Anim. Res. 50 (2001) 239–250
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Original article

Effects of separate calcium feeding on laying hens selected for low (R^-) or high (R^+) residual feed consumption

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(Received 16 December 1999; accepted 22 May 2001)

Abstract — The experiment was carried out with a sample of females from the 21st generation of lines R^- and R^+ selected divergently for residual food intake in the laying period. After a breeding period of 18 weeks the hens of each line had been distributed among climatic rooms into two groups, one fed with a complete commercial feed (control group) and the other one with both a low calcium feed and oyster shells given in two separate troughs (treated group). Egg production was recorded during 77 days, egg and shell traits were obtained during the third and fourth weeks of the experiment, and the voluntary consumption of feed was measured over a period of 28 days. The treatment had a significant effect for both lines on average egg weight ($p < 0.05$), shell weight ($p < 0.01$), shell thickness ($p < 0.01$), and albumen thickness ($p < 0.05$). However, the line × treatment interaction was significant for yolk weight ($p < 0.05$) and voluntary calcium consumption ($p < 0.001$), indicating that the under-consuming line (R^-) showed a better response to separate calcium feeding with a 40% decrease of its residual feed consumption, and better egg and shell qualities. The advantage of line R^- might be related to the expression of a specific calcium appetite which is masked in line R^+ which ingests excess nutrients.

laying hen / selection/ residual food consumption / separate calcium feeding / interaction

Résumé — Réponse à l'alimentation calcique séparée de poules sélectionnées pour une faible (R^-) ou forte (R^+) consommation alimentaire résiduelle. L'expérience a été réalisée sur un échantillon de poules pondeuses issues de la 21e génération des lignées R^- et R^+ sélectionnées de façon divergente sur la fraction résiduelle de la consommation alimentaire en période de ponte. Après une phase d'élevage de 18 semaines les poules de chaque lignée ont été réparties dans des chambres conditionnées

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en deux lots : l'un recevant un aliment commercial complet (lot témoin), l'autre, un aliment de base appauvri en calcium d'une part et des coquilles d'huîtres d'autres part, distribués dans deux mangeoires distinctes (lot traité). Les mesures individuelles ont porté sur la ponte pendant 77 jours, celles relatives à la consommation alimentaire sur une période de 28 jours. Entre la 3^{e} et la 4^{e} semaine de l'expérience, étaient effectuées des mesures sur la qualité de l'œuf et de la coquille. Le traitement, indépendamment de la lignée, a eu un effet significatif sur le poids moyen de l'œuf (p < 0,05), le poids de la coquille (p < 0,01), l'épaisseur de la coquille (p < 0,01) et l'épaisseur de l'albumen (p < 0,05). Pour deux variables, le poids du jaune (p < 0,05) et la consommation du nutriment calcique (p < 0,001), l'interaction lignée × traitement s'est révélée significative indiquant que la lignée sous-consommatrice d'aliment (R^-) répond davantage à l'alimentation calcique séparée avec une diminution de 40 % de sa consommation résiduelle, et une augmentation de 6 % de sa masse d'œufs. Ces réponses favorables de la lignée sous-consommatrice d'aliment (R^-) peuvent être expliquées par l'expression d'un appétit calcique spécifique qui est mal exprimé par la lignée sur consommatrice R^+ à cause de l'ingestion excessive du nutriment énergétique.

poules pondeuses / sélection / consommation alimentaire résiduelle / alimentation calcique séparée / interaction

1. INTRODUCTION

In laying hens, feed conversion to egg production (kg feed consumed per kg eggs produced) has been improved by selection lowering body weight and increasing egg production. However, with equal egg production and body weight, differences between individual hens in the same flock persist and may reach as much as 40 per cent of the average feed consumption corresponding to differences in food intake and efficiency of utilisation of ingested nutrients [9]. Based on this "residual" variability Bordas and Mérat [2], starting from a Rhode Island Red base population, selected two lines of laying hens, respectively, with low (R^-) and high (R^+) residual feed intake.

The difference in residual food intake between lines increased rapidly and reached 25 per cent of the mean food intake of the two lines at the 21st generation. Correlatively, the difference in observed total food intake between lines is of the same order since the laying performances (egg number, mean egg weight) are similar. Paradoxically, in spite of its higher food intake the R^+ line shows a significantly higher percentage of shell-less, cracked and broken eggs than the R^- line [4, 5].

