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Synthesis of stocks and phenotypic effects of dwarf and bantam sex-linked major genes in egg-type chickens

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ABSTRACT

The present study describes the production of stocks segregating dwarf (dw), bantam (dw^B) and normal (dw^+) alleles, as well as the characters, shank length, adult body weight, age at sexual maturity and egg production. Heterozygous K dw^+/k dw^B sires were mated to normal (dw^+) dams to produce stock D6.a, and mated to dw^B females to produce stock D6.b. Stock D4.a came from mating F1 heterozygous dw^B dw sires to dwarf Leghorns. In a third series of matings, 7/8 Sebright and 1/8 dw-Leghorn dw^B dw sires were crossed to three groups of dams of different genotypes. The progeny of the normal (dw^+), dwarf (dw), and bantam (dw^B) dams were designated as stocks D4.b, D4.c and D4.d, respectively. The dw+ dams were White Leghorn strain cross females. The difference between the rate of laying of normal (69.7%) and their bantam sisters (68.6%) was not statistically significant when the average 32-week body weight of the dw+ sisters was 1,897 g. However, when the 32-week body weight of the normal daughters from the same sires and smaller dams was around 1,646 g, the difference between the rate of laying of the normal (78.1%) and their bantam sisters (75.9%) was significant ($P < 0.05$). The dw^B gene may have a similar but smaller effect on the rate of egg laying than its dwarf allele. The difference between sexual maturity of normal and bantam daughters of either the largest or the smallest dams was not statistically significant, even though the smallest dw^B pullets were in average 2.9 days older at first egg. The use of shank length combined with adult body weight allowed a precise discrimination between bantams and dwarfs.

INTRODUCTION

In laying hens the feed consumed is utilized for three main purposes: egg production, body weight gain, and body maintenance. Smaller birds need less food for maintenance than larger ones (Brody *et al.*, 1938). Consequently, when two birds produce the same number of eggs of equal size, the smallest bird consumes less feed and therefore, is more economical. The dwarf (dw) gene (Hutt, 1949) has been used to produce layers of a smaller body size. Three alleles are known to exist at the dwarf locus in the Z sex chromosome of chickens; they are the non-identifiable (dw^+) wild type, the dwarf (dw) and the bantam (dw^B) allele (Custódio and Jaap, 1973). The dw^+ gene is responsible for what is considered normal size and normal body proportions in chickens. The dw allele is responsible for a reduction in body size and for a disproportional shortening of the shank. This paper provided evidence that the bantam gene (dw^B) is located at the dw locus. The bantam gene (dw^B) also reduces body size, but much less than does the dwarf gene (dw). While the dw gene reduces body weight about 30% in females, the third allele (dw^B) reduces adult body weight by less than 10%. This third allele is probably the same sex-linked gene reported by Maw (1935) and by Godfrey (1953). The objectives of this research were: 1) to produce stocks segregating dwarf, bantam or normal alleles; 2) to compare the influences of dw, dw^B and dw^+ genes in small and large White Leghorns.

