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Feed Allowance—Genotype Interactions in Broiler Breeder Hens

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ABSTRACT Ad libitum feeding reduces livability and reproductive fitness in broiler breeder hens. Two genotypes, a standard (S) and an experimental dwarf broiler breeder (E), were fed ad libitum (SA and EA, respectively), restricted at 55% of ad libitum feed intake (intermediate restriction) from 6 to 15 wk of age (SI and EI, respectively), or restricted (SR and ER, respectively) to match a standard growth curve with a diluted mash feed (2,400 kcal/kg). The experiment was repeated at 2 locations (experiment 1 = 672 hens in pens from 0 to 40 wk; experiment 2 = 420 hens in pens and cages from 0 to 53 wk). Feed restriction reduced adult BW by 20% compared with ad libitum feeding, delayed sexual maturity by 2 to 4 wk, and improved livability. Hens fed the intermediate diet immediately compensated after 15 wk of age to reach BW, sexual maturity, and livability close to those of ad libitum-fed hens. The E genotype exhibited better tolerance to ad libitum feeding than the S genotype in all measured aspects. Average laying rate during the first 24 wk of lay was 66.4, 77.4, 69.9, 47.2, 57.9, and 72.4% for EA, EI, ER, SA, SI, and SR respectively in experiment 2. Egg abnormalities (double yolk, shell problems) decreased after the peak of lay but remained consistently higher for S compared with E, and for ad libitum and intermediate diets compared with the restricted diet. Yolk deposition rate was measured by a double dye technique. Duration of yolk rapid growth was 8.8 d in E and 9.3 d in S hens ($P < 0.001$), but this difference did not explain the observed variations in laying rate. The potential to increase feed allowances even with a diluted diet in broiler breeder hens requires adapted genotypes.

(*Key words*: broiler breeder, feed allowance, age, follicular growth, egg production)

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INTRODUCTION

Genetic selection for fast growth in broilers has increased feed intake in broiler breeders, with negative consequences on their reproductive performances. Because reproduction has low heritability, only hypothetical modern genomic technologies might resolve this dilemma in the future (Bulfield, 2004). Limiting feed intake is currently the only practical tool to limit the negative effects of selection for growth on egg and chick production. However, the severity and duration of feed restriction to broiler breeder chickens have to be continuously adapted according to changing genotype and selection goals, and feed restriction remains a subject of debate among welfare groups (Hocking et al., 2001; Mench, 2002). To counteract, in part, the application of severe feed restriction, several authors have investigated modified rearing programs to reconcile good reproductive performance with a less severe feeding regimen (qualitatively or quantitatively during certain periods) and improved welfare (Robbins et al., 1986, 1988; Hocking, 1993; Savory et al., 1996; Bruggeman et al., 1999; Renema et al., 1999; Savory and Larivière, 1999; Hocking et al., 2001, 2004).

Some genotypes exhibit better tolerance to ad libitum feeding. Dwarf sex-linked breeder hens tolerate ad libitum feeding with better reproductive fitness than regular broiler breeders (Hocking et al., 1987; Whitehead et al., 1987; Triyuwanta et al., 1992). Some dilution with fiber may improve the welfare of female broiler breeders (Hocking et al., 2004) even if its efficiency to limit growth rate is not adequate (Savory et al., 1996). In a recent experiment with promising results, a feed diluted with wheat bran was provided ad libitum to an experimental strain of dwarf breeders selected for viability and reproductive traits (Heck et al., 2004). However, the control normal breeders in that experiment received a regular undiluted feed and thus, the actual factor responsible for the positive results remained unclear.

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Abbreviation Key: EA = experimental dwarf genotype fed ad libitum; EI = experimental dwarf genotype on intermediate feed allowance; ER = experimental dwarf genotype on restricted feed allowance; SA = standard genotype fed ad libitum; SI = standard genotype on intermediate feed allowance; SR = standard genotype on restricted feed allowance.

TABLE 1. Composition and characteristics of the diets

Ingredient (%)	Starter	Grower	Breeder
Corn	22.84	10.00	18.00
Wheat	30.00	38.65	27.05
Soybean meal (48%CP)	17.00	8.00	9.00
Peas	5.00	2.00	4.00
Wheat bran	20.00	37.25	32.00
Soybean oil	1.00	1.00	2.00
Calcium carbonate	1.40	1.28	6.20
Dicalcium phosphate	1.50	0.70	0.67
L-Lysine HCl	0.16	0.07	0.04
DL-Methionine	0.15	0.10	0.09
Salt	0.35	0.35	0.35
Vitamins[1]	0.05	0.05	0.05
Trace minerals[1]	0.01	0.01	0.01
Calculated analysis (%)			
AME_n (kcal/kg)	2,600.00	2,400.00	2,400.00
Crude protein	17.70	15.20	14.70
Lysine	0.98	0.71	0.70
Methionine + cysteine	0.73	0.63	0.60
Ca	1.00	0.76	2.61
Available P	0.45	0.39	0.35

[1]Vitamin and trace mineral complexes provided (per kg of diet): vitamin A (retinyl palmitate, 10,000 IU; cholecalciferol, 1,500 IU; vitamin E (DL-α-tocopheryl acetate), 15 mg; vitamin B_1, 1.5 mg; vitamin B_2, 3.2 mg; D-pantothenic acid, 25 mg; vitamin B_6, 1 mg; vitamin B_{12}, 0.008 mg; biotin, 0.2 mg; niacin, 3.6 mg; vitamin K_3, 1.25 mg; folic acid, 1.5 mg; choline chloride, 750 mg; cobalt, 1.2 mg; copper, 8.8 mg; zinc, 84 mg; manganese, 106 mg; iron, 44 mg; iodine, 1.2 mg; selenium, 0.2 mg.

