

Increase of egg weight with age in normal and dwarf, purebred and crossbred laying hens

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Summary – An exponential curve, $W = P - Q \exp(-Rt)$ was fitted to egg weights (W) of individual hens from 8 genetic groups tested for egg production from 18–51 weeks of age (t). The groups were constituted of the combination of genotype at the sex-linked dwarfism locus (normal or dwarf) and line (White Leghorn, Brown Egg and both reciprocal crosses). The least-squares mean of the residual standard deviation about the curve was between 1.27 and 1.74 g in the 8 groups and estimated values of the initial $P - Q$ and mature egg P weights were between 26.9 and 33.9 g and 56.9 and 65.8 g, respectively. Effects of genotype and line as well as heterosis were estimated for both egg weights and for rate of growth relative to the remaining expected growth (R). R was smaller for dwarf hens which thus reached mature egg weight later than normal females. Significant heterosis was found for both egg weights of dwarf hens (12.6 and 9.5%) and for the initial egg weight of normal ones (12.8%). Negative heterosis for R obtained for dwarf hens (–17.4%) corresponded to a flatter egg weight curve of these crossbreds.

egg weight / age of hen / heterosis / dwarfism / exponential curve

Résumé – Évolution comparée du poids de l'œuf avec l'âge de la poule chez des femelles normales ou naines et pures ou croisées. On a ajusté individuellement une courbe de la forme $W = P - Q \exp(-Rt)$ au poids de l'œuf (W) mesuré entre 18 et 51 sem d'âge (t) chez des poules de 8 groupes génétiques définis par la combinaison du génotype au locus de nanisme lié au sexe (normal ou nain) et de la lignée (souche Leghorn blanche, souche à œuf brun et leurs croisements réciproques). L'écart type résiduel après ajustement de la courbe exponentielle aux valeurs de poids, évalué pour chaque groupe par la méthode des moindres carrés, a pris des valeurs comprises entre 1,27 et 1,74 g. De la même manière, les estimations des poids du premier œuf ($P - Q$) étaient situées entre 26,9 et 33,9 g, et celles de l'œuf à maturité entre 56,9 et 65,8 g d'autre part. On a évalué les effets du génotype et de la lignée et l'hétérosis pour les poids de l'œuf et l'accroissement de poids journalier relativement au poids restant à gagner (R). La valeur de R était inférieure pour les poules naines qui par conséquent ont atteint leur poids d'œuf à maturité plus tard

que les femelles normales. Un hétérosis significatif a été obtenu pour les 2 poids d'œuf chez les poules naines (12,6 et 9,5%) et pour le poids du premier œuf chez les femelles normales (12,8%). L'hétérosis négatif trouvé pour R chez les poules naines (-17,4%) correspond au fait que la courbe du poids de l'œuf étaient plus aplatie chez les croisés de ce génotype.

poids de l'œuf / âge de la poule / hétérosis / nanisme / courbe exponentielle

INTRODUCTION

Egg weight increases curvilinearly with age of hen (Cowen *et al*, 1964). Although it might be advantageous to have egg-laying hens producing quickly and regularly eggs within a limited weight range (Poggenpoel and Duckitt, 1988), few works have analyzed the relationship between egg weight and age, or evaluated its variability. A non-linear equation with 3 parameters (mature egg weight, egg weight range and rate of increase of egg weight) was proposed by Weatherup and Foster (1980). They compared parameters of the curves fitted for pure and crossbred hens but they did not evaluate the effect of heterosis on the shape of the curve. The same type of curve was used by Foster *et al* (1987) to help produce a weekly forecast of the number of class A (British grading) eggs in several commercial flocks. Recently, Shalev and Pasternak (1993) applied the method of Weatherup and Foster to egg weight and grading for several avian species. An analogous but exponential curve was developed by Yoo *et al* (1983) who estimated the heritability of the 3 parameters of the curves obtained for hens from 2 selected lines.

The sex-linked dwarfism gene *dw* is associated with several unfavourable effects on egg traits, and particularly on egg weight (Mérat, 1990). In a recent work, the influence of heterosis on the reduction of production associated with *dw* was explored and some advantage was found for crossbred dwarf hens (Mérat *et al*, 1994). However, the egg weight at the age of 43–45 weeks was still about 4 g lighter in dwarf than in normal crossbred hens. In the present study, the egg weight increase of normal and dwarf hens of 2 parental pure lines (White Leghorn and Brown Egg) with age and their reciprocal crosses were compared and the effects of *dw* and heterosis on the shape of the exponential curve of egg weight with time were estimated in order to explore the dynamics of egg weight in relation to *dw* and crossbreeding.

