

# Correlated Responses to Long-Term Selection for Clutch Length in Dwarf Brown-Egg Layers Carrying or Not Carrying the Naked Neck Gene

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**ABSTRACT** Two dwarf brown-egg layer lines, differing in their genotype for the naked neck gene (*NA*), line L2 (*NA\*NA/\*NA*) and line L1 (*NA\*N/\*N*), have been selected for 16 generations for increased average clutch length. A control line from the same base population, dwarf and segregating for the *NA* gene, was maintained by random mating. Genetic parameters were estimated by a multivariate derivative-free restricted maximum likelihood procedure, and the *NA* gene effect was estimated within the unselected control line. The studied traits included clutch traits, egg production traits, abnormal eggs, egg weight at 36 wk, and BW at 42 wk. The average clutch length, egg number, and maximum clutch length were normalized using the Box-Cox transformation. In response to 16 generations of direct selection for increased average clutch length, other egg production traits, such as laying rate and total egg number, have been

indirectly improved in a dwarf layer genetic background. The estimated heritabilities were 0.406 to 0.424 for transformed average clutch length (TCL), 0.373 to 0.411 for transformed egg number (TEN), 0.529 to 0.559 for age at first egg (AFE), 0.275 to 0.282 for laying rate (LR), 0.455 for clutch number (CN), and 0.319 for the number of double-yolked eggs (DYEN). The TCL had high genetic correlations with TEN (0.777), LR (0.863), maximum clutch length (0.902), and CN (-0.845). Selection for increased average clutch length was an effective method for increasing egg production. Line L2 showed a higher egg weight than L1, which indicates that the combined effect of *NA* and *DW* genes was favorable to maintain egg weight when egg number could be improved. Line L1 showed a higher number of DYEN, suggesting that the regulation of follicular maturation was changed in this line.

(Key words: dwarf layer, naked neck gene, clutch length, correlated response, genetic parameter)

2003 Poultry Science 82:709–720

## INTRODUCTION

Selection for part- or whole-record egg number or laying rate is a usual approach to improving egg production, which has been shown to yield positive genetic progress, as reviewed by Fairfull and Gowe (1990). In order to better identify the genetic factors underlying egg production variability, some genetic studies have focused on the time interval between consecutive ovipositions (McClung et al., 1976), the mean time of oviposition (Yoo et al., 1988; Lillpers and Wilhelmson, 1993), and the intraclutch mean lag of oviposition time (Luc et al., 1996), in which the view for increasing egg production was ascribed to an increase in the rate of passage of egg through the oviduct and to an increase in the follicular maturation rate. Clutch length (CL) is inversely related to the interval between

ovipositions, and its measurement is easier than monitoring the oviposition time every day, although it may be influenced by false recording due to atypical very short sequences and internal ovulations (Lillpers and Wilhelmson, 1993). Furthermore, in the turkey, Nestor (1980) investigated the genetic variability of average CL and of the number of total days lost from broodiness. Both traits were moderately heritable, and the selection for decreased total days lost from broodiness was found to be the most efficient method to increase egg number and number of poults, but it decreased markedly adult BW.

In broiler production, the sex-linked dwarf gene, *DW*, is used in dam lines, where it can improve feed efficiency. In egg-laying strains, the *DW* gene has been shown to decrease egg production (Bernier and Arscott, 1972), and

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Received for publication July 22, 2002.

Accepted for publication December 10, 2002.

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**Abbreviation Key:** AFE = age at first egg; BE = broken eggs; BW16, BW42 = body weight at 16 and 42 wk, respectively; CL = clutch length; CN = clutch number; DYEN = number of double-yolked eggs; EBV = estimated breeding values; EN = egg number; EW = egg weight; EWG = egg weight gain from 29 to 36 wk; EW36 = egg weight at 36 wk; LR = laying rate; MCL = maximum clutch length; SSE = soft-shelled eggs; TCL = transformed clutch length; TEN = transformed egg number; TMCL = transformed value of maximum clutch length.

more particularly CL (Amin-Bakhche and Mérat, 1975). Consequently, selection for CL is proposed as a special approach for improving egg production of dwarf layers. Furthermore, the association of the naked neck gene, *NA*, with the *DW* gene, was found previously to have a favorable effect on egg weight and feed efficiency (Bordas and Mérat, 1984). Thus, a selection experiment was initiated in 1985 with the aim to improve CL in two lines of dwarf brown-egg layers differing in their genotype for the *NA* gene. The objectives were to investigate the genetic variability of CL in dwarf hens and the effect of the naked neck gene on the selection response in a dwarf background.

Selection for increased CL has achieved a significant direct response, with an average CL of 15.16, 14.87, and 3.63 at generation 16 in two selected lines and a control line, respectively (Chen and Tixier-Boichard, 2002). The purposes of the present study were to estimate genetic correlations of average CL with other production traits in dwarf brown-egg layers and to assess the correlated responses to a long-term selection for CL.

## MATERIALS AND METHODS

### *Animals and Housing*

The selection procedure in the current study has been previously described by Chen and Tixier-Boichard (2002). Briefly, a selection experiment was conducted at the Institut National de la Recherche Agronomique (INRA) in Jouy-en-Josas beginning in 1985. The unselected base population consisted of 99 dams and 23 sires, carrying the sex-linked dwarf gene and segregating for the *NA* gene. Selected line L1 was normally feathered, homozygous for the nonnaked neck allele (*NA*\**N*), line L2 was homozygous for the naked neck allele (*NA*\**NA*), and control line C was segregating for the three possible genotypes at the *NA* locus with a 50% frequency of *NA*\**NA* mutant allele. The average CL was calculated as the arithmetic mean of all clutches recorded from the first egg until 42 wk of age. In the first two generations, females were selected on an index incorporating BW with a negative coefficient and egg weight and average CL with positive coefficients, determined according to the expected genetic gains (Yamada et al., 1975). Males were selected on individual BW within each sire family. From generation 2 on, selection was done solely on average CL. Females were selected on a within-sire basis, combining the individual value and the full-sib mean, assuming a heritability value of 0.4 in both lines. Selection of males combined the within-sire full-sister mean and the deviation of the sire family mean from the general mean. The lines were reproduced with a 1-yr generation interval. After pooling the three lines, the data set included a total of 10,595 birds consisting of 2,616 male and 7,979 female chickens. They were produced from 518 sires and 2,609 dams.

Each year, chicks of the three lines were hatched in one to three batches, 2 or 3 wk apart, and were reared on the floor with 10L:14D cycle. Sexes were separated and lines were intermingled. They were vaccinated against the ma-

ior poultry infectious diseases (Marek's disease, Newcastle, and Gumboro diseases, infectious bronchitis). Between 16 and 17 wk of age, pullets were moved into individual cages of a three-tier system. The light cycle in the laying house was set to 16L:8D from the day of housing. Beginning in 1987, the layer mash containing 2,600 cal/g ME and 15.5% CP was provided for ad libitum consumption. Ambient temperature was held constant at 23°C for females, in order to avoid interaction between lines and environment that could be due to the *NA*\**NA* allele in the case of fluctuating temperatures. Males were housed in collective cages between 16 and 17 wk of age.