Moreover, taking account of the physiological processes implied in egg formation, research works aimed at satisfying the specific calcium requirement and improving shell quality have led several authors [12–14, 17] to separate a calcium source from the rest of the food. From a genetic point of view, Bordas and Mérat [3] and Picker [19] studied separate calcium feeding on populations of dwarf and naked-neck hens. Other investigations were conducted on Fayoumi and crossed Fayoumi × Leghorn hens [1]. All these authors reported that separate calcium feeding better satisfied the specific energetic and calcium requirements associated with egg formation.

The main purpose of the present work is to verify whether separate calcium feeding has the same effects in lines with low (R^-) and high (R^+) food intake, or whether selection for food intake caused differences in calcium utilisation between these lines.

2. MATERIALS AND METHODS

2.1. Birds and experimental conditions

The experiment included 176 female Rhode-Island Red day-old chicks issued from the 21st generation of lines with low (R$^-$) and high (R$^+$) residual food intake. The chicks were obtained in one hatch. In each line they were issued from 9 sires mated to 6 dams each. The two lines were previously described [2]. The chicks were first raised in floor pens on litter till the age of 18 weeks. Then the pullets were transferred to 4 climatic rooms each containing a battery of flat-deck type individual cages. Each cage was equipped with an automatic water supply and one or two feed troughs according to the type of food given. All rooms were subjected to the same artificial lighting schedule of 14 h per 24 h during the entire experimental period and they were maintained at a constant ambient temperature of 21 ± 1 °C.

2.2. Composition of feeds

The females of both lines (R$^+$ and R$^-$) were distributed into two groups, each family being represented in both groups. Hens of the control group (n = 87) received a complete commercial feed. Conversely, hens of the treated or separate calcium feeding (SCF) group (n = 85) received a similar commercial feed with a lower calcium level (1.51 per cent, see Tab. I), suppressing the calcium carbonate meal, and calcium carbonate as oyster shell was given in a second trough. It is noted that this level of 1.51 per cent calcium was also contained in the single commercial feed, excluding its carbonate meal component. All feeds were

Table I. Composition and chemical analysis of feeds.

Composition	Complete feed (control)	Low-calcium feed (treatment)
	(%)	
Wheat	10.00	10.70
Maize	39.90	42.70
Barley	10.00	10.70
Wheat bran	1.60	1.70
Animal fat	0.50	0.50
Peas	12.00	12.80
Soybean	2.10	2.20
Sunflower	7.00	7.50
Protein conc. Car. 500	4.80	5.20
Alfalfa meal	4.30	4.60
Calcium carbonate meal	6.40	0
Minerals and vitamins	1.00	1.00
Pigment / supplementation	0.40	0.40
Chemical composition (%)[1]		
Water	11.30	12.00
Minerals	11.94	6.35
Fat	3.35	3.26
Calcium	3.83	1.51
Cellulosis	5.91	5.73
Crude protein	14.86	15.96
Total phosphorus	0.62	0.69
Metabolisable energy (kcal)	2651.10	2833.00

[1] Source: UFAC (1997).

distributed ad libitum and their composition is shown in Table I. The separate source of calcium called calcicoque consisted in marine shell with particles varying from 1 to 4 mm and containing 32.5 per cent calcium.

2.3. Measurements

Three classes of variables were measured: variables concerning egg production; those related to egg and shell quality and those concerning food consumption. The complete list of variables in each group is given in Tables II, III and IV.

2.3.1. Egg production variables

Following the transfer of pullets to cages, individual egg production was recorded every day from the first laid egg till the age of 33 weeks. These data allowed to calculate the age at first egg, number of eggs laid, average length of laying series, percentage of "pause" days, percentage of broken eggs and of shell-less eggs. In our conditions, eggs laid on consecutive days without interruption formed a laying series, and any interruption of laying of at least 2 days was considered as a pause.

2.3.2. Egg and shell quality variables

From the age of 32 weeks, measurements related to egg quality (yolk weight, albumen height) and shell quality (weight, thickness) were recorded in 3 eggs per hen. In one egg per hen which was weighted and then broken, the yolk was separated from the albumen and weighted. The shell was washed, dried and weighted the following day.

