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# Genetic background of body reserves in laying hens through backfat thickness phenotyping

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## ABSTRACT

In this study, we pursued three primary objectives: firstly to test and validate the phenotyping of backfat thickness as an indicator of the overall fatness of laying hens; secondly, to estimate genetic parameters for this trait; thirdly, to study the phenotypic and genetic relationships between this trait and other traits related to production and body composition. To address these questions, hens from two lines under divergent selection for residual feed intake, were phenotyped for body weight, body composition traits (backfat, total fat volume, and blood adipokines levels), and egg number. Linear mixed models enabled to estimate variance components and calculate genetic parameters. The two lines largely differed in body fatness: the efficient line had larger backfat and lower chemerin levels compared to the inefficient line. However, there were no significant differences between the two lines concerning body weight, total fat volume, other blood adipokines levels (adiponectin, ghrelin, and visfatin), and egg production. The genetic parameter estimation revealed moderate heritability (0.38 and 0.42) for backfat and body weight, high heritability (higher than 0.80) for blood adipokines levels and low heritability (0.24 and 0.27) for egg production and total fat volume. Backfat and total fat volume were genetically highly and positively correlated (0.91). Body weight and total fat volume were also highly positively correlated (0.67). However, backfat and body weight were moderately positively correlated (0.39). The genetic correlation between backfat and egg number was moderate and negative. In conclusion, backfat could provide additional genetic information to that of the body weight as a selection criterion for body reserves. However, its correlation with laying performance should be taken into account to avoid undesired responses to selection.

**Keywords:** body composition, body reserves, backfat thickness, ultrasonography, CT-scan, adipokines, genetic correlations, heritability, laying hens

35 One of the major challenges of the egg production sector is to extend the career of laying hens, for  
36 ethical, environmental, and economical reasons (reviews: Bain *et al.* 2016; Preisinger 2018). Laying hens  
37 have been selected for laying criteria for more than 60 years, resulting in animals able to maintain  
38 profitable egg production from approximately 20 to 80 weeks of age. The priority of, at least European  
39 stakeholders, is now to extend the laying period to 100 weeks of age, with the aim of producing 500 eggs  
40 per hen. This would further dilute the economic and environmental costs related to non-productive life  
41 periods (growth, laying pauses...), and reduce the number of hens by decreasing the breeder stock.

42 The late-laying period, which goes beyond 80 weeks of age, remains relatively unexplored for what is our  
43 understanding of its physiology, nutrition, and genetics. The existing literature on this laying period is  
44 notably scarce, providing limited insights into these aspects, therefore, further research and investigation  
45 are warranted to enhance our knowledge in these areas.

46 Egg production is a major nutrient expenditure for layers (energy, protein, calcium...) and about 25% of the  
47 gross energy intake goes to egg production (Larbier and Leclercq, 1992; Luiting, 1990). Excessive  
48 investment in egg production may lead to different metabolic diseases, and the longer the production  
49 cycle, the higher the risk. For instance, extending the laying period makes hens more likely to develop  
50 hepatic steatosis, a disease responsible for egg production drop and obese conditions (Bain *et al.*, 2016).  
51 Therefore, we need to monitor both egg production and fattening in laying hens, to select balanced hens  
52 that can ensure cost-effective egg production while maintaining optimal fatness.

53 The monitoring of egg production and the pedigree of laying hens has been facilitated by cage-rearing  
54 systems. In some regions of the world, cages are about to be banned and technical solutions are emerging  
55 for individual recording systems and relevant selection criteria for egg production in alternative systems  
56 (Bécot *et al.*, 2021). Regarding fatness in chicken, like in other species, the gold standard and most common  
57 method to determine body composition are lethal and destructive because it is either a dissection with  
58 adipose tissue weighing or a chemical analysis of the shredded body. This phenotyping method is  
59 unsatisfactory because it requires the euthanasia of the animal, which raises ethical and practical  
60 problems. Indeed, the animals can no longer be used for genetic selection (except as collateral  
61 information), and this method is not suited for longitudinal studies aiming to assess the dynamics of body  
62 reserves at several points in time during the animal life. Alternative and non-invasive methods are now  
63 available to determine body composition in various species (Lerch *et al.*, 2021; Staub *et al.*, 2019; Xavier *et al.*,  
64 2022). In poultry, tomography has proven to be sufficiently accurate to be considered as a reference  
65 method for body composition, with phenotypic correlations above 0.80 in broilers (Cobo *et al.*, 2015;  
66 Mellouk *et al.*, 2018b). However, the routine use of tomography is difficult to implement on a large number  
67 of animals as it cannot easily be performed on the farm and because it requires sedation of the animal,  
68 which is time-consuming and costly and not without risk for the animals. The methods relying on

69 ultrasonography have been used effectively to assess body fatness in chickens. A specific region was  
70 identified on top of the *synsacrum* where subcutaneous adipose tissue thickness was highly correlated to  
71 chemical analyses of the shredded body ( $r=0.92$ ; Mellouk *et al.* 2018), to the abdominal fat pad weight by  
72 dissection ( $r=0.86$ ; Mellouk *et al.* 2018) and the body fat volume estimated by tomography ( $r>0.84$ ; Mellouk  
73 *et al.* 2018; Grandhayé *et al.* 2019). So far, body fatness traits recorded by ultrasonography were all tested  
74 on broilers while no data are available on laying hens. Despite belonging to the same species (*Gallus gallus*  
75 *domesticus*), broilers and layers have been subjected to separate and intense genetic selection for over 60  
76 years. As a result, they differ greatly in terms of growth rate and energy metabolisms. In addition, selection  
77 and phenotype recording target different physiological stages, focusing on young animals in broilers and  
78 adults in layers.

