

Growth to sexual maturity of dwarf and nondwarf White Rock chickens divergently selected for juvenile body weight*

D. J. Zelenka, E. A. Dunnington and P. B. Siegel

Poultry Science Department, Virginia Polytechnic Institute and State University, Blacksburg, VA 24061, USA

Received October 20, 1985; Accepted May 28, 1986

Communicated by A. Robertson

Summary. Growth from hatching to the onset of lay (sexual maturity) was studied in White Plymouth Rock pullets from lines selected for high (HN) and low (LN) 56-day body weight, their reciprocal F_1 crosses, an F_2 cross, and two dwarf populations originating from the HN and LN parental lines. The highest R^2 s for describing growth for all populations except HN were obtained when body weight was expressed relative to body weight at sexual maturity. Modes of inheritance differed depending on whether patterns of growth were expressed in a chronological time frame or on a physiological basis. Heterosis observed for age at sexual maturity and for body weight after the age when selection was made was not in evidence when ages and weights were expressed as a proportion of those at sexual maturity.

Key words: Chickens – Growth – Heterosis – Dwarfism – Sexual maturity

Introduction

Growth, a complex biological phenomenon influenced by genetic and environmental factors, is usually measured in domestic and laboratory animals as change in body weight over time. Such change includes both mass and composition of the individual.

Genetic variation of growth has been measured in chickens (Krause et al. 1967), quail (Marks 1978), and turkeys (Johnson and Gowe 1962), and selection experiments for body weight at specific ages have been conducted with these species (Marks 1985; Nestor 1985; Siegel and Dunnington 1985).

* This research was supported, in part, by BARD Project No. US-675-83C

Similarly, genetic variation in growth rate of rodents has been investigated (Roberts 1966; Eisen 1976 1980), and growth curves of mice have been altered through the use of selection indices (McCarthy and Bakker 1979).

Growth has been viewed as change in weight over elapsed time (Brody 1945), at a specific chronological age (Roberts 1966; Dunnington and Siegel 1985), at a specific physiological stage (Reddy and Siegel 1977a; Dunnington et al. 1983), and in relation to a final body weight (Ricklefs 1967; Grossman et al. 1985). Andrews (1982) related growth to changes in resource allocations during the life cycle, and discussed growth patterns in reptiles with respect to relative size at hatching, sexual maturity, and maximum size. In female chickens, dramatic changes in body weight and carcass composition occur just prior to the onset of egg production (Zelenka et al. 1986).

This paper discusses growth from hatching to the onset of egg production (sexual maturity) in dwarf and nondwarf populations of chickens known to differ in age, in body weight, and in carcass composition at sexual maturity. Comparisons included lines divergently selected for juvenile body weight and their F_1 and F_2 crosses.

Materials and methods

Stocks

Female chickens from five nondwarf and two dwarf populations were used in this experiment. Parental lines were nondwarf White Plymouth Rocks divergently selected for 24 generations for high (HN) and low (LN) juvenile body weight (Siegel 1978; Dunnington and Siegel 1985). The parental lines were mated to produce the reciprocal F_1 crosses (HL and LH) and an F_2 was produced from HL × HL matings. In designation of crosses, the sire population is shown first and the dam second. After 13 generations of selection, the sex-linked recessive allele (*dw*) for dwarfing (Hutt 1959) was introduced into samples of the HN and LN lines by mating females from these lines to males of a commercial meat-type stock which carried the dwarf allele (Reddy and Siegel 1977b). Through

repeated backcrossing of heterozygous males to normal females within each selected line, two populations resulted, HD and LD, which were of the same genetic origin as the HN and LN lines, respectively. After ten generations of backcrossing, the HD and the LD populations were maintained for two generations by random mating of dwarf males and females.

Husbandry

Chicks from all mating combinations were produced from age-contemporary parents. On the 22nd day of incubation, chicks were removed from the hatcher, wing-banded, vaccinated for Marek's disease, vent-sexed, and females were placed in litter-floor pens. Lighting was continuous until the chicks were 14 days of age, after which light was provided from 0600 to 1800 h. At 57 days, the pullets were moved to a windowed house and exposed to natural lighting until 127 days of age. They were then moved to a windowless house, individually caged, and provided a photoperiod which extended from 0600 to 2000 h. Starter, developer, and breeder diets (Siegel 1962) in mash form, and water were provided ad libitum.