The objective of the present experiments was to further explore the possibilities of feeding broiler breeders a diluted diet to compare an experimental dwarf broiler breeder with a conventional strain at 3 feed allowance levels: ad libitum, partial restriction from 6 to 15 wk of age, or feed restriction throughout the experiment. From previous results it was found that the period from wk 6 to 15 during rearing is critical for restricting broiler breeders when improvement of reproductive performance is desired (Bruggeman et al., 1999). The level of restriction between wk 6 and 15 of age was based on a proportion of the feed intake of the ad libitum fed birds, which was fixed at 55%. The experiment was duplicated on the same genotypes in 2 distinct locations and special attention was given to the effects of genotype and feeding regimen on egg production. In addition, we studied the effect of the feeding regimen on yolk deposition rate as an indicator of follicular growth rate, which is assumed different between ad libitum and restricted broiler breeders. Several studies suggest that the increased incidence of erratic ovipositions, double-yolked eggs, and defective eggs in ad libitum birds is the result of the simultaneous development of follicles, resulting in multiple hierarchies of follicles, and of multiple recruitment from the white cohorts into the hierarchy of yellow follicles (Yu et al., 1992; Hocking, 1993; Waddington and Hocking, 1993).

MATERIALS AND METHODS

Experiment 1 (Nouzilly)

Birds and Treatments. Six hundred seventy-two 1-d-old female chicks were delivered by Hubbard (Chateaubourg, France). There were 336 chicks of conventional standard broiler breeder Hubbard (S), and 336 chicks of an experimental dwarf heavy broiler breeder type selected for better viability and reproductive traits at the partial expense of growth (E). One-third of the chicks of each genotype (SR and ER) were feed restricted from 2 wk of age to the end of the experiment, to match a reference body weight curve provided by the breeding company, and one-third (SA and EA) was fed ad libitum. The remaining one-third (SI and EI) received an intermediate feed restriction program from 6 to 15 wk of age only, at 55% of the feed intake of the corresponding ad libitum groups. The 6 experimental treatments (SA, SI, SR, EA, EI, and ER) were replicated 8 times according to a randomized block design. There were 8 blocks of 6 pens of 14 chicks each (1.7 × 1.7 m). Each block was located on half of a pen row in an environmentally controlled poultry shed.

A special feed composition was studied to test the lowest possible energy concentration that might be applied in production (Table 1). From a low-energy starter diet (2,600 kcal of ME/kg), the diet was diluted to 2,400 kcal of ME/kg with wheat bran to 1) limit the energy intake of ad libitum-fed hens, and 2) increase the amount and duration of feed intake in restricted hens. With the same objectives, the particle size of the meal form of the feeds was fine (5 to 10% >2 mm; 30 to 35% <0.5 mm). Feed distributed was weighed every day for each pen to minimize the accumulation of unconsumed feed in the troughs of ad libitum-fed hens.

Transition from grower to breeder feed was at 20 wk of age for the ad libitum-fed hens and the intermediate feed restriction hens (SA, EA, SI, and EI). The restricted hens (SR and ER) received the breeder feed at the start of lay. At sexual maturity, the feed restriction program was adjusted in each pen to reach a consumption of 185 or 165 g of feed/hen per d for the SR and ER hens respectively, when the laying rate in the pen reached 50%. Two weeks after the peak of lay, the feed allocation was stepped back each week in increments of 3 g/hen per d when the actual average body weight increased more than 20 g/hen per wk (from 33 to 40 wk of age in ER and SR hens).

Birds in the 6 treatment groups were exposed to the same photoperiods: wk 1 = 24L:0D, wk 2 to 18 = 7L:17D, and increasing by 2 h/wk to reach 16L:8D after 23 wk of age. Minimum temperature was maintained at 31°C for chicks and decreased progressively to reach 18°C after 3 wk of age. In adult hens, the maximum temperature inside the shed was below 22°C when the external temperature did not exceed 26°C. However, under warmer climatic conditions, the temperature inside the shed increased proportionally to the external temperature.

Individual BW was recorded every 3 wk. Feed restriction was adjusted by pen BW in each SR and ER pen every week based on weight sampling. Feed intake was measured for the same 3-wk periods by weighing feed refusals per pen. At 18 wk of age, 3 nests (30 × 30 × 40 cm) were connected to each pen.

Egg Measurements. Egg production was recorded every day by pen during the week and for all pens on Mondays for weekend production. Eggs with multiple yolks, and soft, cracked, or dirty shells were recorded daily. Egg weights were measured on 4 consecutive days of production every week. Only nondouble-yolked eggs with normal shells were weighed.

The growth of the yellow follicle in terms of yolk deposition was measured using a double dye technique as described by Gilbert (1972), and slightly adapted. Two dyes, one red (Scarlet R[2]) and one black (Sudan Black[2]), were diluted with maize starch and packed into capsules (type 3[3]). A daily dose of 25 mg of each pigment was force fed at 0900 h to all hens in 12 pens (i.e., 2 per treatment) for 3 wk starting at the age of 34 wk. As suggested by Gilbert (1972), irregular distribution of the dyes was a better indicator of the number of days of yolk deposition than regular alternation of the dyes. Starting 2 wk after the beginning of dye ingestion, all eggs laid in the 12 pens during 4 d were collected, weighed, and identified by pen and date. After boiling for 10 min, the yolk of the egg was isolated by manual dissection and weighed. The cooked yolk was cut into 2 equal parts using a cutter and fixed on a tray using a needle in the center of the concentric colored rings. The number of rings was counted taking into account the weekend days (without pigment), and the diameter of each ring (internal lip) was measured using a caliper (Figure 1).

