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Genetic variability of metabolic characteristics in chickens selected for their ability to digest wheat¹

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ABSTRACT: Improving feed efficiency remains crucial for poultry production. Birds have previously been selected on their ability to digest their diet, as assessed by AMEn (Apparent ME corrected for 0 nitrogen). Such selection, for either a high (D+) or a low AMEn (D-), affects energy, nitrogen, lipid, and starch digestibility. The aim of this study was to establish whether selection on the digestive ability of birds modified metabolic traits. A total of 630 broiler chickens of the eighth generation of a divergent selection experiment on AMEn were used for this purpose. A balance trial was performed to determine energy, nitrogen, and phosphorus retention. Growth performance was recorded and body protein and lipid deposition assessed by breast and abdominal fat yields. Tibia development and mineralization were also studied and heat production was indirectly assessed through the measurement of body temperature during fasting and feeding. Phenotypic correlations estimated within line

showed that an increased efficiency was associated to fatter birds and more solid bones in D- but not in D+ line, whereas increased consumption was associated with more solid bones in D+ but not in D- line. The heritability estimates for metabolic traits were relatively high, except for temperature traits (from 0.08 to 0.12), ranging from 0.28 to 0.56 for body composition, and from 0.38 to 0.77 for bone characteristics. Breast meat yield did not differ between the 2 lines whereas a slight increase in abdominal fat yield was observed in the high-digestion line (D+). The relative dry tibia weights and ash weights were greater in D+ birds (+6.56 and +8.06%, respectively) but the lengths and the diameters of the tibia were lower (-7.89 and -3.77%, respectively). Finally, AMEn was poorly correlated with almost all metabolic traits (ranging from -0.10 to 0.20), indicating that the ability of the animal to digest its diet is genetically independent of post-digestion metabolic traits.

Key words: chicken, digestibility, feed efficiency, genetic parameters, metabolic traits, selection

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INTRODUCTION

Feed conversion ratio (**FCR**) and residual feed intake (**RFI**) include proportion of diet digested, heat production, and tissue deposition. They have been extensively used in selection, which has led to

changes in metabolic traits such as tissue deposition and heat production. A greater FCR could reduce the maintenance requirements, tissue growth, and bird activity and affect heat production (Skinner-Noble and Teeter, 2004). Selection for FCR or RFI modified body temperature and heat production both in layers and broilers (Bordas et al., 1992; Gabarrou et al., 1997), which could be due to different basal metabolic rates, diet-induced thermogenesis (**DIT**), and physical activity. Selection of chickens on feed efficiency has also been shown to modify tissue deposition, a better efficiency being associated with a lower abdominal fat yield and a greater breast meat yield (Leenstra and Pit, 1988). Selection can also affect the skeletal

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Table 1. Composition of the diet

Item	Amount (g·kg ⁻¹)
Ingredients	
Corn	60.4
Wheat (Rialto)	525.0
Soybean meal 48	284.0
Corn gluten 60	31.0
Soybean oil	60.0
DL methionine	1.2
L-Lysine 78	2.2
Calcium carbonate	13.4
Dicalcium phosphate	15.8
Sodium chloride	3.0
Mineral and vitamin mix ¹	3.5
Robenidine ²	0.5
Characteristics ³ (calculated)	
AMEn ⁴ (kcal·kg ⁻¹)	2,943
CP, %	20.5
Lysine (%)	1.16
Methionine + Cystine (%)	0.76
Calcium (%)	1.11
Total phosphorus (%)	0.66
Non-phytate phosphorus (%)	0.42

¹Supplied per kilogram of diet: Co, 0.5 mg; Cu, 16 mg; Fe, 47 mg; I, 1.6 mg; Mn, 65 mg; Se, 0.2 mg; Zn, 72 mg; retinyl acetate, 12,000 IU; cholecalciferol, 3440 IU; dl- α tocopheryl acetate, 80 mg; thiamine, 4 mg; riboflavin, 6.4 mg; calcium pantothenate, 20 mg; vitamin B12, 0.02 mg; menadione, 4 mg; pyridoxine hydrochloride, 5.6 mg; folic acid, 0.4 mg; biotin, 0.24 mg; niacin, 80 mg; choline, 440 mg; antioxidant, 40 mg.

²Robenz, Alpharma Animal Health, Bridgewater, NJ.

³Calculated (INRA-AFZ, 2004).

⁴Apparent metabolizable Energy corrected to 0 nitrogen retention.

development of birds. Birds selected on low RFI had a greater bone ash weight than those selected on high RFI (Bordas et al., 1992; Bordas and Minvielle, 1999; Swennen et al., 2007). Phosphorus retention rate of unselected broilers was also 78% greater than that of those selected for FCR (Meschy et al., 2008).

Recently, digestive efficiency (i.e., the proportion of diet digested by birds), has been shown to be a potential criterion of selection for feed efficiency (Mignon-Grasteau et al., 2004) but no information is available on consequences of Apparent ME corrected to 0 nitrogen retention (AMEn) selection on postdigestive metabolism. The aim of this study was to establish whether selection on this trait modified metabolic traits, through comparisons of lines selected for high (D+) or low (D-) digestive efficiency and estimations of genetic correlations between these traits. Previous studies demonstrated that these lines showed differences in feeding activity but not in physical activity (de Verdal et al., 2010b); we therefore focused on DIT, lipid and protein deposition (through body composition), and bone development.

MATERIALS AND METHODS

The experiment was conducted according to the guidelines of the French Ministry of Agriculture for Animal Research.

