Residual Feed Consumption in Laying Hens. 2. Genetic Variation and Correlations

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ABSTRACT The study described here deals with the quantification of the genetic variation of "residual feed consumption" (RFC) of hens of a White Leghorn population during a 44-wk laying period (20 to 64 wk of age) in 11 time segments of 4 wk each, fed either a commercial or a low-energy diet (11.7 and 10.0 MJ ME/kg, respectively, where 1 MJ = .239 Mcal). The RFC is defined operationally as the difference between the observed feed consumption of a laying hen and its consumption as predicted from a model with metabolic body weight, egg mass production, and body weight gain as independent variables.

The RFC was found to be highly heritable in all periods. The heritability of RFC accumulated over the whole laying period (RFC-T) was estimated as .42 to .62. For each time segment between 32 and 56 wk of age, genetic correlations between RFC and RFC-T were estimated to be larger than .91. The genetic sources causing variation in RFC during the first part of lay seem to differ from those causing variation later on, and to be of less importance during the rest of the laying period. It was concluded that RFC shows a considerable systematic and permanent additive genetic variance, and that RFC measurements for selection can be limited to one to three time segments between 32 and 56 wk. Furthermore, less environmental variance and therefore higher heritabilities and genetic correlations seemed to exist for birds fed the low energy diet in comparison with those fed the commercial diet. No clear differences could be found between genetic and phenotypic correlation estimates of RFC with feed consumption, metabolic body weight, egg mass production, and body weight gain.

(*Key words*: residual feed consumption, genetic parameters, maintenance, part-record, dietary energy)

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INTRODUCTION

Luiting and Urff (1991b) concluded from multiple regression analyses in a population of White Leghorn (WL) laying hens, that 10 to 30% of the variance of daily feed consumption (FCD) among hens remained unaccounted for by metabolic body weight ($MBW^{.75}$), daily egg mass production (adjusted for abnormal eggs, EMDc), and body weight gain (BWG). This unexplained term is referred to as "residual feed consumption" (RFC), defined operationally as the difference between the observed feed consumption of a hen and its consumption as predicted from $MBW^{.75}$, EMDc, and BWG. In other words, hens showing equal production levels and body weights may differ considerably with regard to feed consumption, and therefore feed efficiency.

Differences among hens in maintenance requirements per metabolic kilogram (kilogram$^{.75}$ of body weight) seem primarily responsible for this and a large amount of systematic and permanent variation in RFC appears to exist (Luiting and Urff, 1991b). The repeatability of RFC was estimated as .52 to .58. If a large part of this systematic and permanent variation is of genetic origin, it might be exploited in a breeding program.

The study described here deals with the quantification of the genetic variation of RFC of hens of a WL population during a 44-wk laying period in 11 time periods of 4 wk. This is done by estimating 1) heritabilities of RFC in different time segments, 2) genetic correlations between RFC measurements in different time segments, and 3) genetic correlations between RFC and $MBW^{.75}$, EMDc, BWG, and FCD per period of 4 wk. Morris (1972) suggested that differences in partial energetic efficiencies between laying hens are expressed more clearly at a suboptimum energy consumption. To verify this, the hens in the present study were fed with either a commercial diet or a low-energy diet (11.7 and 10.0 MJ ME/kg, respectively, where 1 MJ = .239 Mcal).

MATERIALS AND METHODS

Data

The population of hens described by Luiting and Urff (1991a) was used for the present study. It consisted of 704 hens in 94 half sib groups of 3 or 4 full sib pairs each (for a total of 352 full sib pairs). From 18 wk of age, when the hens were transferred to individual battery cages, one member of each full sib pair was fed a commercial diet (calculated content 11.7 MJ ME/kg and 155 g CP/kg) and the other one a low energy diet (10.0 MJ ME/kg and 152 g CP/kg), both provided for *ad libitum* intake. Details were given by Luiting and Urff (1991a).

According to Luiting and Urff (1991a), multiple regressions of FCD (in grams per day) on $MBW^{.75}$ (in kilograms$^{.75}$), EMDc (in grams per day), and BWG (in grams per day) were performed within each of 11 4-wk periods (starting at 20 wk of age) and within each diet; furthermore, the residual feed consumption (RFC in kiloJoules of ME per day) was calculated per hen and per period by multiplying with the calculated ME contents (Luiting and Urff, 1991b). To investigate the overall performance per hen, RFC was averaged over all 4-wk periods (RFC-T). Following Manson (1972) an averaged RFC per hen was also calculated for the following time segments: 24 to 32, 20 to 32, 32 to 44, 20 to 44, 44 to 64, and 32 to 64 wk of age (RFC_{24-32}, RFC_{20-32}, RFC_{32-44}, RFC_{20-44}, RFC_{44-64}, and RFC_{32-64}, respectively). To investigate the inheritance of individual stability of RFC per hen, the standard deviation of RFC among periods for each hen (sdRFC) was calculated after standardization and log-transformation (Luiting and Urff, 1991b).