Each generation, egg number (EN) was recorded from the age at first egg (AFE) to 42 wk of age. In addition, average egg weights (EW) were obtained at 29 wk and 36 wk, by collecting five eggs per hen laid on consecutive days within a week. Egg production was recorded daily for each hen with the status of each egg, either normal, or broken egg (BE), soft-shelled egg (SSE), and double-yolked egg (DYEN). The BW were measured at 6, 10, and 16 wk, and adult BW was determined at 42 wk of age (BW42), on average, over generations. For each hen, the laying rate (LR) was obtained from the ratio of egg number (whatever the egg status) to laying period. A 1-d break at least between ovipositions was taken as the end of a clutch. The clutch number (CN), average CL, and maximum clutch length (MCL) were calculated.

### *Variables Under Study*

In order to satisfy the classical hypothesis for describing traits with polygenic inheritance via a linear model with normal error, Box-Cox power transformation was used to normalize trait distribution (Besbes et al., 1993). The parameters (*t*) were found to be -0.247, -0.1, and 1.79 for the transformed value of average CL (TCL), for transformed value of maximum CL (TMCL) and for transformed value of total egg number (TEN), respectively (Chen and Tixier-Boichard, 2002). It was not possible, however, to find a suitable transformation, which could satisfy the normality conditions for traits related to egg status (BE, SSE, and DYEN).

There were 13 traits studied, including clutch traits (TCL, MCL, and CN), egg production traits (AFE, TEN, and LR), egg weight at 36 wk (EW36), egg weight gain (EWG = EW36 - EW29), the percentage of abnormal eggs (BE and SSE), the number of double-yolked eggs (DYEN), and BW at 16 and 42 wk (BW16 and BW42). At generations 3, 5, 9, and 12, individual egg mass and feed intake were measured during 36 to 40 and 33 to 37 wk of age in hatch 1 and hatch 2, respectively. Feed efficiency was obtained from egg mass divided by feed intake.

### *Methods of Analysis*

***Phenotypic Trends and Effects of Genotypes at the NA Locus.*** The phenotypic variabilities and year trends were compared among the three lines. The contrast between lines was estimated for each year with model I.

The naked neck gene effect was estimated within the control line by applying model II to generations 6, 8, and 10 to 16, only, because the other generations had either very few birds, or no bird, of each homozygous genotype at the *NA* locus. All statistical analyses were conducted by using SAS software (SAS Institute, 1995).

Model I:  $Y_{ijkl} = \mu + (\text{year} \times h)_{ij} + (\text{year} \times l)_{ik} + e_{ijkl}$

Model II:  $Y_{ijkl} = \mu + (\text{year} \times h)_{ij} + G_k + e_{ijkl}$

where  $Y_{ijkl}$  = individual observation,  $\mu$  = overall mean,  $(\text{year} \times h)_{ij}$  = fixed effect of  $j$ th hatch within  $i$ th year,  $(\text{year} \times l)_{ik}$  = fixed effect of  $k$ th line within  $i$ th year,  $G_k$  = fixed effect of genotype at the *NA* locus within the control line, and  $e_{ijkl}$  = random error.

**Estimation of Genetic Parameters.** Variance and covariance components were estimated using the derivative-free multiple trait Restricted Maximum Likelihood (REML) procedure with the VCE package of Groeneveld (1997). The following animal model was applied to all traits on the whole data set:

$$Y_{ijkl} = \mu + (\text{year} \times h)_{ij} + G_k + a_l + e_{ijkl}$$

where  $Y_{ijkl}$  = individual observation for traits,  $\mu$  = overall mean,  $(\text{year} \times h)_{ij}$  = fixed effect of the  $j$ th hatch within  $i$ th year,  $G_k$  = fixed effect of genotype at the *NA* locus,  $a_l$  = random animal effect, and  $e_{ijkl}$  = random error. Expectation and variance of the vector of performance,  $y$ , were distributed as follows in matrix notation:

$$E \begin{bmatrix} a \\ e \end{bmatrix} = \begin{bmatrix} 0 \\ 0 \end{bmatrix}$$

and

$$V \begin{bmatrix} a \\ e \end{bmatrix} = \begin{bmatrix} A \otimes G & 0 \\ 0 & \bigoplus_{l=1}^m R_l \end{bmatrix}$$

where  $A$  = numerator relationship matrix,  $G$  = variance-covariance matrix for the additive genetic effect,  $m$  = the number of records, and  $R_l$  = residual variance-covariance matrix for animal  $l$ . The direct product and direct sum of matrices are indicated by  $\otimes$  and  $\bigoplus$ , respectively.

All traits could not be analyzed together, because of large computing requirements. Therefore, five analyses with four traits each were implemented in the present study, but these analyses always included the selected trait, TCL. Analyses were also done for each line separately starting from the same base population. The fixed effect of the *NA* locus was not included in the separate analysis of line L1 and line L2.

**Genetic Trends and Inbreeding Effect.** Genetic trends were evaluated in both selected lines for eight traits with the estimated breeding values (EBV) by best linear unbiased prediction (BLUP) using mixed linear model with the PEST package (Groeneveld, 1990). In this analysis, variance components were obtained from the above re-

stricted maximum likelihood analysis. Concomitantly, the individual inbreeding coefficient was used as a covariable, with the following model:

$$Y_{ijkl} = \mu + bI + (\text{year} \times h)_{ij} + G_k + a_l + e_{ijkl}$$

where  $Y_{ijkl}$  = individual observation for traits,  $\mu$  = overall mean,  $b$  = regression coefficient,  $I$  = inbreeding coefficient,  $(\text{year} \times h)_{ij}$  = fixed effect of the  $j$ th hatch within  $i$ th year,  $G_k$  = fixed effect of genotype at the *NA* locus within the control line,  $a_l$  = random animal additive genetic effect, and  $e_{ijkl}$  = random error. In the first generation, the coefficient of inbreeding was assumed to be 0, then individual inbreeding coefficients were computed by using the PEDIG package (Boichard, 2002).