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MATERIAL AND METHODS

Stocks D6.a and D6.b

Phenotypically the effect of the bantam sex-linked gene, dw^{B}, is not qualitative. Therefore, a linked marker gene is used to detect its presence (Jaap, 1971). The slow feathering K allele was used as a marker for the normal dw^{+} gene and its rapid feathering allele k as a marker for the dw^{B} gene (Custódio and Jaap, 1973). Heterozygous C sires (K dw^{+}/k dw^{B}) were produced as shown in Table I. Initially 50 dwarf (dw) Leghorns were artificially inseminated with semen from two k dw^{B}/k dw^{B} Golden Sebright cocks to produce group A progeny. Although 132 of these progeny were alive at 12 weeks of age, they proved to be very susceptible to Marek disease. Only 19 daughters and 22 sons survived until 42 weeks of age. At this age the average body weight of the daughters was 959 ± 20 g and the sons averaged 1402 ± 42 g. The 22 F1 males were back-crossed to the remaining dwarf Leghorn dams and 59 bantam-type non-dwarf daughters (progeny B) were retained for test matings. Daughters of the F1 generation (progeny A) were mated to a broiler-type male known to be K dw^{+}/k dw^{+} to produce progeny C males. This was the only male available which had at least one Z sex chromosome marked with the K gene. These matings were performed in order to obtain heterozygous sires (K dw^{+}/k dw^{B}) with the Z sex chromosome derived from the broiler-type sire marked by the K slow feathering gene. Only the late feathering (K dw^{+}/k dw^{B}) males were retained for breeding. These males averaged 2764 ± 68 g adult body weight and 116.6 ± 1.4 mm shank length. They were utilized in two test matings to produce progenies D6.a and D6.b (Table I). In test mating 1, 11 C sires were mated to 39 dw^{+} Leghorn dams weighing 1978 ± 51 g, with an average shank length of 101.3 ± 0.8 mm. These Leghorns were chosen as test dams so that their female progeny (D6.a) would be approximately equal in size to a large-size Leghorn. In test mating 2, 10 C sires were mated to 46 non-dwarf females (progeny B, Table I). These dams weighed 1240 ± 26 g with an average shank length of 81.7 ± 0.6 mm. These females were chosen as test dams so that the adult body weight of their female progeny (D6.b) would be equivalent to that of small Leghorns. Since the A sires and the dw-Leghorn dams were common ancestors to both C males and B dams, their D6.b progeny were inbred. The coefficient of inbreeding of the D6.a females was equal to 15.6%. All matings were performed by artificial insemination. The classification of slow and rapid feathering birds was made at hatching time and was checked for accuracy 10 days later. Shank length was measured at 16 weeks of age and body weights were taken at 32 weeks of age. Egg production and sexual maturity were determined for the progeny of test matings 1 and 2. The eggs laid were recorded during a 40-week laying period, for the daughters of the Leghorn dams (test mating 1), and for

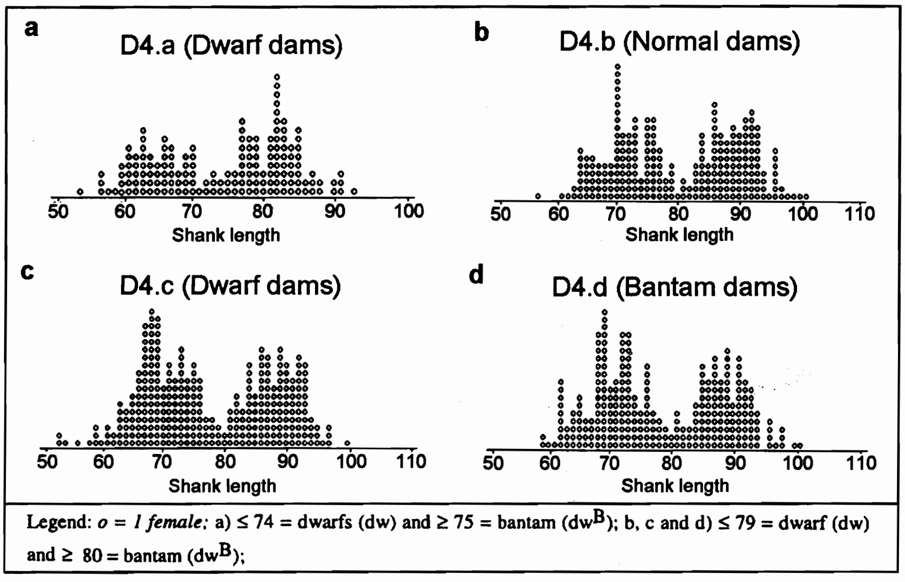
Table I - Matings which provided heterozygous sires for producing stocks segregating normal (dw+), dwarf (dw) and bantam (dw^{B}) genes.

Parents	Mature body weight of dams	Non-crossover genotypes of sons and/or daughters retained for breeding	Progeny notation
2 ♂♂ Sebright x 50 ♀♀ dw-Leghorn	1070 g	F1 (22 ♂♂ k dw^{B}/k dw and 19 k ♀♀	A
22 ♂♂ A x ♀♀ dw-Leghorn	1070 g	BC$_1$ (59 ♀♀ dw^{B} and ♀♀ dw^{B} dw)	B
1 ♂ Broiler-type K dw^{+}/k dw^{+} x 19 ♀♀ k dw^{B} - A	959 g	♂♂ K dw^{+}/k dw^{B}	C
10 ♂♂ B x ♀♀ dw-Leghorn	1070 g	BC$_2$ (104 ♀♀ dw^{B}, 69 ♀♀ dw)	D4.a
		and ♂♂ dw^{B} dw	B′
Test mating No. 1			
11 ♂♂ C x 39 ♀♀ dw^{+}-Leghorn	1978 g	♀♀ K dw^{+} and ♀♀ k dw^{B}	D6.a
Test mating No. 2			
10 ♂♂ C x 46 ♀♀ dw^{B}-Progeny B	1240 g	♀♀ K dw^{+} and ♀♀ k dw^{B}	D6.b
Test mating No. 3			
18 ♂♂ B′ x 49 ♀♀ Leghorn (dw^{+})	large	♀♀ dw^{B} and ♀♀ dw	D4.b
18 ♂♂ B′ x 55 ♀♀ D4.a (dw)	980 g	♀♀ dw^{B} and ♀♀ dw	D4.c
18 ♂♂ B′ x 53 ♀♀ D4.a (dw^{B})	1262 g	♀♀ dw^{B} and ♀♀ dw	D4.d

