Heritability of Digestibilities and Divergent Selection for Digestion Ability in Growing Chicks Fed a Wheat Diet

S. Mignon-Grasteau,*[,1] N. Muley,* D. Bastianelli,† J. Gomez,* A. Péron,* N. Sellier,* N. Millet,* J. Besnard,* J.-M. Hallouis,* and B. Carré*

*INRA, Animal Genetics, 37380, Nouzilly, France; and †CIRAD-EMVT, 34398, Montpellier, France

ABSTRACT The genetic parameters of digestibilities for a wheat-based diet were estimated on 864 broilers. Two divergent lines (D+ and D–) were developed based on AME_n. The Rialto wheat variety was used as it is known to result in low digestibility values. Digestibility of lipids (DL), starch (DS), and proteins (DP) were measured individually using Near Infrared (NIR) analysis of freeze-dried excreta. Body weight, feed consumption (FC), feed conversion ratio (FCR) and residual feed consumption (RES) were recorded to evaluate their correlation with AME_n.

The mean AME_n value was 3,093 kcal/kg DM (CV = 9.0%), with a range of 1,001 to 4,022 kcal/kg DM, and was highly heritable (0.36 to 0.38) based on the Restricted Maximum Likelihood method. Genetic correlations with BW were low (–0.10 to –0.15). Selection for AME_n can thus be performed without modifying BW. In contrast, the estimated genetic correlations between AME_n and the other traits were highly negative (–0.53 to –0.60 for FC, –0.77 to –0.80 for RES, and –0.77 to –0.84 for FCR). Finally, digestibilities of feed components were moderately to highly heritable (0.33 to 0.47) and highly correlated with AME_n (0.91 for DL, 0.83 for DS, and 0.86 for DP). Selecting for improved AME_n should thus improve digestibility of proteins, starch, and lipids. The first generation of divergent selection on AME_n confirmed these results, D+ and D– lines showing a 13% difference in AME_n ($P < 0.0001$) and similar BW.

(*Key words*: chicken, genetic parameter, digestibility, selection, growth)

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INTRODUCTION

Feed supply represents a large part of the total cost of poultry production. Improving feed efficiency by selection of poultry is thus a major goal. Many genetic studies measuring heritability of growth, feed intake, and feed efficiency have been conducted (reviewed by Pym, 1990). Pym (1990) described several factors that improved feed efficiency, such as an increase in feed intake, a reduction in maintenance requirements, a reduction in body fat, and an increase in digestibility or metabolizability (in growing chicks, about 97% of the metabolizability variations come from variation in digestibility).

Significant differences between chicken lines have been observed in terms of ME (Sibbald and Slinger, 1963; Proudman et al., 1970; Laurin et al., 1985; Jørgensen et al., 1990; Pym, 1990; Ten Doeschate et al., 1993) but they were rather low, except in the study by Pym et al. (1984). Pym et al. (1984) compared lines selected for high BW, feed consumption, or feed efficiency and after 10 generations observed a noticeable difference in ME between the high feed consumption (2,622 kcal/kg) and the high feed efficiency lines (2,916 kcal/kg). Despite this result, it has been generally accepted that genetics was hardly involved in the determinism of metabolizability (Pym, 1985; Jørgensen et al., 1990), although no estimate of genetic parameters was available.

However, most studies used common diets based on corn and soybean meal. These ingredients generally show high digestibility values, which may mask individual differences. Thus, selection for feed efficiency in such conditions progressed on the basis of increased growth rate,

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[1]To whom correspondence should be addressed: grasteau@tours.inra.fr.

Abbreviation Key: BW20 = body weight at 20 d; BW23 = body weight at 23 d; D+ = line selected for a high AME_n; D– = line selected for a low AME_n; DDM = digestibility of dry matter; DL = digestibility of lipids; DP = digestibility of proteins; DS = digestibility of starch; FC = feed consumption; FC1 = feed consumption between 13 and 20 d; FC2 = feed consumption between 20 and 23 d; FCR = feed conversion ratio; FCR1 = feed conversion ratio between 13 and 20 d, FCR2 = feed conversion ratio between 20 and 23 d; NIR = near infrared spectrophotometry; RES = residual feed consumption; RES1 = residual feed consumption between 13 and 20 d; RES2 = residual feed consumption between 20 and 23 d; RWG = difference between recorded weight gain (13 to 20 d) and regressed weight gain on digestible protein consumption and ratio of digestible protein content digestibility to AME_n value; WG1 = weight gain between 13 and 20 d; WG2 = weight gain between 20 and 23 d.

decreased fat deposition, or reduced maintenance requirement, and very little through increased digestibility.

The study that showed a rather high difference in ME between lines (Pym et al., 1984) was conducted with a diet containing a high level (33.6%) of wheat. Wheat diets given to growing chicks were often observed to result in low digestibilities compared with corn diets (Mollah et al., 1983; Rogel et al., 1987; Nicol et al., 1993; Carré et al., 2002). Moreover, high variability in digestibilities between birds was also observed with wheat diets (Choct et al., 1999; Carré et al., 2002). These problems of wheat digestion largely depend on wheat samples, those with high viscosity and hardness resulting in lowest digestibilities (Carré et al., 2002). However, the management of wheat sample variability by feed manufacturers may prove difficult. An alternative approach to solve this problem could be the selection of birds showing high digestibilities with low quality wheat varieties.