MATERIALS AND METHODS

Birds

Genetic types and genotypes have been described previously by Mérat *et al* (1994). Briefly, pure and crossbred, normal and dwarf progenies were obtained in a single hatch from a White Leghorn line and a Brown Egg line (11 *DW dw* males per line mated to 3 or 4 females each) maintained in our laboratory. Hens were housed in individual cages in a single room under 14 h light and 10 h dark, at 22°C, from 18 to 52 weeks of age. A commercial egg layer diet (15.5% total

protein, 2 600 kcal/kg metabolizable energy, 3.4% calcium) was provided *ad libitum*. Performances reported elsewhere (Mérat *et al*, 1994) can be summarized as follows. Both normal and dwarf Brown Egg purebred females were heavier at 17 weeks (by 513 and 366 g, respectively) and at 52 weeks (by 743 and 495 g, respectively) than their White Leghorn counterparts. They also started laying earlier (14.8 and 17.7 d earlier, respectively), and laid more eggs (22.6 and 23.9 more up to 51 weeks of age, respectively), which were heavier (by 3.8 and 5.1 g, respectively). Finally, crossbreds had intermediate body weights but performed at the same level as the pure Brown Egg line for egg production traits.

Data and statistical analysis

A total of 430 birds were tested for egg production from 18 to 51 weeks of age. Weekly, and then every other week, 3 consecutive eggs were collected from each bird. Double-yolk, soft-shelled or broken eggs were discarded, the total weight of 2 normal eggs was recorded and the corresponding mean weight was calculated. A maximum number of 29 weights could be obtained for each hen. Fifty-three hens were excluded because they died or stopped laying early.

An exponential curve, $W = P - Q \exp(-Rt)$, was fitted to the series of egg weights of each remaining hen, using the Nlin procedure (SAS Institute, 1988). Under this model described by Brody (1964) and applied to egg weight by Yoo *et al* (1983), egg weight (W) increases with age (t) and R is the rate of growth relative to the growth yet to be made: $R = (dW/dt)/(P - W)$. The parameter Q is the range of weights from initial egg weight to mature egg weight and $P - Q$ is the egg weight for $t = 0$, *ie* at the age of 18 weeks in this experiment. Residual standard deviation about the curve was also calculated as a measure of the goodness of fit of the curves to the data. The iterative process failed to converge for 22 hens (11 normal and 11 dwarf). Correspondingly, reasonable estimations of P , Q and R could not be obtained for them. Inspection of the actual egg weight curves of these hens revealed that they did not reach the self-inhibiting phase of decreasing slope during the whole span of the experiment. For every variable describing the shape of the egg weight curve (namely P , $P - Q$, R and the residual standard deviation) of the remaining 356 hens, a 2-way analysis of variance with interaction was performed. The main effects were genotype at the sex-linked dwarfism locus (normal or dwarf) and genetic type (Leghorn, Brown Egg, Leghorn \times Brown Egg, Brown Egg \times Leghorn). Variables with significantly positively skewed distributions (P , Q , and R) were transformed with the log transformation (Gill, 1978) and then analyzed, without changing the significance of the effects or the heterosis. Therefore results are given on untransformed data. Means of lines within each phenotype, normal and dwarf, were compared also by the Student–Newman–Keuls procedure. Correlations with parameters of the exponential egg weight curve and with egg production traits (egg number, age at first egg, egg weight at end of test and body weights at 17 and 52 weeks of age) were calculated both within and across genotypes. From linear combinations of least-squares means, heterosis was estimated for both normal and dwarf hens, crossbred advantage was calculated for each reciprocal cross and reciprocal crossbred performances were compared. All analyses were performed using the general linear model procedure (SAS Institute, 1988).