## RESULTS

### Phenotypic Trends and Effects of Genotypes at the *NA* Locus

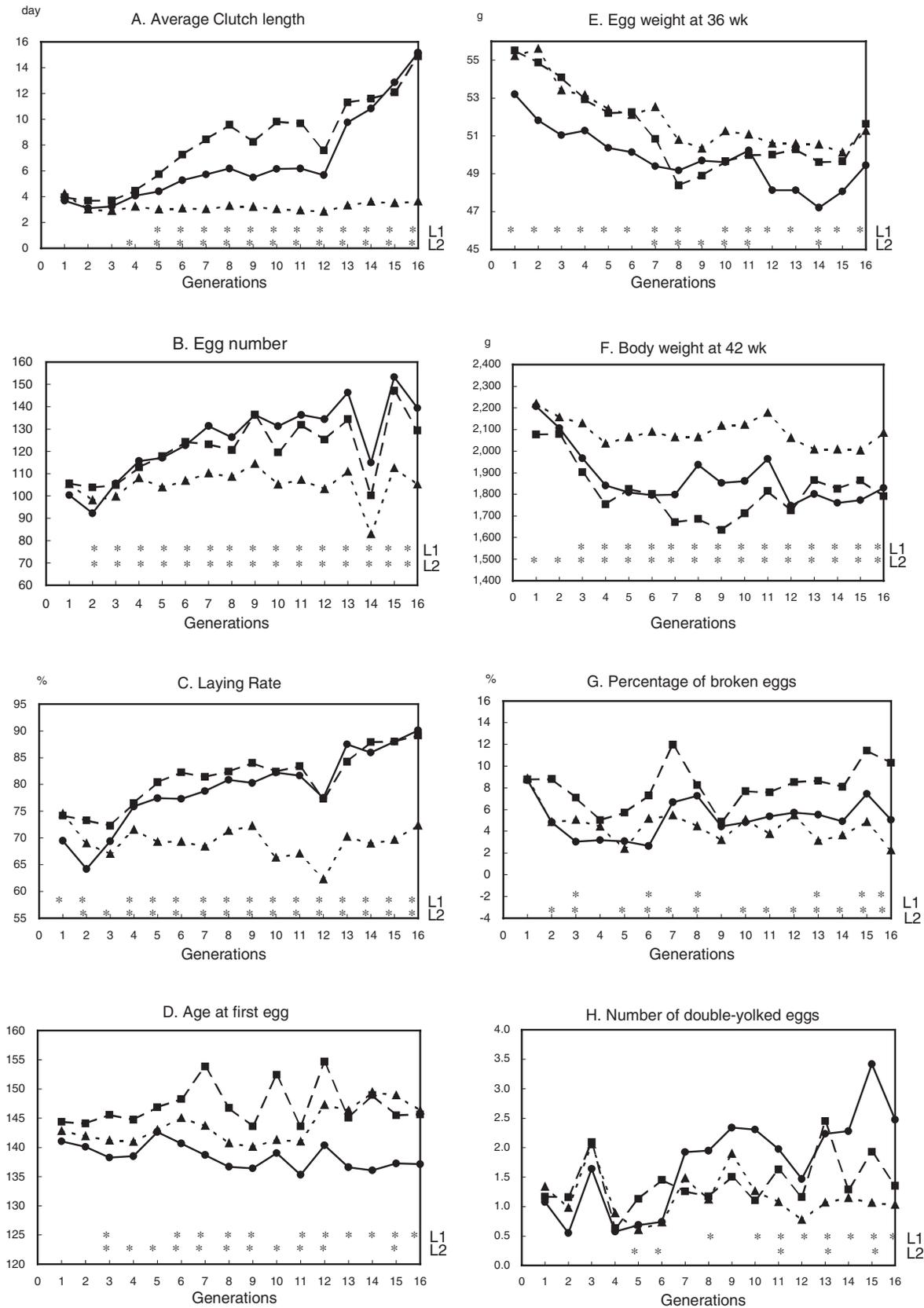
**Clutch Traits.** Selection for average CL in the dwarf laying hens resulted in significant progress. The naked neck line exhibited a faster response to selection, but no significant difference was observed between the selected lines in the last generations (Figure 1A). The related traits, MCL and CN, also showed significant changes after 16 generations of selection. At the 16th generation, MCL was 49.6, 49.0, and 9.8 for L1, L2, and C, respectively, and CN was 12.3, 11.9, and 30.9 for L1, L2, and C, respectively. At generation 12, the marked decrease in CL was due to an acute failure in water distribution, which on a relative basis impaired egg production more severely in the selected lines than in the control line.

**Egg Number.** The EN from housing to 42 wk of age significantly improved in both selected lines (Figure 1B). The dramatic drop in generation 14 was associated with a shorter recording period by 1 mo due to a housing problem. At the 16th generation, EN was 139, 129, and 105 for L1, L2, and C, respectively. Regarding the two selected lines, line L1 showed a higher value of EN than line L2, due to an earlier value of AFE in line L1 than in line L2.

**Laying Rate.** The LR, which is generally less influenced by AFE than is EN, showed a significant improvement in both selected lines, which did not differ significantly from each other (Figure 1C). In generation 12, a marked decline was associated with the acute failure in water distribution. At the 16th generation, LR was 90.1, 89.2, and 72.3% for L1, L2, and C, respectively.

**Age at First Egg.** At the 16th generation, AFE was 137, 146, and 146 for the L1, L2, and C lines. Compared to initial values, AFE has declined in Line L1 but not in Line L2 (Figure 1D).

**Egg Weight.** The EW36 declined slightly in all lines (Figure 1E). At the 16th generation, EW36 was 49.5, 51.6, and 51.3 for the L1, L2, and C lines, respectively. In each generation, EW36 in line L1 was significantly lower than



**FIGURE 1.** Phenotypic trends in females for eight studied traits in three lines. ....▲.....: dwarf control line, segregating for allele *NA\*NA* at the naked neck locus; —●—: dwarf and normally feathered selected line (*NA\*N/\*N*); - -■- -: dwarf and homozygous naked neck selected line (*NA\*NA/\*NA*). The significance level of comparison between each selected line and the control is indicated by an asterisk along the absciss line.

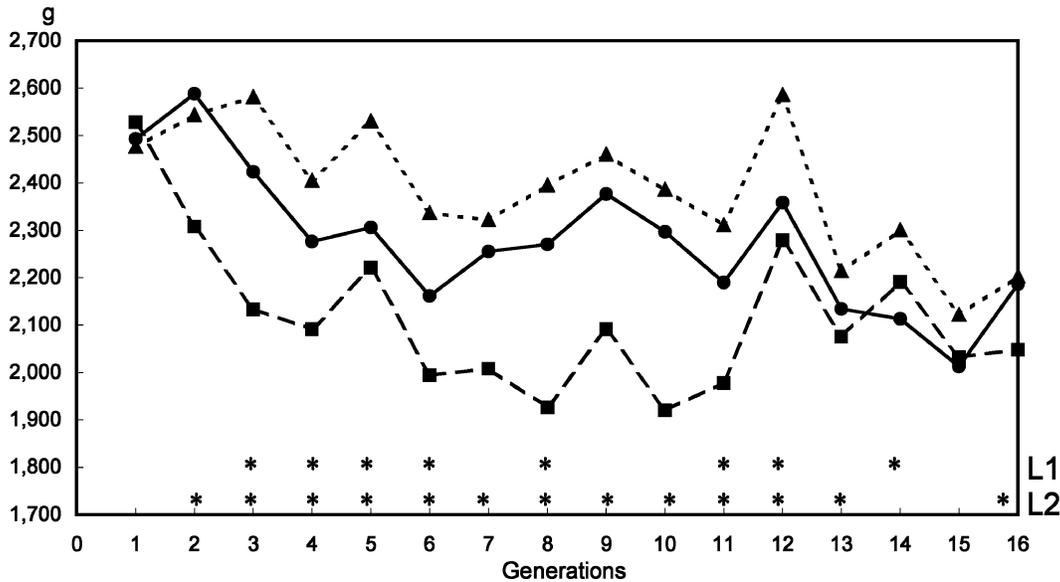


FIGURE 2. Phenotypic trends in males for body weight at 42 wk of age in three lines. ....▲.....: dwarf control line, segregating for allele  $NA^*NA$  at the naked neck locus; —●—: dwarf and normally feathered selected line ( $NA^*N/^*N$ ); -\_■\_-: dwarf and homozygous naked neck selected line ( $NA^*NA/^*NA$ ). The significance level of comparison between each selected line and the control is indicated by an asterisk along the absciss line.

in line C, but this was only the case from generations 6 to 11 and at generation 14 in line L2.