The same individual measured all eggs. The diameters measured along 2 perpendicular directions were averaged. The volume of the yolk was obtained using the formula: $4/3\ \pi \times D^3$. The thickness and volume of yolk deposited daily was calculated from the difference between 2 consecutive days.

Slaughter and Carcass Dissection. At 40 wk of age, 20 birds per treatment were selected according to BW at 39 wk to match the average of each treatment. After 16 h of feed removal, birds were slaughtered by bleeding after electro-narcosis, and feather-plucked in the experimental abattoir at Nouzilly. After 16 h at 4°C, carcasses were weighed and dissected. The digestive tract (from under the crop down to cloaca), abdominal fat, liver without gall bladder, left pectoralis minor and major without skin, and left thigh without foot were dissected according to standard procedures (Marche, 1985). The ovaries were removed and the yellow follicles were counted and weighed, as were the residual ovaries after removal of the yellow follicles.

Experiment 2 (Leuven)

Two hundred and ten type E and 210 type S 1-d-old chicks were delivered by Hubbard. The same experimental treatments were followed as in experiment 1 with ad libitum, intermediate-fed, and restricted treatments for each line, resulting in 6 groups of birds (SA, SI, SR, EA, EI, ER). The hens were distributed to 12 pens, having 2 replications per group. During the rearing period, all birds were raised on floor pens littered with wood shavings and supplied

[2]Sigma Chemical Co., St. Louis, MO.
[3]LGA, Bandol, France.

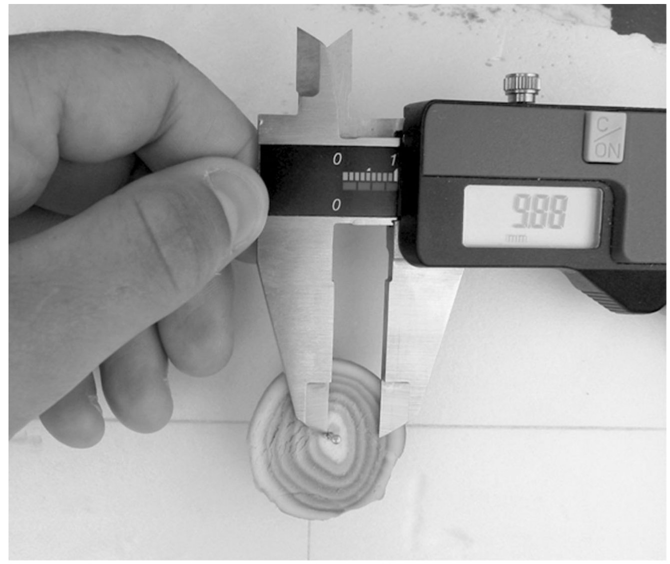

FIGURE 1. Measure of the daily deposition of vitellus by the colored ring method. The radius of the internal fringe of each band is measured in 2 orthogonal directions.

with suspended drinkers. The same feeds, feed recommendations, photoperiods, and temperature schedules were used as described for experiment 1 (in Nouzilly).

Body weights of all birds were recorded every 3 wk until BW stabilized. A number of restricted birds were weighed weekly to adapt the amount of feed according to the recommended target BW curve. Feed intake of ad libitum-fed birds was measured weekly by weighing feed refusals per pen. At the start of lay, 12 birds per group were individually caged (50 × 50 × 40 cm) to follow individual egg laying in a temperature controlled room maintaining a temperature of 18 to 20°C. Normal eggs and multiple-yolk, soft-shell, or cracked eggs were recorded daily. The remaining birds were kept on the floor.

At 36 wk of age, the follicular growth of the yellow follicles was followed using the same double dye technique and protocol as described above. For this purpose, 12 caged hens per group were used.

Statistical Analysis

Body weight, feed intake, and egg production were averaged per pen and analyzed by 2-way (genotype × regimen) repeated measurements ANOVA. Body and egg composition and ovarian characteristics were analyzed by 2-way ANOVA using individual measurements as replications.

Abnormal eggs were counted by pen for 2 consecutive 8-wk periods after the onset of lay (laying rate >5% in the pen). The double-yolked eggs were distinguished from those with shell problems (soft and broken shells). The number of settable eggs was computed by further elimination of the dirty eggs. All data were expressed as percentage of the total number of eggs laid in the pen during the 8-wk period. Two-way ANOVA was applied on arc sinus square root transformed percentages.

Follicular growth was first measured by counting the number of days of yolk deposition during the rapid growth phase per egg. The dimensions of the layer of yolk deposited into follicles (thickness and volume) were calculated from the averaged measure of diameters for each egg and analyzed by regression with the number of days of rapid growth.

In all cases, the Newman and Keuls multiple comparison test was applied to compare means when interactions were significant, or to measure regimen differences ($P \leq 0.05$).

RESULTS

Livability, BW, and Body Composition

In experiment 1 (Nouzilly), mortality was low (5 hens), and 9 birds were culled for accident or leg disorders during the growing period (0 to 20 wk). The major cause of mortality during the laying period was a period of hot weather (34°C in the breeder house) at 37 wk of age that killed 4, 4, 11, and 10 birds in groups EA, EI, SA, and SI, respectively, and none in ER or SR. After this initial heat stress, feed was withdrawn from the hens at 0800 h and returned at 1600 h on days expected to be warm; no more mortality due to heat (up to 36°C in the shed) was recorded. When culling and mortality were combined, average percentages of livability to 40 wk of age were: EA = 91%, EI = 92.5%, ER = 99%, SA = 81.5%, SI = 88.5%, and SR = 97.5%. Birds in SR and ER groups had significantly higher livability in these weather conditions than the other regimens, and EA and EI had significantly higher livability than SA and SI, respectively.