Heritabilities of Residual Feed Consumption

A univariate restricted maximum likelihood procedure (the EM algorithm by Meyer, 1986) was used to estimate variance components of RFC within diet, for each single period, for cumulative periods and for the defined time segments, from the following random model:

$$RFC_{ij} = \mu + s_i + e_{ij} \qquad [1]$$

where i = 1, . . . , s; s = number of sires in the analysis; j = 1, . . . , n; n = number of hens per sire; RFC_{ij} = residual feed consumption of hen ij (kJ ME/day); μ = overall mean; s_i = random effect of sire i; e_{ij} = random effect of hen j within sire i.

Estimates from Henderson's Method III were used as starting values for variance components. Iteration was stopped when differences in variance components between successive rounds were less than .01%. Genetic variances (σ^2_A) were calculated from between-sire variances (σ^2_S) as $\sigma^2_A = 4\sigma^2_S$, phenotypic variances (σ^2_P) as $\sigma^2_P = \sigma^2_S + \sigma^2_e$, where σ^2_e is the error variance, and environmental variances (σ^2_E) as $\sigma^2_E = \sigma^2_P - \sigma^2_A$. Heritabilities ($h^2$) were derived as $h^2 = \sigma^2_A/\sigma^2_P$. Sampling errors of genetic parameters were approximated according to Meyer (1986); no formal significance tests of parameter diet-contrasts and time trends have been performed in view of the non-normal distributions of the parameters or the dependence of estimates. The same procedure was followed for sdRFC.

Genetic Correlations of Residual Feed Consumption Over Time and with Economic Traits

Covariance components of RFC during each single period with RFC-T, of RFC accumulated over successively longer periods with RFC-T, and among RFC in the defined time segments, were estimated per diet by the same procedure as described for variance components, but now from a bivariate random model with the same structure as [1], using a multivariate restricted maximum likelihood procedure with equal designs. Genetic covariances (σ_{Aij}, where the subscripts i and j denote the traits) were computed from the between-sire covariances (σ_{Sij}) as $\sigma_{Aij} = 4\sigma_{Sij}$, phenotypic covariances (σ_{Pij}) as $\sigma_{Pij} = \sigma_{Sij} + \sigma_{eij}$, where σ_{eij} is the error covariance, and environmental covariances (σ_{Eij}) as $\sigma_{Eij} = \sigma_{Pij} - \sigma_{Aij}$. Genetic ($r_A$) and environmental ($r_E$) correlations were derived as $r_A = \sigma_{Sij}/(\sigma_{Si}\,\sigma_{Sj})$ and $r_E = \sigma_{Eij}/(\sigma_{Ei}\,\sigma_{Ej})$. The same procedure was followed for covariances of RFC-T with sdRFC. The same procedure was followed for (co)variances of RFC with $MBW^{.75}$, EMDc, BWG, and FCD per diet and per period, and per diet averaged over periods.

RESULTS

Heritabilities of Residual Feed Consumption Over Time

The left side of Figure 1 shows the estimated σ^2_A, σ^2_E, and h^2 of RFC for single periods. Sampling errors of h^2 estimates were within the range of .16 to .24. The h^2 estimates varied considerably among periods, and had a tendency to decrease with time (about 1.5 to 2 times the sampling error). The estimates of σ^2_A showed a large amount of variation among periods but there was no clear time trend. In contrast, σ^2_E increased gradually over time. Also h^2 estimates of the low-energy diet were on average slightly higher than those of the commercial diet. For σ^2_A no clear difference between the diets was observed, in contrast to σ^2_E, which had lower values on the low-energy diet.