Birds and Housing

The experiment included 630 birds (307 males and 323 females) of the eighth generation of selection of D+ and D- lines, divergently selected either for high or low digestive efficiency, assessed through AMEn recorded at 3 wk of age. They were reared in 3 hatches, each separated by 4 wk. The pedigree file included animals from all generations (i.e., 4495 birds: 122 and 132 sires for D+ and D-, respectively, corresponding to 16.5 and 15.5 birds per sire for D+ and D-, respectively). They were individually weighed at hatching and groups of 4 or 5 chicks were placed in metal cages (36 cm long \times 22 cm wide \times 40 cm high) for 3 d. After 3 d, chicks were randomly allocated to individual cages in 3 different rearing cells. The environmental conditions were controlled for ventilation, lighting program (24 light: 0 h dark from 1 d to 7 d and 23 h light: 1 h dark from 8 d to 23 d, dark periods beginning at midnight), and temperature (from 33°C at d 1 to 22°C at d 23). Mortality was recorded daily. The birds had free access to water and feed. They were fed a wheat-based diet similar to that used during the selection experiment (Table 1; Mignon-Grasteau et al., 2004).

Performance and Excretion Measurements

All the birds were individually weighed at 17 d and at 23 d (BW23) of age. Individual total feed intake (FI) was recorded from 17 to 23 d and FCR was calculated. Nitrogen (NI) and phosphorus (PI) intake for each bird was calculated as the product of FI and nitrogen and phosphorus concentration in the diet. Excreta were collected individually between 17 and 23 d, using the method of individual collection of total excreta (Bourdillon et al., 1990). Total excreta were dried and weighed (DEW) and DM digestibility (CDU-DM) was calculated as:

$$\text{CDU-DM} = 100 - 100 \times \frac{\text{DEW}}{\text{FI}} \quad [1]$$

AMEn and nitrogen excretion (NE) were measured for all birds using Near Infrared spectrophotometry (NIRS; Foss NIRS Systems, Inc., Silver Spring, MD), following the method of Bastianelli et al. (2010). Phosphorus excretion (PE) was measured by colorimetric analysis. Nitrogen and phosphorus excretion rates were calculated as ratio of NE to NI and PE to PI, respectively.

The RFI was calculated as the deviation between the real feed consumption and its estimate obtained by linear regression on metabolic BW ($BW^{0.75}$) and the BW gain (BWG) between 17 and 23 d.

Temperature and Body Composition Measurements

At 22 d of age, temperature after 12 h fasting was measured under the wing with an oxymeter (Vet/Ox G2 digital monitor; Heska Corp., Loveland, CO) as an indicator of the basal metabolic temperature, and thus metabolic rate (FT). After 2 h of refeeding, the temperatures of fed birds were measured again using the same method. The difference between temperatures of fed and fasted birds corrected for the feed intake during these 2 h was used as an indicator of DIT.

Body Composition and Bone Measurements

At 23 d of age, all remaining chicks were sacrificed by CO₂ inhalation. Breast muscle and abdominal fat were weighed for each bird and their yields (BR_Y and AF_Y, respectively) were calculated in relation to BW.

The right tibia was removed and cleaned of muscle and then stored at -20°C until the other measurements were performed. After bone defrosting, the tibia length and diameter were measured with a caliper. Tibia lengths and diameters were calculated in relation to BW23. A 3-point loading test using an Instron Universal Testing Instrument (Model 5543; INSTRON SA, Buc, France) was used to measure the bone breaking strength (BBS) using the method described by Letourneau-Montminy et al. (2008). To measure bone DM, all the bones were maintained at 105°C for 12 h and then weighed. For tibia ash weight, the dried tibias were placed in a muffle furnace at 550°C for 12 h and then weighed. The relative dry and ash tibia weights were calculated as the ratio of the dry or ash tibia weight to BW23. The ash percentage of the tibia was calculated as the ash weight to the dry tibia weight ratio.

Statistical Analyses

To determine the order of magnitude of the difference between lines, all data of the last generation were analyzed according to the GLM procedure (SAS Inst. Inc., Cary, NC) using this model:

$$y_{ijklm} = \mu + L_i + C_j + H_k + S_l + LC_{ij} + LH_{ik} + e_{ijklm} [2]$$

where y_{ijklm} is the performance of animal m , μ the general mean, L_i the fixed effect of line i ($i = D+$ or $D-$), C_j the effect of rearing cell j ($j = 1$ to 3), H_k the fixed effect of hatch k ($k = 1$ to 3), S_l the fixed effect of sex

l , LC_{ij} the effect of the interaction between line i and cell j , LH_{ik} the effect of the interaction between line i and hatch k , and e_{ijklm} the residual pertaining to animal m . Least square means and SD were calculated for D+ and D- lines for each trait. Differences were considered significant when the P -value was less than 0.05.

Estimation of Phenotypic Correlations

To check whether relationships between traits have been modified differently by selection in D+ and D- lines, phenotypic correlations were calculated using the procedure PROC CORR of SAS on data collected during the last generation ($n = 630$). Calculations were made separately for each line. Taking into account the number of birds in the experiment, the limit of significance ($P = 0.05$) for these phenotypic correlations was 0.115.

Estimation of Genetic Parameters

Analyses were performed on all data recorded during this experiment ($n = 574$ to 608 depending on the trait). However for some traits as AMEn, BW23, FCR, RFI, and FI, data collected during the 8 former generations of selection were also included in the genetic analyses ($n = 2300$ to 4412 depending on the trait). The pedigree file included all generations (i.e., 4554 birds). Genetic parameters were estimated by the REML method with VCE4 software (Neumaier and Groeneveld, 1998). For all the estimations, the model used included the additive genetic effect of animal, and the main fixed effects of sex, hatch ($n = 23$), and cell. Preliminary analyses indicated the presence of a significant maternal effect for BW23, FCR, AMEn, breast meat yield, and abdominal fat yield. A maternal permanent environment effect was thus included in the model for these traits (c_m , $n = 4495$). For breast meat yield, although the likelihood of the model with maternal permanent environment effect was better than the model without maternal effect, estimates were surprising compared with the literature, probably due to overparametrization of the model. The results presented below for this trait are therefore those obtained with the simplest model, without the maternal environment effect.

As several traits were strongly correlated, it was not possible to run a single analysis including all traits, and distinct multi-trait analyses were performed, always including traits used in the selection experiment (i.e., AMEn and BW23). A total of 135 analyses were performed. When a parameter (heritability or genetic correlation between 2 traits) was estimated in several analyses, the parameter estimates and the SE of parameters presented below are the means of those obtained in various analyses.