a 27-week laying period for the daughters of the Bantam dams (test mating 2). For both kinds of pullets, egg production was recorded three days per week, starting at 22 weeks of age. Sexual maturity was recorded as the age in days when the first egg was laid.

Stock D4.a

This stock was developed from repeated backcrossing of heterozygous (k dw^B/k dw) A sires to dw-Leghorn dams (Table I). Initially 3/4 dw-Leghorns and 3/4 Sebright Bantams were produced by backcrossing 22 A males to dw-Leghorn dams. Dwarf and non-dwarf females were obtained from these matings. In the next step, 10 non-dwarf males were backcrossed to dw-Leghorn dams. In the resulting 7/8 dw-Leghorn and 1/8 Sebright Bantam progeny, dwarfs and bantams were identified at 16 weeks of age and shank length was measured on each individual. At housing time, 104 birds were classified as bantams (dw^B) and 69 were classified as dwarfs (dw). Dwarf and bantam females were identified phenotypically by the disproportionate shortening of the shank in the dw birds. The bantams had a shank length equal to or larger than 75 mm whereas the dwarfs had shanks equal to or shorter than 74 mm. The distribution of shank lengths at 16 weeks of age is shown in Figure 1. Both bantams and dwarfs were individually weighed at 32 weeks of age. These birds were brooded and reared on floor pens and were housed in individual cages prior to starting laying.



Legend: *o = 1 female;* a) ≤ 74 = dwarfs (dw) and ≥ 75 = bantam (dw^B); b, c and d) ≤ 79 = dwarf (dw) and ≥ 80 = bantam (dw^B);

Figure 1 - Distribution of shank length of females in stock D4.a., and of daughters from dw^B dw sires and normal (dw^+), dwarf (dw) and bantam (dw^B) dams.

Stocks D4.b., D4.c. and D4.d

Three experimental stocks were produced by mating heterozygous B′ sires (dw^B dw) to normal (dw^+), dwarf (dw), and bantam (dw^B) dams (test mating 3). The heterozygous B′ sires and both the bantam and dwarf dams came from a flock (D4.a) having 7/8 dw-Leghorn and 1/8 Sebright Bantam inheritance (Table I). The D4.a stock was obtained by backcrossing 10 dw^B dw progeny B males (Table I) to dwarf Leghorn dams (mass matings). From this stock, 18 heterozygous (k dw^B/k dw) B′ sires were pedigree-mated to 55 dwarf (dw) and 53 bantam (dw^B) dams from the D4.a stock, together with 49 normal (dw^+) large Leghorn dams to produce, respectively, the experimental stocks D4.b, D4.c and D4.d. The normal (dw^+) dams were strain crosses of White Leghorn commercial layers. Each sire was used to inseminate dams of each of the three genotypes. The average number of normal, dwarf, and bantam dams allocated to each sire was 2.7, 3.0, and 2.9, respectively. A total of 2280 chicks was obtained in two hatches at two-week intervals, and these were distributed by genotype of dam as follows:

Genotype of dam	First hatch	Second hatch
dw^+	295	288
dw	420	452
dw^B	406	419

Chicks from the first hatch were brooded intermingled until eight weeks of age, after which the males were discarded. At 16 weeks of age in both hatches, individual body weights and shank lengths were recorded and the largest and smallest females were housed in separate pens. All pullets were transferred from the floor pens to individual cages when those of the second hatch reached 20 weeks of age. At this time the pullets were classified as bantams or dwarfs on the basis of their body size and shank length proportions. The birds classified as bantams had shank lengths equal to or larger than 80 mm whereas the dwarfs had shanks equal to or shorter than 79 mm. The distribution of shank lengths at 16 weeks is shown in Figure 1. The dwarf pullets were placed in cages and received 15 h of artificial light daily. Individual body weights were obtained at 32 weeks of age for all pullets. Differences between averages were analyzed by the *t*-test outlined by Snedecor and Cochran (1969).