The weight of the albumen was estimated as the difference between total egg weight and the sum of the yolk and shell weights. The albumen height (in mm) was measured with a tripod micrometer at about 1 cm from the yolk from another egg broken on a flat surface. The thickness (in 1/100 mm) of the shell was measured with a caliper on a piece of dried shell.

2.3.3. Food consumption variables

Over a period of 28 successive days between the ages of 29 to 33 weeks, the food intake, or food and calcium source intake (for the SCF group), was measured per hen together with the body weight and its variation from the beginning to the end of the period. During this same period the eggs laid by each hen were weighted. The mean egg weight was calculated for the 3rd and 4th weeks of the period.

2.3.4. Derived estimations: calcium carbonate intake, residual food intake, food efficiency

From the measurements performed during the 28-day period previously described, two variables concerning food consumption were obtained: 0_1 which is the total consumption including the calcium-rich fraction, and 0_2 which is the food intake excluding this calcium carbonate fraction. For hens receiving the complete feed, the calcium ingested as carbonate was estimated from food intake 0_1 multiplied by the percentage of $CaC0_3$ meal and 0_2 was estimated by removing this part. Under SCF, 0_2 is directly measured and 0_1 is the sum of 0_2 and the calcium carbonate source.

"Residual" food consumption was then estimated including or not the calcium carbonate source. In the first case, i.e. with calcium supply included (0_1), a multiple regression equation similar to that devised by Byerly et al. [7] was estimated for all hens:

$$T_1 = 54.6\ W^{0.5} + 1.77\ \Delta W + 1.89\ E - 1546$$

where W is the mean body weight, ΔW the variation of body weight during the 28-d period, and E the egg mass during this period. The difference between T_1 (theoretical estimate) and observed food intake 0_1 represents residual consumption R_1.

Table II. Effects of separate calcium feeding and line on egg production traits.

Variables	Mode of calcium feeding				Ratio (%)[2]		Significance		
	in the feed		separate						
	R^-	R^+	R^-	R^+	R^-	R^+	Mode of calcium feeding	Line	Interaction[1]
Age at 1st egg (d)	157.8	156.4	157.2	155.4	99.6	99.4	NS	NS	NS
Egg number	59.8	68.0	63.6	69.2	106.3	101.8	+	**	NS
Laying intensity (p. cent)	77.0	85.8	81.7	87.0	106.1	101.4	+	***	NS
Length of series (d)	4.5	7.6	5.3	7.2	117.8	94.7	NS	**	NS
Pauses (p. cent)	8.2	5.8	4.5	4.6	54.9	79.3	+	NS	NS
Soft-shelled eggs (p. cent)	4.0	5.0	2.8	5.5	70.0	110.0	NS	NS	NS
Number of double-yolked eggs	0.64	1.4	0.54	1.6	84.4	114.3	NS	+	NS
Broken eggs (%)	14.5	21.7	14.5	20.9	100.0	96.3	NS	NS	NS
Mean egg weight (g)	50.0	49.9	51.6	50.8	103.2	101.8	*	NS	NS

[1] Line × mode of calcium feeding; [2] treated/control.
NS = non-significant; + = $p < 0.10$; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

Table III. Effects of separate calcium feeding and line on egg and shell quality.

Variables	Mode of calcium feeding				Ratio (%)[2]		Significance		
	in the feed		separate						
	R^-	R^+	R^-	R^+	R^-	R^+	Mode of calcium feeding	Line	Interaction[1]
Weight of broken egg (g)	50.9	50.1	51.7	51.2	101.6	102.2	*	NS	NS
Shell weight (g)	4.2	3.7	4.3	3.9	102.4	105.4	**	**	NS
Shell (%)	8.2	7.4	8.3	7.7	101.2	104.0	+	**	NS
Shell thickness (0.01 mm)	31.6	29.5	32.3	30.6	102.2	103.7	**	**	NS
Albumen thickness (0.1 mm)	72.2	63.7	70.3	61.3	97.4	96.2	*	***	NS
Albumen weight (g)	33.3	33	34	33.7	102.1	102.1	+	NS	NS
Yolk weight (g)	13.4	13.3	13.4	13.8	100.0	103.8	+	NS	*
Yolk/albumen	40.5	40.4	39.6	41.2	97.8	102.0	NS	NS	NS

[1] Line × mode of calcium feeding; [2] treated/control.
NS = non-significant; + = $p < 0.1$; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

Table IV. Effects of separate calcium feeding and line on feed consumption and feed conversion traits.