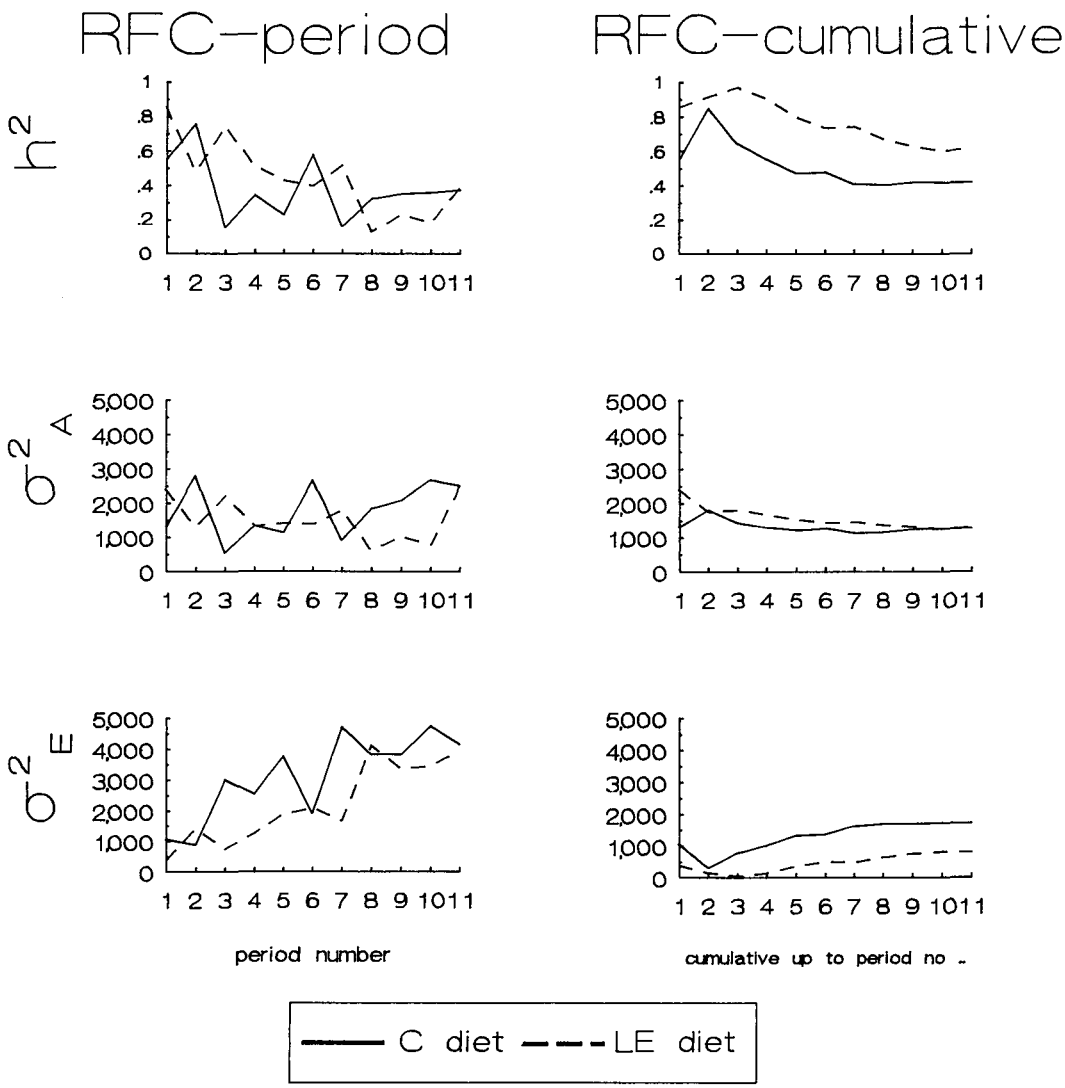

FIGURE 1. Heritabilities (h^2) and genetic (σ^2_A) and environmental (σ^2_E) variances of residual feed consumption on the commercial diet (C) and on the low-energy (LE) diet (11.7 and 10.0 MJ ME/kg, respectively, where 1 MJ = .239 Mcal) during each single period (RFC-period in kiloJoules of ME per day) and during successively longer accumulated periods (RFC-cumulative in kiloJoules of ME per day).

The right side of Figure 1 shows the estimated σ^2_A, σ^2_E, and h^2 of RFC over accumulated periods. Sampling errors of h^2 estimates ranged from .21 to .23. The same time trends and diet differences were noted as was observed for RFC for single periods, but the graphs were more stable, the h^2 estimates were higher and the σ^2_E estimates were lower. Cumulative h^2 estimates over the first three periods were very high (.68 and .93 for the commercial and the low-energy diet, respectively), whereas σ^2_A estimates were somewhat larger and σ^2_E estimates much smaller than in later periods. After that, cumulative h^2 decreased gradually to .42 and .62 for the commercial and low-energy diet, respectively; σ^2_A was stable and σ^2_E increased to a stable level after cumulation to six or eight periods.