Individual body weights were obtained at 1, 8, 15, 22, 29, 42, 57, 71, 85, 99, 113, 127, and 141 days of age. After 141 days of age, each pullet was weighed weekly until all pullets within a mating combination commenced lay.

Analyses

Body weights within mating combinations were expressed as a function of time using the Logistic, Gompertz, and von Bertalanffy equations (Ricklefs 1967) and as linear regressions

Table 1. Number of individuals, means and standard errors for weight (g) and age (days) at sexual maturity by population

Population	<i>n</i>	Weight	Age
HN	32	2,714 ± 36 ^a	171 ± 2 ^d
HL	25	1,969 ± 25 ^c	164 ± 2 ^d
LH	36	1,968 ± 27 ^c	165 ± 2 ^d
LN	24	1,239 ± 25 ^d	253 ± 8 ^a
F ₂	25	1,927 ± 49 ^c	176 ± 2 ^d
HD	28	2,184 ± 48 ^b	195 ± 4 ^c
LD	31	864 ± 18 ^e	219 ± 5 ^b

Any two means in a column with the same superscript are not significantly different ($P < 0.05$)

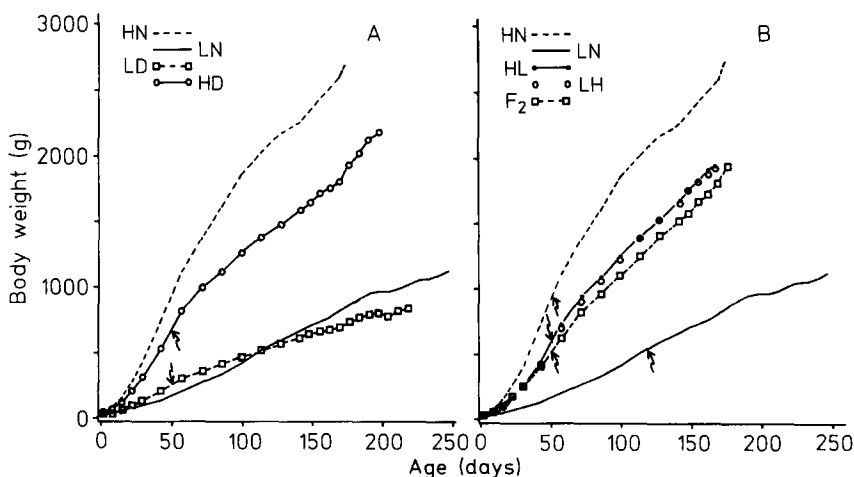


Fig. 1. Growth patterns illustrating single allelic (A) and polygenic (B) influences on body weight from hatching to sexual maturity. Arrows show points of inflection

of body weight expressed as a proportion of weight at sexual maturity, i.e., degree of maturity (DM) with the equation:

$$W = a + bt$$

where *W* was body weight expressed as a percentage of body weight at sexual maturity, and *t* was time.

Standardization to describe age and body weight in terms of degree of sexual maturity involved expressing chronological ages relative to age at sexual maturity with values on the x-axis ranging from 0 to 100%. Body weights were expressed on the y-axis as actual values and standardized (% BW) as a proportion of weight at sexual maturity. Since populations differed greatly in age and body weight at sexual maturity (Table 1), standardization placed all populations on the same physiological scale.

For genetic analyses, data for lines HN and LN were used both in comparisons of alleles at the dwarf locus and those involving reciprocal F₁ and F₂ crosses. In the latter case, inferences about the modes of inheritance were made from nonorthogonal linear contrasts (Scheffe 1970).

Results and discussion

Growth to sexual maturity

Growth patterns from hatching to sexual maturity are presented for each population in Fig. 1.