Table 2. General mean (\pm SD) on all generations and least square means (\pm SE) on the last generation for all traits analyzed in D+ and D- birds, selected respectively for their high or low digestive efficiency

Variable ¹	<i>n</i>	Mean \pm SD	D+ ²	D- ²	D+/D- (%) ³	Line effect (<i>P</i> -value)	
BW23, g	– last generation	592	453 \pm 78	490 \pm 3.62	428 \pm 3.62	+14.5	< 0.001
	– all generations	4412	449 \pm 70				
FI, g	– last generation	586	324 \pm 73	285 \pm 3.19	363 \pm 3.25	–21.5	< 0.001
	– all generations	4214	313 \pm 85				
AMEn, kcal·kg MS ⁻¹	– last generation	584	2879 \pm 592	3278 \pm 25.6	2460 \pm 25.7	+33.3	< .0001
	– all generations	4384	2875 \pm 637				
FCR, g·g ⁻¹	– last generation	586	2.15 \pm 0.67	1.72 \pm 0.08	2.72 \pm 0.08	–36.8	< .0001
	– all generations	4278	2.09 \pm 0.75				
RFI, g	– last generation	586	0.00 \pm 69.1	–33.2 \pm 3.15	34.9 \pm 3.20	–195.1	< .0001
	– all generations	2300	0.00 \pm 44.6				
CDU-DM, %	– last generation	584	67.2 \pm 12.2	75.4 \pm 0.56	58.8 \pm 0.56	+28.2	< .0001
	– all generations	4396	60.2 \pm 13.5				
FT, °C		598	40.2 \pm 0.4	40.2 \pm 0.02	40.2 \pm 0.02	0.0	0.724
DIT, °C·g ⁻¹		574	0.021 \pm 0.024	0.023 \pm 0.001	0.019 \pm 0.001	+21.1	0.079
Breast meat yield, g·kg ⁻¹		587	52.3 \pm 4.29	52.4 \pm 0.25	52.2 \pm 0.25	+0.4	0.531
Abdominal fat yield, g·kg ⁻¹		588	11.6 \pm 5.31	12.5 \pm 0.30	10.8 \pm 0.30	+15.7	< .0001
Ash content, %		592	41.0 \pm 2.13	41.1 \pm 0.12	41.0 \pm 0.12	+0.2	0.597
Relative dry tibia weight, g·kg ⁻¹		600	3.15 \pm 0.35	3.25 \pm 0.02	3.05 \pm 0.02	+6.6	< .0001
Relative ash weight, g·kg ⁻¹		591	1.29 \pm 0.14	1.34 \pm 0.01	1.24 \pm 0.01	+8.1	< .0001
Relative tibia length, mm·kg ⁻¹		590	145 \pm 21.5	140 \pm 1.06	152 \pm 1.05	–7.9	< 0.001
Relative tibia diameter, mm·kg ⁻¹		598	10.3 \pm 1.29	10.2 \pm 0.07	10.6 \pm 0.07	–3.8	< 0.001
BBS, N		608	104 \pm 31.3	116 \pm 1.51	87.9 \pm 1.51	+32.0	< 0.001
PE, g DM		592	1.06 \pm 0.44	0.81 \pm 0.02	1.28 \pm 0.02	–36.7	< 0.001
PI, g DM		601	1.97 \pm 0.45	1.72 \pm 22.4	2.17 \pm 22.5	–20.7	< 0.001
PE:PI, g·g ⁻¹		592	0.52 \pm 0.12	0.47 \pm 0.01	0.58 \pm 0.01	–19.0	< 0.001
NE, g DM		598	5.07 \pm 2.48	3.40 \pm 0.11	6.59 \pm 0.11	–48.4	< 0.001
NI, g DM		595	9.30 \pm 2.09	8.15 \pm 0.10	10.3 \pm 0.10	–20.9	< 0.001
NE:NI, g·g ⁻¹		591	0.52 \pm 0.15	0.41 \pm 0.01	0.63 \pm 0.01	–34.9	< 0.001

¹BW23 = BW at 23 d of age; FI = Feed intake between 17 and 23 d; AMEn = Apparent metabolisable energy corrected for 0 nitrogen; FCR = feed conversion ratio between 17 and 23 d; RFI = residual feed intake; CDU-DM = coefficient of digestive use of the DM; FT = Basal metabolic temperature; DIT = diet-induced thermogenesis; BBS = Bone breaking strength; PE = phosphorus excreted between 17 and 23 d; PI = phosphorus intake between 17 and 23 d; PE:PI = phosphorus excreted to phosphorus intake ratio; NE = nitrogen excreted between 17 and 23 d; NI = nitrogen intake between 17 and 23 d; NE:NI = nitrogen excreted to nitrogen intake ratio.

²D+ line is selected for high digestive efficiency and D- line is selected for low digestive efficiency.

³Relative difference between D+ and D- calculated as $100 \times (\text{D+ mean} / \text{D- mean} - 1)$ when D+ mean > D- mean, as $100 \times (1 - \text{D+ mean} / \text{D- mean})$ when D+ mean < D- mean.

RESULTS

Differences between Lines

Elementary statistics for all traits are reported in Table 2. For the performance traits, the D+ birds showed 33.3% greater AMEn. The FCR and RFI were consistently greater for D+ than for D- birds. The CDU-DM was 28.2% greater in D+ than in D- birds. Finally, nitrogen and phosphorus intake and excretion were lower for the D+ line (–20.9% and –20.7% for nitrogen and phosphorus intake and –48.4% and –36.7% for nitrogen and phosphorus excretion, respectively). The excretion rates were thus 34.9 and 18.9% lower in D+ than in D- for nitrogen and phosphorus, respectively.