One of the aims of the current study was to estimate the proportion of individual digestibility variation coming from genetics, with birds being fed a diet based on a low quality wheat (Rialto variety). Depending on the heritability estimate, the subsequent aim was to select 2 divergent lines on the basis of their digestion ability assessed by AME_n measured for this wheat diet.

MATERIALS AND METHODS

Birds

The data originated from 2 generations of a pure sire line of chickens developed for meat production. The first generation (432 birds) was produced from chicks supplied by a commercial breeder, who provided pedigree information on the 3 former generations. Their progeny (432 birds), that is, the second generation, originated from the selection experiment for digestibility, detailed below. A total of 864 birds of both sexes (425 males and 439 females) were thus evaluated in the current experiment.

At each generation, 432 birds were produced from 3 successive hatchings at 3-wk intervals. Birds were reared on floor until 7 d of age and then placed in 144 individual cages (36 × 22 × 40 cm, length × width × height). Each cage was provided with a feeder, a drinking system, and a plastic tray placed under the cage for collection of total excreta. Feeders were designed to avoid spillage by birds. The cages were placed in 2 ventilated rooms (72 cages per room). Birds were maintained on a lighting schedule of 23L:1D daily from 13 to 23 d and ambient temperature was gradually decreased from 29°C at 13 d to 22°C at 23 d. Between 7 and 23 d, animals were fed a pelleted diet containing 55% wheat (Rialto variety) and 8% rapeseed oil (Table 1). This wheat variety was chosen because of its high viscosity and hardness (Carré et al., 2002) to maximize individual variability. A high dietary oil level was used for the same purpose.

[2]Foss NIRSystems, Inc., Silver Spring, MD.

TABLE 1. Composition of the experimental pelleted diet

Ingredient	
Wheat (Rialto variety)	55.00%
Rapeseed oil	8.00%
48 Soybean meal	33.24%
Calcium carbonate	1.19%
Dicalcium phosphate	1.55%
Sodium chloride	0.35%
Mineral and vitamin premix[1]	0.50%
DL-Met	0.12%
Robenidine[2]	0.05%
Content[3]	
AME_n[4] (kcal/kg)	2,784
Crude protein (%)	21.27
Met + Cys (%)	0.82
Lys (%)	1.13
Calcium (%)	1.11
Available phosphorus (%)	0.41
Crude fat (%)	9.74
Starch (%)	35.68
RAV (mL/g)	2.5

[1]Supplied per kilogram of diet: Ca, 1.6 g; Co, 0.6 mg; Cu, 25 mg; I, 1 mg; Se, 0.25 mg; Zn, 60 mg; Fe, 50 mg; Mn, 85 mg; all-*trans*-retinol, 10,000 IU; cholecalciferol, 2,000 IU; DL-α-tocopheryl acetate, 30 mg; butylated hydroxy toluene, 125 mg; menadione, 2 mg; thiamine, 1.5 mg; riboflavin, 4 mg; calcium pantothenate, 10 mg; niacin, 30 mg; pyridoxine, 2.5 mg; vitamin B_{12}, 15 μg; folic acid, 0.4 mg; biotin, 0.2 mg; choline chloride, 500 mg.

[2]Robenz, American Cyanamid Co., Agricultural Division, Wayne, NJ.

[3]Calculated values except for AME_n, crude protein, crude fat, starch, and real applied viscosity (RAV).

[4]AME_n measured between 20 and 23 d.

Recorded Traits

Birds were weighed at 13, 20 (BW20), and 23 d (BW23) and weight gains were calculated between 13 and 20 d (WG1) and between 20 and 23 d (WG2). The feed consumption (FC) and feed conversion ratios (FCR) were measured individually between 13 and 20 d (FC1 and FCR1) and between 20 and 23 d (FC2 and FCR2). Residual feed intakes for both periods (RES1 and RES2) were calculated as the difference between the measured value and its estimated value obtained by regression on weight gain. Residual weight gain for the period 13 to 20 d (RWG) was also calculated as an indicator of protein efficiency. It was computed as the difference between WG1 and its estimated value obtained by regression on digestible protein consumption and the ratio of percentage of digestible protein to AME_n dietary concentrations measured for each individual. As protein efficiency in chickens largely depends on fatness (Saunderson, 1988), the lowest RWG values are believed to be related to the highest fatness.

The AME_n and digestibilities of dry matter (DDM), proteins (DP), lipids (DL), and starch (DS) were individually measured between 20 and 23 d using a method based on collection of total excreta, similar to that described by Bourdillon et al. (1990). Gross energy, lipids, starch, and protein concentrations of individual freeze-dried excreta were measured for all birds using Near Infrared (NIR) spectrophotometry. The NIR spectra of all individual freeze-dried excreta were recorded on Foss NIR system 6500 spin-cell equipment,[2] between 400 and 2,500 nm.