Since R²s were largest for DM in all populations except HN where the R² was slightly higher for the Gompertz equation (Table 2), results are presented for DM only. Weight at maximum growth rate differed according to population, being 970, 583, 564, 559, 513, 674, and 252 g for HN, HL, LH, LN, F₂, HD, and LD, respectively. Age at inflection was 50 days for all stocks except LN, which was 120 days. Occurrence of the inflection at the same age for dwarf and cross populations was consistent with the suggestion of a stabilizing influence of the dwarf allele in divergently selected weight populations (Reddy and Siegel 1977b). Also, the relaxing of selection during the last two generations in the dwarf populations may have contributed to stabilization.

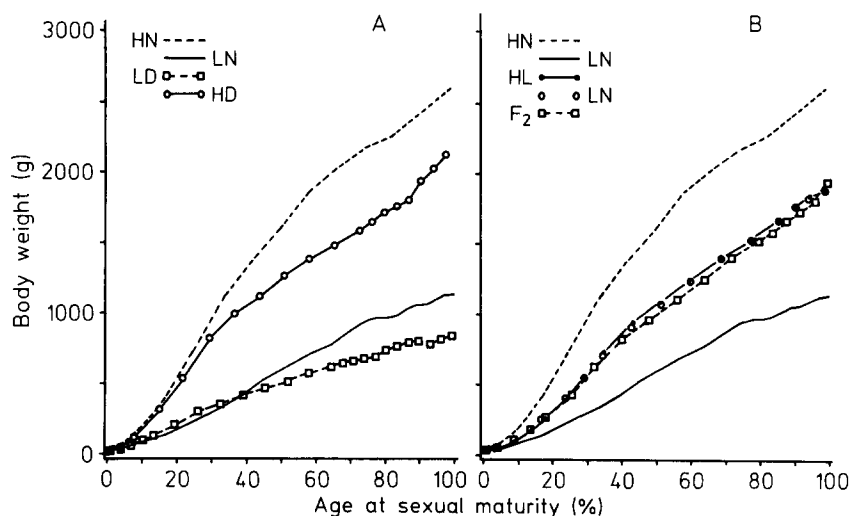


Fig. 2. Growth patterns of dwarf and normal chickens (A) and of crosses and parental stocks (B) when age was expressed as % of age at sexual maturity

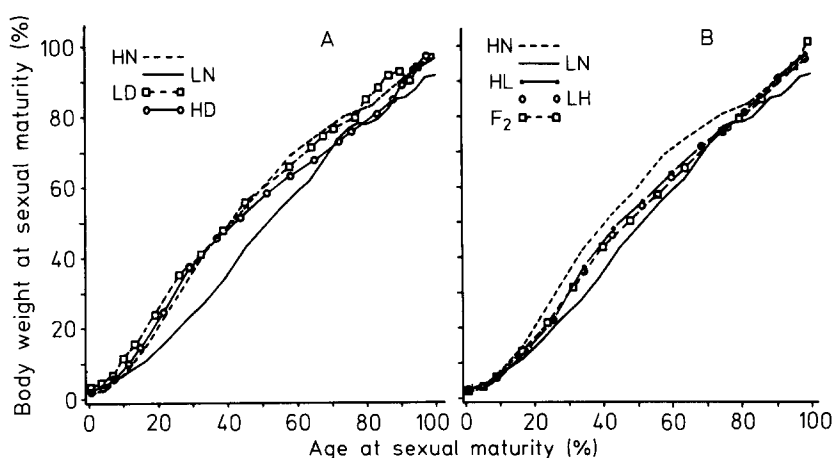


Fig. 3. Growth patterns of dwarf and normal chickens (A) and of crosses and parental stocks (B) when age and body weight were expressed as % of age and of body weight at sexual maturity