Analysis of variance

The shank and adult body weights in stocks D4.b, D4.c and D4.d were subjected to analysis of variance. The analyses of variance were carried out with the LSMLGP computer program (Harvey, 1972). The sire random s_i and the dam within SG subclasses d_{ijk} effects were excluded from the model and the $(GP)_{jl}$, $(GH)_{jm}$ and $(PH)_{lm}$ interaction effects were included. Genotypes of dam (G), hatches (H), and phenotypes of progeny (P) were fixed effects. The following cross-classified fixed model represents each observation:

$$Y_{jlmn} = \mu + G_j + P_l + H_m + (GP)_{jl} + (GH)_{jm} + (PH)_{lm} + e_{jlmn}$$

where, Y_{jlmn} = is the female trait of the nth progeny in the mth hatch and 1th phenotype belonging to the jth genotype of dam; m = overall mean; G_j = effect of the jth genotype of dam; P_l = effect of the lth phenotype of progeny; H_m = effect common to all individuals in the mth hatch; $(GP)_{jl}$ = effect due to interaction between the jth genotype of dam and the lth phenotype of progeny; $(GH)_{jm}$ = effect due to interaction between the jth genotype of dam and the mth hatch; $(PH)_{lm}$ = effect due to interaction between the 1th phenotype of progeny and the mth hatch, and e_{jlmn} = is the random error characteristic of the nth observation in the mth hatch and 1th phenotype of progeny belonging to the jth genotype of dam. As usual, the random deviations were assumed to be independent and normally distributed.

RESULTS AND DISCUSSION

Stocks D6.a and D6.b

Normal and bantam daughters from the normal dams in stock D6.a were available with complete records on 32-week body weight, shank length, rate of lay, and sexual maturity (Table II and III). There were also normal (dw^+) and bantam (dw^B) daughters with complete records on those same traits from the bantam (dw^B) dams, in stock D6.b (Table II and III). Custódio and Jaap (1973) found highly significant differences between the marker gene classes for mature shank length and body weight at 16 weeks of age in crosses originated from Golden Sebright Bantams. It seems evident, therefore, that the dw^B gene influences both rate of growth and adult size. The dw^B gene reduces eight-week body weight of bantam females by 10%. The difference between shank length of normal (dw^+) and bantam (dw^B) sisters was significant ($P < 0.01$) for the progeny of the normal (stock D6.a), as well as for the progeny of the bantam dams (stock D6.b, Table II). However, 32-week body weight differences between normal (dw^+) and bantam (dw^B) sisters from test matings 1 and 2 were not statistically significant, even though the bantam females (dw^B) were 5.0% and 3.9% smaller than the normal females (dw^+) in stocks D6.a and D6.b, respectively. Therefore, the dw^B gene significantly reduced the skeleton (body size), and perhaps fleshing (body weight) as well.

Since the dw, dwarf gene reduced the rate of lay of dwarf pullets compared to their normal sisters, there is a possibility that the dw^B allele also reduces the egg production of bantam pullets compared to their normal sisters. For the D6.a stock, the difference between the egg production of the normal and their bantam sisters

Table II - Mean ± standard deviations body weights and shank lengths of normal (dw^+) and bantam (dw^B) progenies from mating 1 (Stock D6.a) and 2 (D6.b).

Phenotype of progeny	No.[1/]	dw^+ dams (Stock D6.a)	No.	dw^B dams (Stock D6.b)
		32-Week body weight (g)		
dw^+	50	1897 ± 39	40	1646 ± 44
dw^B	38	1802 ± 45	34	1581 ± 48
Reduction (%)		$5.0\%^{ns}$		$3.9\%^{ns}$
		16-Week shank length (mm)		
dw^+	50	98.0 ± 0.8	40	91.7 ± 0.8
dw^B	38	95.2 ± 0.9	34	88.8 ± 0.9
Reduction (%)		2.9%*		3.2%*

[1/] Number of observations; * Statistically significant ($P < 0.05$). ns, Nonsignificant.