79 As they age, layers tend to become fatter, and breeders aim to achieve a balanced target fat level: neither  
80 too thin nor too fat, to maintain sufficient body reserves in case of nutrient scarcity while avoiding  
81 unnecessary energy storage.

82 Consequently, the present study aimed to achieve several objectives. Firstly, it sought to test and validate  
83 the phenotyping by ultrasounds of the subcutaneous adipose tissue thickness on top of the *synsacrum* as  
84 an accurate indicator of the overall fatness of the layer hen. Secondly, it aimed to estimate the heritability  
85 of this new trait in laying hens. Finally, it aimed to study the phenotypic and genetic correlations between  
86 this trait and other traits from the breeding goal of most of the lines of laying hens, in order to evaluate its  
87 potential as a selection criterion.

## 88 **Methods**

### 89 **Laying hen population and rearing condition**

90 The laying hens used in this study belong to two experimental lines originating from the same Rhode  
91 Island Red population, divergently selected since 1976 on the residual feed intake, a trait for feed efficiency  
92 (Bordas *et al.*, 1992). These lines were chosen for this study because the selection process on RFI has also  
93 led to marked differences in carcass adiposity with the efficient line (R-) being fatter than the inefficient  
94 (R+) one, despite a reduced feed intake (El-Kazzi *et al.*, 1995). The RFI was estimated as defined in Byerly  
95 *et al.* (1980) and represents the difference between the observed feed intake and the expected one  
96 estimated based on known maintenance and production requirements.

97 In total, we used 394 animals, 215 from the R+ line and 179 from the R- line. There were 92 and 123 R+  
98 phenotyped in 2019 and 2021 (from 9 sires and 38 dams in 2019, and 10 sires and 42 dams in 2021), and  
99 75 and 104 R- in 2019 and 2021 (from 9 sires and 43 dams in 2019, and 9 sires and 41 dams in 2021). All  
100 animals were hatched in two batches at the INRAE Pôle d'Expérimentation Avicole de Tours (UE PEAT,  
101 Nouzilly, France ; <https://doi.org/10.15454/1.5572326250887292E12>). They were reared under standard  
102 farming conditions in floor pens until 17 weeks of age when 46 birds were euthanized for body composition

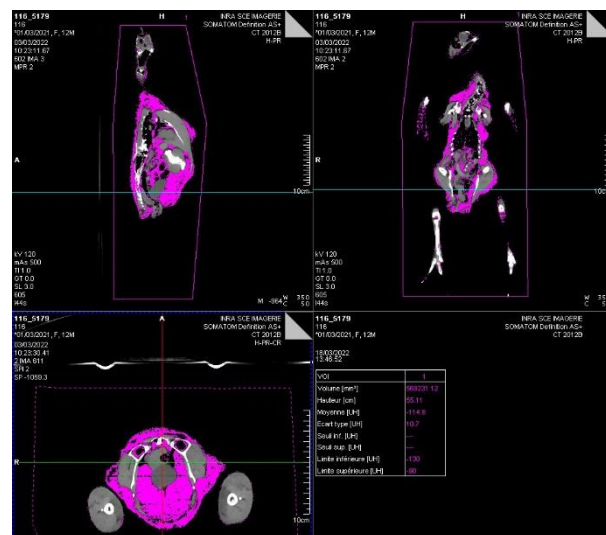
103 recording (23 pullets per line), by neck cut and bleeding, immediately after head electrical stunning. The  
104 remaining animals were transferred to individual cages with a lighting regime set at 14 h of light per day  
105 and fed *ad libitum* a commercial diet (Appendix 1). Egg production was recorded daily up to 53 weeks of  
106 age, when the hens were euthanized as described above. Because of the adaptation of the experimental  
107 facility to both the sanitary situation and lockdown policy caused by the COVID-19 pandemic, only the body  
108 weight (named BodyWeight) and last backfat thickness were recorded in birds from the batch 2019.

## 109 Phenotypes

### 110 Tomography as the Gold Standard for body composition

111 The body composition of euthanized hens was determined soon after death (within the hour because *rigor*  
112 *mortis* occurs rapidly in chickens) with a CT scan (Siemens Somatom Definition AS, Siemens Corp.,  
113 Germany). During the scan, each hen was placed on the back. The X-ray source was set at 120 kV and 500  
114 mA/s. The determination of total fat volume was performed using both an upper and lower threshold of  
115 the Hounsfield Units (HU) scale. Fatty components were located between -130 and -90 HU. The total  
116 volume of pixels within these bounds was used as the total volume of fat in the animal (example in Figure 1;  
117 trait named TotFat).