RESULTS

Least-squares means for the variables that describe the shape of the egg weight curve, with the significance levels of main effects and interactions, are listed in table I. Dwarf birds had smaller egg weights ($P < 0.05$), both initially and at maturity, a lower rate of change of egg weight increment and a smaller residual standard deviation about the curve ($P < 0.001$). Initial egg weight line differences ($P < 0.05$), with larger eggs from crossbreds than from White Leghorn hens, persisted only marginally ($P < 0.10$) in mature egg weight, but more clearly among dwarf hens. Only marginal line differences ($P < 0.10$) were found for the rate of change in egg weight increment but the residual standard deviation about the curve was significantly lower ($P < 0.001$) in the White Leghorn line.

Correlations with parameters of the exponential egg weight curve and several production traits recorded during the experiment are presented in table II.

Correlations between the rate R and the other parameters of the exponential curve were significant ($P < 0.001$) and negative for both normal and dwarf hens. Mature egg weight, P , was associated positively ($P < 0.001$) with Q and $P - Q$ to the same extent in normal and dwarf females. Initial egg weight, $P - Q$, had positive correlations with Q in dwarf hens ($P < 0.05$) and with the residual standard deviation in normal females ($P < 0.05$).

For both types of females, mature egg weight, P , was positively correlated with actual body weight at the beginning ($P < 0.05$) and the end ($P < 0.01$) of the test period and with mean egg weight (2-week egg collection at 43 weeks of age) ($P < 0.001$). However, it was not associated with age at first egg and it was correlated negatively ($P < 0.05$) with egg number of normal hens. Total egg weight gain, Q , was hardly associated with body weights and was not correlated with age at first egg. However, it increased with mean egg weight ($P < 0.01$) and decreased with higher egg number ($P < 0.001$) in normal females. Initial egg weight, $P - Q$, was correlated with all 5 traits, similarly in dwarf and normal hens. Association was negative only with age at first egg ($P < 0.01$). The rate R was significantly correlated with egg number of dwarf females only ($P < 0.05$). Larger residual standard deviation was associated with higher body weights ($P < 0.01$) and egg weight ($P < 0.05$) of normal hens, and with higher 17-week body weight ($P < 0.05$) of dwarf females.

Correlations between production traits are given here for the sake of completeness. They were quite similar for both types of hens. Correlations of egg number with egg weight were the only non-significant values ($P > 0.05$).

Table III contains percentage superiority for each reciprocal cross and heterosis, separately for dwarf and normal hens, with corresponding comparisons of crossbred superiority. Heterosis of initial egg weight, $P - Q$, was significant ($P < 0.01$ or $P < 0.001$) for all crossbred types but it was not different between normal and dwarf hens. At maturity, heterosis for egg weight, P , was significant ($P < 0.05$ or $P < 0.01$) for dwarf hens only. Negative heterosis ($P < 0.10$ or $P < 0.05$) was obtained for the rate of change R of the egg weight curve of dwarf females. Crossbred advantage was not different in the 2 reciprocal crosses, except for R in normal hens ($P < 0.05$). There was some heterosis ($P < 0.10$) of the same magnitude in normal and dwarf hens for the residual standard deviation about the curve.

Table I. Least squares means of the variables describing the exponential egg weight curve and residual standard deviation about the curve according to genotype and genetic type.

	Normal				Dwarf				Significance of effects		
	L	L × BE	BE × L	BE	L	L × BE	BE × L	BE	Genotype	Genetic type	Interaction
Number of birds	46	46	38	43	46	46	45	46			
Initial 18 weeks egg weight, $P - Q$, (g)	29.1 ^c	33.9 ^{ab}	35.0 ^a	31.9 ^b	26.9 ^c	33.0 ^a	31.2 ^{ab}	30.0 ^b	*	*	NS
Rate of change in egg weight increment R	0.00819 ^a	0.01060 ^a	0.00806 ^a	0.00979 ^a	0.00853 ^a	0.00730 ^a	0.00748 ^a	0.00936 ^a	*	+	+
Mature egg weight P , (g)	64.0 ^a	63.6 ^a	65.8 ^a	64.9 ^a	56.9 ^b	65.3 ^a	64.3 ^a	61.4 ^{ab}	*	+	NS
Residual standard deviation (g)	1.39 ^b	1.66 ^a	1.68 ^a	1.74 ^a	1.27 ^b	1.52 ^a	1.50 ^a	1.53 ^a	***	***	NS

+ $P < 0.10$; * $P < 0.05$; *** $P < 0.001$; NS: not significant; L: White Leghorn line, BE: Brown Egg line. Means for lines within genotype with no common superscripts are significantly different ($P < 0.05$).