Body composition was affected by selection only by abdominal fatness, as D+ birds were 15.7% fatter

than D- birds. In contrast, breast yield was not different between D+ and D- birds. No difference was found between lines for either fasted temperature or diet-induced thermogenesis, although there was a slightly greater tendency for DIT in D+ than in D- ($P = 0.08$).

Birds of the D+ line were 14.5% heavier than D- birds, but had 7.9% shorter and 3.8% less wide tibias. The dry tibia and ash weights were 6.6 and 8.1% heavier in D+ than in D-, respectively, but bone ash content was not different between the 2 lines. Bones of D+ birds were also harder than those of D- birds, as BBS was 32.0% greater in the former than in the latter.

Phenotypic Correlations in D+ and D- Lines

Correlations between the different metabolic parameters shown in Table 3 are comparable in D+ and D- lines. At the

Table 3. Estimated phenotypic correlations (below the diagonal in italics) for D+ selected for their high digestive efficiency (before the brackets) and D- selected for their low digestive efficiency (within brackets), and estimations (\pm SE) of heritability (on the diagonal) and genetic correlations (above the diagonal) for temperature, body composition, and bone characteristics

Traits ¹	FT	DIT	BRY	AFY	TAC	TW	TAW	TL	TD	BBS
FT	0.12 \pm 0.04²	-0.53 \pm ne ³	0.33 \pm 0.19	0.06 \pm 0.24	0.06 \pm 0.19	0.44 \pm 0.19	0.42 \pm 0.16	-0.39 \pm 0.19	-0.24 \pm ne	0.37 \pm 0.18
DIT	<i>-0.78⁴(-0.77)⁵</i>	0.13 \pm 0.05	-0.45 \pm 0.17	-0.11 \pm 0.23	0.03 \pm 0.20	-0.67 \pm 0.16	-0.53 \pm ne	0.62 \pm ne	0.33 \pm ne	-0.79 \pm 0.20
BRY	<i>0.04(0.06)</i>	<i>-0.02(-0.10)</i>	0.56 \pm 0.08	-0.39 \pm 0.19	0.12 \pm 0.14	0.18 \pm 0.14	0.25 \pm 0.12	-0.27 \pm 0.14	-0.08 \pm 0.14	0.12 \pm 0.06
AFY	<i>0.06(0.07)</i>	<i>-0.11(-0.03)</i>	<i>0.03(-0.05)</i>	0.28 \pm 0.08	-0.37 \pm 0.16	0.09 \pm 0.16	-0.13 \pm 0.17	-0.31 \pm ne	-0.67 \pm 0.14	0.16 \pm 0.15
TAC	<i>0.15(0.04)</i>	<i>-0.12(-0.01)</i>	<i>-0.03(0.01)</i>	<i>0.00(0.00)</i>	0.41 \pm 0.05	-0.10 \pm 0.14	0.40 \pm 0.11	0.01 \pm 0.15	0.04 \pm 0.14	0.22 \pm 0.11
TW	<i>0.06(0.08)</i>	<i>-0.05(-0.09)</i>	<i>0.09(0.13)</i>	<i>-0.01(-0.04)</i>	<i>-0.15(0.00)</i>	0.38 \pm 0.07	0.85 \pm 0.04	-0.26 \pm ne	0.07 \pm ne	0.69 \pm 0.08
TAW	<i>0.12(0.12)</i>	<i>-0.06(-0.12)</i>	<i>0.06(0.16)</i>	<i>0.06(-0.09)</i>	<i>0.38(0.46)</i>	<i>0.80(0.83)</i>	0.52 \pm 0.07	-0.20 \pm ne	0.06 \pm 0.13	0.67 \pm ne
TL	<i>-0.22(-0.13)</i>	<i>0.28(0.10)</i>	<i>-0.16(-0.28)</i>	<i>-0.23(-0.36)</i>	<i>-0.18(-0.21)</i>	<i>-0.00(-0.04)</i>	<i>-0.09(-0.14)</i>	0.61 \pm 0.05	0.82 \pm 0.04	-0.70 \pm ne
TD	<i>-0.16(-0.13)</i>	<i>0.22(0.10)</i>	<i>-0.02(-0.11)</i>	<i>-0.22(-0.35)</i>	<i>0.00(-0.20)</i>	<i>0.16(0.14)</i>	<i>0.15(0.05)</i>	<i>0.80(0.79)</i>	0.74 \pm 0.07	-0.40 \pm ne
BBS	<i>0.18(0.07)</i>	<i>-0.22(-0.11)</i>	<i>0.09(0.29)</i>	<i>0.15(0.22)</i>	<i>0.39(0.34)</i>	<i>0.41(0.44)</i>	<i>0.58(0.61)</i>	<i>-0.67(-0.71)</i>	<i>-0.42(-0.42)</i>	0.77 \pm 0.07

¹FT = Basal metabolic temperature; DIT = diet-induced thermogenesis; BRY = breast yield; AFY = abdominal fat yield; TAC = tibia ash content; TW = relative tibia weight; TAW = relative tibia ash weight; TL = tibia length; TD = tibia diam.; BBS = Bone breaking strength; ne = not estimated.

²Heritability are written in bold on the diagonal.

³Genetic correlations above the diagonal.

⁴Phenotypic correlations in D+ line (in italics before brackets) below the diagonal.

⁵Phenotypic correlations in D- line (in italics within brackets) below the diagonal.

opposite, correlations between metabolic parameters and either excretion or digestive and feed efficiency (cf. Tables 4 and 5) showed some differences between D+ and D- lines. In D+ birds, bone length, diameter, and solidity are correlated to ingestion traits (PI, NI, and RFI), whereas this correlation is absent in D- birds. In D+ birds, an increased consumption should thus be associated with shorter and more solid bones. At the opposite, bone length, size, and solidity is correlated to efficiency traits (PE/PI, NE/NI, AMEn, and FCR) in D- birds, but not in D+ birds. Finally, efficiency traits (PE/PI, NE/NI, AMEn, RFI, and FCR) are correlated to fatness in D- birds but not in D+ birds. In D- birds, an improvement in efficiency is thus associated to fatter birds and to shorter and more solid bones.