**Body Weight.** At the 16th generation, female BW42 in both selected lines was significantly lower than in line C. A marked decline was observed in BW42 of both selected lines until generation 4 (Figure 1F), as a result of initial selection on this trait in the first two generations. At generation 3, BW42 decreased in all lines, as a result of a change in energy content in the diet. After generation 4, BW42 was relatively stable and remained lower in both selected lines than in line C. Figure 2 showed the phenotypic trends for male BW42. The first generations exhibited a marked decline due to the same reason as for females. At generation 12, avian encephalomyelitis occurred in the second hatch and decreased BW in females. Males were not affected, however, because they were produced in the first hatch only, free of the disease. Consequently, male and female BW42 showed different trends at generation 12, because of husbandry problems only.

**Egg Quality Traits.** The BE in line L2 was significantly higher than in line L1 and line C, except in generations 4 and 9. The BE in line L1 was also significantly higher than in line C in the last four generations (Figure 1G). The SSE did not differ significantly between the three lines at the 16th generation. The DYEN in line L1 slightly increased and was significantly higher than in the other two lines at the last three generations (Figure 1H).

**Feed Efficiency.** Table 1 shows the feed efficiency of each line in four generations. The ratio of egg mass to feed intake in both selected lines was significantly higher than in the control line, and the selected lines showed an increasing trend over generations.

**NA Gene Effect.** Table 2 shows the mean and SEM for each trait after pooling nine generations of the control line. Genotype did not significantly affect EN, MCL, CN,

BE, SSE, and BW42. An additive effect of the  $NA$  gene was observed for AFE, EW36, and DYEN (with higher values for  $NA$  gene carriers) and BW16 (with lower values for  $NA$  gene carriers), when the heterozygous genotype was intermediate between each homozygous. A dominant effect of the  $NA$  gene was observed on CL and LR, when both heterozygous and homozygous mutant genotypes exhibited a higher value than the normal homozygous. The opposite situation occurred for EWG when only the homozygous  $NA^*NA$  had a higher value.

### Estimation of Genetic Parameters

Heritabilities, genetic correlations, and phenotypic correlations for traits recorded over 16 generations are presented in Table 3. The heritability of TCL ranged from 0.406 to 0.424 in the five analyses. Heritability of CN was slightly higher than heritability of TCL. The LR exhibited a lower heritability value (0.28). Other production traits, such as AFE, TEN, TMCL, CN, EW36, and BW42, also showed high values of heritability ranging between 0.37 (TEN) and 0.77 (BW42). Egg quality traits exhibited lower heritability values (0.17 to 0.32).

Genetic correlations exhibited a high value among the clutch traits, when the genetic correlations were 0.902 and  $-0.845$  for TMCL and CN with TCL (Table 3). Genetic correlations between TCL and either TEN or LR were also high, 0.755 and 0.863, respectively, which shows that indirect selection took place on egg number. The correlation between TCL and AFE was low and negative, whereas it was high and negative between TEN and AFE.

The genetic correlations were high between EW36 and BW42, but BW42 was not significantly correlated with TCL, whereas EW36 was negatively correlated with TCL ( $-0.209$ ) (Table 3). The BE and DYEN traits showed a

TABLE 1. Means  $\pm$  SEM of feed efficiency of each line in four generations

| Generations | Lines <sup>1</sup>             |                                |                                |
|-------------|--------------------------------|--------------------------------|--------------------------------|
|             | C                              | L1                             | L2                             |
| 3           | 0.331 $\pm$ 0.007 <sup>b</sup> | 0.376 $\pm$ 0.007 <sup>a</sup> | 0.371 $\pm$ 0.007 <sup>a</sup> |
| 5           | 0.324 $\pm$ 0.011 <sup>b</sup> | 0.394 $\pm$ 0.009 <sup>a</sup> | 0.393 $\pm$ 0.009 <sup>a</sup> |
| 9           | 0.344 $\pm$ 0.013 <sup>b</sup> | 0.399 $\pm$ 0.009 <sup>a</sup> | 0.421 $\pm$ 0.010 <sup>a</sup> |
| 12          | 0.402 $\pm$ 0.010 <sup>b</sup> | 0.440 $\pm$ 0.010 <sup>a</sup> | 0.452 $\pm$ 0.010 <sup>a</sup> |

<sup>a,b</sup>Means within rows with no common superscript differ significantly ( $P < 0.05$ ).

<sup>1</sup>Line C = dwarf control line, segregating for the NA\*NA naked neck allele; line L1 = normally-feathered dwarf selected line; and line L2 = homozygous naked neck dwarf selected line.

slight positive correlation with TCL, but SSE did not show a significant correlation with TCL. These estimates should, however, be considered carefully because of the nonnormal distributions of egg status traits. All phenotypic correlations were in the same direction as genetic correlations.

### Genetic Trends and Inbreeding Effect

Genetic trends for the various traits in the three lines are shown in Figure 3. Linear estimates of genetic gain per generation were calculated either with the deviation from control line (classical method) or with individual EBV and are presented in Table 4. The scale of measure varied according to the trait, except TCL and TEN, which were transformed units. The genetic levels for TEN and LR were notably increased by selection in both lines. On the contrary, CN was notably decreased by selection in both lines. In the EBV method, linear regression equations exhibited high  $R^2$  values ( $>0.90$ ) except for BW42, EW36, and BE (0.25 to 0.48), whereas EW36 did not show a significant linear trend in both selected lines with the classical method. A significantly negative genetic trend was observed on AFE, particularly in line L1. The EW36 and BW42 exhibited slight downward trends according

to the EBV method, which was not significant for BW42 in line L2. In line L1, DYEN significantly increased by 0.116 per generation. The above results were in agreement with the genetic correlations estimated with TCL.