TABLE 2. Model of analysis used for each trait

	Effect				
Trait[1]	Hatch	Floor	Edge of battery cage	Sex	Animal
BW20	✓		✓	✓	✓
BW23	✓		✓	✓	✓
WG1	✓		✓	✓	✓
WG2	✓		✓	✓	✓
FC1	✓		✓	✓	✓
FC2	✓		✓	✓	✓
FCR1	✓	✓	✓	✓	✓
FCR2	✓			✓	✓
RES1	✓	✓			✓
RES2	✓		✓	✓	✓
AME_n	✓			✓	✓
RWG	✓			✓	✓
DL	✓				✓
DS	✓				✓
DP	✓			✓	✓

[1]BW20 = BW at 20 d; BW23 = BW at 23 d; WG1 = weight gain between 13 and 20 d; WG2 = weight gain between 20 and 23 d; FC1 = feed consumption between 13 and 20 d; FC2 = feed consumption between 20 and 23 d; FCR1 = feed conversion ratio between 13 and 20 d; FCR2 = feed conversion ratio between 20 and 23 d; RES1 = residual feed consumption between 13 and 20 d; RES2 = residual feed consumption between 20 and 23 d; RWG = residual weight gain; DL = digestibility of lipid, DS = digestibility of starch; DP = digestibility of protein. AME_n and digestibility values were measured between 20 and 23 d.

However, visible wavelengths were discarded because of the instability they introduced in models.

The NIR spectra were measured in duplicate (with 2 different cup fillings) and averaged. A selection of excreta samples was made on the basis of the Mahalanobis distance between the spectra, with the aim of respecting the spectral variability of the database. Among these selected samples, 170 were analyzed for starch, 120 for gross energy and lipids, and 61 for total and uric acid nitrogens (difference gives protein nitrogen) using the chemical analyses described by Carré et al. (2002) and Marquardt (1983). These analyses were used as standards for calculating NIR statistical calibration models to predict the composition of all individual excreta samples. For protein prediction, the 61 reference measurements were pooled with former databases to increase the calibration set. The calibration models were obtained on the first (for lipids) or second derivative of spectra (for other parameters) with a mathematical pretreatment of spectra. The standard errors of calibrations were 21.03 kcal/kg and 0.60, 0.33, 0.20, and 0.15% for gross energy, starch, lipids, total nitrogen, and uric acid nitrogen, respectively. The corresponding R^2 values were 0.995, 0.994, 0.993, 0.966, and 0.972, respectively.

Statistical Analyses

Transformation of Data. Distributions for some traits were far from normal and thus needed to be normalized before analysis. Residual feed consumption was log-transformed. For FCR1, FCR2, DDM, DL, DS, DP, and AME_n, a Box-Cox transformation was used (Box and Cox, 1964), as follows:

$$y_t = \frac{y^{t-1}}{t y_g^{t-1}}$$

where y_t is the transformed variable, y the initial variable, t the parameter of the transformation, and y_g the geometric mean of y. Parameter t was estimated at –3 for FCR1 and FCR2, 4 for DDM, 6 for DL, 5 for DS and DP, and 5.1 for AME_n.

Choice of Model of Analysis. The effects to be included in the model were determined for each trait with the GLM procedure of SAS (SAS Institute, 1999); it was performed on transformed data for non-normally distributed traits. Genetic parameters were then estimated by restricted maximum likelihood (REML) with the VCE4 software (Neumaier and Groeneveld, 1998), using the following model:

$$y_{ijklm} = \mu + S_i + H_j + E_k + F_l + a_m + e_{ijklm}$$

where y_{ijklm} = performance of animal m, μ the general mean, S_i = fixed effect of the ith sex, H_j = fixed effect of the jth hatch (n = 6), E_k = fixed effect of being on the edge of the battery cages (yes or no), F_l = effect of the lth floor of the battery cage (n = 3), a_m = random additive genetic effect of animal m (n = 3,887), and e_{ijklm} = residual pertaining to animal n. Effects included in the model for each trait can be found in Table 2.

Estimation of Genetic Parameters

Multitrait analyses were used to estimate heritability of recorded traits and their genetic correlations with AME_n. Due to a very high genetic correlation between AME_n and DDM (0.99 ± 0.01, Mignon-Grasteau et al., 2003) only AME_n was used in genetic analyses. The first 2 analyses were aimed at estimating correlations between AME_n and traits recorded during the first period, and between AME_n and traits recorded in the second period. They therefore included FC1, FCR1, BW20, WG1, RES1, and AME_n for