Table III - Egg production and sexual maturity of normal (dw^+) and bantam (dw^B) progenies from mating 1 (Stock D6.a) and 2 (D6.b).

Phenotype of progeny	No.[1/]	dw^+ dams (Stock D6.a)	No.	dw^B dams (Stock D6.b)
		Egg production (%)		
dw^+	50	69.7 ± 1.6	40	78.1 ± 0.7
dw^B	38	68.6 ± 1.9	34	75.9 ± 0.7
Reduction (%)		$1.6\%^{ns}$		2.8%*
		Sexual maturity (days)		
dw^+	50	159.6 ± 1.7	40	149.0 ± 2.2
dw^B	38	159.5 ± 2.0	34	151.9 ± 2.4
Difference		-0.5 days^{ns}		+2.9 days^{ns}

[1/] Number of observations; ns, nonsignificant; *statistically significant ($P < 0.05$).

was not statistically significant when mean body weight of the normal sisters was 1897 g. However, when the mean adult body weight of the normal daughters from the same sires and smaller dams was 1646 g, the difference between the egg production of the normal and their bantam sisters was significant ($P < 0.05$) (Table III). Although sample sizes were small, the possibility that the dw^B allele reduces egg production of the smallest birds exists. The coefficients of variation in stocks D6.a were several times larger than in stock D6.b. Since Prod'homme and Merat (1969) reported that the dwarf gene does not depress egg production in larger meat-type birds, the present results may indicate that the dw^B allele reduces egg production when the dw^B female weighs 1.9 kg or less at 32 weeks of age, or when the dw^B females shank length is less than 90 mm. Although the females in stock D6.b were inbred by 15.6% it is not clear whether this influenced the laying rate. The difference between sexual maturity of normal and bantam daughters of either the largest or the smallest dams was not statistically significant (Table III), even though the smaller dw^B pullets were in average 2.9 days older at first egg. The coefficient of variation estimated for dwarfs in stock D6.b was only about 1.6%.

Table IV - Means and standard errors for adult body weight of females in stocks D4.a, D4.b, D4.c and D4.d.

Phenotype of females		Stocks D4.a	D4.b	D4.c	D4.d	Total
dw^B	No.	50	66	83	76	275
	Ave	1262 ± 25	1505 ± 25	1456 ± 22	1445 ± 23	
dw	No.	38	50	101	112	301
	Ave	980 ± 29	1146 ± 28	1096 ± 21	1069 ± 19	
Reduction (%)		22.3%*	23.8%*	24.7%*	26.0%*	

*Statistically significant ($P < 0.01$). Ave, Average.

Table V - Least-square means and standard errors for 16-week shank length (in mm) of females.

Phenotype of females		Stocks D4.a	D4.b	D4.c	D4.d	Total
dw^B	No.	92	108	127	121	448
	Ave	81.2 ± 3.99	90.8 ± 0.5	89.3 ± 0.5	89.4 ± 0.5	
dw	No.	73	100	159	139	471
	Ave	65.2 ± 4.49	72.6 ± 0.5	69.7 ± 0.4	70.8 ± 0.4	
Reduction (%)		20.4%*	20.0%*	21.9%*	20.8%*	

*Statistically significant ($P < 0.01$). Ave, Average.

Other stocks

Thirty-two-week body weights and shank lengths of bantam and dwarf females are shown in Tables IV and V, for stocks D4.a, D4.b, D4.c and D4.d. These results showed that the shank length was a satisfactory measure for phenotypically discriminating dwarfs and bantams at 16 weeks of age. A second classification, where both shank length and adult body weight were used for classifying birds, resulted in a surplus of 9.4% more dwarfs. Therefore, there seems to have been no misclassification with regard to the data presented. This may be corroborated by the bimodal 16-week shank length distribution presented in Figure 1. In general, the discrimination between dwarf and bantam females seemed to be made accurately by shank length and adult body weight differences. By discarding birds with doubtful phenotypes, possible misinterpretation was avoided. When using shank length only, the estimated misinterpretation was 1.5%, which increased to 8.6% when body weight was also considered.