Genetic Parameters of Metabolic Traits

Heritability estimates of BW23, AMEn, FCR, RFI, and CDU-DM can be found in de Verdal et al. (2011a,b). The genetic parameters of temperature, body composition, and bone characteristics are presented in Table 3. Heritability estimates of FT and DIT were low but significantly different from 0. Heritability estimates for body composition traits were greater, ranging from 0.28 for abdominal fatness to 0.56 for breast meat yield. Abdominal fat yield was also subjected to a significant maternal permanent environment effect (0.06 \pm 0.02). All the bone characteristics were highly heritable (ranging from 0.38 to 0.77) and were not affected by this maternal effect.

As several traits presented very strong genetic correlations, convergence was more difficult in some analyses, making it impossible to estimate SE of genetic correlations.

A strong negative correlation (-0.53) was found between FT and DIT, indicating that birds with a low basal temperature have a greater increase in temperature when fed than those with a high FT. Estimates of genetic correlations also indicated that birds with greater FT (and lower DIT) had heavier, shorter, and more solid bones. They also tended to have more protein deposition, as breast yield was moderately correlated with FT and DIT.

As usually observed, breast meat yield and abdominal fat yield were negatively correlated. On average, these 2 traits were poorly correlated with bone traits. However, fatter animals had shorter, thinner, and less mineralized bones, as genetic correlations between AFY and ash content, tibia length and diameter were negative (from -0.31 to -0.67).

Tibia ash content was weakly correlated with other bone traits, except for relative ash weight. Apart from tibia ash content, all bone characteristics were strongly correlated with bone breaking strength (absolute values of genetic correlations ranging from 0.40 to 0.70), indicating that the most solid bones were heavy, short, and thin. Finally, the 2 weight traits and the 2 dimension traits of bones were strongly correlated with each other, but weight and dimension were independent.

Genetic Correlations between Metabolic Traits and Nitrogen and Phosphorus Characteristics

The genetic correlations between metabolic traits (temperature, body composition, and bone characteristics) and nitrogen and phosphorus intake and excretion are shown in Table 4. Metabolic rate was not

Table 4. Genetic correlations (\pm SE) and phenotypic correlations between nitrogen and phosphorus traits and temperature, body composition, and bone characteristics

Traits ¹	Type ²	PE	PI	PE:PI	NE	NI	NE:NI
FT	G	0.11 \pm 0.19	0.14 \pm 0.20	0.00 \pm 0.16	-0.01 \pm 0.16	0.15 \pm 0.21	-0.16 \pm ne
	P-D+	-0.09	-0.00	-0.10	-0.18	0.01	-0.22
	P-D-	-0.04	-0.01	-0.04	-0.04	0.01	-0.07
DIT	G	-0.32 \pm ne	-0.59 \pm ne	0.03 \pm 0.22	0.30 \pm ne	-0.59 \pm 0.15	-0.05 \pm ne
	P-D+	-0.08	-0.16	-0.01	-0.04	-0.15	0.01
	P-D-	-0.10	-0.13	-0.05	-0.09	-0.15	-0.03
BRY	G	-0.08 \pm 0.13	0.06 \pm ne	-0.30 \pm 0.12	-0.09 \pm 0.11	0.08 \pm ne	-0.33 \pm 0.10
	P-D+	-0.09	0.03	-0.13	-0.10	0.01	-0.12
	P-D-	-0.04	0.07	-0.12	-0.05	0.06	-0.15
AFY	G	0.19 \pm 0.15	0.09 \pm 0.15	0.38 \pm 0.19	0.05 \pm ne	0.09 \pm 0.16	0.06 \pm 0.11
	P-D+	0.15	0.26	0.05	0.19	0.26	0.13
	P-D-	-0.31	-0.28	-0.18	-0.35	-0.28	-0.27
TAC	G	-0.46 \pm ne	-0.13 \pm 0.13	-0.78 \pm ne	-0.29 \pm 0.11	-0.14 \pm 0.13	-0.40 \pm 0.09
	P-D+	-0.07	-0.09	-0.15	-0.02	0.09	-0.10
	P-D-	-0.08	0.05	-0.20	-0.06	0.07	-0.16
TW	G	0.22 \pm 0.13	0.44 \pm 0.11	-0.25 \pm 0.11	0.21 \pm 0.11	0.46 \pm 0.11	-0.11 \pm 0.08
	P-D+	-0.14	-0.01	-0.14	-0.11	0.00	-0.11
	P-D-	0.02	0.09	-0.04	0.0	0.08	-0.07
TAW	G	-0.14 \pm 0.13	0.21 \pm 0.12	-0.69 \pm 0.07	-0.03 \pm 0.11	0.21 \pm ne	-0.36 \pm 0.10
	P-D+	-0.17	0.02	-0.21	-0.11	0.04	-0.14
	P-D-	0.04	0.18	-0.12	0.04	0.19	-0.11
TL	G	-0.33 \pm ne	-0.50 \pm ne	-0.02 \pm ne	0.35 \pm 0.07	-0.50 \pm ne	-0.07 \pm ne
	P-D+	-0.20	-0.51	0.03	-0.04	-0.51	0.21
	P-D-	0.23	0.02	0.31	0.26	0.02	0.37
TD	G	-0.43 \pm 0.08	-0.37 \pm ne	-0.41 \pm ne	-0.16 \pm ne	-0.30 \pm ne	-0.15 \pm ne
	P-D+	-0.20	-0.45	-0.02	-0.06	-0.45	0.15
	P-D-	0.13	-0.01	0.18	0.15	-0.01	0.22
BBS	G	0.11 \pm ne	0.49 \pm 0.06	-0.45 \pm 0.11	0.13 \pm 0.09	0.49 \pm 0.06	-0.32 \pm ne
	P-D+	0.05	0.41	-0.16	-0.02	0.41	-0.24
	P-D-	-0.09	0.11	-0.23	-0.14	0.10	-0.31

¹FT = Basal metabolic temperature; DIT = diet-induced thermogenesis; BRY = breast yield; AFY = abdominal fat yield; TAC = tibia ash content; TW = relative tibia weight; TAW = relative tibia ash weight; TL = tibia length; TD = tibia diam.; BBS = Bone breaking strength; PE = phosphorus excreted between 17 and 23 d; PI = phosphorus intake between 17 and 23 d; PE:PI = phosphorus excreted to phosphorus intake ratio; NE = nitrogen excreted between 17 and 23 d; NI = nitrogen intake between 17 and 23 d; NE:NI = nitrogen excreted to nitrogen intake ratio; ne = not estimated.