118



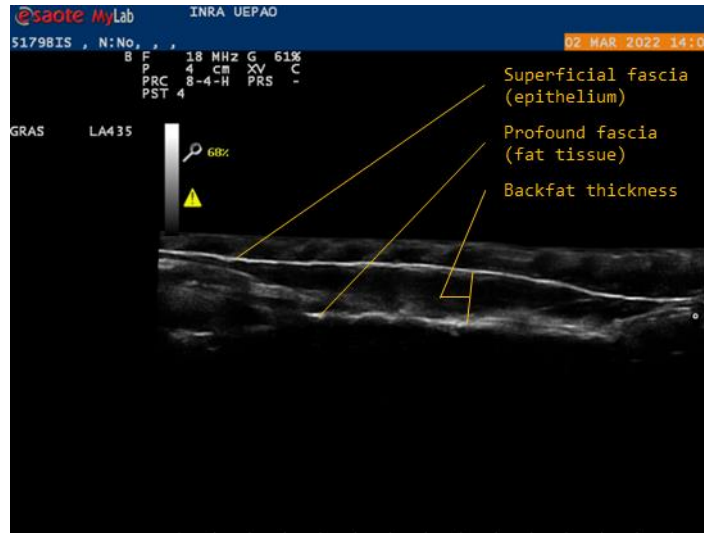
119

120 **Figure 1:** Example of CT-scan image visualizing the 3D axes (hen ID: PEA2021045179).  
121 The pixels set between -130 and -90 HU and colored in pink to display the fatty components

### 122 *In-vivo* indicators for body energy reserves

123 Dorsal subcutaneous adipose tissue thickness (trait named backfat in this study) was recorded using an  
124 ultrasound scanner (MyLab 30 Gold Vet, Hospimedi France, Saint-Crépin-Ibouwillers, France) equipped with  
125 a high-frequency linear probe (18 MHz; L435, Esaote S.P.A., Genova, Italy). In previous studies in broilers,  
126 a specific region was identified on top of the *synsacrum* as a good indicator of total fatness (Figure 2), based  
127 on high correlations with TotFat (Mellouk *et al.* 2018; Grandhay *et al.* 2019). BackFat was recorded

128 according to the same protocol: the plumage was soaked with soapy water and then spread, ultrasound  
129 gel was applied in contact with the epithelium and the probe was put in contact with the gel. The entire  
130 recording process took about 1 min per hen and no feathers were plucked. Backfat was recorded 5 times  
131 at 129, 192, 218, 289, and 371 days of age. Body weight was recorded together with Backfat.  
132



133  
134 **Figure 2:** Ultrasound scan panoramic image of the dorsal subcutaneous adipose tissue thickness  
135 above the *synsacrum*, an example of the same hen as in Figure 1 (hen ID: PEA2021045179)

### 136 *Blood Adipokines levels*

137 A first blood sample was collected from the wing vein at 17 weeks of age and a second blood sample  
138 was collected during the neck bleeding at the slaughter process, at 53 weeks of age. Plasma was isolated  
139 from blood after centrifugation (5000 g for 10 min at 4°C) and then stored at -20°C. Consequently, all hens  
140 had two blood samples available to determine adipokines concentrations. The concentrations of four  
141 adipokines (visfatin, adiponectin, chemerin, and ghrelin) were determined in the plasma using chicken-  
142 specific ELISA kits as previously described (Barbe et al., 2020; Mellouk et al., 2018b). Briefly, MBS269004  
143 (sensitivity 5 pg/mL), MBS016609 (sensitivity 0.1 µg/mL), MBS738819 (sensitivity 0.1 ng/mL), and  
144 MBS2700427 (sensitivity 0.05 ng/mL) were used for visfatin, adiponectin, chemerin, and ghrelin,  
145 respectively (My BioSource, San Diego, USA). The experiment was performed following the manufacturer's  
146 protocol with an intra-assay coefficient of variation ≤ 8%, < 10%, < 5.6%, and < 12%, respectively. The  
147 absorbance was measured at 450 nm and then compared with reference values. The traits are named after  
148 the appropriated adipokines (visfatin, adiponectin, chemerin, and ghrelin).

### 149 *Egg production*

150 Egg production was recorded daily from the first egg laid until the end of the experiment (*i.e.* culling of the  
151 flock; trait named TotEggNum).

152 **Statistical analyses**

153 *Models*

154 To calculate genetic parameters (correlations and heritabilities), variance components were estimated  
 155 using bivariate animal model analyses (Henderson, 1975). Commonly in bivariate analyses, both traits have  
 156 the same two variance strata, genetic and residual, or three strata, genetic, animal, and sampling. This  
 157 common model with two strata can be described as:

158 
$$\begin{bmatrix} \mathbf{y}_1 \\ \mathbf{y}_2 \end{bmatrix} = \begin{bmatrix} \mathbf{X}_1 & 0 \\ 0 & \mathbf{X}_2 \end{bmatrix} \begin{bmatrix} \mathbf{b}_1 \\ \mathbf{b}_2 \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_1 & 0 \\ 0 & \mathbf{Z}_2 \end{bmatrix} \begin{bmatrix} \mathbf{u}_1 \\ \mathbf{u}_2 \end{bmatrix} + \begin{bmatrix} \mathbf{e}_1 \\ \mathbf{e}_2 \end{bmatrix}$$

159 where  $\mathbf{y}_1$  and  $\mathbf{y}_2$  are vectors of the observed values for the first and second trait respectively,  $\mathbf{X}_1$  and  $\mathbf{X}_2$   
 160 are design matrices for fixed effects and  $\mathbf{b}_1$  and  $\mathbf{b}_2$  are vectors of values for fixed effects (details at the end  
 161 of the section),  $\mathbf{Z}_1$  and  $\mathbf{Z}_2$  are design matrices for the additive genetic random effects and  $\mathbf{u}_1$  and  $\mathbf{u}_2$  are  
 162 vectors of breeding values, and  $\mathbf{e}_1$  and  $\mathbf{e}_2$  are vectors of residual values. The variance components are  
 163 fitted as 2x2 matrices of variances-covariances for each stratum:

164 
$$\text{Var} \begin{bmatrix} \mathbf{u}_1 \\ \mathbf{u}_2 \end{bmatrix} = \mathbf{G} \times \mathbf{A} \quad \text{where } \mathbf{G} = \begin{bmatrix} \sigma_{u1}^2 & \sigma_{u1u2} \\ \sigma_{u1u2} & \sigma_{u2}^2 \end{bmatrix} \text{ and } \mathbf{A} \text{ is the additive genetic relationship matrix}$$

165 
$$\text{Var} \begin{bmatrix} \mathbf{e}_1 \\ \mathbf{e}_2 \end{bmatrix} = \mathbf{R} \times \mathbf{I} \quad \text{where } \mathbf{R} = \begin{bmatrix} \sigma_{e1}^2 & \sigma_{e1e2} \\ \sigma_{e1e2} & \sigma_{e2}^2 \end{bmatrix} \text{ and } \mathbf{I} \text{ is the identity matrix}$$

166 For a bivariate analysis where both traits have three strata, the model can be described as:

167 
$$\begin{bmatrix} \mathbf{y}_1 \\ \mathbf{y}_2 \end{bmatrix} = \begin{bmatrix} \mathbf{X}_1 & 0 \\ 0 & \mathbf{X}_2 \end{bmatrix} \begin{bmatrix} \mathbf{b}_1 \\ \mathbf{b}_2 \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_1 & 0 \\ 0 & \mathbf{Z}_2 \end{bmatrix} \begin{bmatrix} \mathbf{u}_1 \\ \mathbf{u}_2 \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_1 & 0 \\ 0 & \mathbf{Z}_2 \end{bmatrix} \begin{bmatrix} \mathbf{pe}_1 \\ \mathbf{pe}_2 \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_1 & 0 \\ 0 & \mathbf{Z}_2 \end{bmatrix} \begin{bmatrix} \mathbf{samp}_1 \\ \mathbf{samp}_2 \end{bmatrix}$$

168 where fixed effects are the same as for the former model, variance components are fitted as 2x2 matrices  
 169 for the genetic strata and the remaining variance is decomposed into an animal (non-genetic) stratum and  
 170 a sampling stratum defined as:

171 
$$\text{Var} \begin{bmatrix} \mathbf{u}_1 \\ \mathbf{u}_2 \end{bmatrix} = \mathbf{G} \times \mathbf{A} \quad \text{where } \mathbf{G} = \begin{bmatrix} \sigma_{u1}^2 & \sigma_{u1u2} \\ \sigma_{u1u2} & \sigma_{u2}^2 \end{bmatrix} \text{ and } \mathbf{A} \text{ is the additive genetic relationship matrix}$$

172 
$$\text{Var} \begin{bmatrix} \mathbf{pe}_1 \\ \mathbf{pe}_2 \end{bmatrix} = \mathbf{P} \times \mathbf{I} \quad \text{where } \mathbf{P} = \begin{bmatrix} \sigma_{pe1}^2 & \sigma_{pe1pe2} \\ \sigma_{pe1pe2} & \sigma_{pe2}^2 \end{bmatrix} \text{ and } \mathbf{I} \text{ is the identity matrix}$$

173 
$$\text{Var} \begin{bmatrix} \mathbf{samp}_1 \\ \mathbf{samp}_2 \end{bmatrix} = \mathbf{S} \times \mathbf{I} \quad \text{where } \mathbf{S} = \begin{bmatrix} \sigma_{samp1}^2 & \sigma_{samp1samp2} \\ \sigma_{samp1samp2} & \sigma_{samp2}^2 \end{bmatrix} \text{ and } \mathbf{I} \text{ is the identity matrix}$$

174 However, when one trait has two strata ( $\mathbf{y}_1$  say) and the other has three strata ( $\mathbf{y}_2$  say), the direct product  
175 variance structure breaks down;  $\sigma_{e1}^2(\sigma_{e1e2})$  cannot be partitioned into  $\sigma_{pe1}^2 + \sigma_{samp1}^2(\sigma_{pe1pe2} +$   
176  $\sigma_{samp1samp2})$ . We can estimate four (three different) parameters:

$$\begin{aligned}177 \quad \sigma_{e1e2}^* &= \sigma_{pe1pe2} + \sigma_{samp1samp2} \\178 \quad \sigma_{e1}^{2*} &= \sigma_{e1}^2 - \sigma_{e1e2}^* = \sigma_{pe1}^2 + \sigma_{samp1}^2 - \sigma_{samp1samp2} \\179 \quad \sigma_{pe2}^{2*} &= \sigma_{pe2}^2 - \sigma_{pe1pe2} \\180 \quad \sigma_{samp2}^{2*} &= \sigma_{samp2}^2 - \sigma_{samp1samp2}\end{aligned}$$

181 The phenotypic variance components are then given by:

$$\begin{aligned}182 \quad \sigma_{total1}^2 &= \sigma_{u1}^2 + \sigma_{e1}^{2*} + \sigma_{e1e2}^* \\183 \quad \sigma_{total1total2} &= \sigma_{u1u2} + \sigma_{e1e2}^* \\184 \quad \sigma_{total2}^2 &= \sigma_{u2}^2 + \sigma_{pe2}^{2*} + \sigma_{samp2}^{2*} + \sigma_{e1e2}^*\end{aligned}$$

185 The variance components were estimated using the average-information restricted maximum likelihood  
186 method (AI-REML algorithm; Gilmour et al., 1995). Reported heritabilities are means calculated with all  
187 bivariate analyses. The fixed effects in the model include the genetic line to account for their mean  
188 differences (levels: R+ or R-) although we assume (because preliminary analyses indicated) that the  
189 variance components do not differ between, the effect of the batch (levels: 2019 or 2021) and the  
190 regression coefficient for the time of recording for the repeated trait. See the provided scripts  
191 “BEDERE\_2023\_ASREMLScript\_bivariate\_2x2strata.as”, “[...]3x3strata.as”, and “[...]3x2strata.as” for  
192 details.