Genetic Correlations of Residual Feed Consumption Over Time

The left side of Figure 2 shows the σ_{Aij}, σ_{Eij}, and correlations of RFC measurements in each single period with the averaged RFC-T. Sampling errors of r_A estimates ranged from .06 to .28. Whereas σ^2_E (Figure 1) increased continuously, σ_{Eij} increased primarily in the beginning. Therefore, r_E was lower at the beginning of the laying period (especially for the low-energy diet). Just as for σ^2_A (Figure 1), the estimates of σ_{Aij} did not show a clear time trend. Thus, r_A estimates show little of a pattern in time (they were all very close to unity), except for a small increase in the first few periods.

The r_A estimates did not differ clearly between the two diets, with the possible exceptions of the first two periods and at the end of the laying period, when the low energy diet had the highest values (Figure 2). The r_E estimates were generally a little lower on the low-energy diet, which was the result of lower σ_{Eij} and somewhat lower σ^2_E (Figure 1).

The right side of Figure 2 shows the σ_{Aij}, σ_{Eij}, and correlations of RFC accumulated over successively longer periods with RFC-T. Sampling errors of r_A estimates ranged from .00 (for estimates close to unity) to .24. Again, the same time trends and diet differences were observed for RFC accumulated over successively longer periods as for RFC in each single period: very high r_A estimates (up to unity), especially after the first two periods; higher σ_{Eij} estimates and, only at the beginning of the laying period, somewhat smaller r_A on the commercial diet than on the low-energy diet.

Heritabilities and Genetic Correlations of Residual Feed Consumption Time Segments

Table 1 gives the estimated h^2 of and r_A among the defined time segments. These parameters followed the same trends as observed for the single and accumulated periods. Up to 32 wk of age h^2 estimates were higher than after that age (especially for the low-energy diet) but estimates of r_A with RFC-T were lower (especially for the commercial diet). Estimates of accumulated h^2 and r_A remained higher and lower, respectively, when the first periods up to 32 wk were included. All genetic parameter estimates were higher on the low-energy diet than on the commercial diet.

The h^2 estimates for sdRFC were .06 and .15 for the low-energy and the commercial diet, respectively (sampling errors .05 to .26). Respective estimates of r_A for sdRFC with RFC-T were .29 and .04 (sampling errors .57 to .82).

Genetic Correlations of Residual Feed Consumption with Economic Traits

Estimates of h^2 for FCD, $MBW^{.75}$, EMDc, and BWG, as presented at the left side of Figure 3, resulted in 16 out of 66 (diets by traits by periods) cases in either nonconvergent (four cases) or impermissible results ($\sigma^2_A<0$; 12 cases); most of these cases apply to EMDc and BWG. The estimates of h^2 for FCD and $MBW^{.75}$ indicate additive genetic variation during the whole laying period. For $MBW^{.75}$ higher h^2 values were obtained for the commercial than for the low-energy diet; for FCD no such diet difference was found. For EMDc and BWG h^2 estimates declined over time and reached zero values.

Estimation of genetic correlation coefficients per period between RFC and FCD, $MBW^{.75}$, EMDc, and BWG resulted in 15 more cases of impermissible results ($|r_A|>1$); most of these cases apply to EMDc and BWG in periods with very low h^2. When the traits were averaged over all periods, two r_A estimates were $|r_A|>1$. The r_A estimates obtained often had very high sampling errors (.16 to .94), especially when h^2 estimates