After 16 generations, the cumulative inbreeding level was the lowest in line C (11.1%) and showed very similar values in lines L1 and L2 with 18.0% and 18.4%, respectively. The average increment of percentage inbreeding coefficient per generation was 0.74, 1.20, and 1.23% in lines C, L1, and L2, respectively. Table 5 showed the inbreeding effect on the mean EBV per 10% inbreeding coefficient. The values were estimated from either three lines together or each line in the model, where the inbreeding coefficient was included as a covariable. A 10% increase of inbreeding reduced TCL, TMCL, TEN, LR, and DYEN, and delayed the AFE but slightly increased or did not affect the BW and EW.

## DISCUSSION

In response to 16 generations of direct selection on CL, other egg production traits, such as LR, and EN, have been indirectly improved in a dwarf layer genetic background. Phenotypic trends, genetic parameters, and correlated responses need to be compared carefully between the two

TABLE 2. Least square means  $\pm$  SEM of analyzed traits by pooling nine generations in the control line for each genotype

| Variables <sup>1</sup> | Phenotypes                   |                               |                              |
|------------------------|------------------------------|-------------------------------|------------------------------|
|                        | Normally feathered           | Heterozygous naked neck       | Homozygous naked neck        |
| CL                     | 3.09 $\pm$ 0.06 <sup>a</sup> | 3.28 $\pm$ 0.05 <sup>b</sup>  | 3.34 $\pm$ 0.06 <sup>b</sup> |
| AFE                    | 143.5 $\pm$ 0.6 <sup>a</sup> | 145.2 $\pm$ 0.5 <sup>b</sup>  | 147.6 $\pm$ 0.6 <sup>c</sup> |
| EN                     | 103.1 $\pm$ 1.3 <sup>a</sup> | 105.1 $\pm$ 1.0 <sup>a</sup>  | 105.7 $\pm$ 1.2 <sup>a</sup> |
| LR, %                  | 66.4 $\pm$ 0.7 <sup>a</sup>  | 68.7 $\pm$ 0.6 <sup>b</sup>   | 70.2 $\pm$ 0.7 <sup>b</sup>  |
| MCL                    | 9.33 $\pm$ 0.36 <sup>a</sup> | 9.94 $\pm$ 0.30 <sup>a</sup>  | 9.81 $\pm$ 0.36 <sup>a</sup> |
| CN                     | 35.9 $\pm$ 0.56 <sup>a</sup> | 35.1 $\pm$ 0.46 <sup>a</sup>  | 34.5 $\pm$ 0.56 <sup>a</sup> |
| EW36, g                | 49.7 $\pm$ 0.2 <sup>a</sup>  | 51.0 $\pm$ 0.2 <sup>b</sup>   | 52.1 $\pm$ 0.2 <sup>c</sup>  |
| EWG, g                 | 3.66 $\pm$ 0.12 <sup>a</sup> | 3.90 $\pm$ 0.10 <sup>a</sup>  | 4.28 $\pm$ 0.11 <sup>b</sup> |
| BE, %                  | 3.65 $\pm$ 0.37 <sup>a</sup> | 4.31 $\pm$ 0.31 <sup>a</sup>  | 4.44 $\pm$ 0.36 <sup>a</sup> |
| SSE, %                 | 2.11 $\pm$ 0.26 <sup>a</sup> | 2.38 $\pm$ 0.21 <sup>a</sup>  | 2.25 $\pm$ 0.25 <sup>a</sup> |
| DYEN                   | 0.84 $\pm$ 0.09 <sup>a</sup> | 0.99 $\pm$ 0.08 <sup>ab</sup> | 1.23 $\pm$ 0.09 <sup>b</sup> |
| BW16, g                | 1,385 $\pm$ 8 <sup>a</sup>   | 1,376 $\pm$ 7 <sup>ab</sup>   | 1,360 $\pm$ 8 <sup>b</sup>   |
| BW42, g                | 2,092 $\pm$ 16 <sup>a</sup>  | 2,061 $\pm$ 13 <sup>a</sup>   | 2,057 $\pm$ 15 <sup>a</sup>  |

<sup>a-c</sup>Means within rows with no common superscript differ significantly ( $P < 0.05$ ).

<sup>1</sup>CL = average clutch length; AFE = age at first egg; EN = egg number; LR = laying rate; MCL = maximum clutch length; CN = clutch number; EW36 = egg weight at 36 wk; EWG = egg weight gain; BE = % of broken eggs; SSE = % of soft-shelled eggs; DYEN = number of double-yolked eggs; BW16, BW42 = body weight at 16 and 42 wk.

TABLE 3. Heritabilities and genetic and phenotypic correlations<sup>1</sup> estimated using the multiple trait restricted maximum likelihood procedure for transformed clutch length value, egg production, and body weight traits

| Traits <sup>2</sup>        | Records (n) | Clutch traits |                |                |                |
|----------------------------|-------------|---------------|----------------|----------------|----------------|
|                            |             | TCL           | TMCL           | CN             | LR             |
| TCL                        | 7,979       | 0.424 ± 0.017 | 0.902 ± 0.008  | -0.845 ± 0.018 | 0.863 ± 0.013  |
| TMCL                       | 5,826       | 0.893         | 0.412 ± 0.016  | -0.739 ± 0.025 | 0.769 ± 0.013  |
| CN                         | 5,826       | -0.780        | -0.666         | 0.455 ± 0.019  | -0.539 ± 0.045 |
| LR                         | 7,979       | 0.787         | 0.724          | -0.0348        | 0.282 ± 0.019  |
| Egg production traits (1)  |             |               |                |                |                |
|                            |             | TCL           | AFE            | TEN            | LR             |
| TCL                        | 7,979       | 0.406 ± 0.019 | -0.058 ± 0.039 | 0.756 ± 0.020  | 0.861 ± 0.014  |
| AFE                        | 7,979       | -0.108        | 0.529 ± 0.019  | -0.591 ± 0.029 | -0.101 ± 0.046 |
| TEN                        | 7,979       | 0.697         | -0.432         | 0.373 ± 0.021  | 0.832 ± 0.015  |
| LR                         | 7,979       | 0.787         | -0.141         | 0.780          | 0.275 ± 0.021  |
| Egg production traits (2)  |             |               |                |                |                |
|                            |             | TCL           | AFE            | TEN            | EW36           |
| TCL                        | 7,979       | 0.423 ± 0.020 | -0.115 ± 0.039 | 0.767 ± 0.017  | -0.213 ± 0.028 |
| AFE                        | 7,979       | -0.108        | 0.559 ± 0.022  | -0.626 ± 0.028 | -0.045 ± 0.030 |
| TEN                        | 7,979       | 0.697         | -0.432         | 0.400 ± 0.022  | -0.097 ± 0.033 |
| EW36                       | 7,494       | -0.291        | 0.082          | -0.241         | 0.639 ± 0.019  |
| Egg and body weight traits |             |               |                |                |                |
|                            |             | TCL           | EW36           | BW42           | TEN            |
| TCL                        | 7,979       | 0.423 ± 0.019 | -0.209 ± 0.027 | -0.056 ± 0.025 | 0.777 ± 0.018  |
| EW36                       | 7,494       | -0.291        | 0.644 ± 0.018  | 0.549 ± 0.021  | -0.096 ± 0.036 |
| BW42                       | 7,955       | -0.252        | 0.449          | 0.768 ± 0.015  | -0.010 ± 0.031 |
| TEN                        | 7,979       | 0.697         | -0.241         | -0.206         | 0.411 ± 0.023  |
| Abnormal eggs              |             |               |                |                |                |
|                            |             | TCL           | BE             | SSE            | DYEN           |
| TCL                        | 7,979       | 0.410 ± 0.019 | 0.222 ± 0.039  | 0.099 ± 0.053  | 0.203 ± 0.036  |
| BE                         | 7,979       | 0.021         | 0.221 ± 0.017  | 0.558 ± 0.037  | 0.449 ± 0.028  |
| SSE                        | 7,979       | -0.079        | 0.263          | 0.169 ± 0.019  | 0.662 ± 0.042  |
| DYEN                       | 7,645       | 0.194         | 0.153          | 0.192          | 0.319 ± 0.016  |