TABLE 3. Elementary statistics on recorded traits

Trait[1]	n	Mean ± SD	Range	Skewness	Kurtosis
BW20 (g)	848	340.1 ± 54.0	117.0 to 506.7	–0.2	0.3
BW23 (g)	849	421.3 ± 65.4	140.0 to 634.3	–0.2	0.6
WG1 (g)	848	165.0 ± 28.6	40.7 to 254.0	–0.4	1.1
WG2 (g)	848	81.5 ± 17.6	7.0 to 217.0	–0.1	5.3
FC1 (g)	849	262.0 ± 44.9	75.0 to 475.0	0.3	1.9
FC2 (g)	848	146.7 ± 26.7	35.0 to 295.0	0.8	3.1
FCR1 (g:g)	846	1.65 ± 0.36	1.12 to 5.36	4.9	34.1
FCR2 (g:g)	847	1.93 ± 1.33	1.27 to 29.50	14.7	267.2
RES1 (g)	846	0.0 ± 33.9	–71.0 to 272.0	2.4	12.1
RES2 (g)	848	0.0 ± 23.8	–65.0 to 175.0	2.3	10.2
AME_n (kcal/kg DM)	842	3,093 ± 280	1,001 to 4,022	–1.9	4.6
RWG (g)	836	0.03 ± 18.21	–91.62 to 82.55	–0.7	3.2
DDM (%)	845	64.3 ± 7.9	20.2 to 85.3	–2.1	5.8
DL (%)	841	70.9 ± 17.3	2.2 to 93.01	–1.3	1.4
DS (%)	841	91.9 ± 9.8	27.4 to 99.6	–3.1	11.0
DP (%)	841	75.2 ± 5.7	34.1 to 88.4	–1.7	7.8

[1]BW20 = BW at 20 d; BW23 = BW at 23 d; WG1 = weight gain between 13 and 20 d; WG2 = weight gain between 20 and 23 d; FC1 = feed consumption between 13 and 20 d; FC2 = feed consumption between 20 and 23 d; RES1 = residual feed consumption between 13 and 20 d; RES2 = residual feed consumption between 20 and 23 d; FCR1 = feed conversion ratio between 13 and 20 d; FCR2 = feed conversion ratio between 20 and 23 d; RWG = residual weight gain; DDM = digestibility of dry matter; DL = digestibility of lipids; DS = digestibility of starch; DP = digestibility of proteins. AME_n and digestibility values were measured between 20 and 23 d.

the first analysis, and FC2, FCR2, BW23, WG2, RES2, and AME_n for the second analysis. The third analysis was aimed at estimating the genetic correlations between the components of digestibility, thus including DL, DS, DP, AME_n, and either FCR1 or FCR2. Finally, an analysis was performed to provide an estimate of the genetic correlation between AME_n and RWG.

Creation of Divergent Lines Based on Selection for AME_n

Estimated values of (co)variance were used to estimate genetic values of AME_n and BW23 by BLUP (Best Linear Unbiased Prediction) for animals of the first generation, using PEST software (Groeneveld et al., 1990). A divergent selection was then performed on the genetic value for AME_n, thus creating a high digestibility line (D+) and a low digestibility line (D–). In both lines, BW23 was kept constant. Twelve males and 36 females of the 432 birds of the first generation for each line were retained as parents of birds of the second generation.

RESULTS

Elementary Statistics

Elementary statistics on recorded traits are shown in Table 3. Mean values for AME_n and DDM were 3,093 kcal/kg DM and 64.3%, respectively. Their respective CV values were 9.0% and 12.3%, ranges being 1,001 to 4,022 kcal/kg DM for AME_n and 20.2 to 85.3%, for DDM. The DDM, DL, DP, and DS were highly variable, especially DL and DS, with CV values of 20.7% and 22.4%, respectively. The CV of DP was much lower (7.6%). Growth traits were consequently highly variable, and the difference between animals for BW23 was more than 4-fold. A sex effect was significant on most traits, females being smaller (3.5% and 4.4% at 20 and 23 d, respectively) and consuming less feed (4.9% and 6.4% for FC1 and FC2, respectively). During the first period, FCR was lower in males than females and no sex difference was found for RES. However, during the second period, females showed better FCR2 (1.89 g:g vs. 1.98 g:g), RES2 (–3.0 g vs. +3.2

TABLE 4. Estimates of genetic parameters[1] for growth traits during the first period (13 to 20 d) and AME_n

Variable[2]	BW20	WG1	FC1	RES1	FCR1	AME_n
BW20	0.55[3]	0.96	0.88	0.53	–0.23	–0.15
WG1		0.35	0.84	0.43	–0.36	–0.04
FC1			0.47	0.85	0.19	–0.53
RES1				0.36	0.68	–0.80
FCR1					0.27	–0.77
AME_n						0.38

[1]Heritabilities are on the diagonal, and genetic correlations are above the diagonal.

[2]BW20 = BW at 20 d; WG1 = weight gain between 13 and 20 d; FC1 = feed consumption between 13 and 20 d;RES1 = residual feed consumption between 13 and 20 d, FCR1 = feed conversion ratio between 13 and 20 d. AME_n was measured between 20 and 23 d.

[3]Standard errors were not available for this analysis.

TABLE 5. Estimates of genetic parameters[1] for growth traits during the second period (20 to 23 d) and AME_n

Variable[2]	BW23	WG2	FC2	RES2	FCR2	AME_n
BW23	0.59 ± 0.05	0.90 ± 0.03	0.80 ± 0.04	0.64 ± 0.05	–0.10 ± 0.11	–0.10 ± 0.09
WG2		0.31 ± 0.05	0.63 ± 0.06	0.39 ± 0.08	–0.42 ± 0.08	0.13 ± 0.09
FC2			0.47 ± 0.05	0.96 ± 0.01	0.36 ± 0.09	–0.60 ± 0.07
RES2				0.44 ± 0.05	0.62 ± 0.07	–0.77 ± 0.05
FCR2					0.32 ± 0.04	–0.84 ± 0.05
AME_n						0.37 ± 0.04

[1]Heritabilities (± SE) are on the diagonal, and genetic correlations (± SE) are above the diagonal.
[2]BW23 = BW at 23d; WG2 = weight gain between 20 and 23 d; FC2 = feed consumption between 20 and 23 d; RES2 = residual feed consumption between 20 and 23 d, FCR2 = feed conversion ratio between 20 and 23 d; AME_n was measured between 20 and 23 d.

g), AME_n (3,114 kcal/kg DM vs. 3,071 kcal/ kg DM), and DP (75.7% vs. 74.8%).