²Type P-D+ = phenotypic correlation estimated in the D+ birds; Type P-D- = phenotypic correlation estimated in the D- birds; Type G = genetic correlation.

correlated with nitrogen or phosphorus consumption and excretion. In contrast, DIT was negatively correlated with nitrogen and phosphorus intake.

As expected, birds depositing more protein, and therefore having heavier breast muscle, had a better ability to retain nitrogen, the genetic correlation between BRY and NE:NI being negative (-0.33). Birds depositing more proteins or less fat were more efficient retainers of phosphorus, genetic correlations between PE:PI and BRY or AFY being estimated at -0.30 and $+0.38$, respectively.

As could be expected, most of the bone characteristics were correlated with the ability of the birds to retain phosphorus, the only trait being uncorrelated with PE:PI being tibia length. Heavier, more mineralized, thicker and more resistant bones were associated with an improved

capacity to retain phosphorus. However, depending on the bone characteristics under consideration, this association with PE:PI was more closely linked to reduced excretion (e.g., in relation to ash content) or to an increased phosphorus intake (e.g., in relation to BBS or relative tibia weight). Correlations between bone traits and nitrogen retention were weaker and more erratic. Only ash content and relative ash weight were significantly correlated with nitrogen retention, the most highly mineralized bones being associated with a greater capacity to retain nitrogen.

Table 5. Genetic correlations (\pm SE) between BW at 23 d (BW23), apparent metabolizable energy (AMEn), feed conversion ratio (FCR), residual feed intake (RFI), and coefficient of digestive use of DM (CDU-DM) and temperature, body composition, and bone traits

Traits ¹	Correlations	BW23	AMEn	FCR	RFI	CDU-DM
FT	G ²	0.56 \pm 0.24	0.00 \pm 0.09	-0.11 \pm ne	0.43 \pm 0.20	0.06 \pm 0.11
	P-D+ ³	0.23	0.18	-0.14	0.05	0.25
	P-D- ⁴	0.16	0.11	0.02	0.01	0.10
DIT	G	-0.82 \pm 0.09	0.18 \pm 0.08	-0.08 \pm ne	-0.64 \pm 0.14	0.23 \pm ne
	P-D+	-0.29	-0.05	-0.02	-0.16	-0.04
	P-D-	-0.16	0.03	-0.05	-0.15	0.06
BRY	G	0.29 \pm 0.20	0.05 \pm 0.08	-0.11 \pm 0.09	0.31 \pm 0.16	0.05 \pm 0.11
	P-D+	0.14	-0.08	-0.05	0.05	0.11
	P-D-	0.27	0.03	0.03	0.07	-0.02
AFY	G	0.73 \pm 0.15	0.20 \pm 0.08	-0.20 \pm 0.10	0.03 \pm ne	0.10 \pm 0.11
	P-D+	0.24	0.04	0.15	0.24	0.09
	P-D-	0.35	0.45	-0.25	-0.31	0.40
TAC	G	-0.22 \pm 0.20	0.08 \pm 0.08	0.07 \pm 0.11	-0.07 \pm 0.13	0.19 \pm 0.10
	P-D+	0.08	0.02	0.02	-0.00	0.04
	P-D-	0.22	0.08	-0.01	-0.02	0.10
TW	G	0.69 \pm 0.16	0.08 \pm 0.08	-0.16 \pm ne	0.47 \pm 0.11	0.03 \pm 0.09
	P-D+	0.15	-0.01	-0.09	0.01	0.10
	P-D-	0.06	0.06	0.28	0.05	0.09
TAW	G	0.38 \pm 0.19	0.09 \pm 0.08	-0.17 \pm 0.10	0.34 \pm 0.13	0.07 \pm ne
	P-D+	0.18	0.02	-0.06	-0.01	0.13
	P-D-	0.25	0.02	0.02	0.13	0.07
TL	G	-1.00 \pm 0.01	0.15 \pm 0.07	0.23 \pm ne	-0.52 \pm ne	-0.11 \pm ne
	P-D+	-0.94	0.10	-0.09	-0.49	-0.07
	P-D-	-0.95	-0.40	0.27	0.08	-0.31
TD	G	-0.95 \pm 0.02	-0.09 \pm 0.06	0.07 \pm ne	-0.37 \pm 0.07	-0.05 \pm ne
	P-D+	-0.81	0.07	-0.05	-0.43	-0.09
	P-D-	-0.79	-0.27	0.10	0.05	-0.22
BBS	G	0.93 \pm 0.04	0.15 \pm 0.07	-0.21 \pm ne	0.54 \pm 0.07	0.13 \pm ne
	P-D+	0.75	-0.058	0.01	0.37	0.20
	P-D-	0.77	0.26	-0.05	0.04	0.24

¹FT = Basal metabolic temperature; DIT = diet-induced thermogenesis; BRY = breast yield; AFY = abdominal fat yield; TAC = tibia ash content; TW = relative tibia weight; TAW = relative tibia ash weight; TL = tibia length; TD = tibia diam.; BBS = Bone breaking strength; ne = not estimated.

²Genetic correlations.

³Phenotypic correlations in D+ line selected for high digestive efficiency.

⁴Phenotypic correlations in D- line selected for low digestive efficiency.