### 193 *Bartlett’s test*

194 Descriptive statistics of the data suggested a bimodal distribution of backfat. This type of distribution may  
195 highlight the presence of a major gene controlling the trait. A simple test to detect a major gene effect on  
196 a trait is to test the homogeneity of the variances between families (Le Roy and Elsen, 1992). A Bartlett test  
197 was performed to test this hypothesis, using the sire as the family identifier (Bartlett, 1937). See the  
198 provided script “BEDERE\_2023\_RScript\_BartlettTest.R” for details.

### 199 *Programs used*

200 Data handling, graphs, and the Bartlett test were performed in base R (R Core Team, 2023). Variance  
201 components and genetic parameters estimations were performed with the software ASReml 4.2 (Gilmour  
202 et al., 2021).



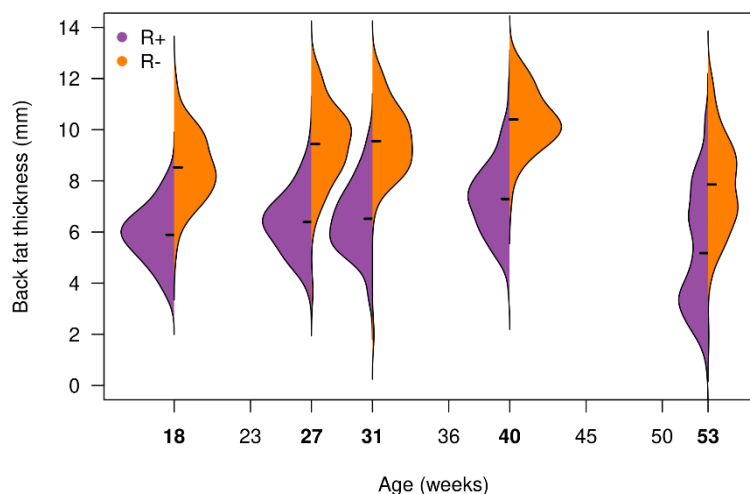
**Table 1:** Summary statistics for the traits studied, for both lines: R+ and R-.

Trait <sup>1</sup>	TotFat (mm <sup>3</sup> )	BackFat (mm)	BodyWeight (g)	Adiponectin (µg/ml)	Chemerin (ng/ml)	Ghrelin (ng/ml)	Visfatin (ng/ml)	TotEggNum (count)	
<i>Summary statistics of observed values</i>									
	number of records	111	580	771	233	233	233	192	
	mean	<b>540,367</b>	<b>6.1</b>	<b>2,339</b>	<b>2.4</b>	<b>39.5</b>	<b>57.0</b>	<b>158</b>	
R+	standard deviation	167,107	1.8	323	0.4	15.9	12.1	43	
	minimum	114,366	0.6	1,524	1.1	26.0	32.0	1	
	maximum	955,873	11.5	3,234	3.2	78.0	88.0	218	
	number of records	86	460	611	191	190	190	155	
	mean	<b>633,050</b>	<b>8.9</b>	<b>2,304</b>	<b>2.0</b>	<b>27.5</b>	<b>60.3</b>	<b>150</b>	
R-	standard deviation	141,608	1.8	351	0.4	11.9	14.3	56	
	minimum	380,231	1.9	1,375	1.0	3.0	34.0	0	
	maximum	1,087,374	12.7	3,465	3.2	68.0	112.0	194	
<i>Fixed effect of the genetic line estimated by the mixed models (R+ compared to R-)</i>									
	Estimated effect	-80,028	-3.11	22.57	0.33	12.13	-2.55	-1.78	-4.25
	P-value	0.23	<.001	0.82	0.40	<.001	0.84	0.74	0.82

<sup>1</sup>The traits are named after their phenotypes: BackFat for dorsal subcutaneous adipose tissue thickness, BodyWeight for body weight, TotFat for the total volume of pixels of fat components, then the blood Adipokines levels named after the appropriate adipokine, and TotEggNum for the total number of eggs laid.