Variables	Mode of calcium feeding				Ratio (%)[2]		Significance		
	in the feed		separate				Mode of calcium feeding	Line	Interaction[1]
	R^-	R^+	R^-	R^+	R^-	R^+			
Mean body weight between 29 and 33 wks (g)	2054.1	1972.2	2009.0	2006.7	97.8	101.7	NS	NS	NS
Egg mass/28 d (g)	1067	1182.5	1132.4	1186	106.1	100.3	NS	***	NS
Feed intake, calcium carbonate excluded (g)	2511.1	3381.2	2595.9	3428.5	103.4	101.4	NS	***	NS
Calcium carbonate intake (g)	171.6	231.2	160.2	147.4	93.4	63.7	***	**	***
Total feed intake (g)	2682.8	3612.4	2756.1	3583.1	102.7	99.2	NS	***	NS
Residual feed intake R_1 (g)[3]	–281	+444.4	–395	+345.4	140.6	77.7	***	***	NS
Residual feed intake R_2 (g)[4]	–292	+387.1	–384.6	+368.5	131.7	95.2	*	***	NS
Feed conversion 1[5]	2.53	3.11	2.43	3	96.0	96.0	NS	***	NS
Feed conversion 2[6]	2.37	2.91	2.3	2.9	97.0	100.0	NS	***	NS

[1] Line × mode of calcium feeding; [2] treated/control; [3] calcium carbonate included; [4] calcium carbonate excluded; [5] Total food intake/egg mass; [6] (total food intake – calcium carbonate intake)/egg mass.
NS = non-significant; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

From food consumption, after excluding the calcium-rich source (0_2), a second equation was calculated in the same way:

$$T_2 = 48.7\ W^{0.5} + 1.73\ \Delta W + 1.79\ E - 1288.$$

The difference between observed food intake 0_2 and theoretical consumption T_2 is a residual food intake R_2 which represents the ingestion of the ration without the calcium-rich source.

Two feed conversion indexes were derived:

IC_1 is the ratio of total food consumed 0_1 to the egg mass E.

IC_2 is the ratio of total food consumed, calcium source excluded, to egg mass E.

2.3.5. Statistical analysis

Analyses of variance were performed according to the following linear model.

$$X_{ijkl} = \mu + L_i + F_j + LF_{ij} + S_k + e_{ijkl}$$

where X_{ijkl} represents the value of individual l issued from the kth sire (S) of the ith line (L) and receiving the jth type of feeding (F). L_i is the fixed effect of the line, F_j is the effect of treatment, LF_{ij} is the interaction effect between line and treatment, S_k is the random effect of the sire, and e_{ijkl} is the random individual deviation.

All these analyses were performed with the GLM procedure of the SAS software [20].

3. RESULTS

During the experiment, only one hen died, in the R^+ line and the receiving SCF treatment.

The mean values of the different variables according to line and treatment are given in Tables II, III and IV. Additionally, these tables present the ratios SCF group/control group within line and the significance of the main effects and of the line × treatment interaction.

3.1. Effects on egg production traits

The results are presented in Table II. No significant interaction was observed between the line and mode of calcium supply. However, the data suggest that SCF had a not significant positive effect on egg number, length of laying series, laying intensity and percentage of pause days (limit of significance on both lines taken together). Besides, in both lines SCF significantly increased mean egg weight, by 2.5 per cent ($p < 0.05$). Conversely, the SCF has no significant effect on the percentage of shell-less or cracked eggs and the number of double-yolked eggs.

In the present experiment, the R^+ line differed significantly from the R^- line for egg number (+10 per cent), as well as for the derived variables, egg-laying intensity and length of series (respectively + 9 and + 4 per cent). Finally, the R^- line seemed to lay less double-yolked eggs than the R^+ line but the difference was not significant.

3.2. Egg and shell quality

Results are given in Table III. Only one significant interaction was significant between treatment and line, for yolk weight ($p < 0.05$): yolk weight did not vary according to the mode of feeding in the R^- line while it increased under SCF as compared to the control group in the R^+ line.

