCCT - 3') and UBC-788 (5' - CCTTCCCTCT - 3'), were clearly different between the pools. These two primers were further investigated on single DNA samples to determine the proportion of animals carrying the pool-specific DNA fragments. Primer UBC-788 revealed one (≈ 300 bp) D- line-characteristic RAPD fragment, while UBC-563 amplified two (≈ 1000 bp and ≈ 600 bp) D- line specific RAPD fragments which can be useful markers in the linkage analysis with quantitative trait loci (QTLs) for body weight.

In the twenty-fifth generation of divergent selection for 8-week body weight an experiment was conducted to determine what effect genotype [D(+) versus D(-) line] has on nitrogen balance. The birds were kept in individual metabolism cages and fed on a practical feed mixture in pellet form which was calculated to contain (expressed on dry matter basis) 12.86 MJ ME/kg, 235.53 g/kg crude protein, 23.34 g/kg crude fat, 26.81 g/kg crude fibre and 64.40 g/kg crude ash. At the beginning of the trial animals were 42 days old, and the trial period lasted for 16 days. The entire trial period was divided on four four-day periods. Nitrogen balance was analysed for 6 males and 6 females from each line. Body-weights were recorded at the end of four-day periods. At the end of each daily collection, excreta were weighed and stored at -20 C until chemical analyses. The birds were fed once daily on 220 g (D+) and 120 g (D-) of the test diet, a quantity that was not completely consumed. Unconsumed feed was collected for each bird on daily basis and fresh feed was weighed and offered to the birds. The nitrogen content in feed and excreta was determined using the Kjeldahl method and crude protein was calculated as Kjeldahl N $\times 6.25$. Nitrogen balance was calculated as the difference between the nitrogen intake in an individual bird and the total nitrogen excretion. There were differences ($P < 0.05$) between lines in daily nitrogen retention. Animals from the D(+) line retained more nitrogen than animals from the D(-) line. Males retained more nitrogen than females irrespective of line. In the last four-day period D(+) males and females retained less ($P < 0.05$) nitrogen in comparison with the first four-day period, whereas in D(-) males and females this difference was not significant. In chickens 42 to 58 days of age, protein retention expressed in grams per kilogram of body weight decreased from 10.1 to 5.2 g/kg in D(+) males, from 11.1 to 5.1 g/kg in D(+) females, from 16.1 to 6.6 g/kg in D(-) males and from 16.9 to 7.6 g/kg in D(-) females. In all trial periods except in the first period for D(-) females, D(-) chickens showed greater feed nitrogen utilization efficiency than D(+) birds.

CONCLUSIONS

A divergent selection experiment with chickens, using body weight at eight weeks of age as the selection criterion, was undertaken for 31 generations. A high (D+) line and a low (D-) line were made up in 1979 with 50 females and 10 males each. Despite the fact that the body weight at 8 weeks of age was the only selection criterion variation within and between lines in other production/physiological traits was recorded in some generations and the genetic control of different traits involved was assessed, as well as direct and correlated responses to selection. This paper is a review of experiments conducted over a period of twenty-eight years on abovementioned lines of chickens.

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