Unravelling the genetic architecture of persistence in production, quality, and efficiency traits in laying hens at late production stages

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Abstract (350 words max. Now at 349)

Background: The laying hen industry aims to extend production for the economic and environmental benefits it offers, while at the same time facing the challenges of declining egg production and quality in aging hens. To explore trait persistence, we studied 998 Rhode Island Red purebred hens from the Novogen nucleus. We recorded daily egg production from 70 to 92 weeks of age and measured individual feed intake twice a week for three weeks, starting at 70, 80, and 90 weeks, as well as body weight at the start and at the end of each feed intake recording period. Random regression models were used to study trait trajectories over time, and PCA and hierarchical clustering were applied to identify groups of hens based on estimated breeding values for the intercept and slope of traits trajectory.

Results: Results showed different aging trajectories among traits. Daily body weight variation, Haugh unit and yolk percentage showed persistence (i.e. stability) over the measured period. On the contrary, daily feed intake, residual feed intake, laying rate, egg mass, eggshell breaking

strength and stiffness decreased over time, while body weight, mean egg weight, eggshell colour and feed conversion ratio increased. To assess the feasibility of selecting for trait persistence, we estimated the genetic variance of the slope and its correlation with the intercept. We found that, for egg weight and eggshell colour, genetic variance of the slope was negligible, indicating that selection for persistence on these traits requires other means. On the contrary, the slope for other traits such as laying rate and residual feed intake showed significant additive genetic variance. Strong genetic correlations between trait estimates at different ages were also observed and heritabilities estimates were low to high depending of the traits and period.

Conclusion: The study explores hens' trait persistence from 70 to 92 weeks, suggesting potential for improved egg production persistence. Challenges arise from low genetic variances impacting the efficiency of the potential selection on persistence. Clustering analysis reveals distinctive response patterns to elongation of production and underlined that selecting for enhanced persistence of different traits will necessitate compromises in breeding goals.

Keywords: Persistence, genetic architecture, laying hens, egg production, egg quality, efficiency

Background

The egg production sector is an important player in food security as eggs represent one of the most affordable animal protein sources, worldwide. The projected development of global egg production over the next 10 years is of 1% increase per year, leading to an expected global production of 96 million tons in 2030 [1]. The layer breeding industry is looking for strategies to conciliate a constant increase in egg demand due to a growing human population, ever larger climatic and political constraints, and a new societal environmental and animal welfare awareness.

One promising strategy implemented to maintain profitability while remaining socially responsible and environmentally friendly is the extension of the laying period beyond 70 weeks of age. The practice of extending the laying period of commercial hens can offer numerous benefits. From an economic perspective, keeping hens beyond 70 weeks of age can yield significant gains by increasing the number of saleable eggs per hen and cushioning the non-productive period. With a longer laying cycle the unproductive periods are reduced, as well as the costs related to bird replacement, while higher revenue for egg producers due to increased egg production are expected. Additionally, keeping hens for a longer period can reduce the frequency of hen replacements, depopulation, and cleaning of the poultry unit, which can translate to lower costs and fewer resources needed in the long term [2]. Ethically, extending the laying period reduces the size of flocks and the number of hens that are sacrificed at the end of the production period. As shown in Great Britain, increasing of 25 units the number of eggs per hen during the production life will lead a reduction of the number of productive hens of 2.5 million birds per annum [3], that corresponds to a decreasing of the hen population in England of 7.6% [4]. Environmentally, reducing the number of layers flocks helps decrease feed requirements and associated environmental costs, such as energy and land use [5, 6]. It would

also contribute to reduce the eutrophication impact as it was estimated that nitrogen excretion decreases by around 1 g per dozen eggs for 10 weeks production extension [3].