### 208 Phenotypic description of the divergent lines

209 The two lines used, diverging for RFI, were very different regarding backfat thickness and chemerin  
 210 blood concentration (Table 1, Figure 3): the R- line had a larger backfat (+34%) and lower chemerin levels  
 211 (-31%) than the R+ line. However, the lines were not significantly different regarding TotFat, BodyWeight,  
 212 Adiponectin, Ghrelin, Visfatin, and TotEggNum. Fort the P-value for TotFat which is 0.23, given the  
 213 difference in mean and the variance, there may be some lack of power in the analysis due to the fact that  
 214 the tomography could be performed one batch only. Previous studies about these lines reported that the  
 215 R+ line (inefficient ones) has a higher feed intake, higher diet-induced thermogenesis and different  
 216 endocrine responses, resulting in different lipid metabolism between the lines (Gabarrou et al., 2000, 1998,  
 217 1997; Swennen et al., 2007) which could explain the observed differences in adiposity between lines.  
 218 Interestingly, in pigs, the selection on residual feed intake was also associated with a difference in backfat  
 219 with the efficient line being fatter, although the magnitude of difference was smaller (Gilbert et al.,  
 220 2017).The results on fat content observed in our study corroborate previous results about the R+ and R-  
 221 lines, with the R+ being liner than the R-. However, contrary to our expectation, no differences were  
 222 observed in the blood level of adiponectin and ghrelin, which are hormones associated with feed intake  
 223 acting as appetite-regulating signals (Mellouk et al., 2018a).



224

225 **Figure 3:** Distribution of the raw values for BackFat according to age in both lines. R+ are in purple on the  
 226 left side of the beanplot, R- are in orange on the right side of the beanplot. The dash is the mean for each  
 227 level.

### 228 BackFat thickness is an indicator of body reserves

229 BackFat and TotFat were genetically highly positively correlated, and phenotypically moderately  
 230 positively correlated (Table 2). Previous studies reported a high phenotypic correlation between BackFat  
 231 and TotFat in chicken ( $r > 0.84$ ; Mellouk *et al.* 2018; Grandhaye *et al.* 2019) but neither heritability, nor

232 phenotypic and genetic correlations with other traits of interest were calculated.. The lower phenotypic  
 233 correlation reported in Table 2 takes into account the effects of the model, which can influence the  
 234 correlation estimate (genetic line, the batch, the repetition of recording, and the genetic and permanent  
 235 environment variances). When we repeated the estimation using the same approach as the previously  
 236 mentioned papers (i.e. Person correlation using raw data), we obtain a correlation value of 0.71 (0.77 in R+  
 237 and 0.60 in R-), which is consistent with the findings previously published.

238 BodyWeight and TotFat were also highly positively correlated. However, BackFat and BodyWeight were  
 239 moderately positively correlated. The overall results show that BackFat is a good indicator of fatness in  
 240 adult layers, consistent with previous findings in young broilers, where it exhibited a high phenotypic  
 241 correlation with the fat fraction from chemical analyses of the shredded body ( $r=0.92$ ) and the abdominal  
 242 fat pad weight obtained by dissection ( $r=0.86$ ; Mellouk *et al.* 2018). Given the genetic correlations between  
 243 BackFat, TotFat, and BodyWeight, we can conclude that BackFat and BodyWeight hold different  
 244 information related to fatness in chickens. Compared to TotFat, BackFat offers notable advantages as an  
 245 easy-to-record trait: it is fast to record, does not require the animal to be asleep, and can be done with a  
 246 portable machine. Our results combined with these technical aspects, make BackFat a very good indicator  
 247 trait of fatness in chicken.

248 **Table 2:** Mean heritability estimates (in diagonal together with their associated mean standard errors),  
 249 genetic correlation estimates (below the diagonal together with their associated standard errors), and  
 250 phenotypic correlations (above the diagonal with their associated standard errors).

	TotFat	BackFat	BodyWeight	Adiponectin	Ghrelin	Visfatin	TotEggNum
TotFat	<b>0.27</b> ( <b>0.04</b> )	0.39 (0.04)	0.54 (0.04)	-0.24 (0.06)	-0.32 (0.06)	-0.06 (0.07)	-0.01 (0.09)
BackFat	0.91 (0.13)	<b>0.38</b> ( <b>0.06</b> )	0.31 (0.04)	-0.18 (0.08)	-0.23 (0.07)	-0.07 (0.06)	-0.01 (0.06)
BodyWeight	0.67 (0.16)	0.39 (0.12)	<b>0.42</b> ( <b>0.08</b> )	-0.24 (0.07)	-0.28 (0.07)	-0.08 (0.07)	-0.17 (0.05)
Adiponectin	-0.37 (0.15)	-0.28 (0.22)	-0.42 (0.18)	<b>0.92</b> ( <b>0.02</b> )	0.39 (0.05)	-0.03 (0.06)	0.01 (0.08)
Ghrelin	-0.80 (0.16)	-0.44 (0.20)	-0.39 (0.18)	0.41 (0.06)	<b>0.91</b> ( <b>0.02</b> )	0.17 (0.06)	0.11 (0.08)
Visfatin	-0.32 (0.19)	-0.19 (0.13)	-0.26 (0.21)	-0.05 (0.07)	0.18 (0.07)	<b>0.80</b> ( <b>0.03</b> )	0.27 (0.06)
TotEggNum	-0.49 (0.34)	-0.34 (0.32)	-0.82 (0.19)	0.02 (0.16)	0.20 (0.20)	0.36 (0.15)	<b>0.24</b> ( <b>0.05</b> )

251 **Genetic background of BackFat thickness**

252 BackFat displayed a moderate heritability (Table 2). The distribution of the values for BackFat in both  
 253 lines displayed a large variance, with apparently two modes, which seems to become exacerbated with  
 254 time (Figure 3). The sire-family variances were heterogeneous according to the Bartlett test (P-  
 255 value=0.008). Both the multimodal distribution and the heterogeneity of sire-family variance are evidence  
 256 of a major gene effect (Le Roy and Elsen, 1992).