Heritability Estimates

Genetic parameters of traits recorded in the first and second period are presented in Tables 4 and 5, respectively. Standard errors were not available in the first analysis due to more difficult convergence. However, the results for both periods were very consistent. The AME_n, BW, FC, and RES showed high heritability, whereas FCR showed lower heritability. Heritabilities of DL, DS, and DP (Table 6) were similar to that of AME_n, DP being less heritable and DL more heritable.

Genetic Correlations Among Traits

The AME_n was nearly independent of BW (–0.15 to –0.10, Tables 4 and 5). In contrast, it was highly and negatively correlated with RES and FCR. Body weight, FC, and RES were highly and positively correlated. In contrast, BW and FC showed very low correlations with FCR, negative with BW and positive with FC.

Genetic correlations between AME_n and digestibilities were very high, ranging from 0.83 to 0.91 (Table 6). However, DL and DS showed a substantially different genetic relationship, with more moderate positive correlations of 0.54 and 0.55 between the traits.

Selection Experiment

Distributions of AME_n and BW23 after one generation of selection are shown in Figure 1. Least square means of all recorded traits are reported in Table 7. They confirmed the estimates of heritability of AME_n and genetic correlations of AME_n and BW, as the line effect was for AME_n ($P < 0.0001$) but not for BW23 ($P = 0.22$). Body weights least square means at 23 d were 390 g in the D+ line and 382 g in the D– line. On average, AME_n reached 3,308 kcal/kg DM in the D+ line and 2,921 kcal/kg DM in the D– line. In the D– line, 55% of birds were under 3,107 kcal/kg DM compared with 13% in the D+ line. The DP, DS, and DL were also higher ($P < 0.0001$) in the D+ line (80.0 vs. 64.8 for DP, 96.2 vs. 88.4% for DS, and 78.3 vs. 74.0% for DL).

DISCUSSION

Metabolizable Energy and Digestibility Values

The mean AME_n value (3,093 kcal/kg DM) in the current study was very close to that reported in a previous study (3,081 kcal/ kg DM; Carré et al., 2002) obtained in 3-wk-old broilers fed a similar diet (55% Rialto wheat and 7% rapeseed oil). In the previous experiment, a comparison of 22 wheat varieties (Carré et al. 2002) showed

TABLE 6. Estimates of genetic parameters[1] for digestibility traits and feed conversion ratios

Variable[2]	DL	DS	DP	FCR	AME_n
DL	0.47 ± 0.03	0.54 ± 0.06	0.70 ± 0.05	–0.89 ± 0.04	0.91 ± 0.02
DS	0.55 ± 0.06	0.37 ± 0.03	0.74 ± 0.04	–0.51 ± 0.06	0.83 ± 0.03
DP	0.71 ± 0.06	0.73 ± 0.04	0.33 ± 0.03	–0.55 ± 0.07 0.30 ± 0.03[3]	0.86 ± 0.03
FCR	–0.70 ± 0.05	–0.70 ± 0.05	–0.79 ± 0.05	0.33 ± 0.04[4]	–0.82 ± 0.04
AME_n	0.92 ± 0.02	0.83 ± 0.03	0.85 ± 0.03	–0.81 ± 0.04	0.36 ± 0.03

[1]Heritabilities (± SE) are on the diagonal; genetic correlations (± SE) are above the diagonal for FCR1 and below the diagonal for FCR2.
[2]DL = digestibility of lipids; DS = digestibility of starch; DP = digestibility of proteins; FCR1 = feed conversion ratio between 13 and 20 d; FCR2 = feed conversion ratio between 20 and 23 d; AME_n and digestibilities were measured between 20 and 23 d.
[3]Heritability estimate of FCR1.
[4]Heritability estimate of FCR2.

TABLE 7. Least square means (± SE) of recorded traits in both lines after one generation of selection

Variable[1]	D+	D–	*P*
BW20 (g)	312.4 ± 4.1	308.0 ± 4.1	NS
BW23 (g)	389.9 ± 4.9	382.3 ± 4.9	NS
WG1 (g)	158.1 ± 2.1	152.3 ± 2.1	0.01
WG2 (g)	78.1 ± 1.3	74.2 ± 1.3	0.02
FC1 (g)	239.2 ± 3.4	263.3 ± 3.4	<0.0001
FC2 (g)	130.5 ± 2.0	147.3 ± 2.0	<0.0001
RES1 (g)	−13.86 ± 2.09	13.52 ± 2.05	<0.0001
RES2 (g)	−12.44 ± 1.85	6.52 ± 1.84	<0.0001
FCR1 (g:g)	1.549 ± 0.024	1.780 ± 0.024	<0.0001
FCR2 (g:g)	1.710 ± 0.118	2.300 ± 0.117	<0.0001
AME_n (kcal/kg DM)	3,308 ± 251	2,921 ± 249	<0.0001
DDM (%)	68.14 ± 0.58	60.79 ± 0.58	<0.0001
DL (%)	80.03 ± 0.99	64.76 ± 0.98	<0.0001
DS (%)	96.25 ± 0.66	88.36 ± 0.65	<0.0001
DP (%)	78.32 ± 0.36	73.97 ± 0.36	<0.0001
RWG	3.57 ± 1.19	−2.75 ± 1.17	0.0001