As was noted concerning Table II, SCF increased mean egg weight ($p < 0.05$). This increase was also found in the shell: shell weight was 4.3 per cent higher under SCF ($p < 0.01$), besides, shell percentage was 2.4 per cent higher and shell thickness was 2.9 per cent higher with this same treatment.

To a lesser extent, internal egg composition appeared to be modified by the SCF treatment with a 1.9 per cent increase for albumen weight and a 1.6 per cent increase for yolk weight. On the contrary, albumen thickness decreased by 3.1 per cent ($p < 0.05$) with SCF compared to the single feed.

Lastly, the R^- line layed eggs with a higher average shell thickness and shell weight ($p < 0.01$), both in absolute terms and in percentage, and with a thicker albumen ($p < 0.001$). For yolk weight, a treatment × line interaction appeared ($p < 0.05$), but the effect was rather small in absolute terms.

3.3. Feed intake and feed conversion

The corresponding results appear in Table IV. The line × treatment interaction for ingestion of the calcium carbonate supply was highly significant ($p < 0.001$). Thus the intake of the calcium-rich nutrient was close for the two treatments in the R^- line (0.4 $g \cdot d^{-1}$) whereas it was considerably reduced by SCF (83.6 g per 28 d or about 3 $g \cdot d^{-1}$) in the R^+ line. Conversely, and although the interaction is not significant, it may be noticed that under SCF, residual food intake R_1 was lowered by 40 per cent (increased in absolute terms) in the R^- line and only by 22 per cent in R^+ in comparison with the control. The tendency was the same but less marked in the R_2 variable. Similarly, it can be noted that the egg mass was 6 per cent higher with SCF in R^- while it remained unchanged in R^+.

Independently of the treatment, Table IV shows that the line effect was highly significant for all traits. This was expected as regards total food intake, as the two lines has been divergently selected for more than 20 years on intake at equal body weight and egg production. This difference in total food intake including the calcium-rich source amounted to 929 g, i.e. 29.5 per cent of the mean food intake of the two lines taken together, while it was slightly reduced when the calcium carbonate was distributed separately (827 g, i.e. 26 per cent). On the contrary, the difference in food consumption excluding the carbonate source was close irrespective of the treatment and represented 870 g and 826 g, respectively (i.e. 29.5 and 28.6 per cent of the mean feed consumption). Finally, no effect was obtained for the body weight of hens in each line.

4. DISCUSSION

4.1. Effects of SCF

The results presented above suggest that separate feeding of the calcium-rich nutrient tends to improve the egg number, the laying rate, and results in a longer laying series, a lower percentage of pause days, and a significant increase of mean egg weight. Correlatively, albumen and yolk weight and shell quality (weight and thickness) are higher. Most of these results have been previously pointed out [3, 11, 17, 18, 21, 22]. However, the effects of SCF on egg production are detailed in the present work as regards the mean length of laying series and percentage of pauses; we are not aware of other results for these variables in the literature.

Furthermore, the residual food intake was reduced under SCF, especially with the calcium source excluded (R_2), which reflects a better utilisation of the basal ration.

4.2. Effect of the line

The observed differences between lines for egg production, abnormal eggs (soft-shell and double-yolked eggs) and shell quality agree with the results of Bordas et al. [4–6] obtained during years of selection of these lines, as well as the results concerning total and residual food intake.

4.3. Response of lines to SCF and line × treatment interaction

It has been noted already that the total food intake differs somewhat less between

R^+ and R^- lines under SCF (827 g per 28 d) than between lines receiving a complete feed (929 g). This 120 g decrease in the excess of the R^+ line over R^- corresponded approximately to the lower ingestion of the calcium source by R^+ in SCF as compared with the single feed. Moreover, the intake of the base ration (without the calcium source) was increased by SCF by 3.5 per cent in the R^- line and only 1.4 per cent for R^+.

An improvement of feed conversion by SCF may explain that the replacement of a complete feed by SCF seems to be associated, in the R^- line, with an improvement in egg production performances with an increase in egg number (+6.3 per cent), of laying rate (+6.1 per cent), of length of laying series (+17.8 per cent) and a reduction in pauses (–45 per cent). Contrary to results obtained in dwarf hens [3], feed conversion (IC1) appears to be slightly (not significantly) improved by SCF with a more important increase in egg production and the absence of effects on body weight.

However, in the present study only two interactions between treatment and line were statistically significant, the interaction on yolk weight, and that on ingestion of the calcium source.