257 In quails, a study reported a low heritability of 0.17 for fat skin percentage (recorded as the fat content  
258 of the shredded skin) as an indicator similar to BackFat (Lotfi et al., 2011). In pigs, BackFat displayed a high  
259 heritability (from 0.63 to 0.72; Cai et al., 2008; Gilbert et al., 2007; Suzuki et al., 2005) while in cattle,  
260 BackFat presented moderate ones (from 0.36 to 0.59; Arnold et al., 1991; Nkrumah et al., 2007; Schenkel  
261 et al., 2004). Many quantitative trait loci (QTL) associated with fatness in chickens are reported: there are  
262 129 QTL listed in chickenQTLdb (<https://www.animalgenome.org/QTLdb/chicken/>) from 69 scientific  
263 articles. Some genes are known to be involved in lipogenesis and differently expressed in lean and fat  
264 broilers (Bourneuf et al., 2006; Resnyk et al., 2017). Yet, major genes for BackFat were not explicitly  
265 identified, further analyses including segregation analyses and genome-wide association studies  
266 accounting for dominant effects would help to identify them.

### 267 **Genetic background of other traits related to fatness**

268 Moderate heritabilities were observed for TotFat and BodyWeight (Table 2), with the latter aligning with  
269 previous studies reporting estimates ranging from 0.32 to 0.53 (Rowland et al., 2019; Wolc et al., 2011,  
270 2009). Heritability in the R+ and R- lines may have changed a little because estimates for BodyWeight were  
271 reported to be 0.56 and 0.61 in females and males respectively in the 15 first generations (Tixier-boichard  
272 et al., 1995). Carcass percentage of fat displayed a moderate heritability in other studies using other  
273 chicken lines (0.43 to 0.55; Moreira et al., 2018; Nunes et al., 2011).

274 The chosen adipokines in this study are known to be indicators of body reserve status and dynamics  
275 (review: Mellouk et al., 2018a). Adiponectin is used as an indicator of energy deficit: the leaner the bird the  
276 higher the level of adiponectin. Chemerin is used as an indicator of body lipid mobilization: the lower the  
277 abdominal fat pad, the higher the level of chemerin. Ghrelin is used as an indicator of general body reserves  
278 accretion: it is known to stimulate intake and growth hormone release. Visfatin is acting like a myokine in  
279 birds (Krzysik-Walker et al., 2008) and it is used as an indicator of lean body reserve status compared to  
280 body lipid reserves. The genetic background, particularly the genes coding for these proteins are well  
281 described. All adipokines except chemerin displayed very high heritability (Table 2). This indicates that  
282 genetics is the primary source of phenotypic variation, and that environmental fluctuations have minimal  
283 influence in our setup, where hens are housed in individual cages and fed *ad libitum*. Genetic parameters  
284 for chemerin could not be estimated because the estimated additive genetic variance was too close to the  
285 zero boundary. This means that almost none of the observed variance is due to genetics, despite a  
286 phenotypic coefficient of variation close to 40%. We hypothesize that there may be a single haplotype per  
287 line in the population, explaining why there is no genetic variance observed despite a significant difference  
288 in mean between the lines. Consequently, no genetic correlation with other traits could be estimated  
289 (explaining why chemerin is not in Table 2).

290 Adiponectin displayed a moderate and positive genetic correlation with Ghrelin, no correlation with  
291 Visfatin and TotEggNum, and moderate and negative genetic correlations with TotFat, BackFat, and

292 BodyWeight. This is consistent with its role in chicken: increased blood level of adiponectine is associated  
293 with decreased lipid deposition, decreased body weight and increased feed intake (Mellouk et al., 2018a).  
294 Ghrelin displayed low and positive genetic correlations with Visfatin and TotEggNum, moderate and  
295 negative genetic correlations with BackFat and BodyWeight, and a high and negative genetic correlation  
296 with TotFat. This is consistent with its role in chicken: increased blood level of ghrelin is associated with  
297 decreased feed intake and increased lipolysis (Murugesan and Nidamanuri, 2022). These correlations  
298 further support BackFat as a good indicator trait for fatness and energy reserves in chickens. Chemerin  
299 levels were significantly higher in the R+ line, which is consistent with the fact that it is associated with  
300 lower body fatness (Mellouk et al., 2018a). Visfatin displayed a low and positive genetic correlation with  
301 TotEggNum, and low-to-moderate and negative genetic correlations with TotFat, BackFat, and  
302 BodyWeight. We were expecting a lower genetic correlation between visfatin and fat-related traits given  
303 its biological function: visfatin is acting like a myokine in chicken (Krzysik-Walker et al., 2008). Increased  
304 blood levels of visfatin are associated with increased feed intake and body weight (lean part; Mellouk et  
305 al., 2018a). It is important to note the high standard errors reported for genetic correlations between  
306 adipokines and other traits, pinpointing they could gain from additional data.

#### 307 **Tradeoff between body reserves and egg production**

308 TotEggNum displayed a moderate heritability (Table 2). This phenotype is capturing two distinct  
309 biological processes: puberty (age at first laying) and laying rate. Total egg number displayed a low  
310 heritability in other studies (from 0.01 to 0.20; Bedere et al., 2022; Liu et al., 2019; Wolc et al., 2011a), but  
311 in most papers the early period (before 25 weeks of age) is skipped to start recording after the laying peak.  
312 Again, the same trait in the first 15 generations was reported to be more heritable ( $h^2 = 0.48$ ; Tixier-  
313 boichard et al., 1995).