<sup>1</sup>Diagonal = heritability ± SE; upper diagonal = genetic correlation ± SE; lower diagonal = phenotypic correlation.

<sup>2</sup>TCL = transformed clutch length; AFE = age at first egg; TEN = transformed egg number; LR = laying rate; TMCL = transformed maximum clutch length; CN = clutch number; EW36 = egg weight at 36 wk; BE = % of broken eggs; SSE = % of soft-shelled eggs; DYEN = number of double-yolked eggs; BW42 = adult body weight at 42 wk.

selected lines, L1 and L2, differing by their genotype at the *NA* locus.

### Phenotypic and Genetic Trends

Phenotypic trends exhibited larger fluctuations between years than genetic trends, as reported in other selection experiments (Sharma et al., 1998). One of the reasons is that the phenotypic variability of the selected trait has increased along with selection and that this trait has become more sensitive to environment in the selected lines than in the control line. The mixed model approach makes possible to evaluate the genetic gain, while taking into account the effects of selection on genetic variances, as reported in other studies (e.g., Meyer and Hill, 1991; Pinard et al., 1992; Chen and Tixier-Boichard, 2002). In the present work, the linear regression of mean genetic values on generation number was significant for most of the traits, but a higher goodness of fit with high  $R^2$  values was obtained with the mixed model approach as compared to the deviation from control line. For most of the traits, the genetic trends estimated by averaging EBV

exhibited a smoother curve than the linear contrasts estimated each year between selected and control lines.

Since all data used for selection have been included in the estimation of EBV, any selection effect should have been accounted for. The model, including the *NA* gene as a fixed effect, takes into account the additive effect of the *NA* locus on performance. Indeed, a positive effect of *NA* gene on EW36 was observed at the phenotypic level, but after accounting for this additive effect in the animal model, a decrease in genetic values for EW36 was observed in line L2 to a larger extent than in line L1. For the LR, the ranking of the L1 and L2 lines differed between phenotypic and genetic trends, because the positive effect of the *NA*\**NA*/*NA* genotype on LR was taken into account in the estimation of genetic trends but was confounded with the line effect in the phenotypic trends.

The difference in genetic trends between both selected lines could be due either to an effect of the *NA* gene on the genetic variances, an effect of random drift, genotype-by-environment interactions, or a change in selection intensity, which had been discussed by Chen and Tixier-Boichard (2002) regarding direct selection response; how-

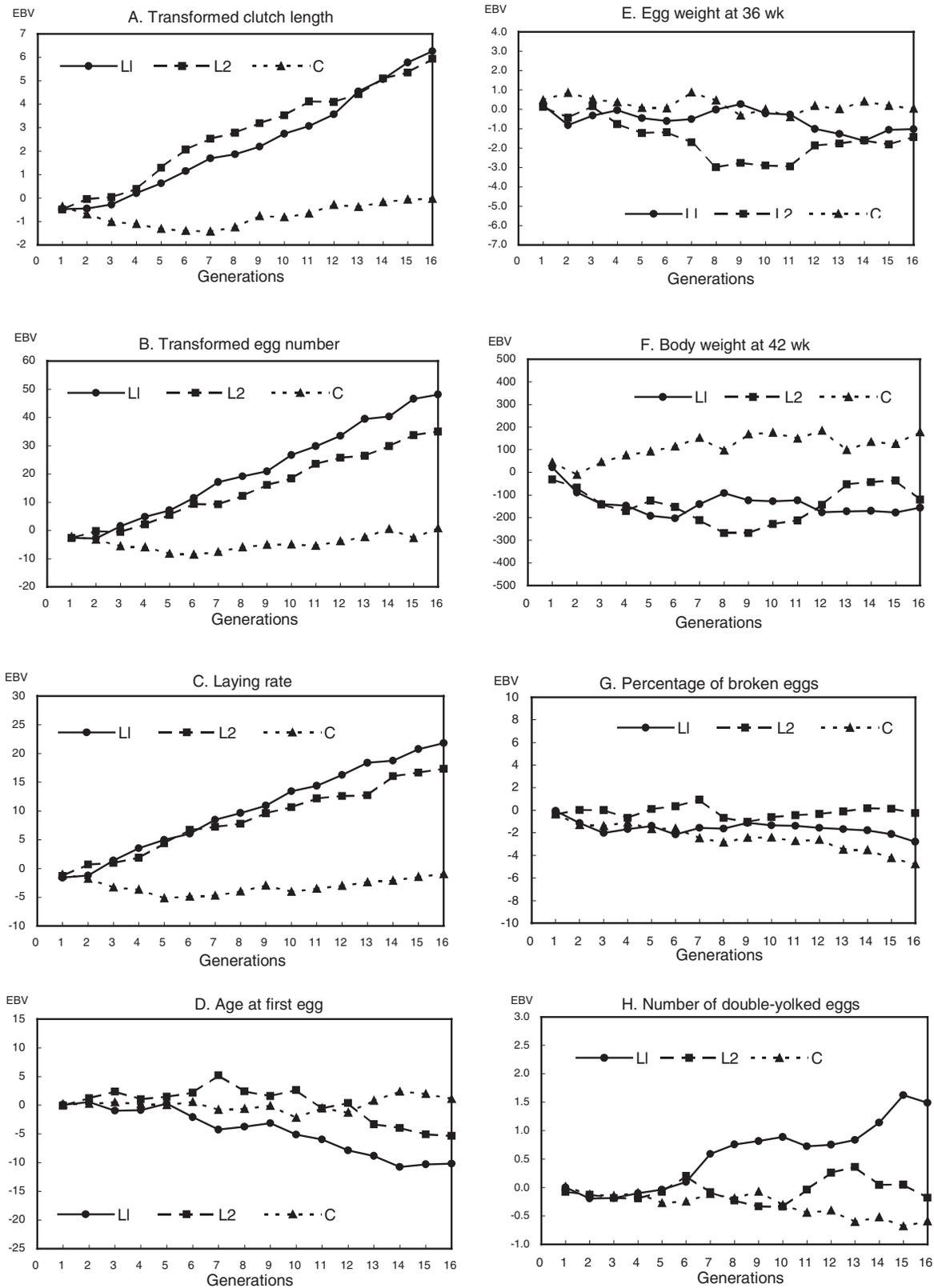


FIGURE 3. Genetic trends in females for eight studied traits in three lines, obtained from the average of individual breeding values. ....▲.....: dwarf control line, segregating for allele  $NA^*NA$  at the naked neck locus; —●—: dwarf and normally feathered selected line ( $NA^*N/*N$ ); -■-: dwarf and homozygous naked neck selected line ( $NA^*NA/*NA$ ).