[1]BW20 = BW at 20 d; BW23 = BW at 23 d; WG1 = weight gain between 13 and 20 d; WG2 = weight gain between 20 and 23 d; FC1 = feed consumption between 13 and 20 d; FC2 = feed consumption between 20 and 23 d; RES1 = residual feed consumption between 13 and 20 d; RES2 = residual feed consumption between 20 and 23 d, FCR1 = feed conversion ratio between 13 and 20 d, FCR2 = feed conversion ratio between 20 and 23 d; DDM = digestibility of dry matter; DL = digestibility of lipids; DS = digestibility of starch; DP = digestibility of proteins; RWG = difference between recorded weight gain (13 to 20 d) and regressed weight gain on digestible protein consumption and ratio of digestible protein content to AME_n value. Digestibilities and AME_n values were measured between 20 and 23 d.

that the Rialto wheat diet was in the lowest range of AME_n values (2,997 to 3,294 kcal/kg of DM). Thus, as in the previous experiment, birds showed some limitations in their digestive processes.

Starch digestibility was similar and low in both experiments (about 91%). However, DL was somewhat higher in the previous experiment compared with the current study (79.5 vs. 70.9%). Birds in the present study were different from those of the previous experiment, as their weight was about half that of those previously used (Carré et al., 2002). It is thus not possible to rule out that this difference in lipid digestibility between experiments was related to differences in the genetic origins of birds.

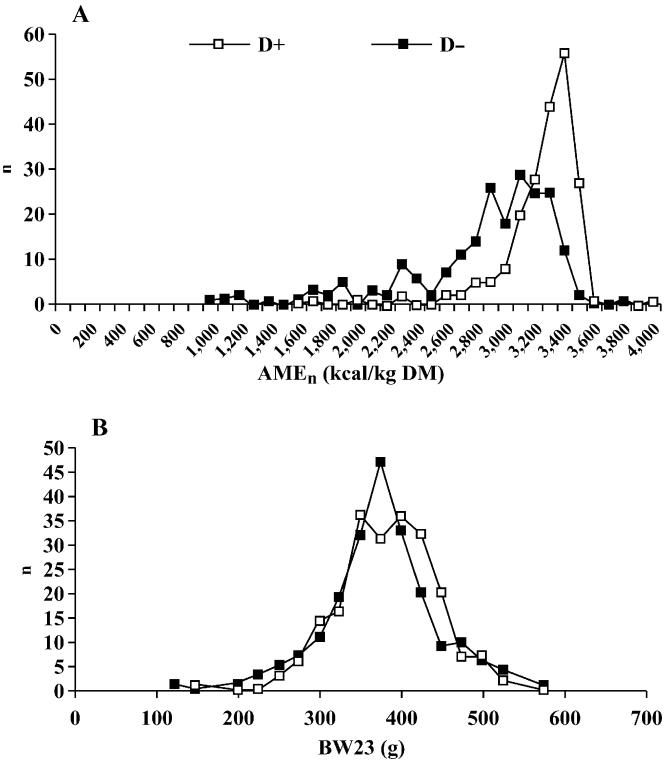

FIGURE 1. Distribution of AME_n (panel A) and BW at 23 d (BW23) (panel B) after one generation of selection. Line D+ was selected for a high AME_n and line D– was selected for a low AME_n.

Genetic Parameters and Selection Experiment

The heritability estimates for FC (0.47) and FCR (0.27 to 0.32) in the current study are consistent with previous results obtained in broilers between 18 and 63 d, that is, 0.33 to 0.55 for FC (Bernon and Chambers, 1988; Grunder and Chambers, 1988; Pym et al., 1991; Wang et al., 1991; Chambers et al., 1994; Su and Sorensen, 2000) and 0.14 to 0.50 (with most values between 0.20 and 0.40) for FCR (Bernon and Chambers, 1988; Grunder and Chambers, 1988; Leenstra and Pit, 1988; Pym, 1990; Chambers et al., 1994; Koerhuis and Hill, 1996; Su and Sorensen, 2000).

To our knowledge, no heritabilities of AME_n or digestibilities of feed macrocomponents have been reported, probably because the procedures for these determinations are not rapid. The use of NIR analyses of excreta in the current experiment enabled these procedures to be performed more rapidly, providing the possibility of testing a greater number of birds, as required for heritability estimations.