Genetic Correlations between Metabolic Traits and Performance and Feed Efficiency

The genetic correlations between metabolic traits and performance and feed efficiency are shown in Table 5. The genetic correlations between all the metabolic traits and AMEn, CDU-DM, and FCR were very low and in most cases not significant, except between AMEn and DIT, relative fat weight, relative tibia length, and BBS (genetic correlations ranging from 0.15 to 0.20).

The BW23 and RFI presented on average a similar pattern of correlations with metabolic traits, with much stronger correlations than those observed with AMEn, FCR or CDU-DM. Heavier animals and those that had a greater residual feed intake were associated with an increased basal temperature, reduced diet-induced thermogenesis and shorter, heavier, thinner and more

solid bones. In contrast, correlations of AFY with BW23 were very strong but they were close to 0 with RFI, heavier animals having decreased abdominal fatness.

DISCUSSION

Selecting animals on feed efficiency or residual feed intake in laying hens and pigs has been shown to have a high impact on several metabolic traits but a low impact on digestibility (de Haer et al., 1993; Luiting et al., 1994). The aim of our study was to establish whether selecting on a trait specific to the digestive process (AMEn) also modified metabolism in the chicken. de Verdal et al. (2011b) have already reported that nitrogen and phosphorus retention rates were modified by selection on AMEn in relation to a differential development of the

digestive tract (de Verdal et al., 2010a). It is important to understand the genetic links between AMEn and heat production (basal temperature and diet-induced thermogenesis), tissue deposition (abdominal fat and breast meat yields), and bone development (tibia ash content, dry and ash tibia weights, tibia length and diameter, and BBS).

Phenotypic and Genetic Characteristics of Metabolic Traits

Temperature. Metabolic rate was not significantly different between D+ and D- birds, which is consistent with the absence of genetic correlation between AMEn and this trait. The basal requirement for maintenance thus appears very similar. Nevertheless, FT was significantly correlated with RFI and BW23. Luiting et al. (1994) showed that laying hens with low RFI have a lower basal metabolic rate, as also found in growing pigs (Barea et al., 2010).

Nevertheless, FT was highly negatively correlated with DIT, which is consistent with the previous phenotypic results reported by El-Gendy and Washburn (1995), who found that chickens with a high basal metabolic temperature tended to have smaller temperature variations after heat stress. As temperature is strongly regulated in homeostatic animals, it is probable that the temperature cannot exceed a certain threshold, which leaves a smaller margin of variation in animals whose basal temperature is high.

Diet-induced thermogenesis tended to be greater in D+ than in D- ($P=0.08$). The greater postprandial thermogenesis observed in D+ birds reflects energy expenditure related to nutrient storage. The low correlation estimates between DIT and AMEn and between DIT and CDU-DM indicated that animals with a better ability to digest would have a slightly greater increase in DIT, which is consistent with the nonsignificant tendency observed for DIT between D+ and D-. It was expected that the birds digesting more feed would have a greater DIT. Indeed, it could be hypothesized that birds digesting more from the same feed consumed would retain more feed, and consequently their metabolism would be more active (Renaudeau et al., 2004). Renaudeau et al. (2004) reported that the heat production associated with the digestive and metabolic use of feed varies with the consumption and the nutrient content of the feed and the final use of these nutrients at the metabolic level.

Using divergently selected for high (R+) and low (R-) residual feed intake laying hens, Swennen et al. (2007) showed a difference in DIT when this trait was not corrected for feed intake but the difference disappeared when correction for difference in consumption was applied. According to these authors, the lack of difference in DIT corrected for feed intake indicates that DIT had no

feedback effect on feed consumption. These results are the opposite of ours, because differences in DIT between D+ and D- birds were only observed when the correction for feed consumption was applied (data not shown). It could be hypothesized that a feedback effect of DIT on feed intake exists in the 2 divergent lines used in the present study, as has been shown in mammals (Stubbs and O'Reilly, 2000).

Heritability estimates of FT and DIT were low, and for FT they were in the same range as reported by Washburn and Pinson (1990) and El-Gendy and Washburn (1995; i.e., between 0.09 and 0.19). These low heritability estimates could be due to the fact that body temperature and heat production are highly regulated characteristics of homeostasis (Yahav et al., 2009) and consequently have low variability, as can be seen from the very low CV of FT (1%). Moreover, the measurement of body temperature is probably not sufficiently precise in view of the range of variation of the trait (0.1 vs. 38.8 to 41.2°C for minimum and maximum FT, respectively). Lack of precision of the measurement of temperature was increased by the fact that chickens were handled, which could cause stress and thus increase body temperature (Sufka and Hughes, 1991; Cunnick et al., 1994). At the opposite of FT, DIT thus showed a very high CV (111%).

Body temperature was poorly correlated with body composition, in agreement with the results of Swennen et al. (2007) in laying hens. In contrast, there was a genetic link between temperature and bone characteristics. Indeed, tibia length relative to BW23 was negatively correlated with FT, and positively correlated with DIT, possibly explained by the fact that the leg is a heat exchange surface (Bordas et al., 1992). An increase in tibia length could therefore provide an increase in the heat dissipation surface, and consequently a decrease in FT and an increase in DIT. Gabarrou (1996) similarly concluded that the increase heat exchange surfaces (e.g., legs, barbs) are an adaptation of birds to increase heat dissipation.

Body Composition. Heritability estimates for body composition characteristics were consistent with the literature (Le Bihan-Duval et al., 2001; Rance et al., 2002; Gaya et al., 2006) although they were in the lower end of the range for AFY. This difference in AFY was probably due to the young age of the birds (23 d) whereas most of the literature deals with older chickens (42 d). Furthermore, a permanent maternal environmental effect was included in the estimation model, which probably reduced the heritability estimate.