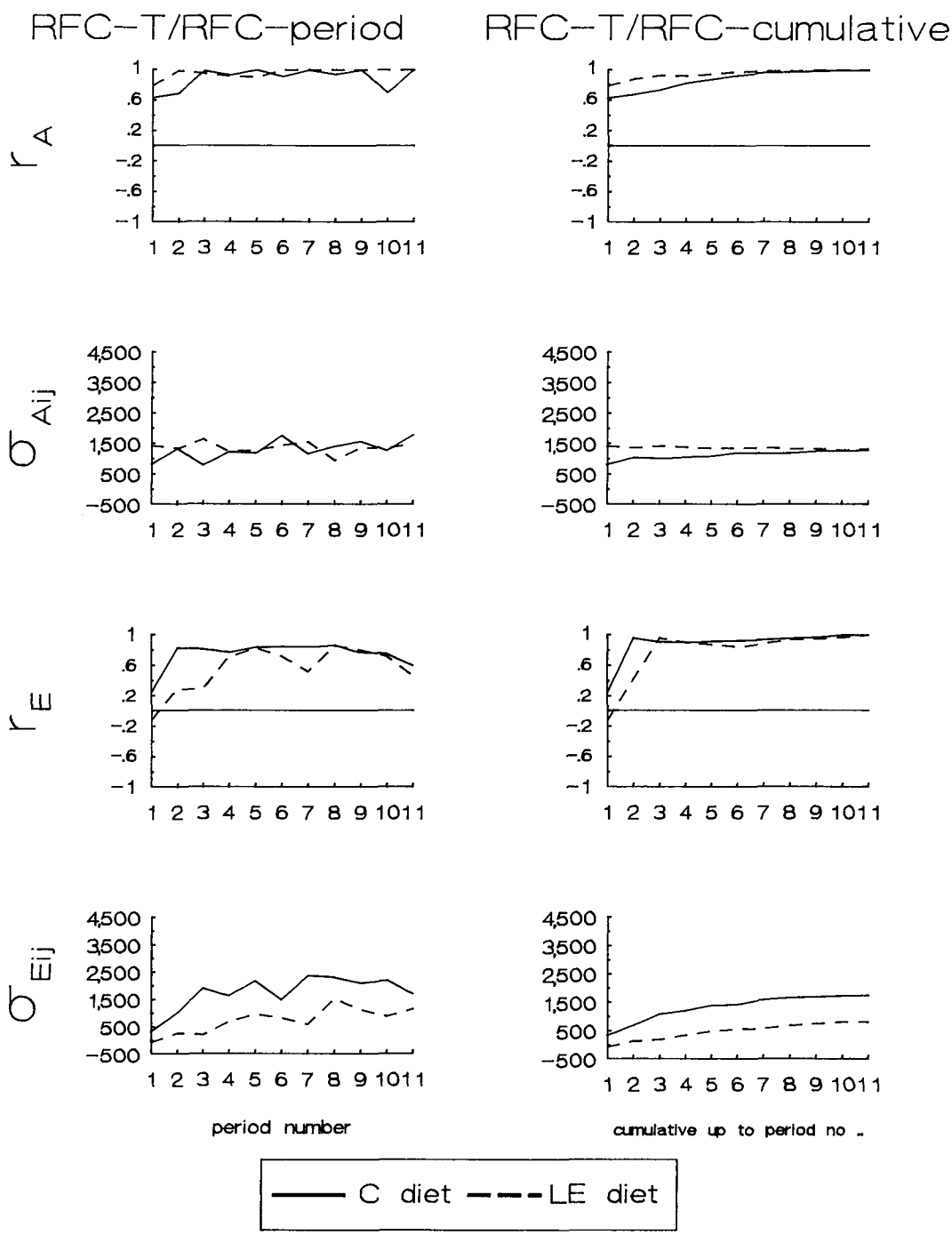

FIGURE 2. Genetic and environmental covariances (σ_{Aij} and σ_{Eij}) and correlations (r_A and r_E) of residual feed consumption (RFC) during each single period (RFC-period in kiloJoules of ME per day) with the total RFC (RFC-T in kiloJoules of ME per day); and, of the RFC accumulated over successively longer periods (RFC-cumulative in kiloJoules of ME per day) with RFC-T, on the commercial diet (C) and on the low-energy (LE) diet (11.7 and 10.0 MJ ME/kg, respectively, where 1 MJ = .239 Mcal).