In the least-squares analysis of variance for shank length and adult body weights, the mean squares for shank length were statistically highly significant ($P < 0.01$) for genotype of dams (G) and phenotype of progenies (P) (Table VI). The interaction P x H was significant at the 5% level but G x P and G x H were not significant. Therefore, dwarfs and bantams showed sensitivity and some differential reactions to the environment in terms of skeletal growth. On the other hand, there is indication of an absence of a gene x genotype interaction for shank length involving sex-linked alleles and the background genotype of the dams. For adult body weight, phenotypes (P) were highly significant ($P < 0.01$) whereas G and H were significant at the 5% level. It seems that genotypes of dams diverged more in body size (skeleton) than in fleshing (body weight). Also, fleshing, as expected, was more influenced by the environment, further indicating that body size and fleshing (body weight), although highly correlated, are actually different traits.

The percent reduction in weight of the dwarf allele varied 16.6% (Table IV). Despite the high coefficient of variation observed, the differences between the 32-week body weight of dw^B and dw progeny were highly significant ($P < 0.01$) in all mating types. The reduction in the 32-week body weight of

Table VI - Least-squares analysis of variance for shank length (mm) and 32-body weight (g) of progeny from heterozygous sires (dw^B dw) mated to D4.b normal (dw^+), D4.c dwarf (dw) and D4.d bantam (dw^B) dams.

Source of variation	d.f.	Mean squares	
		16-Week shank length	32-Week body weight
Genotype of dam (G)	2	93.7223**	167001.0325*
Phenotype (P)	1	37877.7513**	14913577.6923**
Hatch (H)	1	72.5030^{ns}	182305.5133*
G x P	2	8.6993^{ns}	3877.8838^{ns}
G x H	2	19.1046^{ns}	37280.4164^{ns}
P x H	1	86.6189*	4450.9542^{ns}
Remainder	478	19.1955	40382.8950

ns - Nonsignificant; *statistically significant ($P < 0.05$); **statistically significant ($P < 0.01$).

dwarfs in all stocks, however, was smaller than that reported for dwarfs in relation to normal egg-type chickens (Bernier and Arscott, 1960; Mohammadian, 1969, and others). As the dw^B gene is expected to reduce 32-week body weight by 10%, this result was expected (Custódio and Jaap, 1973). All differences between means of dwarfs and bantams were highly significant ($P < 0.01$) with regard to shank length. The percent reduction due to the dwarf allele varied little.

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RESUMO

Neste trabalho descreve-se a obtenção de seis plantéis experimentais, segregantes para os alelos ligados ao sexo, dwarf (dw), bantam (dw^B) e normal (dw^+), em galinhas para ovos. Comparações entre desempenhos entre plantéis hemizigóticos para genes maiores no locus dwarf também foram efetuadas com relação a comprimento de canela medida na 16ª semana de idade, peso do corpo adulto, produção de ovos e maturidade sexual. Machos heterozigotos (K dw^+ / k dw^B) foram acasalados com fêmeas normais (dw^+) e com fêmeas bantam (dw^B). As progênies fêmeas, nos referidos acasalamentos, foram denominadas de D6.a e D6.b, respectivamente. Galos 7/8 Sebright e 1/8 dw-Leghorn heterozigotos (dw^B dw) foram acasalados com três grupos de galinhas de diferentes genótipos (dw^+, dw e dw^B). As progênies das mães normais (dw^+), dwarf (dw) e bantam (dw^B) foram denominadas de plantéis D4.b, D4.c e D4.d, respectivamente. As seguintes conclusões foram relatadas: a) a redução no peso corporal adulto de fêmeas dwarf, em todos os plantéis, em relação a fêmeas bantam, foi menor que a relatada em relação a galinhas normais do tipo ovo; b) a diferença entre a taxa de postura de galinhas normais e suas irmãs bantam não foi estatisticamente significativa em fêmeas dw^+ (filhas de mães dw^+), pesando 1897 g. Porém, em galinhas dw^B com peso médio de 1646 g (filhas de mães dw^B), a diferença entre a taxa de postura de galinhas normais e de suas irmãs bantam foi significativa ($P < 0{,}05$). Portanto, o alelo dw^B pode ter um efeito semelhante, porém menor sobre a taxa de postura do que seu alelo dwarf; c) a diferença entre maturidade sexual de galinhas normais e bantam, filhas de mães maiores ou menores, não foi estatisticamente significativa, muito embora a postura do primeiro ovo tenha ocorrido 2,9 dias mais tarde em frangas dw^B menores; d) o comprimento de canela associado ao peso adulto possibilitou a discriminação precisa entre bantams e dwarfs.

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