Nonetheless, extending the production period is not without consequences, as it impacts both animal productivity and egg quality. Several studies have shown that egg production declines beyond 60 weeks of age at a rate of approximately 7 to 10 % every 10 additional weeks of laying cycle [2, 7, 8]. Therefore, at 100 weeks of age, laying rates of 65-70% are quite common in commercial laying hens [9, 10]. Another aspect to consider when extending the laying period is that egg weight increases with bird age whilst shell quality tends to deteriorate. This is evidenced by more fragile egg shell, a reduction in the Haugh unit (HU) [2, 11], and an increase in egg deformities [12]. The mean decrease in quality is also associated with an increase in the variability of egg quality [3], with nearly 25% of eggs being unmarketable [6]. Finally, body weight tends also to increase with the hen age and the gain in weight is often due to abdominal fat accumulation, which, if excessive, can negatively affect hens' reproductive performance [13, 14]. Furthermore, as egg production is a demanding process for the overall metabolism of laying hens, extending the production period may elevate the prevalence of metabolic diseases [3].

The decades of genetic selection of commercial lines of layers to improve laying rate, has resulted in a remarkable egg production improvement [15]. Research on the genetic architecture of traits related to egg production during early production periods up to 60 weeks of age is abundant. Studies have primarily focused on genetic improvement of the number of egg laid on the production period [12, 16–19], estimating the possibility of selection directly on laying curve [20], or identifying proxies for selecting on egg quality traits [21]. On the contrary, there is a scarcity of research concerning late production periods, despite the current priority to increase egg production through breeding for increased persistence in lay at later laying cycle stages [22].

While the concept of persistence in egg-laying hens is well known and has been discussed among scientists [23] , the literature on the genetic determinism of this trait remains limited [2, 20]. Previous research has mainly focused on the genetic architecture of egg production throughout the animals' productive life, examining either the whole production period [17, 24] or specific intervals within it [18], the former being the closest to the selection objective, while the latter being theoretically the best approach [25]. As a result, improving persistence has often involved increasing the number of eggs laid during these different periods. However, this approach does not consider the trait trajectory over time for each individual animal, which is essential for improving trait persistence. A way to select animals on traits that are measured sequentially is to use random regression models (RRM). These models make it possible to predict the trajectory of the animals' estimated breeding value for a given trait over time, and thus in particular to identify the most persistent individuals from a genetic point of view. Moreover, this approach allows selecting animals based on the complete pattern of performances rather than performances at specific times, that are often considered as multiple traits [26]. Random regression models are commonly used in dairy cattle evaluations [27–33], and their application to layer performance is less common and mainly restricted to egg production [20, 25, 34, 35]. In our study we applied RRM on a variety of traits in laying chickens measured from 70 to 92 weeks of age (weeks of age), a production period seldom studied, to i) investigate the dynamic of genetic parameters of egg production, egg quality, and feed efficiency traits over this period of time, ii) evaluate the potential of selecting animals on genetic random regression coefficient estimates to improve traits persistence after 60 weeks of age ; iii) identify specific hen types based on their traits' persistence.

Materials and Methods

In this study we employed random regression models to analyse the dynamics of variance components and breeding values for the traits over time. This approach allowed us to investigate individual reactions to prolonged production periods and identify potential strategies for selecting chickens with enhanced persistence.

Birds and farming system

This study used 998 hens from a Rhode Island Red Line selected for egg production and quality, body weight and feather pecking, from the nucleus of the Novogen breeding company (Pledran, France). The hens were produced in two consecutive batches of 501 and 497 animals. The hens were reared on floor pens up to 17 weeks of age. After that, all hens from the first batch and 377 from the second one were transferred in a barn with collective cages of full sibs (five birds per cage), while the remaining 120 animals from the second batch were transferred in a barn with floor pens. At 55 weeks, all animals were moved to individual cages until they were slaughtered at 93 weeks of age. The collective cages had a living area containing food and water, while the floor system had nests overlaid in two rows.

The animals were fed *ad libitum* a commercial laying diet (11.47 MJ/kg metablolizable energy, 16.5% of crude protein, 3.70% of Ca) and the lighting regime was the standard 16h of light and 8h of darkness and ambient temperature in the barn was kept at 20°C constant.

To ensure precise pedigree records, we traced the relationship between animals over at least five generations. This allowed to retrace a pedigree encompassing 27390 animals, organized into sire-based families with an average of 22 offspring per sire and 5 offspring per dam. For our study, this translates to an average of 27 sires and 111 dams per batch.