Body weights of ad libitum-fed hens rapidly diverged from their restricted counterparts (Figure 2). Body weights of ad libitum and intermediate S and E birds stabilized around 24 wk of age; in contrast, BW of restricted birds of both genotypes increased continuously until the end of the experiment. Intermediate feed restriction resulted in intermediate growth when applied (6 to 15 wk). During that period, SI hens exhibited the same average BW as EA hens. However, immediately after feed restriction was released (end of wk 15), a compensatory feed intake for 9 wk led to similar adult BW for EA and EI hens, and for SA and SI hens (Table 2). There was a significant genotype × feeding regimen interaction for BW. This was mainly due to the larger BW differences between the fully restricted birds and the ad libitum S birds compared with the EA and ER birds. No other interaction reached significance for body composition. Relative to BW, the E hens had relatively more blood and feathers than the S hens but no genotype effect on gut weight could be measured. Permanent feed restriction reduced abdominal fat and increased the weight of the liver relative to BW but not the absolute weight of the liver. Intermediate feed restriction did not change the fat and liver weights compared with ad libitum feeding. Hens of the E genotype had heavier livers and less fat relative to S hens. The ovaries of E hens exhibited on average one yellow follicle less than S hens regardless of feeding regimen. However, within genotype, there was no effect of feeding regimen on the number of yellow follicles at 40 wk of age. The breast meat and thigh yields were smaller (2 and 1% BW, respectively) in E compared with the S genotype. Within a genotype, feed restriction significantly reduced the relative thigh weight but not the breast meat yield (Table 2).

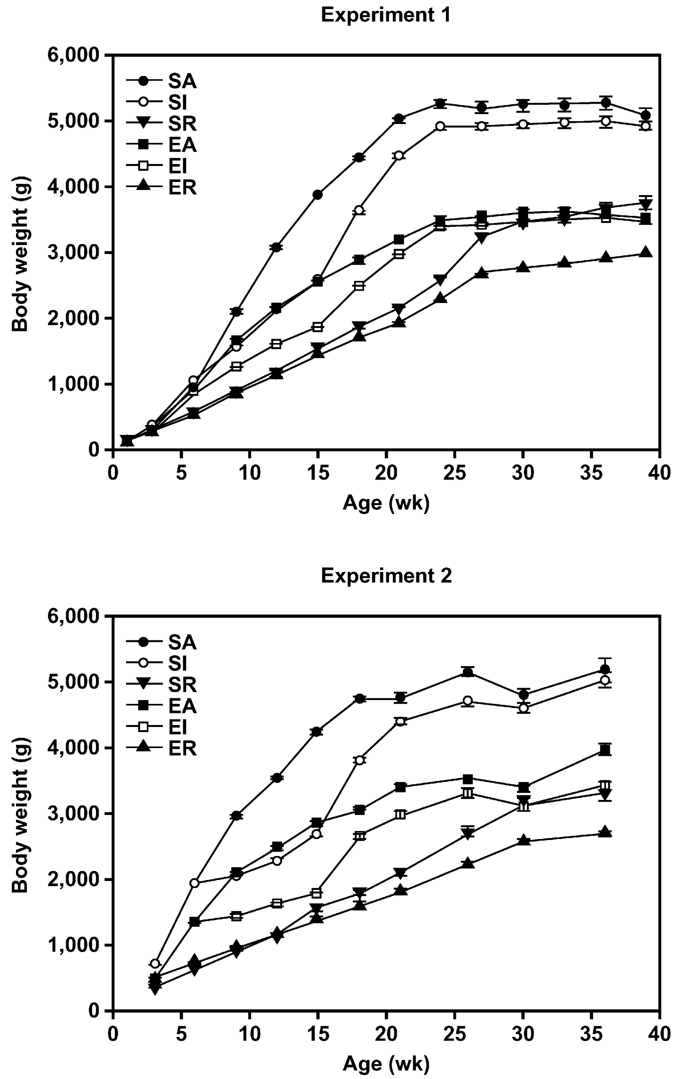

FIGURE 2. Mean BW (± SE) of hens of 2 genotypes [standard (S) and experimental dwarf (E) genotype] receiving 3 feeding regimens [ad libitum (A), intermediate feed restriction (I), and feed restriction (R)] to 40 wk of age (n = 8 pens of 14 hens in experiment 1; n = 2 pens of 35 hens in experiment 2).

In experiment 2 (Leuven), mortality at the end of the experiment (wk 53) was 45.7% for SA, 35.7% for SI, 12.8% for SR, 2.8% for EA, 1.4% for EI, and 2.8% for ER. No mortality occurred from 40 to 53 wk of age. The highest mortality was due to the extremely high temperatures from wk 26 to 31. In this period, 20 SA hens, 18 SI, 3 SR, 1 EA, and no EI or ER birds died. The patterns of BW curves of the hens were comparable to those obtained in experiment 1 (Figure 2) with the exception that the BW curve of the SA birds was somewhat steeper until 18 wk of age. The small weight loss in the ad libitum- and intermediate-fed S and E hens around wk 30 coincides with the period of

TABLE 2. Effects of genotype and feed allowance on body composition (% of BW) and number of yellow follicles per ovary at 40 wk of age (n = 20 hens per treatment)

	Treatment[1]						ANOVA			
	EA	EI	ER	SA	SI	SR	Genotype (G)	Regimen (R)	G × R	SEM
BW (g)	3,530[b]	3,438[b]	2,944[a]	4,928[d]	4,869[d]	3,765[c]	<0.001	<0.001	<0.001	40
Blood + feather,[2] % of BW	8.32	8.48	8.61	6.90	7.89	7.36	<0.001	—	—	0.30
Gut, % of BW	3.20	3.32	3.39	3.29	3.24	3.57	—	—	—	0.11
Liver, % of BW	1.21	1.21	1.34	1.00	1.18	1.22	<0.001	<0.001	—	0.04
Abdominal fat,[3] % of BW	3.63	3.99	2.98	5.17	4.91	3.56	<0.001	<0.001	—	0.24
Yellow follicles,[4] n	5.90	5.50	6.00	6.75	6.85	7.10	<0.001	—	—	0.28
Breast, % of BW	15.55	14.54	14.43	17.51	17.00	17.24	<0.001	—	—	0.37
Thigh, % of BW	22.31	22.45	21.75	23.09	23.60	22.82	<0.001	0.04	—	0.29

[a–d]Means without common superscript letters within a line are signficantly different ($P < 0.05$).