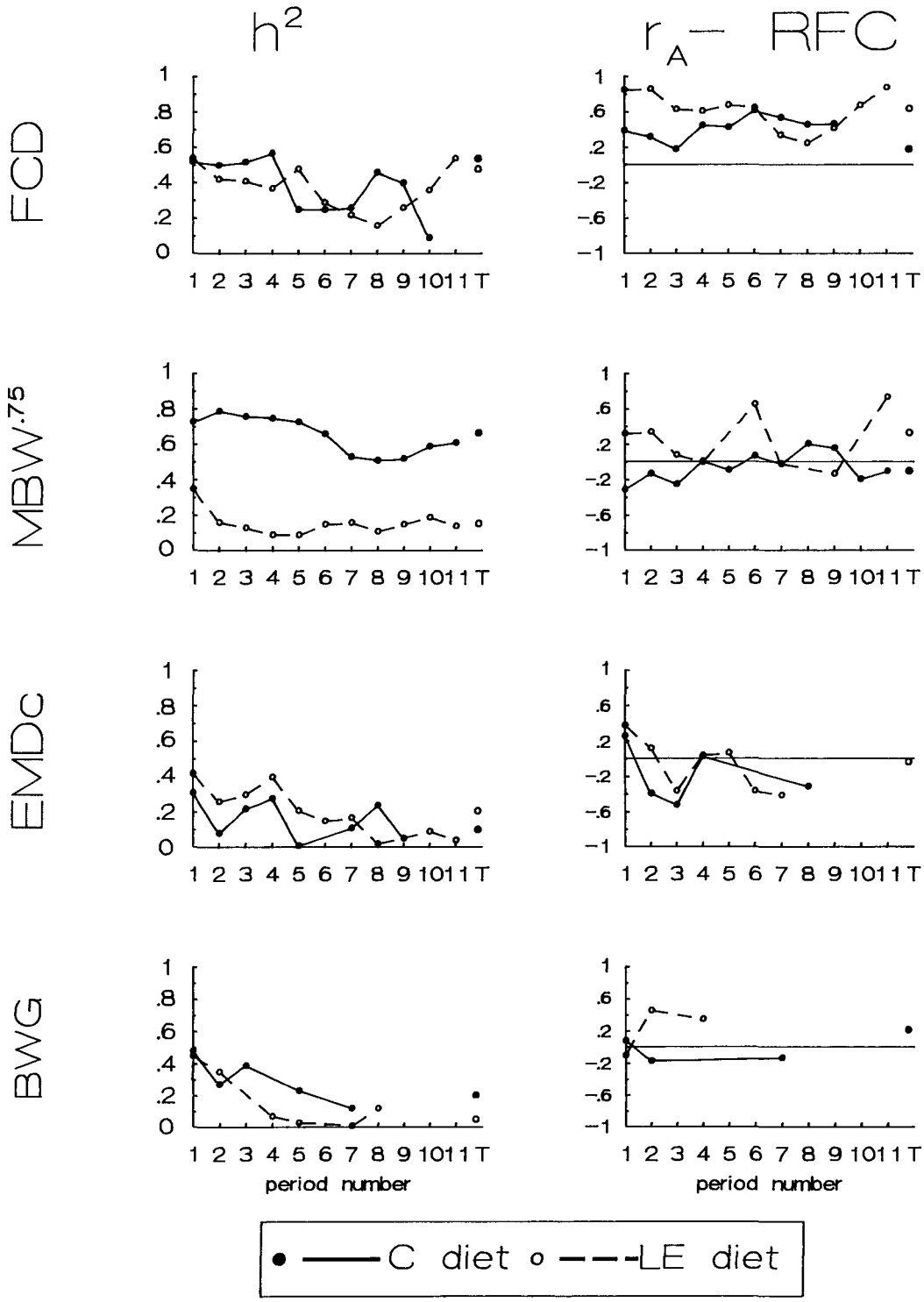

FIGURE 3. Heritabilities (h^2) of feed consumption (FCD), metabolic body weight ($MBW^{.75}$), egg mass production (EMDc), and body weight gain (BWG), and genetic correlations of residual feed consumption (r_A-RFC) with FCD, $MBW^{.75}$, EMDc, and BWG during each single period and accumulated over all periods (T), on the commercial diet (C) and on the low-energy (LE) diet (11.7 and 10.0 MJ ME/kg, respectively, where 1 MJ = .239 Mcal).

TABLE 1. *Heritabilities (h^2) of and genetic correlations (r_A) between residual feed consumption of different time segments of the two diets (commercial diet[1]: r_A and h^2 above the diagonal, with h^2 on the diagonal; low-energy diet[1]: r_A and h^2 below the diagonal)*

Variable	RFC_{20-24}[2]	RFC_{24-32}	RFC_{20-32}	RFC_{32-44}	RFC_{20-44}	RFC_{44-64}	RFC_{32-64}	RFC_{20-64}–T[3]
RFC_{20-24}[2]	.86 .55	.77	.88	.36	.69	.43	.42	.63
RFC_{24-32}	.84 .80	.57	.98	.71	.92	.43	.55	.71
RFC_{20-32}	.94 .98	.97	.65	.63	.90	.46	.54	.74
RFC_{32-44}	.71 1.00	.93	.45	.43	.91	.90	.97	.95
RFC_{20-44}	.86 1.00	.99	.98	.74	.48	.74	.83	.93
RFC_{44-64}	.66 .86	.80	1.00	.92	.43	.41	.98	.93
RFC_{32-64}	.67 .92	.86	1.00	.94	1.00	.48	.41	.97
RFC_{20-64}–T[3]	.79 .95	.93	1.00	.98	.98	.99	.62	.42

[1]Commercial and low-energy diet containing 11.7 and 10.0 MJ ME/kg, respectively, where 1 MJ = .239 Mcal.