Traits recorded

A large range of traits were recorded between 70 and 92 weeks of age and they are summarised in Figure 1. Egg production was recorded daily from 70 weeks to 92 weeks of age. Laying rate (LR) was calculated weekly by dividing the number of eggs laid during the considered week (EggLaid) by 7 and multiplying the result by 100. Laying rates below 50% were considered as outliers and removed from the analysis. Individual feed intake (FI) was measured during three periods of three weeks each, starting at 70, 80, and 90 weeks of age (i.e. from 70 to 82 wk, from 80 to 82 wk and from 90 to 92 wk). Feed intake was recorded twice a week, every 3-4 days, by weighing the individual feeders. The weekly feed intake (WFI) and daily feed intake (DFI) were calculated as follows:

$$WFI_{ij} = \sum_{r=1}^{2} FI_{ijr}$$

$$DFI_{ij} = \frac{WFI_{ij}}{7}$$

Where FI_{ijk} is the feed intake of animal i during the week j for the weekly recording records r .

Body weight (BW) was measured for every hen at the start and end of each period of 3 weeks (at 70, 72, 80, 82, 90 and 92 weeks of age). The egg weight (EW) was recorded daily from 70 weeks of age to 92 wk and the mean egg weight (MEW) was determined for each week by averaging the weight of eggs laid during each recorded week.

The egg mass (EGGM) and feed conversion ratio (FCR) were calculated weekly as follows:

$$EGGM_{ij} = EggLaid_{ij} * MEW_{ij}$$

$$FCR_{ij} = \frac{WFI_{ij}}{EGGM_{ij}}$$

where $EggLaid_{ij}$ is the number of eggs laid, $MEWij$ the mean egg weight and WFI_{ij} the weekly feed intake for the animal i on the week j.

Daily body weight variation (DBWV) and residual feed intake (RFI) were calculated for each of the three feed recording periods. DBWV was calculated as the difference between the body weight measured at the end and at the start of the 3-week feed intake measure period, divided by 21, as described in the formula:

$$DBWV_{ik} = \frac{BWend_{ik} - BWstart_{ik}}{21}$$

with $BWend_{ik}$, $BWstart_{ik}$, being the body weight for the animal i recorded at the end and at the start of the period k.

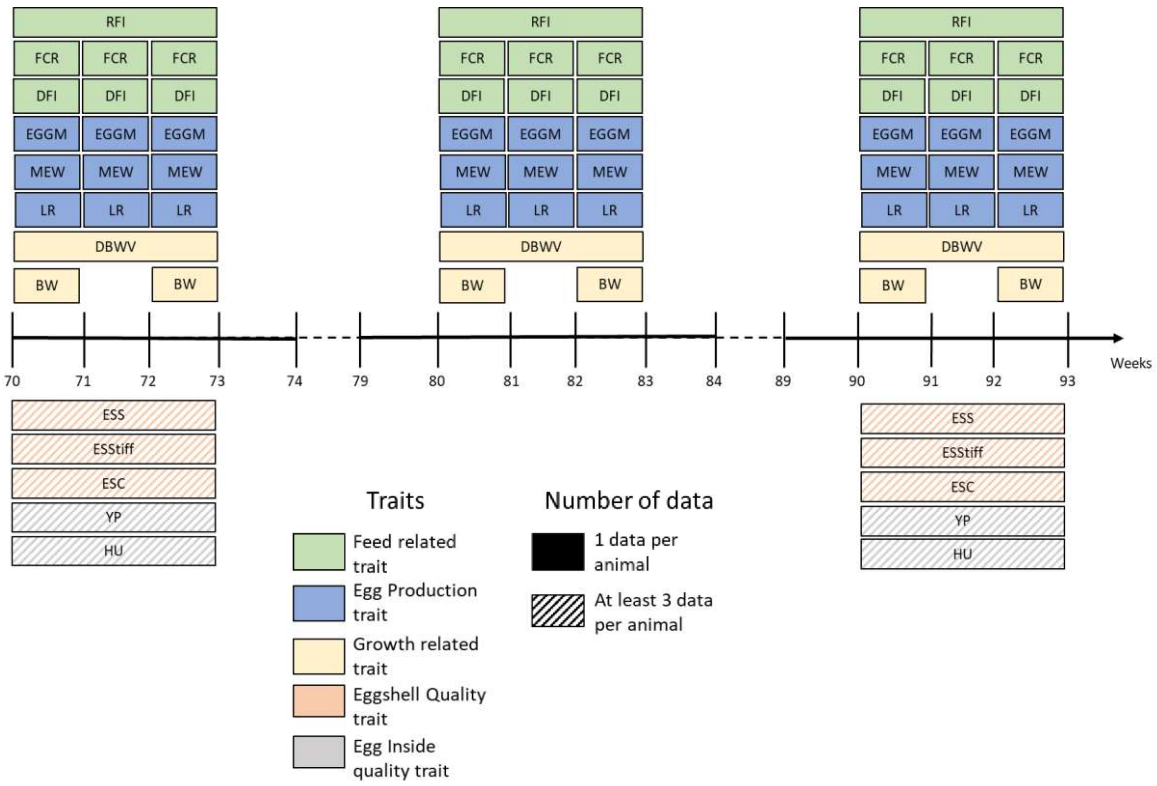
For each of the 3-week recording periods k for every individual animal i, the Residual Feed Intake (RFI_{ik}) was computed as the difference between the overall feed intake throughout the period (calculated as the sum of the three recorded WFI_{ij} values for period k) and the corresponding predicted feed intake (PFI_{ik}) for the same period ($RFI_{ik} = \sum_{j=1}^{3} WFI_{ijk} - PFI_{ik}$). The predicted feed intake was determined through a multiple regression equation detailed in references [36, 37]. This equation, applied to all hens, utilized three independent variables recorded during the respective 3-week periods (70-72; 80-82; 90-92 weeks of age): mean body weight (BW_{meanik}), $DBWV_{ik}$, and egg mass ($EGGM_{ik}$). The equation's parameters underwent adjustment using the *nls* function in the R programming language [38], and the equation was fitted to the combined data of all animals over the three 3-week periods :