The R^- line, which produced lighter eggs with the complete feed, gave eggs heavier by 3.2 per cent under SCF, but without an increase in yolk weight, whereas the R^+ line had a yolk weight heavier by 3.8 per cent with SCF. Similar results were obtained by Picker on dwarf lines [19].

The most significant interaction concerned the decreased intake of the calcium carbonate source under SCF ($p < 0.001$). This decrease was considerable in the R^+ line (–36.3 per cent) while it was only of 6.7 per cent in the R^- line.

To complete the interpretation of this result, it is useful to take account, in addition, of the supply of calcium by the base ration excluding the calcium carbonate: both in the single feed and under SCF this calcium supply of the calcium element represented 1.51 per cent of the ingested basic feed. Combining this with the calcium atoms brought under the form of carbonate, it was observed that the total calcium ingested in the R^+ line was 138.3 g and 99.7 g, respectively, with the single feed and under SCF; for the R^- line the corresponding figures were 102.5 g and 91.3 g. This shows clearly enough that, while the R^- line ingested about the same total amount of calcium irrespective of the treatment, the R^+ line ate a large excess of calcium with the single feed, but tended to absorb about the same quantity as the R^- line when given SCF.

From the point of view of the specific calcium appetite and of its regulating role compared in the two lines, our results suggest the following interpretation: irrespective of the type of feeding, the low consuming R^- line regulates its calcium intake similarly. Moreover, the observed decrease of the residual fraction of food intake with SCF as compared to a complete ration suggest that when a complete feed is offered, the calcium requirement somewhat limits underconsumption. Concerning the R^+ line, a single feed caused an overconsumption of calcium. In other words, the tendency to overconsume the base ration has priority and causes a considerable excess of calcium ingestion, inhibiting its regulation. In contrast, under SCF, a regulation of calcium intake can be expressed, and it seemed to be as complete as in the R^- line, while the consumption of the base ration remained in excess. Finally, the appetite for calcium is completely separate from the appetite for the rest of the ration in both lines.

Variables concerning shell quality (weight, thickness percentage of shell) were improved by about 3 per cent by SCF in both lines, which agrees with other results in the literature. It seems, however, that the calcium ingested ($3.67\ g{\cdot}d^{-1}$) with the complete feed was sufficient in the R^- line for its requirements, while it was in excess ($4.94\ g{\cdot}d^{-1}$) in the R^+ line, where it is not efficiently utilised and/or assimilated in relation to the needs associated with shell calcification [15, 16]. This might be caused by the feeding behaviour of this line which eats the major part of the feed at the beginning of the day [10] and consequently less in the afternoon, at the time when the calcium requirement is maximum, corresponding to shell formation. Thus the "specific appetite" could be masked by the large energetic requirement of the R^+ line which could be expressed earlier in the day.

5. CONCLUSION

To conclude, SCF seems to be more beneficial, on the whole, to the low-consuming R^- line. More generally, it would be interesting to assess whether hens having a tendency to underconsume benefit more from SCF. Moreover, selection that tends to modify the appetite of laying hens may possibly be associated with a feeding schedule taking into account the specific requirements and feeding behaviour of the selected line. Additional studies from the physiological point of view would be necessary to explain the inefficient utilisation of calcium by the R^+ line. For instance, a comparison of R^+ and R^- lines under SCF or fed the single feed might include observations on feeding behaviour throughout the day and also on days with or without eggshell formation.

Incidentally, since in other experiments on SCF, the calcium level of the base ration (excluding the carbonate source) was generally between 0.8 and 1.0 per cent [8, 15] while in the present work it was 1.5 per cent, our observations on the effects of SCF were possibly relatively underestimated as compared to those of other authors.

ACKNOWLEDGMENTS

The first author expresses his gratitude towards the Laboratoire de Génétique Factorielle and the Fondation Lefranc for financial support. The authors also wish to thank David Gourichon and Anne Françoise Ameline for technical assistance.

REFERENCES

[1] Abdelatif M., Bordas A., Mérat P., Consommation alimentaire chez des poules Fayoumi et Fayoumi × Leghorn en fonction de la formation de l'œuf et de l'oviposition, avec ou sans source calcique séparée, Génét. Sél. Évol. 18 (1986) 63–72.