[1]Treatments: EA, EI, and ER represent groups of E genotype birds (experimental dwarf broiler breeder) fed ad libitum, fed an intermediate feed allowance, and fed a restricted feed allowance, respectively. Groups SA, SI, and SR were standard genotype birds fed ad libitum, fed an intermediate feed allowance, and fed a restricted feed allowance, respectively. 2Blood + feather weight obtained by difference between the plucked weight and the live BW.

[3]Abdominal fat content.

[4]Number of yellow follicles per ovary.

high temperature in the breeder house where birds were kept on the floor during that period.

Egg Production

In experiment 1, the onset of lay was similar for the EA, EI, SA, and SI groups (21 wk) and was delayed by 2 wk for ER and 3 wk for SR. The time necessary to reach the peak of lay was on average 2 wk longer in the S hens than in the E hens (Figure 3). The peak laying rate was significantly improved by permanent feed restriction (SR > SI and SA) in birds of the S genotype, but not in the E genotype (interaction $P \leq 0.05$). The overall laying rate of the E genotype was higher than the S genotype ($P \leq 0.001$). Considering the post peak period (29 to 37 wk of age), a significant genotype × regimen interaction was measured, illustrating a greater persistency of the intermediate feed-restricted SI hens (68.5%) than the SA hens (61.6%; New-

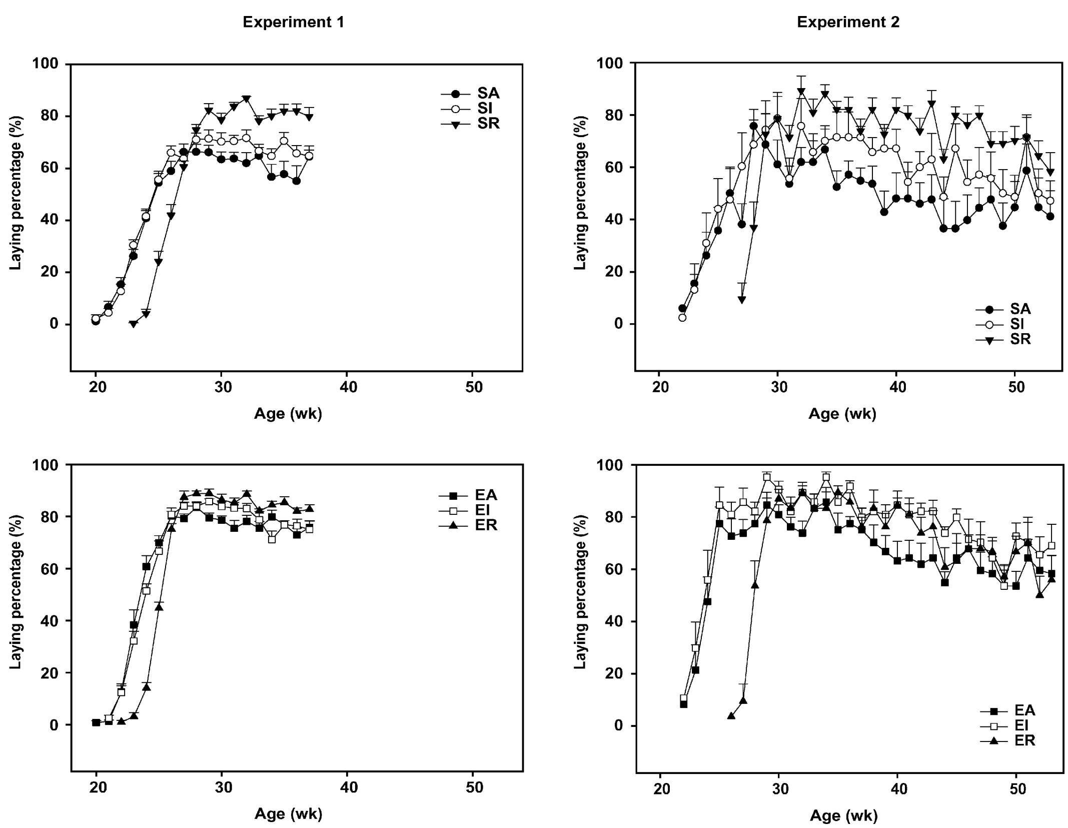

FIGURE 3. Mean laying rate (± SE) of 2 broiler breeders genotypes [standard (S) and experimental dwarf (E) genotype] exposed to 3 feeding regimens [ad libitum (A), intermediate feed restriction (I), and feed restriction (R)] to 40 wk of age (n = 8 pens of 14 hens in experiment 1; n = 12 individual caged hens in experiment 2).