$$RFI_{ik} = \sum_{j=1}^{3} WFI_{ijk} - (33.06 * (BWmean_{ik})^{\frac{1}{2}} + 26.47 * DBWV_{ik} + 0.96 * \sum_{j=1}^{3} EGGM_{ijk} - 76.31)$$

Egg quality traits were measured by the Zootests company (Ploufragan, France) on at least three individual egg records per hen per period on the first and last 3-week recording periods.

Eggshell breaking strength (ESS) and egg shell stiffness (ESStiff) were measured by compressing eggs between two flat plates moving at constant speed, using a compression machine (model Synergie 200, MTS Systems Corporation, Minnesota, United-States). ESS is the maximum force recorded before eggshell fracture. ESStiff represents deformation of the shell under a constant force of 15 Newton. Eggshell color (ESC) was obtained by recording redness (a*), yellowness (b*) and lightness (L*) with a portable chromameter (model CR400, Konica Minolta, Osaka, Japan). Yolk percentage was estimated as the ratio between yolk weight and egg weight multiplied by 100 and the Haugh unit, was calculated using the formula by Haugh [39].

Fig. 1 : Summary of the data used in the study.



Models

Weekly phenotypes over the 3 3-week recording periods were analysed with random regression models, whose variance components were estimated with an average information restricted maximum likelihood (REML) method [40, 41], using the ASRemL software [42]. To do so, we modelled the trajectory of the traits with first degree polynomials, over the three recording periods, our aim being to study the persistence of the performances rather than perfectly modelling their kinetics. The model fitted for all the traits is the following :

$$y_{ijlmn} = \mu + DOB_l + ENVT55wk_m + PosCage_n + \beta_1 t_{ijlmn} + p_{int_i} + p_{slp_i} t_{ijlmn} + a_{int_i} + a_{slp_i} t_{ijlmn} + e_{ijlmn} \quad (1)$$