Table II. Correlation between parameters of the exponential egg weight curve, between production traits and between both types of character in normal and dwarf hens.

	P	Q	P - Q	R	Residual sd	Egg number	Age first egg	Egg weight	17-week body weight
<i>Q</i>									
Normal	0.86***								
Dwarf	0.93***								
<i>P - Q</i>									
Normal	0.45***	-0.07							
Dwarf	0.53***	0.18*							
<i>R</i>									
Normal	-0.66***	-0.38***	-0.63***						
Dwarf	-0.65***	-0.48***	-0.63***						
Residual standard deviation									
Normal	0.08	0.01	0.15*	-0.02					
Dwarf	-0.05	-0.08	0.05	0.02					
Egg number									
Normal	-0.15*	-0.33***	0.28***	0.12	-0.08				
Dwarf	0.10	-0.03	0.34***	-0.15*	0.09				
Age at first egg									
Normal	-0.03	0.09	-0.22**	-0.13	-0.05	-0.43***			
Dwarf	-0.12	-0.05	-0.20**	0.00	-0.06	-0.43***			
Egg weight at 43-45 weeks									
Normal	0.43***	0.22**	0.42***	-0.13	0.20*	0.14	-0.25***		
Dwarf	0.45***	0.33***	0.49***	-0.09	-0.01	0.10	-0.29***		
17-week body weight									
Normal	0.19*	0.02	0.32***	-0.02	0.36***	0.25***	-0.42***	0.42***	
Dwarf	0.16*	0.03	0.35***	0.05	0.15*	0.36***	-0.46***	0.49***	
52-week body weight									
Normal	0.21**	0.07	0.28***	-0.05	0.28***	0.20**	-0.30***	0.50***	0.76***
Dwarf	0.26***	0.13	0.39***	-0.04	0.03	0.26***	-0.40***	0.61***	0.73***

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; P = mature egg weight; Q = range of egg weights; $P - Q$ = initial egg weight; R = rate of change in egg weight increment relative to the increment needed to reach mature weight; $n = 168-183$.

Table III. Percentage crossbred superiority over pure lines evaluated for each reciprocal cross and overall (heterosis), and corresponding comparisons between normal and dwarf hens.

	Percentage crossbred superiority						Comparison of crossbred superiority between normal and dwarf hens		
	Normal			Dwarf			Value of F and significance of the contrast		
	L × BE	BE × L	Heterosis	L × BE	BE × L	Heterosis	L × BE	BE × L	Heterosis
Initial egg weight <i>P - Q</i>	11.0***	14.7***	12.8***	15.8***	9.5***	12.6***	0.8	1.8	0.1
Rate of change <i>R</i> (in egg weight increment)	17.9 [†]	-10.3	3.8	-18.4 [†]	-16.4 [†]	-17.4*	7.0***	0.2	3.5 [†]
Mature egg weight <i>P</i>	-1.2	2.2	0.5	10.3**	8.6*	9.5**	4.8*	1.3	4.1*
Residual standard deviation	6.0	7.5	6.8 [†]	8.5	7.0	7.8 [†]	0.1	0.0	0.0

+ *P* < 0.10; * *P* < 0.05; ** *P* < 0.01; *** *P* < 0.001; L = White Leghorn line, BE = Brown Egg line.

DISCUSSION

Residual standard deviation about the non-linear curve fitted to egg weights is a measure of the goodness of fit of the curve to the data. Values between 1.27 and 1.74 g obtained in this experiment (table I) compare favourably with those around 2 g reported by Weatherup and Foster (1980) and Yoo *et al* (1983). While the former authors did not find any effect of the breed on the residual standard deviation, a consistently smaller value (table I) was found for the White Leghorn line used in this study, and more generally for dwarf hens. However, this observation may be scale related as both White Leghorn and dwarf hens laid smaller eggs. Indeed, correlation of residual standard deviation with mean egg weight was 0.20 for normal hens and was -0.01 (not significant) for dwarf females while the correlation with initial egg weight, $P - Q$, was 0.15 for normal hens (table II). On the other hand, no association was found between residual standard deviation and mature egg weight, P , in either type of hens. Moreover, as dwarf hens produce fewer defective eggs (Mérat, 1990), their egg weight increase with age might also be more regular.