[2]RFC_{i-j} = residual feed consumption of the time segment between i and j weeks of age.

[3]T = total recording period.

were almost zero. The r_A estimates between RFC and FCD seemed to be positive, whereas no clear values could be obtained for the ones for RFC with $MBW^{.75}$, EMDc, and BWG (at the right side of Figure 3).

DISCUSSION

The limited size of the two populations (i.e., diet groups) causes difficulties when interpreting the results. In view of the large sampling errors for the genetic parameter estimates, the derivation of variance components due to additive genetic and environmental effects is not very likely to result in consistent and meaningful figures for the two diets. Nevertheless, some tentative conclusions will be drawn by generalizing the contrasts among the time periods over the two diets, and the contrasts between diets over the various periods, so that combination with present (and future) other estimates may provide more reliable information.

Heritabilities of Residual Feed Consumption

The h^2 estimates of RFC were very high (>.5) up to about 28 wk of age in the commercial diet and up to about 32 wk in the low-energy diet. After that the h^2 estimates stabilize around .3 to .4 for both diets. Similar estimates and age trends in h^2 were found for RFC in WL populations by Bentsen (1983) from 16 to 66 wk of age (starting at about .5 and stabilizing around .2 to .3) and by Katle (1987) from 16 to 40 wk of age (starting at about .6 and stabilizing around .4), whereas the estimates from Wing and Nordskog (1982) for RFC in WL between 32 and 36 wk of age (.15 to .29) are rather low but fall within the range of the present study. In contrast, Arboleda *et al.* (1976) obtained in WL for two 4-wk periods with 8 wk in between (before and after the peak of lay) estimates of h^2 for RFC that were near zero.

A decrease in h^2 with age has often been reported for traits related to egg production, egg quality, and body weight (Clayton and Robertson, 1966; Tawfik *et al.*, 1976; Flock, 1977; Liljedahl *et al.*, 1984; Engström *et al.*, 1990). In most cases this involves an increasing σ_E^2 with age. The most probable explanation for this phenomenon is that the hens have increasing difficulties in coping with cumulative environmental stress (see Orgel, 1963; Gavora *et al.*,

1980). Liljedahl *et al.* (1984) and Engström *et al.* (1990) also found increasing σ^2_A with age for egg production. In the present study, σ^2_E increased, but σ^2_A did not increase. The steady increase in σ^2_P of RFC with age in both diets, as described by Luiting and Urff (1991b), is primarily the result of this increase in σ^2_E, because no clear pattern can be seen in σ^2_A (see Figure 1).

Accumulation of periods gave more stable and higher h^2 estimates than per period, presumably by the fact that random error on the estimates was diminishing with increasing accumulation, which also became evident from the lower σ^2_E and the similar σ^2_A levels. Accumulated h^2 estimates for the whole laying period from 20 to 64 wk of age (RFC-T) were .42 and .62 for the commercial diet and the low-energy diet, respectively. Furthermore, cumulative h^2 estimates remained high because of inclusion of the first periods up to 32 wk of age. Accumulation of periods after 32 wk of age (Table 1) gave h^2 estimates of about .4 for both diets. In most reports concerning light laying hens, similar estimates for accumulated whole laying periods were observed (Hagger and Abplanalp, 1978, .30 to .61 from 20 to 60 wk; Bentsen, 1983, .53 from 16 to 66 wk; Katle, 1987, .77 from 16 to 40 wk; Pauw, 1987, .4 from 20 to 72 wk), and accumulation after the first weeks often gave somewhat lower estimates (Hagger and Abplanalp, 1978, .22 to .64 from 40 to 60 wk; Bentsen, 1983, .35 from 34 to 66 wk).