TABLE 4. Estimates of genetic gain  $\pm$  SEM per generation based upon difference with control line (classical) and individual estimated breeding values (EBV) for both selected lines

| Traits <sup>1</sup> | Lines <sup>2</sup> |                     |                     |                     |                     |
|---------------------|--------------------|---------------------|---------------------|---------------------|---------------------|
|                     | C                  | L1                  |                     | L2                  |                     |
|                     | $\sigma_P$         | Classical           | EBV                 | Classical           | EBV                 |
| TCL                 | 1.90               | 0.37** $\pm$ 0.045  | 0.46** $\pm$ 0.018  | 0.35** $\pm$ 0.045  | 0.43** $\pm$ 0.014  |
| CN                  | 10.22              | -1.28** $\pm$ 0.156 | -1.30** $\pm$ 0.080 | -1.28** $\pm$ 0.271 | -1.27** $\pm$ 0.085 |
| AFE                 | 12.46              | -0.59** $\pm$ 0.116 | -0.81** $\pm$ 0.059 | -0.326 $\pm$ 0.280  | -0.44** $\pm$ 0.123 |
| TEN                 | 20.89              | 3.076** $\pm$ 0.244 | 3.60** $\pm$ 0.076  | 2.20** $\pm$ 0.304  | 2.65** $\pm$ 0.072  |
| LR, %               | 14.36              | 1.46** $\pm$ 0.154  | 1.61** $\pm$ 0.028  | 1.125** $\pm$ 0.146 | 1.25** $\pm$ 0.039  |
| BW42, g             | 322.1              | -11.07* $\pm$ 4.06  | -5.67* $\pm$ 2.62   | -0.914 $\pm$ 7.733  | 1.09 $\pm$ 4.52     |
| EW36, g             | 4.37               | 0.017 $\pm$ 0.046   | -0.071* $\pm$ 0.024 | -0.024 $\pm$ 0.063  | -0.127* $\pm$ 0.046 |
| BE, %               | 8.02               | 0.255** $\pm$ 0.027 | -0.070* $\pm$ 0.027 | 0.42** $\pm$ 0.107  | -0.0026 $\pm$ 0.027 |
| DYEN                | 2.04               | 0.153** $\pm$ 0.023 | 0.116** $\pm$ 0.011 | 0.072* $\pm$ 0.027  | 0.013 $\pm$ 0.011   |

<sup>1</sup>TCL = transformed clutch length; CN = average clutch length; AFE = age at first egg; TEN = transformed egg number; LR = laying rate; BW42 = adult body weight at 42 wk; EW36 = egg weight at 36 wk; BE = percentage of broken eggs; DYEN = number of double-yolked eggs.

<sup>2</sup>Line C = dwarf control line, segregating for the *NA\*NA* naked neck allele; line L1 = normally feathered dwarf selected line; and line L2 = homozygous naked neck dwarf selected line.

\* $P < 0.05$ .

\*\* $P < 0.01$ .

ever, some comments may be added regarding correlated responses. The AFE in the control line exhibited an increasing trend in later generations and, this could be explained by a higher proportion of homozygous *NA* layers, in which *NA* gene is known to delay the AFE. During the course of selection, an opposite trend for EW36 was observed between the two selected lines from generations 7 to 15, but an almost parallel trend was found between line L2 and the control line. This could be related to the occurrence of Marek's disease in the laying hens of generation 7 with a higher mortality in line L2 (about 30%) than in line L1 (about 15%); thus, hens remaining available for selection may not be a representative sample of line L2 before the disease. Since generation 12, natural selection may have also taken place, because hatchability decreased in line L2 (unpublished data), which could be influenced by egg size. The EW36 and BW42 for line L1 at 12th generation showed a more dramatic decline than for the other lines. In this generation, avian encephalomyelitis was diagnosed, and line L1 appeared to be more sensitive to this disease. In this line, survivors had a lower BW and laid small-sized eggs because of a high correlation between EW36 and BW42 (0.45).

Considering the initially faster response to selection for CL in naked neck layers, as well as the effects of the *NA\*NA* allele on egg production in the control line, one could speculate that a similar selection experiment with a base population segregating for the *NA* gene would have resulted in an increased frequency of the *NA\*NA* allele.

Regarding egg quality traits, the DYEN significantly increased by 0.116 in line L1 only, which suggests a change in the regulation of follicular maturation. The follicular maturation rate may have increased above an optimum value required for normal egg formation and oviposition. Selection for an increased DYEN has been done previously in White Leghorn chickens (Abplanalp et al., 1977), and the effect of introducing the *DW* gene in these lines was clearly to reduce the DYEN (Leenstra

et al., 1986). Thus, the present finding of an increased DYEN in dwarf layers provides evidence that selection on CL affected follicular maturation. An increase in CL is also associated with a decrease in oviposition interval and may also affect the duration of eggshell formation, which would result in a decreased shell percentage and, possibly, a decreased shell strength. In the present study, both lines L1 and L2 did exhibit a slightly negative trend for the BE, which was significant only in line L1. Curiously, the control line exhibited also a negative genetic trend on BE. As compared to the control line, mean EBV for BE was higher in lines L1 and L2 and was consistently higher in line L2 than line L1.

Inbreeding depression was observed in most egg production traits but not in BW and EW36. This result agreed with most studies of inbreeding effects on reproduction traits (Flock et al., 1991; Sewalem et al., 1999). Regarding BW and EW36, the lack of inbreeding depressions was surprising. One possible reason could be that the dominance effect was neglected in the model. Kennedy et al. (1988) proposed a model with an additive relationship matrix, dominance relationship matrix, and inbreeding coefficient as a covariate to provide unbiased prediction of additive and dominance values and unbiased estimation of inbreeding depression under random as well as phenotypic selection. The simulation study showed a biased estimation when using a model neglecting the dominance effect; however, it is difficult to compute the inverse of dominance relationship matrix with large data sets (Uimari and Kenney, 1990).