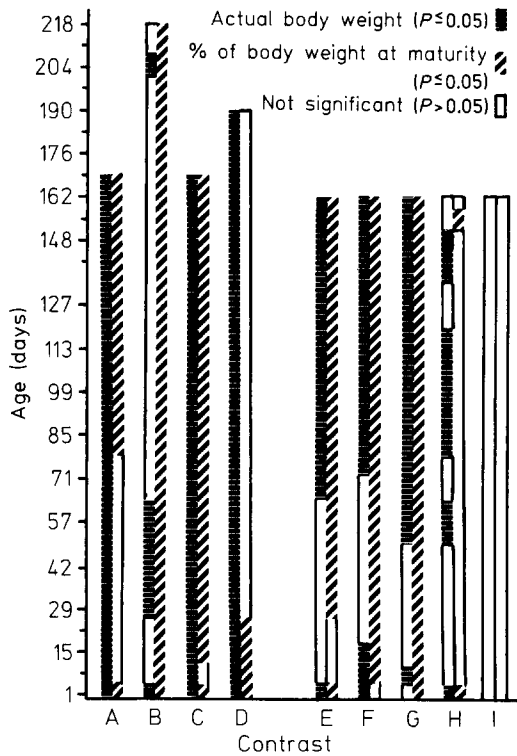
When body weight was expressed in the context of age relative to age at sexual maturity, LN pullets differed from LD, HN, and HD pullets in that their early growth was slower and the curve remained concave for an extended period (Fig. 2A). As a result, LN pullets were not heavier than the LD birds until attaining a weight of about 400 g. After point of inflection, growth of LD and HD pullets slowed considerably. Growth of the F_1 and F_2 crosses approximated the midpoint of the parental lines (Fig. 2B).

When ages and body weights were simultaneously standardized for their respective values at sexual maturity, patterns for dwarfs were similar to those for the HN chickens (Fig. 3A), while those for the crosses were intermediate to the parental populations (Fig. 3B). Thus, growth relative to body weight and age at sexual maturity, while influenced by additive genetic variation, may have been compensated for by the stabilizing effects of the *dw* allele (Reddy and Siegel 1977b).

Genetic analyses

Characterization of growth of normal and dwarf chickens differed depending on the background genome and whether expressed as actual body weight or % BW (Fig. 4). HN pullets were heavier than HD pullets at all ages (Contrast A). When expressed as % BW, however, HD pullets were larger than HN ones at one day of age with no difference from then until 85 days and subsequent ages when the pattern reversed. The difference observed at one day of age, which can be attributed to egg weight (Payne et al. 1957; Reddy and Siegel 1977b), was overcome at subsequent ages by the faster growth of HN than HD chickens. The minor influence of allele *dw* on growth at young ages was consistent with previous reports (Hutt 1959; Reddy and Siegel 1977b).

Growth relationships between normal and dwarf pullets in the low-weight line (Contrast B) differed from



Contrast	Genetic context
A HN-HD	Influence of <i>dw</i> allele in high line
B LN-LD	Influence of <i>dw</i> allele in low line
C HN-LN	Direct effect of selection
C HD-LD	Influence of selection in genomes containing <i>dw</i>
E [(HN + LN)/2]-HL	Heterosis
F [(LN + HN)/2]-LH	Heterosis
G (HN + LN)-(HL + LH)	Nonadditivity
H HL-F ₂	Recombination
I [(2HL + HN + LN)/4]-F ₂	Recombination

Fig. 4. Nonorthogonal linear contrasts of body weight and body weight expressed as a percentage of body weight at sexual maturity (% BW) at each age. For each contrast, the left-hand column refers to body weight and the right-hand column refers to % BW. Age is represented by the vertical axis. The columns are cross-hatched over the ages at which the contrast is significant ($P \leq 0.05$), and are left blank where it is not significant.

those just described in the high-weight line. Although LN chicks were heavier than LD chicks at one day of age due to differences in egg weight, the latter grew faster than LN ones from 29 to 57 days of age. Thereafter, the only difference in body weight between these populations was at 204 days when weights of LD chicks declined slightly. Contrary to results for absolute body weight, % BW of LD pullets was higher at all ages than that of LN pullets.