Breast meat yield was not different between D+ and D- birds, which was consistent with the genetic correlation between AMEn and breast meat yield ($r_g = 0.05$). As efficiency of nitrogen retention was very different between the 2 lines, this suggests that the digestive processes were modified. On the other

hand, D+ showed a 15.7% greater abdominal fat yield than D- birds. Nevertheless, according to phenotypic correlations, abdominal fat yield was correlated positively with AMEn and negatively with FCR and RFI in D- birds. This observation suggested a prioritization toward fat deposition in D- birds when increasing their efficiency. It thus seems that, in that case, the genetic correlation between efficiency and fatness is an average of the phenotypic correlations in both lines.

According to our estimates of genetic correlations between the body composition and the nitrogen and phosphorus traits, protein deposition is more linked to the efficiency of nitrogen retention, but not specifically to either intake or excretion. Bouvarel et al. (2006) demonstrated that a 20 to 18.5% reduction in body protein fixation resulted in a 10% increase in excretion. Similarly, although birds were deficient in AA, which is possible when protein retention is low, Smith et al. (1998) showed a decrease in growth performance and BMY. Moreover, the significant negative correlation between BMY and PE:PI could be explained by the high genetic correlation between NE:NI and PE:PI (de Verdal et al., 2011b) or by the involvement of phosphorus in the absorption of AA. Indeed, it has previously been shown that improvement in phytic phosphorus (PP) hydrolysis by phytase is linked to an increase in retention of AA (Selle et al., 2003). The negative effect of PP on the retention of AA could be explained by the formation of complexes between PP and proteins in the upper part of the gastrointestinal tract, inhibiting protein hydrolysis by pepsin (Selle et al., 2000) and phosphorus absorption. An improvement in phosphorus absorption could thus be linked to an increase in both protein retention and the BMY. Furthermore, Martinez-Amezcuca et al. (2006) suggested that phosphorus is essential in the activation of the Na/K ATPase pump, which is involved in the absorption of AA.

Bone Characteristics. Several measurements were performed in the present study and, except for TAC, all the bone characteristics were significantly different between D+ and D- lines. This is also for these bone characteristics that the phenotypic correlations with efficiency were the most frequently different between D+ and D- lines. According to Meschy et al. (2008) and Acosta et al. (2009), tibia ash content is the best indicator of phosphorus bioavailability. For example, improving the bioavailability of P by addition of phytase to the diet increases TAC (Selle et al., 2003; Manangi et al., 2009). These studies were confirmed by our estimation of the strong genetic correlation between PE:PI and TAC (-0.78).

The D+ birds had shorter, thinner but denser bones than D- birds, which was consistent with their better BBS. Moreover, tibia length and BBS were negatively genetically correlated. These results were consistent with those of Williams et al. (2000a), showing a reduction in

the leverage of the breaking moment for shorter bone. McDevitt et al. (2006) showed that BBS was linked to the inorganic bone component (i.e., ash weight), which is an indicator of the hardness of the bone. In the present study, the tibia ash weight was heavier in D+ than in D- birds, suggesting harder bone in the former. Bone breaking strength is also linked to the organic bone component (i.e., dry tibia weight), which provides flexibility. In our case, the relative dry tibia weight was heavier in D+ than in D-. These results are consistent with the positive genetic correlations estimated between BBS, TW, and TAW.

Furthermore, Alexander et al. (2010) showed a negative link between the bone integrity traits, such as BBS, and phosphorus deficiency. This negative link was consistent with the present negative correlation between PE:PI and BBS (-0.45). Furthermore, McDevitt et al. (2006) showed that the reduction in BBS could be due to a decrease in mineral consumption or a decrease in mineral use. The most likely hypothesis according to our study would be a reduction in mineral use because D-birds showed lower BBS but a greater feed intake than D+ birds. This hypothesis is supported by the study of Williams et al. (2000b) who did not find a significant link between intake (NI and PI) and ash content.

These differences in bone characteristics between D+ and D- were not explained by the divergent selection experiment, because the genetic correlations between AMEn and bone traits were low and in most cases not significant. However, in contrast to TAC, all these traits presented very strong genetic correlations with BW23, which was moderately affected by selection on AMEn. These traits were strongly heritable (ranging from 0.38 to 0.77), in agreement with the results of Suchy et al. (2009) showing that 70 to 80% of bone mass was determined by genetics. Moreover, if a direct genetic link between AMEn and bone characteristics has not been shown in this study, phenotypic correlations estimated at the last generations in both lines can suggest an indirect link between these traits. Indeed, there is an association between efficiency and bone characteristics only in D- birds. It can be hypothesized that D+ birds are very efficient, and that they are close to optimal values for bone characteristics. At the opposite, efficiency in D- birds is very low, and in their case, an improvement of efficiency could be associated to an increase in the capacity to use minerals and their bone quality.

Genetic Correlations between Growth Performance, Feed Efficiency, and Metabolic Traits. The impact of genetic selection of FCR and RFI on metabolism has been studied in poultry, cattle, and pigs (Gilbert et al., 2007; Aggrey et al., 2010; Bouquet et al., 2010). In our study, the genetic correlations between AMEn, FCR, RFI, and the metabolic traits showed that FCR and AMEn were less closely correlated with metabolic characteristics than

RFI. For example, it had already been shown that selecting poultry for high RFI values is linked with increased heat production during feed deprivation (Luiting et al., 1994; Swennen et al., 2007). Furthermore, Luiting et al. (1994) reported that the differences in digestibility of feed energy did not have an important role in the differences in RFI and FT between the divergent lines selected for RFI. Moreover, Skinner-Noble and Teeter (2004) showed that body temperature was not a good indicator of FCR, in agreement with our low genetic correlation between FT and FCR. Similarly, pigs selected for high or low RFI values showed differences in fasting heat production but no differences were found in energy and DM digestibility coefficients (Barea et al., 2010).

Finally, the results of the study presented here showed independence of digestibility characteristics such as AMEn and CDU-DM, and heat production and metabolism characteristics were not highly genetically correlated. Selecting for digestibility could have a very low impact on metabolism characteristics, whatever the trait being selected. It seems therefore that the selection experiment based on AMEn modified the digestion phase but not the postdigestion phase. Indeed, what the animal does with digested nutrients does not change with selection for digestibility characteristics.

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