TABLE 3. Effects of genotype and feed allowance on nonsettable egg (as % of total eggs laid) at different periods of production after sexual maturity (n = 8 pens of 14 hens in experiment 1; n = 12 individual caged hens in experiment 2)

Period amd experiment	Item	Treatment[1]						ANOVA			
		EA	EI	ER	SA	SI	SR	Genotype (G)	Regimen (R)	G × R	SEM
0 to 8 wk											
Experiment 1	Settable	88.5	89	96.4	81.2	82	93.9	—	—	—	
	Double yolk	5.5	5.7	1.7	9.0	10.0	2.2	<0.001	<0.001	—	0.7
	Shell problems	4.4	3.7	1.1	5.6	5.4	2.5	<0.001	<0.001	—	0.6
	Laying percentage	64.3	63.5	70.3	46.2	46.5	61.7	<0.0001	<0.0001	—	2.1
Experiment 2	Settable	90.3	84.3	98.8	77.9	77.6	97.9	0.06	<0.0001	—	4.4
	Double yolk	2.9	1	0.4	6.6	6.5	0.3	0.005	0.0004	—	1.2
	Shell problems	6.8	12.7	0.8	15.4	15.9	1.8	—	0.0003	—	1.1
	Laying percentage	57.9	65.6	61	39.5	42.6	65.9	—	—	—	7.4
9 to 16 wk											
Experiment 1	Settable	94.2	94.5	97.3	88.5	90.6	95.3	—	—	—	—
	Double yolk	2.1	2.0	0.3	3.4	3.2	1.4	<0.001	<0.001	—	0.3
	Shell problems	2.4	2.0	1.2	3.9	3.5	1.5	0.05	0.006	—	0.6
	Laying percentage	76.3	78.3	83.0	61.2	68.5	77.5	<0.0001	<0.0001	—	2.1
Experiment 2	Settable	96.9	97.8	95.9	89.1	94.5	96.8	0.04	—	0.03	1.5
	Double yolk	0.2	0	2.9	3.2	1.7	0	—	—	<0.0001	0.5
	Shell problems	3.1	2.2	1.1	8.4	3.8	3.2	0.02	0.04	—	1.2
	Laying percentage	78.4	87.5	82.4	58.7	69.9	78.6	0.0001	<0.0001	0.0001	5.2
17 to 24 wk											
Experiment 2	Settable	97.9	95.6	99.1	86.9	95.2	97.5	0.0007	0.005	0.0004	0.9
	Double yolk	0	0	0	2.4	1.5	0	0.0015	—	—	0.3
	Shell problems	2.4	4.3	0.8	10.63	3.4	2.5	—	0.01	0.03	0.9
	Laying percentage	63.7	78.8	67.1	44.3	60.4	72.7	<0.0001	<0.0001	<0.0001	6.7
Mean laying, % (0 to 24 wk)		66.4	77.4	69.9	47.2	57.9	72.4	0.0001	0.0006	0.003	6.6

[1]Treatments: EA, EI, and ER represent groups of E genotype birds (experimental dwarf broiler breeder) fed ad libitum, fed an intermediate feed allowance, and fed a restricted feed allowance, respectively. Groups SA, SI, and SR were standard genotype birds fed ad libitum, fed an intermediate feed allowance, and fed a restricted feed allowance, respectively.

man and Keuls test, $P \leq 0.05$), whereas the average laying rate of the EI hens (79.3%) did not differ from that of the EA hens (76.9%).

Egg weights compared for corresponding periods after sexual maturity showed no significant effect of regimen or genotype. However, the number of nonsettable eggs was significantly higher in ad libitum or intermediate feed restricted hens than in restricted hens (Table 3). During the first 8 wk of lay there were 2 to 4 times more double-yolk and abnormal shell (soft and broken) problems among the eggs laid by ad libitum-fed hens than restricted breeders (ER and SR). The E genotype exhibited less than half the abnormalities of the S genotype regardless of feeding regimen ($P \leq 0.001$). The same effect was observed during the subsequent 8 wk of production with lesser acuity. Laying rate calculated after sexual maturity showed major effects of the feed restriction program (restricted higher than intermediate and ad libitum) and genotype (E higher than S) without significant interaction between the 2 factors.

In experiment 2 (Figure 3), start of lay was attained at 21 wk of age for the SA and EA birds and at 22 wk for SI and EI hens. The first egg of the restricted E and S hens was observed at 25 and 26 wk of age, respectively. The maximum laying rate in the SA birds was attained at 28 wk of age (75.7%) and gradually decreased thereafter to reach 41.1% at the end of the experiment (wk 53). Birds in the SI group reached peak production at wk 30 (78.6%). The decrease in egg production was slower than in the ad libitum fed-birds, which is reflected in the significantly higher egg production after wk 31 compared with the SA birds. This resulted in a significantly higher average laying rate in SI (57.9%) compared with the SA (47.2%) birds throughout the 24 wk following start of lay. Restricted feeding of the S hens significantly improved average egg production (72.4%) compared with the SI and SA birds. Laying rates of EA and EI hens peaked at wk 29 (84.5 and 95.2%, respectively). Throughout the 24 wk after first oviposition, average egg production was significantly higher in the EI (77.4%) compared with the EA (66.4%) birds. Restriction of the E hens resulted in an overall egg production (69.9%) rate that was between that of the EI and EA groups. Significant differences in laying percentage occurred after 8 wk of lay and persisted until the end of the experiment (Table 3). This effect could be clearly observed in the S line, with significant differences between feeding groups (SA < SI < SR). The decline in egg production due to ad libitum or intermediate feeding was less pronounced in the E line. Intermediate feeding of the E birds resulted in better mean laying percentages than feed restriction of E birds in all 3 periods after start of lay.