The high heritabilities observed for AME_n (0.36 to 0.38) confirmed that selection for AME_n is possible, if diet composition emphasized variations among birds. The very low genetic correlations between AME_n and BW show that selecting AME_n should not modify growth. This was confirmed by means of the high (D+) and low (D–) lines

after one generation of selection. The D+ and D– lines were significantly different for AME_n, but not for BW.

It is not surprising to observe high values for genetic correlations between AME_n and FC, as birds adjust FC on AME_n values to meet their energy requirements (Pym, 1990). However, this correlation may raise the question of whether the high FC is a cause or a consequence of genetic variation in AME_n. The FC could be a part of the cause of genetic variations in AME_n, as the protein efficiency assessed by RWG was lower in the D– line than in the D+ line. This difference shows that fat deposition was probably slightly higher (Saunderson, 1988) in the D– line. Thus, despite a similar BW, birds from the D– line would need to eat more, even in the case of similar digestibilities in both lines. Thus, selection of future generations will try to reduce differences in RWG between lines, to select for AME_n independently of fat deposition. Such independence is probably easy to obtain because previous divergent lines selected on fat deposition have shown no difference or very small differences in AME_n values (MacLeod and Geraert, 1988). Moreover, as RWG and AME_n in the current study were only moderately genetically correlated (0.43 ± 0.13) and RWG exhibited low heritability (0.14 ± 0.05), it should be possible to select further on AME_n, even if a constraint on RWG is included.

The considerable negative genetic correlations between AME_n and RES or FCR were expected, so these traits should evolve together. The D+ and D– lines differed significantly for all these traits.

According to the high genetic correlations between FCR and AME_n (–0.77 and –0.84), digestion parameters were major factors for the variation in FCR. This was somewhat different from most of the previously published experiments, as AME_n differences between lines selected on FCR were observed to be low in most cases (Pym, 1990), and indicates that most of the FCR variation in previous experiments came from metabolic parameters, not from digestion parameters. This difference from previous experiments has to be related to the composition of the diet in the current study that emphasized digestion variability.

Finally, AME_n was highly correlated with digestibilities of all components, i.e., digestibilities should evolve homogenously with selection on AME_n. Ten Doeschate et al. (1993) compared 3 lines (commercial, selected for growth, selected for FCR) and also found that they had the same rank for AME_n, digestibilities of amino acids and dry matter. Consistently, DL, DS, and DP were significantly higher in the D+ line than in the D– line. The greatest difference between lines was found for DL (23.6% vs. 8.9% for DS and 5.9% for DP), which is probably due to the highest heritability of DL (0.47 vs. 0.37 for DS and 0.33 for DP) and to its greater genetic correlation with AME_n (0.91 vs. 0.83 for DS and 0.86 for DP).

In conclusion, the magnitude (0.36 to 0.38) of heritability of AME_n of a wheat-based diet indicated that selection on this trait is possible. This was confirmed by the significant (P = 0.0001) 13% difference in AME_n obtained between divergent lines (D+ and D–) after one generation of selection. The genetic correlation between growth traits and AME_n showed that this selection can be achieved without modifying BW, and this was also confirmed by the selection experiment. The considerable genetic correlations between AME_n and digestibilities of feed components showed that selection for increased AME_n should improve DL, DS, and DP homogeneously. Further investigations will be needed to confirm whether differences observed between the D+ and D– lines on a wheat diet will still be present with other diets, particularly corn-based diets. Finally, the D+ and D– lines will be used in the future to study the physiological factors that explain variations in digestibility between birds.

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REFERENCES

Bernon, D. E., and J. R. Chambers. 1988. Genetic parameters of unadjusted and adjusted age-constant feed consumption and efficiency of meat-type chickens. Poult. Sci. 67:1497–1504.

Bourdillon, A., B. Carré, L. Conan, M. Francesch, M. Fuentes, G. Huychebaert, W. M. M. A. Jansen, B. Leclercq, M. Lessire, J. MacNab, M. Rigoni, and J. Wiseman. 1990. European reference method of in vivo determination of metabolizable energy in poultry: Reproducibility, effect of age, comparison with predicted values. Br. Poult. Sci. 31:567–576.

Box, G. E. P., and D. R. Cox. 1964. An analysis of transformations. J. Res. Stat. Soc. 26:211–243.

Carré, B., S. Idi, S. Maisonnier, J. P. Melcion, F. X. Oury, J. Gomez, and P. Pluchard. 2002. Relationships between digestibilities of feed components and characteristics of wheats (*Triticum aestivum*) introduced as the only cereal source in a broiler chicken diet. Br. Poult. Sci. 43:404–412.

Chambers, J. R., L. Wang, and I. MacMillan. 1994. Genetic variation of broiler feed consumption and efficiency corrected for differences in test body weight. Poult. Sci. 73:1196–1203.

Choct, M., R. J. Hughes, and M. R. Bedford. 1999. Effects of a xylanase on individual bird variation, starch digestion throughout the intestine, and ileal and caecal volatile fatty acid production in chickens fed wheat. Br. Poult. Sci. 40:419–422.

Groeneveld, E., M. Kovac, and T. Wang. 1990. PEST, a general purpose BLUP package for multivariate prediction and estimation. Pages 488–491 in Proceedings of the 4th World Congress on Genetics Applied to Livestock, Edinburgh, UK.