Although the differences in h^2 estimates between diets were usually not much larger than the respective sampling errors, the general pattern seems to point to higher h^2 estimates on the low-energy diet than on the commercial diet, often as a result of a lower σ^2_E and a similar σ^2_A. This means a lower σ^2_P, which has been discussed already by Luiting and Urff (1991b). In that study it was concluded that the low energy diet results in a reduction of BWG and RFC in order to maintain a high egg production level. This effect must be largely environmental: it seems that hens that spend surplus energy for RFC-related processes simply adapt when being fed on a low-energy diet, but σ^2_A appears to be unaffected. However, the difference in h^2 estimates that was observed in the cumulative figures seemed to be caused only by differences in h^2 estimates before 32 wk of age (see also Table 1). The latter estimates on the low-energy diet were probably overestimates due to sampling errors. It was suggested by Luiting and Urff (1991b) to estimate h^2 for sdRFC as a measure of individual stability over time. This hypothesis was supported by the small positive phenotypic correlation (r_P) between sdRFC and RFC-T (Luiting and Urff, 1991b). The genetic parameter estimates from the present study were rather low and not very conclusive because of the high sampling errors.

Genetic Correlations of Residual Feed Consumption Over Time

On both diets, the time trend in r_P of RFC during each single period with RFC-T, as described by Luiting and Urff (1991b), was similar to the time trend in r_E given in the present study. The values of r_E and r_P were very similar after the first few periods. It follows that r_A estimates were very close to unity with the exception of the first periods. Also it seemed that the small difference in r_P between the two diets, as described by Luiting and Urff (1991b), was primarily the result of a small difference in r_E. Furthermore, the conclusion of diminishing random error on the estimates of cumulative variances (Figure 1), leading to more stable-looking graphs, holds here as well for the cumulative covariances and correlations. On the commercial diet, r_A estimates between the first three periods and the total accumulated RFC (.6 to .8) were somewhat lower than in later periods (almost unity). For birds fed the low-energy diet, this lower value was only observed for the first period. Table 1 also shows that r_A estimates between RFC measured up to 32 wk of age and later measurements were relatively low. Together with the time trend in h^2, this indicated that the genetic sources causing variation in RFC during the first part of lay differ from those causing variation later on, and were of less importance during the rest of the laying period. Clayton and Robertson (1966) drew the same conclusions with regard to body weight (gain) and egg weight. Flock (1977) observed the same phenomenon with egg production, both on part-time (8-wk periods) and cumulative records. Liljedahl (1989) interpreted low r_A estimates

(.58 to .74) between early and later egg production data as an indication of genotype by environment interaction. In this interpretation, age is considered as an internal environment. Following Liljedahl's reasoning, in hens used in the present experiment about 29% of gene action responsible for RFC would be common to the two ages (RFC_{20-32} versus RFC_{32-64}, Table 1) on the commercial diet.

Genetic Correlations of Residual Feed Consumption with Economic Traits

Just as r_P of RFC with $MBW^{.75}$, EMDc, and BWG per period, estimates of r_A did not clearly differ from zero. The r_A between RFC and FCD per period seem to be positive just as r_P (square root of $1 - R^2$; see Luiting and Urff, 1991b); on the commercial diet they have the same magnitude as r_P, whereas on the low-energy diet they were somewhat higher. For breeding purposes it would be better to estimate RFC by using genetic rather than phenotypic parameters. Of course, this would require estimates of r_A per period, which demand data from large numbers of related animals. This is the reason why the estimates are scarce in the literature or have large sampling errors. The fact that no clear differences could be found in the present study between the estimates of r_P and r_A of RFC with $MBW^{.75}$, EMDc, and BWG per period, suggests that calculation of RFC by phenotypic multiple regression analyses is an acceptable alternative in a breeding program if no reliable estimates of r_A are available.

In conclusion, the h^2 of the total accumulated RFC-T was .42, and the σ_P was 4.7 g/day (Luiting and Urff, 1991b) on the commercial diet. The expected response from direct selection of nucleus females for a low RFC, with selection intensity i = 1, would be about 2.0 g/day on the nucleus level. Because of the high h^2 and r_A with RFC-T, recording during a short time segment would still result in a high expected selection response: one period of 4 wk after 32 wk of age (h^2 about .3 and r_A with RFC-T about .95) would result in 1.6 g/day, three successive periods from 32 to 44 wk of age (h^2 .43 and r_A with RFC-T .95) would result in 1.9 g/day. Measuring during one or a few periods would improve the ratio between savings and costs of RFC selection. A similar measurement period was recommended for phenotypic studies, based on the estimated repeatabilities (Luiting and Urff, 1991b).

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