For the first 2 periods after onset of lay, results on the percentage of settable, double-yolked, and eggs with shell problems showed the same trends compared with the results of experiment 1 (Table 3). Ad libitum and intermediate feeding clearly increased the percentage of eggs with abnormalities compared with restricted feeding in both lines. The percentage of double-yolked eggs was significantly higher in the ad libitum and intermediate fed S birds compared with their counterparts in the E line. With advancing age, the percentage of abnormal eggs decreased in both genotypes but differences between ad libitum/intermediate fed birds and restricted birds within the S line persisted

TABLE 4. Effects of genotype and feed allowance on the duration of the rapid growth of the yellow follicles measured by the double dye method (see Figure 1) on 12 hens per treatment at 34 wk of age

	Treatment[1]						ANOVA			
	EA	EI	ER	SA	SI	SR	Genotype (G)	Regimen (R)	G × R	SEM
Experiment 1										
Eggs (n)	43	46	52	59	50	57				
Duration (d)	8.83	9.04	8.75	9.28	9.52	9.39	<0.001	—	—	0.13
Experiment 2										
Eggs (n)	46	45	48	30	39	46				
Duration (d)	8.76	8.69	8.62	9.47	9.25	8.91	<0.0001	—	—	0.13

[1]Treatments: EA, EI, and ER represent groups of E genotype birds (experimental dwarf broiler breeder) fed ad libitum, fed an intermediate feed allowance, and fed a restricted feed allowance, respectively. Groups SA, SI, and SR were standard genotype birds fed ad libitum, fed an intermediate feed allowance, and fed a restricted feed allowance, respectively.

until the end, with the restricted birds showing more settable eggs. In the E line, the differences observed during the first period due to the feeding regimen disappeared in the 2 subsequent periods, explaining the interaction factor between genotype × feeding regimen for double-yolked eggs, shell problem eggs, and settable eggs.

Yolk Deposition

Eggs with questionable or missing rings were excluded from the experiments on yolk deposition at both locations. The measured average duration of the rapid yolk growth was 9 d in both experiments. Most eggs (92.9%) showed rapid yolk deposition varying between 8 and 10 d. Only 8% of the eggs showed shorter (2.5% with 7 d) or longer (4.6% with 11 d) periods of rapid growth. Duration of rapid yolk growth was one-half day shorter in E hens than S hens ($P \leq 0.001$) regardless of regimen and there was no detectable effect of regimen on yolk rapid deposition (Table 4).

The yolk material deposited during the first 4 d of rapid development averaged 2.02 ± 0.07 mm/d. After the fourth day, the thickness of the deposited yolk decreased linearly to reach 1 mm after the seventh day of rapid development. During this period, the volume of daily deposited yolk material reached a plateau at 3.0 cm^3/d without significant effect of genotype or regimen (Figure 4).

DISCUSSION

The results of this study show that the heavy dwarf broiler breeder genotype E fed a diluted feed partly restricted from 6 to 15 wk gave the best results regarding livability and reproductive performance. Moreover, it is tempting to suggest that the current practice of long-term feed restriction to broiler breeder females is not necessary for the improvement of laying performance in heavy dwarf broiler breeders, as illustrated by the small differences in laying performance between the 3 groups of E birds. The lower laying rate in the permanently restricted E group compared with the partially restricted birds in experiment 2 indicates a negative effect of over-restriction. This is consistent with an earlier finding by Whitehead et al. (1987), who found that dwarf broiler breeders should not be restricted too severely. The potential to relax feed restriction in dwarf genotype E is important in view of recent concerns on welfare of broiler breeders. The added cost of an ad libitum-fed broiler breeder would have to be precisely quantified taking into account the extra feed consumed during the growing phase compared with a restricted standard broiler breeder hen as well as the performance of progeny. A recent study by Tona et al. (2004) indicates that the progeny of these dwarf broiler breeders perform well compared with the established standard S lines taking into account posthatch growth and feed conversion ratio. However, the relative role of the dw gene and of the genetic selection of genotype E in those positive results remains open to debate and further investigation.

In heavy standard broiler breeders, the need for feed restriction remained crucial to obtain acceptable egg production, although improved laying persistency can be obtained with intermediate feeding strategies compared with ad libitum feeding. The intermediate feeding strategy in a specific period before rearing (6 to 15 wk) also affected (albeit to a lesser extent) later egg production, which was reflected by a better laying persistency in the S line. This indicates a carryover effect of restricted feeding during critical rearing periods on later reproductive performance in standard broiler breeder genotypes, confirming the results of Yu et al. (1992) and Bruggeman et al. (1999). The dwarf heavy breeder E showed capabilities to tolerate ad libitum feeding while maintaining acceptable reproductive fitness although intermediate and restricted feeding still slightly improved laying performance. The occurrence of egg abnormalities was not consistently improved by the intermediate feeding strategy and fertility was not measured in the present experiments. Application of intermediate-like feeding strategies deserves additional research to evaluate further their impact on chick production.

The broiler breeders approached adult BW around the age at onset of sexual maturity in both ad libitum- and intermediate-fed S and E genotypes. The intermediate- and ad libitum-fed birds started lay at the same age despite different growth curves during rearing. This illustrates the importance of reaching a threshold BW and a minimum age for triggering the necessary changes in reproductive hormones that determine the onset of lay (Sharp et al., 1990; Bruggeman et al., 1998; Heck et al., 2004). The shape of the growth curve during the rearing period was not an important factor in determining the age at first egg.

Overall, intermediate feed restriction from 6 to 15 wk of age had no persistent effect on BW and body composition at 40 wk of age. Permanent feed restriction reduced fat deposition and to a lesser extent thigh muscle growth. The E birds had less abdominal fat and less muscle than the S breeders and this was more pronounced for breast than for thigh. The lower thigh/breast yield could be related to the presence of the dwarf gene. Goddard et al. (1996) showed a decreased muscle cell proliferation in young broiler chicks with the absence of a functional growth hormone receptor.