Grunder, A. A., and J. R. Chambers. 1988. Genetic parameters of plasma very low density lipoproteins, abdominal fat lipase, and protein, fatness and growth traits of broiler chickens. Poult. Sci. 67:183–190.

Jørgensen, H., P. Sorensen, and B. O. Eggum. 1990. Protein and energy metabolism in broiler chickens selected for either body weight gain or feed efficiency. Br. Poult. Sci. 31:517–524.

Koerhuis, A., and W. G. Hill. 1996. Predicted response in feed conversion ratio for growth by selection on the ratio or on linear combination in a sequential selection program. Br. Poult. Sci. 37:317–327.

Laurin, D. E., S. P. Touchburn, E. R. Chavez, and C. W. Chan. 1985. Methods of measuring energy utilization in broilers: Effect of genetic line and presence of supplementary dietary fat. Poult. Sci. 64:969–978.

Leenstra, F. R., and R. Pit. 1988. Fat deposition in a broiler sire strain. 3. Heritability of and genetic correlation among body weight, abdominal fat, and feed conversion. Poult. Sci. 67:1–9.

MacLeod, M. G., and P. A. Geraert. 1988. Energy metabolism in genetically fat and lean birds and mammals. Pages 109–120 in Leanness in Domestic Birds. Genetic, Metabolic and Hormonal Aspects. B. Leclercq and C. C. Whitehead, ed. Butterworths, London.

Marquardt, R. R. 1983. A simple spectrophotometric method for the direct determination of uric acid in avian excreta. Poult. Sci. 62:2106–2108.

Mignon-Grasteau, S., N. Muley, D. Bastianelli, J. Gomez, J. M. Hallouis, J. Besnard, N. Millet, and B. Carré. 2003. La variabilité des capacités de digestion des régimes à base de blé a une forte composante génétique chez le poulet de chair. Pages 359–361 in Proceedings of the 5th Journées de la Recherche Avicole. World Poultry Science Association, Tours, France.

Mollah, Y., W. L. Bryden, I. R. Wallis, D. Balnave, and E. F. Annison. 1983. Studies on low metabolisable energy wheats for poultry using conventional and rapid assay procedures and the effect of processing. Br. Poult. Sci. 24:81–99.

Neumaier, A., and E. Groeneveld. 1998. Restricted maximum likelihood of covariances in sparse linear models. Genet. Sel. Evol. 30:13–26.

Nicol, N. T., J. Wiseman, and G. Norton. 1993. Factors determining the nutritional value of wheat varieties for poultry. Carbohydr. Polym. 21:211–215.

Proudman, J. A., W. J. Mellen, and D. L. Anderson. 1970. Utilization of feed in fast- and slow-growing lines of chickens. Poult. Sci. 49:961–972.

Pym, R. A. E. 1985. Genetic and physiological aspects of feed efficiency. Pages 60–64 in Proceedings of the 17th World Poultry Congress. World Poultry Science Association, Helsinki, Finland.

Pym, R. A. E. 1990. Nutritional genetics. Pages 847–876 in Poultry Breeding and Genetics. R. D. Crawford, ed. Elsevier, Amsterdam, The Netherlands.

Pym, R. A. E., R. J. Johnson, D. B. Etse, and P. Eason. 1991. Inheritance of plasma insulin-like growth factor I and growth rate, feed intake, feed efficiency and abdominal fatness in chickens. Br. Poult. Sci. 32:285–293.

Pym, R. A., P. J. Nicholls, E. Thomson, A. Choice, and D. J. Farrell. 1984. Energy and nitrogen metabolism of broilers selected over ten generations for increased growth rate, feed consumption and conversion of feed to gain. Br. Poult. Sci. 25:529–539.

Rogel, A. M., E. F. Annison, W. L. Bryden, and D. Balnave. 1987. The digestion of wheat starch in broiler chickens. Aust. J. Agric. Res. 38:639–649.

Saunderson, C. L. 1988. Amino acid and protein metabolism in genetically lean and fat lines of chickens. Pages 363–374 in Leanness in Domestic Birds. Genetic, Metabolic and Hormonal Aspects. B. Leclercq and C. C. Whitehead, ed. Butterworths, London.

SAS Institute. 1999. SAS/STAT User's guide. Version 6, 4th ed, SAS Institute Inc., Cary, NC.

Sibbald, I. R., and S. J. Slinger. 1963. The effects of breed, sex, an arsenical and nutrient density on the utilization of dietary energy. Poult. Sci. 42:1325–1332.

Su, G., and P. Sorensen. 2000. Genetic parameters of feed and growth traits and responses to selection for feed conversion ratio in broiler chickens. Page 3 in Proceedings of the 21st World Poultry Congress. World Poultry Science Association, Montreal, Canada.

Ten Doeschate, R. A. H. M., C. W. Scheele, V. V. A. M. Schreurs, and J. D. Van der Klis. 1993. Digestibility studies in broiler chickens: Influence of genotype, age, sex and method of determination. Br. Poult. Sci. 34:131–146.

Wang, L., J. R. Chambers, and I. MacMillan. 1991. Heritabilities of adjusted and unadjusted feed and abdominal fat traits in a broiler dam populations. Poult. Sci. 70:440–446.