The observed egg weight was larger in the Brown Egg line than in the White Leghorn line (Mérat *et al*, 1994), as was the case for the initial egg weight ($P - Q$) estimated for normal and for dwarf hens (31.9 *versus* 29.1 g and 30.0 *versus* 26.9 g). This could be expected as the Brown Egg line was a heavier line (Mérat *et al*, 1994). However, the corresponding values of heterosis (table III) were surprisingly large, and yet agreed well with actual values above 10% (data not shown) measured from all 68 eggs obtained at 20 weeks of age. Heterosis for initial egg weight was the same in the 2 genotypes, a reflection of the fact that $P - Q$ was associated with all main production traits to the same extent in normal and dwarf females (table II). As anticipated, adjusted mature egg weight was larger than the observed mean egg weight at 43–45 weeks of age reported by Mérat *et al* (1994) but the ranking of the purebreds and crossbreds within genotype was quite similar to that in their report, with little differences between lines (table I). At maturity, while normal Leghorns had caught up with the 3 other normal types for egg weight, dwarf Leghorns still had smaller egg weight (table I), which induced the significant positive heterosis reported for dwarfs (table III). Negative correlation of P with egg number (table II) in normal hens buffered mature egg weight differences between crossbreds and purebreds that could have been anticipated from initial egg weights, thereby reducing heterosis. On the contrary, the absence of a similar correlation in dwarf hens allowed maintenance of heterosis at maturity for this genotype.

Good correlations between Q and P were to be expected as the range of egg weight, Q , is extended more by raising its upper limit, P , than by decreasing its lower end, $P - Q$. As a matter of fact, no significant negative correlation was found between Q and $P - Q$. Furthermore, the positive correlations found between initial and mature egg weights reflect the obvious biological association between the 2 traits. On the other hand, the positive correlation between Q and $P - Q$ in dwarf hens does not have a straightforward explanation. As initial egg weight was smaller in those birds, the strong correlation between Q and P may have combined its effects with those of the smaller rate R , observed for dwarfs (table I), to allow for a simultaneous positive association with $P - Q$.

The smaller rate of change in egg weight increment (table I) for dwarf hens (egg weight curve was flatter) delayed attainment of mature egg weight. Moreover, negative heterosis for dwarf crossbreds (table III) indicates that within the range of ages and weights observed in this experiment the curve was flatter for those 2 genetic types. This is confirmed by the only significant (and negative) correlation involving R , with egg number in dwarfs (table II), which indicates that, among dwarfs, mature egg weight would be reached later by hens laying more eggs. On the contrary, positive heterosis obtained only for normal Leghorn \times Brown Egg crossbreds, showed that curvilinearity was enhanced by this cross and, therefore, that mature egg weight could be reached earlier.

As the exponential curve was flatter (for smaller R values), mature egg weight, P , was reached later, thereby allowing for larger extreme egg weights and egg weight range, and for the negative correlations found between those traits and R .

An ideal egg weight curve would be one starting at a high initial weight and quickly increasing towards a high mature egg weight. In this work, favourable combinations for the 3 parameters of the curve were obtained for all normal size genetic types except the pure Leghorn, and particularly for the Leghorn \times Brown Egg cross with its fast rate of increase. Among dwarf groups, pure Leghorns were even more at a disadvantage as their initial and mature egg weights were both smaller. Reciprocal crossbreds had higher initial egg weight than purebreds but took longer to reach their mature weight, which was also larger, while pure Brown Egg had a better rate of change. The interest of the dwarf gene in crossbred hens reported by Mérat *et al* (1994) for egg production traits was somewhat confirmed here for the evolution of egg weight, but increasing R in crossbred dwarfs would make them even more acceptable for egg production.

More generally, the present study confirmed the value of the exponential curve to describe the increase of egg weight with age for several genetic types. It has also shown that the shape of the curve was affected by genetic differences between lines through its 3 parameters. The expected crossbred advantage for egg weight was also obtained by comparing values of the corresponding parameters for purebreds and crossbreds. Heterosis, however, was generally higher than usually reported from actual measurements, maybe because they were made before maturity (constant egg size) was reached.

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