The consistent difference in body weight of the two parental lines (Contrast C) was a function of divergent

Table 2. R^2 of growth curves of various populations expressed by Logistic, Gompertz, von Bertalanffy, and degree of maturity (DM)

Populations	Equation			
	Logistic	Gompertz	Bertalanffy	DM
HN	0.951	<u>0.986</u>	0.978	0.980
HL	0.966	<u>0.976</u>	0.943	<u>0.994</u>
LH	0.961	0.920	0.889	<u>0.995</u>
LN	0.964	0.918	0.882	<u>0.992</u>
F ₂	0.964	0.987	0.975	<u>0.997</u>
HD	0.921	0.881	0.847	<u>0.987</u>
LD	0.967	0.956	0.937	<u>0.986</u>

DM = body weight expressed as a proportion of weight at sexual maturity

The largest value of R^2 for each population is underlined

selection for juvenile body weight and correlated responses in egg weight (Dunnington and Siegel 1985). For % BW, although LN pullets were relatively heavier at hatch than HN pullets, the latter made up this difference by eight days and thereafter were proportionately heavier than LN chicks.

Contrast D, which evaluated weight differences between dwarfs of the selected lines was consistent with the pattern for additive genetic variation observed for nondwarf pullets from these lines. Yet, while the *dw* allele decreased body weight, the extent of the reduction was influenced by the background genome. For example, weights from 1 to 22 days of age represented a greater % BW in LD than in HD pullets. After 29 days, growth of HD and LD chicks was proportionately similar, indicating that the differences observed at younger ages disappeared.

After discrepancies observed at early ages due to effects of egg weight disappeared, heterosis was similar and in the same direction for the HL and LH crosses (Contrasts E and F, respectively). This pattern was evidenced by significance of contrasts for body weight differences at one day of age for HL and LH crosses but not when the crosses were pooled (Contrast G). The difference in hatching weight of reciprocal crosses was because the dams of the HL cross laid smaller eggs than dams of the LH cross. Effects of egg weight on body weight disappeared by 8 and 15 days, respectively, in HL and LH chicks. Contrasts involving either or both HL and LH crosses were not significant until after 57 days of age. Heterosis of % BW was significant whenever HL and LH crosses were analyzed simultaneously (Contrast G), and almost always significant when analyzed separately (Contrasts E and F) with the difference again being due to egg weight. These results illustrate that crosses were physiologically more advanced than their parental populations at fixed chro-

nological ages, i.e., developmental rates were greater for the crosses than the parental lines.

Recombination effects differed depending on whether the F_2 was compared to its parental F_1 (Contrast H) or if the parental lines were included (Contrast I). Contrast H was significant at young ages and reflected differences in egg weight. Compensation for these differences occurred during the first few days after hatch for both absolute body weight and % BW. Recombination effects for body weight were significant at several ages; all prior to sexual maturity in cross HL. For contrast H, % BW was not significant until 15 to 20 days prior to the onset of lay because, shortly before lay began, proportionate growth rate accelerated in HL pullets relative to F_2 pullets. Similar rapid growth was noted in F_2 pullets which commenced lay shortly after HL pullets. Some of this increased growth was likely associated with yolk development (Zelenka et al. 1986). Conversely, no recombination effects were observed when the HN and LN parental lines were included (Contrast I). Recombination and lack of linkage, therefore, brought the F_2 closer to the mean of its parent and grandparent populations than the HL cross per se.

For body weight at sexual maturity, Contrasts A, B, C, and D were significant, indicating that HN, LN, HD, and LD stocks all commenced lay at different body weights (Table 1). Contrast E, F, G, H, and I were not significant, illustrating that, when weights were compared at sexual maturity, regardless of chronological age, heterosis and recombination for body weight were small (-0.4 to -2%). Hence, heterosis and recombination for body weight at younger ages in these populations were associated with different physiological stages at specific chronological ages. Although there was heterosis for age at first egg, an observation consistent with the literature (e.g., Warren 1927; Zelenka et al. 1986), it disappeared when values were standardized according to degree of maturity, i.e., standardization removed the artifact of scaling due to the greater developmental rate of the crosses.

To determine whether directional selection for a trait such as body weight is effective, weights can be compared at the same chronological ages or as days to reach the same body weight. The data presented in this paper demonstrated that patterns of growth exhibited different modes of inheritance in a chronological time frame than on a physiological basis. Therefore, when comparing stocks, consideration should be given to the biological and physiological importance of the specific characters being studied because resource allocations vary according to stages in the life cycle.