[2] Bordas A., Mérat P., Correlated responses in a selection experiment on residual feed intake of adult Rhode Island Red cocks and hens, Ann. Agric. Fenniae 23 (1984) 233–237.

[3] Bordas A., Mérat P., Effet d'une alimentation calcique séparée sur les performances de poules pondeuses naines, in: Conf. Eur. d'Aviculture de Paris (24–28 août), Eds World's Poultry Science Association Branche française, 1986, pp. 186–190.

[4] Bordas A., Tixier-Boichard M., Mérat P., Direct and correlated responses to divergent selection for residual food intake in Rhodes Island red laying hens, Brit. Poult. Sci. 33 (1992) 741–754.

[5] Bordas A., Mérat P., Minvielle F., Heterosis in egg laying lines under divergent selection for residual feed consumption, Poult Sci. 75 (1996) 20–24.

[6] Bordas A., Minvielle F., Réponse à la chaleur de poules pondeuses issues de lignées sélectionnées pour une faible (R^-) ou forte (R^+) consommation alimentaire résiduelle, Génét. Sél. Évol. 29 (1997) 279–290.

[7] Byerly T.C.J., Kessler W., Gous M., Thomas O.P., Feed requirement for egg production, Poultry Sci. 59 (1980) 2500–2507.

[8] Cabrera M.C., Alimentation calcique chez la pondeuse : effets d'une alimentation calcique séparée combinée ou non à un rationnement alimentaire sur l'énergie métabolisable du régime et la rétention d'azote, calcium et phosphore chez la poule, Mémoire de DEA de Nutrition, Université Pierre et Marie Curie, Paris VI, France, 1981.

[9] Fairfull R.W., Chambers J.R., Breeding for feed efficiency , Poultry Can. J. Anim. Sci. 64 (1984) 513–527.

[10] Gabarrou J.F., Geraert P.A., Francois N., Guillaumin S., Picard M., Bordas A., Energy balance of laying hens selected on residual food consumption, Brit. Poult. Sci. 39 (1998) 78–89.

[11] Larbier M., Leclercq B., L'œuf et l'alimentation des poules pondeuses, in: Nutrition et alimentation des volailles, INRA édition, 1992, pp. 195–226.

[12] Leeson S., Summers J.D., Voluntary food restriction by laying hens mediated through dietary self selection, Brit. Poult. Sci. 19 (1978) 417–424.

[13] Leeson S., Summers J.D., Dietary self-selection by layers, Poult. Sci. 58 (1979) 646–651.

[14] Leeson S., Summers J.D., Effect of early light treatment and diet self-selection on laying performance, Poult. Sci. 59 (1980) 11–15.

[15] Mongin P., Sauveur B., Voluntary food and calcium intake by the laying hens, Brit. Poult. Sci. 15 (1974) 349–359.

[16] Mongin P., Sauveur B., The specific calcium appetite of the domestic fowl, in: Boorman K.N, Freeman B.M. (Eds.), Food intake regulation in poultry, Brit. Poult. Sci., Edinburgh, 1979, pp. 171–189.

[17] Mongin P., Sauveur B., Données et applications nouvelles concernant la solidité de la coquille de l'œuf. Alimentation calcique séparée, Courrier Avicole, Paris 553 (1975) 6–9.

[18] Picard P., Antoine H., Sauveur B., Influence de l'alimentation calcique séparée sur l'ingéré énergétique de la poule pondeuse soumise à un stress thermique, Conférence Européenne d'aviculture de Paris du 24 au 28 août, 1986, pp. 406–411.

[19] Picker I., Influence du gène cou nu Na sur les consommations alimentaires en fonction de la formation de l'œuf et sur les performances de ponte de poules naines DW, en contexte d'alimentation calcique séparée, Mémoire de DEA, Université de Paris VII, 1987, 80 p.

[20] SAS Institute, SAS User's Guide: Statistics, Statistic Institute Inc., Cary NC, 1988.

[21] Sauveur B., Picard M., Effet de la température et de l'éclairement appliqués à la poule sur la qualité de l'œuf, Options méditeranéeennes, séries A, n° 7, L'aviculture en Méditerannée, 1990, pp. 211–226.

[22] Uzu G., L'alimentation de la poule pondeuse en climat chaud : deux voies d'amélioration, L'aviculture, France, n° 504, 1989, pp. 40–48.

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