314 TotEggNum genetic correlation was moderate and negative with BackFat, and high and negative with  
315 BodyWeight (Table 2). The few studies mentioning genetic correlations between egg production and body  
316 weight reported moderate and negative correlations (-0.29 to -0.42; Yoo et al., 1988) or no correlation  
317 (Wolc et al., 2011b). The very high value estimated in our study may be a specificity of the R+ and R- lines.  
318 Both the size and fatness are optimum-based breeding goals: a targeted neither too big nor too small size  
319 and fatness are desired, whereas egg production is mostly maximized. This means that the selection index  
320 must consider these genetic correlations to combine selection criteria such as TotEggNum, BackFat, and  
321 BodyWeight to breed multi-performing laying hens.

322

323

## Conclusion

324 To conclude, this study showed, on two Rhode Island lines diverging for feed efficiency differing also in  
325 fat content, that backfat thickness is an accurate indicator of the overall fatness of laying hens. Backfat  
326 thickness can be recorded repeatedly during the production cycle, creating opportunities to better  
327 understand body reserve dynamics in chickens. In addition, backfat thickness displayed a moderate  
328 heritability, implying that there is room for genetic improvement, probably canalization around an  
329 optimum to be defined. Both the bimodal distribution of the trait and the heterogeneity of the variances  
330 between families are signs of the presence of a major gene segregating backfat thickness in the population.  
331 The genetic correlation with body weight was moderate, implying that backfat holds complementary  
332 genetic information about fatness that is currently not considered in breeding programs including body  
333 weight in their breeding goal. Finally, the genetic correlation with egg production was moderate and  
334 unfavorable. This correlation should be taken into account to avoid undesired responses to selection. It is  
335 important to keep in mind that all the reported results are based on particular genetic lines, divergently  
336 selected since 1976 on the residual feed intake. They need to be confirmed on regular commercial genetic  
337 lines to consider backfat thickness in the breeding goal.

338

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344

## Ethics statement regarding animals

345 All data coming from living animals were recorded as part of the breeding program of INRAE Poultry  
346 experimental facility (UE PEAT, Nouzilly, France ; <https://doi.org/10.15454/1.5572326250887292E12>)  
347 conducted in compliance the French Ministry of higher education, research and innovation authorization  
348 (number agreement 02414.01). The traits involved are egg number, body weight, and backfat thickness.  
349 The other traits were recorded *post-mortem*, after the animals were euthanized in compliance with  
350 national regulations pertaining to livestock production and according to procedures approved by the  
351 French Veterinary Services. The traits involved are body composition by tomography, blood adipokines  
352 concentrations, and carcass traits (*e.g.* abdominal fat pad weight).

CRediT (Contributor Roles Taxonomy, <https://credit.niso.org/>)

Initials <sup>1</sup>	NB	JD	YB	CS	DG	FE	PLR	TZ	BR	FL	CR	MCI	MD	MCh	LG	AG
Conceptualization	✓	✓		✓	✓		✓	✓		✓						
Data curation	✓															
Formal Analysis	✓															
Funding acquisition	✓															
Investigation	✓	✓	✓	✓	✓	✓			✓	✓	✓	✓	✓	✓	✓	
Methodology	✓															
Project administration	✓															
Resources		✓	✓	✓	✓	✓										
Software																✓
Supervision	✓	✓		✓	✓		✓	✓								
Validation		✓	✓	✓	✓	✓	✓	✓								✓
Visualization	✓			✓		✓										
Writing – original draft	✓															
Writing – review & editing	✓	✓		✓			✓	✓								✓

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358 **Data, scripts, code, and supplementary information availability**

359 Data are available online: [link forthcoming upon acceptance](#)

360 Scripts and code are available online: [link forthcoming upon acceptance](#)

361 **Conflict of interest disclosure**

362 The authors declare that they comply with the PCI rule of having no financial conflicts of interest  
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527

529 **Appendix 1: Diet composition (AVRIL NUTRITION ANIMALE, Bruz, France)**

530 **Ingredients:** wheat, soybean meal, corn, sodium carbonate, dried and soluble corn distillers grains, barley,  
531 monocalcium phosphate, sodium chloride, soybean oil, soybeans, wheat bran, rapeseed meal.

532

533 **Additional feedstuff:** vitamins (A: 10 000 UI/kg, D3: 3 000 UI/kg, E: 21 UI/kg), oligoelements (iron sulfate:  
534 50.3 mg/kg, anhydrous calcium iodate: 1.5 mg/kg, copper sulfate: 10 mg/kg, manganese oxide II: 50 mg/kg,  
535 hydrated glycine manganese chelate 30 mg/kg, zinc oxide: 50 mg/kg, hydrated glycine zinc chelate  
536 30 mg/kg, sodium selenite: 0.3 mg/kg), amino-acids (L-lysine sulfate: 545 mg/kg), digestibility enhancer  
537 (endo-1.4-beta-xylanase: 560 TXU/kg, endo-1.4-beta-glucanase: 250 TGU/kg, 3-phytase: 5000 FTU/kg)  
538 other (lutein extract: 6.0 mg/kg, carotenoids: 4.6 mg/kg, canthaxanthine: 2.0 mg/kg), grappeseed dried  
539 extract, organic acids).

540

541 **Proximate analyses:** 17.3% protein, 3.2% cellulose, 2.3% fat, 13.0% ashes, 0.9% Lysine, 0.4% Methionine,  
542 3.9% calcium, 0.1% sodium, 0.4% phosphorus.