References

Andrews R (1982) Growth of reptiles. In: Gans C (ed) *Biology of the reptilia*, vol 13. Fovanovich, London, pp 273-320

- Brody S (1945) *Bioenergetics and growth*. Reinhold, New York
- Dunnington EA, Siegel PB (1985) Long-term selection for 8-week body weight in chickens. Direct and correlated responses. *Theor Appl Genet* 71:305-313
- Dunnington EA, Siegel PB, Cherry JA, Soller M (1983) Relationship of age and body weight at sexual maturity in selected lines of chickens. *Arch Geflügelkd* 47:85-89
- Eisen EJ (1976) Results of growth curve analyses in mice and rats. *J Anim Sci* 42:1008-1023
- Eisen EJ (1980) Conclusions from long-term selection experiments with mice. *Z Tierzücht Züchtungsbiol* 97:305-319
- Grossman M, Bohren BB, Anderson VL (1985) Logistic growth curve of chickens: a comparison of techniques to estimate parameters. *J Hered* 76:397-399
- Hutt, FB (1959) Sex-linked dwarfism in the fowl. *J Hered* 50:209-221
- Johnson AS, Gowe RS (1962) Modification of growth pattern of the domestic turkey by selection at two ages. In: 12th World's Poultry Cong pp 57-62
- Krause GF, Siegel PB, Hurst DC (1967) A probability structure for growth curves. *Biometrics* 23:217-225
- Marks HL (1978) Growth curve changes associated with long term selection for body weight in Japanese quail. *Growth* 42:129-140
- Marks HL (1985) Direct and correlated responses to selection for growth. In: Hill WG, Manson JM, Hewitt D (eds) *Poultry genetics and breeding*. Br Poult Sci Ltd Longman, Harlow, pp 45-57
- McCarthy JC, Bakker H (1979) The effect of selection for different combinations of weights at two ages on the growth curve of mice. *Theor Appl Genet* 55:57-64
- Nestor KE (1985) Egg production consequences of improving growth and efficiency in turkeys. In: Hill WG, Manson JM, Hewitt D (eds) *Poultry genetics and breeding*. Br Poult Sci Ltd, Longman, Harlow, pp 73-83
- Payne L, Siegel PB, Ortman L (1957) Correlation of dam, egg, poult, and adult weights in Broad Breasted Bronze turkeys. *Poult Sci* 36:572-575
- Reddy PRK, Siegel PB (1977a) Selection for body weight at eight weeks of age. 12. Egg production in selected and relaxed lines. *Poult Sci* 56:673-686
- Reddy PRK, Siegel PB (1977b) Selection for body weight at eight weeks of age. 14. Effects of the sex-linked dwarf gene. *Poult Sci* 56:1004-1013
- Ricklefs RE (1967) A graphical method of fitting equations to growth curves. *Ecology* 48:978-983
- Roberts RC (1966) The limits to artificial selection for body weight in the mouse. 1. The limits attained in earlier experiments. *Genet Res* 8:347-360
- Scheffe H (1970) Multiple testing versus multiple estimation. Improper confidence sets. Estimation of directions and ratios. *Ann Math Stat* 41:1-29
- Siegel PB (1962) Selection for body weight at eight weeks of age. 1. Short term responses and heritabilities. *Poult Sci* 41:954-962
- Siegel PB (1978) Response to twenty generations of selection for body weight in chickens. In: Proc 16th World's Poultry Cong, pp 1761-1772
- Siegel PB, Dunnington EA (1985) Reproductive complications associated with selection for broiler growth. In: Hill WG, Manson JM, Hewitt D (eds) *Poultry genetics and breeding*. Brit Poult Sci Ltd, Longman, Harlow, pp 59-72
- Warren DC (1927) Hybrid vigor in poultry. *Poult Sci* 7:1-8
- Zelenka DJ, Siegel PB, Dunnington EA, Cherry JA (1986) Inheritance of traits associated with sexual maturity when populations of chickens reach 50% lay. *Poult Sci* 65:233-240