### Genetic Parameters

Genetic parameters and genetic trends were estimated with an animal model, considering year  $\times$  hatch effects and genotype at the *NA* locus as fixed effects. The animal model, however, can not estimate an effect of the *NA* locus on genetic variances. Indeed, line-specific analyses

TABLE 5. Inbreeding effect on studied traits: changes in mean estimated breeding values per 10% inbreeding coefficient estimated either from three lines (average) or each line separately<sup>1</sup>

| Traits <sup>2</sup> | Averages | Lines <sup>3</sup> |        |        |
|---------------------|----------|--------------------|--------|--------|
|                     |          | L1                 | L2     | C      |
| TCL                 | -0.828   | -1.161             | -1.193 | -0.289 |
| TMCL                | -2.503   | -4.595             | -3.232 | -1.250 |
| CN                  | 2.178    | 3.437              | 3.609  | 0.809  |
| AFE                 | 4.634    | 7.424              | 4.803  | 0.636  |
| TEN                 | -9.254   | -10.706            | -8.866 | -5.441 |
| LR                  | -3.085   | -4.794             | -2.579 | -2.471 |
| BW16, g             | 12.165   | 7.852              | 39.144 | -2.148 |
| BW42, g             | 76.289   | 122.65             | 125.90 | 18.891 |
| EW36, g             | 0.837    | 1.367              | 1.322  | -0.387 |
| EWG, g              | 1.746    | 1.343              | 0.395  | 1.803  |
| BE, %               | 1.746    | 1.343              | 0.395  | 1.803  |
| SSE, %              | 1.392    | 1.648              | -0.473 | 1.017  |
| DYEN                | -0.298   | -0.088             | -0.407 | 1.067  |

<sup>1</sup>The fixed effect of genotypes was not used in the model for the two selected lines.

<sup>2</sup>TCL = transformed clutch length; TMCL = transformed maximum clutch length; CN = clutch number; AFE = age at first egg; TEN = transformed egg number; LR = laying rate; BW16, BW42 = body weight at 16 and 42 wk; EW36 = egg weight at 36 wk; EWG = egg weight gain; BE = percentage of broken eggs; SSE = percentage of soft-shelled eggs; DYEN = number double-yolked eggs.

<sup>3</sup>Line C = dwarf control line, segregating for the *NA\*NA* naked neck allele; line L1 = normally feathered dwarf selected line; and line L2 = homozygous naked neck dwarf selected line.

yielded higher heritabilities for TEN and LR in line L1 (0.441 and 0.355) than in line L2 (0.345 and 0.208), as well as different genetic correlations between TCL and AFE (-0.383 in line L1, -0.119 in line L2 and 0.051 in the control line) or between TCL and EW36 (-0.289 in line L1, -0.164 in line L2, and -0.222 in the control line). The TCL appeared to be significantly and negatively correlated with AFE in line L1 only; however, this value was still lower than the correlation estimated between TEN and AFE. The EW36 appeared also to be negatively correlated to TCL in both lines with a higher value in line L1. The TEN was also negatively correlated with EW36 but to a lesser extent than was TCL. Genetic correlations between BW42 and either TCL or TEN were weak or close to zero. The EW36 had a higher negative genetic correlation with TCL than that of BW42 with TCL, which agreed with most of previous studies. It should be noticed that in spite of the marked reduction in BW due to the *DW* mutation, heritability of adult BW was still very high. Body weight traits may be affected by maternal effects or dominance effects that were not taken into account in the present analysis; thus, an overestimation of heritability may not be ruled out for weight traits.

In another poultry species, such as the turkey (Nestor, 1980), the genetic parameters estimated for average CL exhibited also a high correlation with the rate of lay but a lower correlation with the number of clutches (-0.49) than in the present study (-0.845). This could be related to the importance of long pauses between clutches due to broodiness in turkeys, which does not take place in the dwarf hens. In addition, average CL in turkeys was not correlated to the sexual maturity and appeared to be less correlated to BW than was the total number of days lost from broodiness after seven generations of selection (Nestor, 1980).

Compared to previous results (Fairfull and Gowe, 1990; Besbes et al., 1992), the present heritability estimates of egg production traits were higher, and this difference may be due to the genetic origin of the lines under study or to the method used; indeed, before the 1990s, normalization of egg number was not a current practice, and estimates were obtained by hierarchical analysis of variance, which did not account for selection effects and underestimated heritability values. Furthermore, the dominance effects were not included in the present analysis; they might take place for egg production traits but to a lesser extent than for weight traits.

### CL as a Selection Criterion for Layers

Generally, direct selection on egg number is expected to decrease AFE, egg weight, and, to a lesser extent, BW (Poggenpoel and Erasmus, 1978; Sharma et al., 1998) unless a multiple trait selection is performed to maintain or improve the genetic values for correlated traits (Gowe and Fairfull, 1985). In the present study, a significant improvement for egg number to 42 wk of age was achieved with 2.86 egg per generation in line L1 and 1.68 egg per generation in line L2. The genetic gain for EW was slightly negative in both selected lines, and line L2 showed a stronger decrease in egg size (-0.127 per generation) than line L1 (-0.071 per generation), but phenotypic means for EW were generally higher in line L2 than in line L1. These results suggest that the *NA* gene had a favorable effect on egg weight when egg number was improved, which totally agreed with the original idea to combine naked neck and dwarf genes in a layer population. Except for a favorable effect on egg weight, the other advantage of *NA* for laying performance was reviewed by Mérat (1986), including also a favorable effect on feed

efficiency. Furthermore, at high ambient temperature, it seems also that naked neck layers had a better shell strength and a higher laying rate than that of normally feathered layers (Bordas and Mérat, 1984). An unfavorable effect of *NA* gene was observed here on the AFE. For this reason, the TEN in an early recording period was significantly less in line L2 than in line L1. However, for maximizing annual egg output, laying persistency should be studied on a longer period. Ultimately, a selected dwarf and naked neck layer could be proposed as an alternative genotype for egg production in tropical countries, where the advantage of the naked neck for heat tolerance would be fully exploited, as documented by Mérat (1986).

In conclusion, the improvement of CL has been accomplished, while other important traits have either been improved or have shown a limited decline. The results indicated that selection for CL was an effective method for increasing the egg production, in which the TCL was more heritable than laying rate and EN. The CL as a selection criteria for layers was a feasible approach to modify LR with less consequence on AFE than selecting on egg number, but effects on EW36, BE, and DYEN should be carefully monitored in nonnaked neck dwarf layers. The DYEN increased, indicating that the regulation of follicular maturation had been changed in line L1. To estimate the response to selection free from environmental effects, a smoother linear regression was obtained with the EBV than with the classical method, but the animal model relies on genetic assumptions that may not be fulfilled. Comparing results of EBV with the classical method may provide a way to test the adequacy of these genetic assumptions. Results differed mainly for correlated responses on EW and BW traits, which are known to be influenced by the *NA* gene and by maternal effects not accounted for in the current study.

## ACKNOWLEDGMENTS

The technical help of the staff of animal caretakers all along the selection experiment is gratefully acknowledged. The authors are grateful to M. Boitard, computer engineer, for programming the data recording and CL computing. We are grateful to D. Boichard and E. Groeneveld for their helpful advices in using VCE, PEST, and PEDIG software. C. F. Chen was supported by a Ph.D. scholarship from INRA.

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