Long-term feed restriction resulted in fewer egg abnormalities than ad libitum feeding (double-yolked eggs, shell problems) according to the literature (Hocking et al., 1987; Yu et al., 1992; Hocking et al., 2002; Heck et al., 2004) and the effect was much more pronounced in the S line. Moreover, the ad libitum and intermediate E birds showed lower numbers of egg abnormalities compared with the S birds. These findings point to the fact that feed restriction/genotype not only affect the number of eggs, possibly by interfering in the process of follicular recruitment, growth, and ovulation, but also postovulation processes such as eggshell formation, which takes place in the oviduct.

There was a significant genotype effect on the number of yellow follicles at 40 wk and on the speed of yolk deposition at wk 37. The E line had, on average, one yellow follicle less and showed a faster yolk deposition needing 0.5 d less to reach maximal follicle weight compared with the S genotype, irrespective of feeding regimen. The introduction of the dwarf gene or specific goals of selection or both in E type broiler breeders not only affected their growth potential and improved their tolerance to ad libitum feed intake but also affected the number and rate of deposition of yolk before reaching maximal follicle weight. It remains speculative how the introduction of the dwarf gene in broiler breeders changes the follicular hierarchy and yolk deposition speed. The rate of yolk deposition measured by the dye technique was not significantly affected by regimen or genotype. It was consistent in thickness during the first 4 d of rapid yolk development, and the volume of yolk material deposited daily reached a plateau after 4 d. This result suggests a relatively steady flow of yolk material toward the follicles, the volume of yolk deposited being limited by the small size of the follicles during the first 4 d of rapid growth.

The lack of effect of feeding regimen on the number of yellow follicles at wk 40 was rather surprising. In the broiler breeder literature, it is well known that feed restriction decreases the number of yellow follicles in the ovary especially during the first weeks of lay (Yu et al., 1992; Hocking, 1993). It is not known if the feed dilution used in this study was responsible for the lack of difference in the number of yellow follicles in the ovary at wk 40. Another possibility is that differences in follicle numbers disappeared because of the older age of the birds (40 wk). This is strengthened by the fact that with age, the number of double-yolked eggs, which is mainly linked with the presence of double

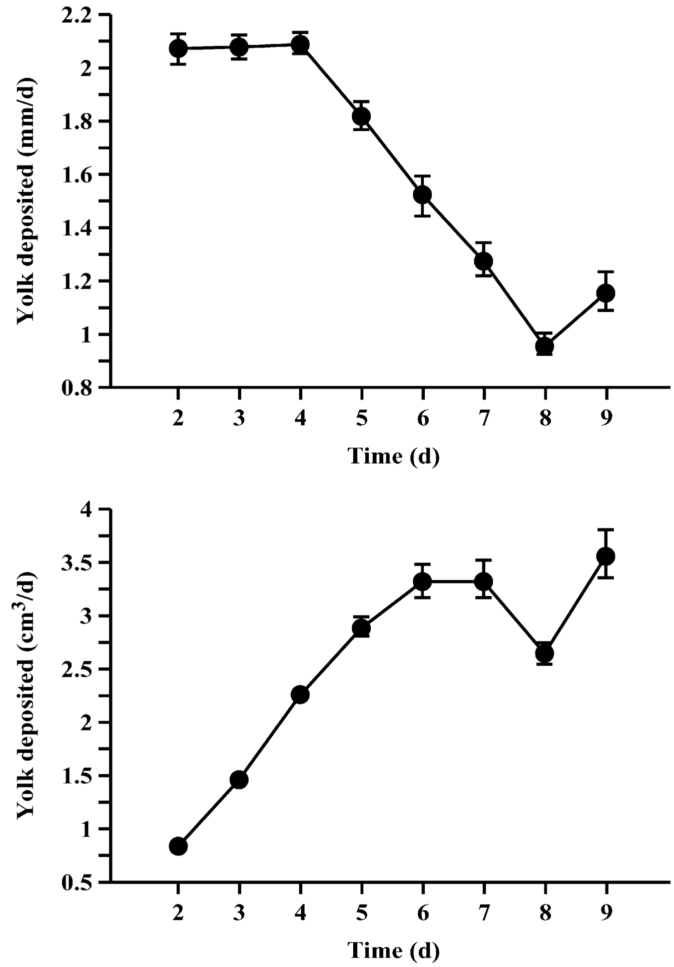

FIGURE 4. Daily yolk deposition in thickness (mm/d) and volume (cm^3/d) measured by the double dye technique (Figure 1) during the days of rapid development of the follicles.

hierarchies of follicles in the ovary, decreased. However, it is clear that the number of yellow follicles or the yolk deposition speed before reaching maximal follicle weight are not the most important factors in determining the obvious differences in laying percentages and number of abnormal eggs found between different genotypes as well as between differently fed birds within a genotype. Changes in the responsiveness of the follicular steroidogenic cells (granulosa and theca) to growth factors or gonadotropins ultimately leading to follicular ovulation of the mature follicle, differences in the rate of atresia, or in the recruitment of white follicles seem to be more important mechanisms in determining the rate of lay in broiler breeders differing in genotype or feeding strategy.

In conclusion, tolerance to ad libitum feeding of a diluted diet in broiler breeders depends on the genotype, and the dw gene is probably a favorable factor. Intermediate feeding strategies such as moderate feed allowance only from 6 to 15 wk of age does not change adult BW, has a limited effect on egg abnormalities, and improves laying rate. A severe feed restriction was the only way to maintain reproductive fitness in the tested heavy standard broiler breeder hen. The rate of yolk deposition in the follicles is probably not related to the large variations in laying rate observed between genotypes and feeding regimens in the present study.

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