where y_{ijlmn} represents the dependent variable for the hen or egg *i* of the batch *l,* from the rearing system *m,* and cage position *n* on the week *j*, μ the intercept, DOB_l the fixed effect of the date of birth of animals in the batch *l*, $ENVT55wk_m$ the fixed effect of rearing system before 55 weeks (*m* = floor or collective cage), $PosCage_n$ the fixed effect of the cage location in the barn (n = 1:32, each value identifying a sequence of 16 cages), β_1 the fixed regression coefficient of the animal's age t (which is the environmental gradient of the reaction norm, from t_{70w}= 0 to t_{92w}= 22). For egg quality phenotypes an additional fixed regression coefficient, whose covariate was the time span between the day of egg lay and the day of quality measurement, was added to the model. The linear function modelling the random permanent environmental effect of the animal *i* is $(p_{int_i} + p_{slp_i} t_{ijmn})$, where p_{int_i} and p_{slp_i} are the random intercept and random slope of the random regression on the age t, respectively, with $\begin{bmatrix} p_{int} \\ p_{slp} \end{bmatrix} \sim N\left(\binom{0}{0}, \boldsymbol{I} \times \begin{bmatrix} \sigma^2_{p_{int}} & \sigma_{p_{int}, p_{slp}} \\ \sigma_{p_{int}, p_{slp}} & \sigma^2_{p_{slp}} \end{bmatrix} \right)$,

where **I** is the identity matrix, σ^2_{pint} is the permanent environment variance for the intercept

term, σ^2_{pslp} the permanent environment variance for the slope term, and $\sigma_{pint,pslp}$ the permanent environment covariance between intercept and slope term.

Similarly, $(a_{int_i} + a_{slp_i} t_{ijkl})$ models the random additive breeding value of animal i, where a_{int_i} and a_{slp_i} are the random intercept and random slope of the random regression on the age t, respectively, with

$$\begin{bmatrix} a_{int} \\ a_{slp} \end{bmatrix} \sim N\left(\binom{0}{0}, \boldsymbol{A} \times \begin{bmatrix} \sigma^2_{a_{int}} & \sigma_{a_{int},a_{slp}} \\ \sigma_{a_{int},a_{slp}} & \sigma^2_{a_{slp}} \end{bmatrix} \right),$$

where **A** is the pedigree-based relationship matrix, σ^2_{aint} is the additive genetic variance for the intercept term, σ^2_{aslp} is the additive genetic variance for the slope term, and $\sigma_{aint,aslp}$ the covariance between the two aforementioned effects.

Finally, e_{ijkl} is the random residual effect, with

$$\begin{bmatrix} e_{70w} \\ e_{71w} \\ e_{72w} \\ e_{80w} \\ e_{81w} \\ e_{82w} \\ e_{90w} \\ e_{91w} \\ e_{92w} \end{bmatrix} \sim \boldsymbol{N}\left(\binom{0}{0}, \begin{bmatrix} I_{70w}\sigma^2_{e_{70w}} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & I_{71w}\sigma^2_{e_{71w}} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & I_{72w}\sigma^2_{e_{72w}} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & I_{80w}\sigma^2_{e_{80w}} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & I_{81w}\sigma^2_{e_{81w}} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & I_{82w}\sigma^2_{e_{82w}} & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & I_{90w}\sigma^2_{e_{90w}} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & I_{91w}\sigma^2_{e_{91w}} & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & I_{92w}\sigma^2_{e_{92w}} \end{bmatrix} \right)$$

where $\mathbf{I}_{70w}$ to $\mathbf{I}_{92w}$ are the identity matrices and $\boldsymbol{\sigma}^2_{e_{70w}}$ to $\boldsymbol{\sigma}^2_{e_{92w}}$ are the residual variances at the corresponding age of measure.

Significance of the genetic (co)variances has been tested by comparing our model with reduced models, by log-likelihood ratio tests, where either the genetic variances of a_{slp_i} or the genetic covariance between a_{int_i} and a_{slp_i} have been set to 0.

Genetic parameters

The additive genetic and permanent environment variances for a trait at the time t_1, ($\sigma^2_{a_{t_1}}$ and $\sigma^2_{p_{t_1}}$, respectively), and the genetic and permanent environment covariances for a trait between two times t_1 and t_2, along the gradient of t, ($\sigma_{a_{t_1},a_{t_2}}$ *and* $\sigma_{p_{t_1},p_{t_2}}$, respectively), have been computed using the formulas:

$$\sigma^2_{a_{t_1}} = \begin{bmatrix} 1 \\ t_1 \end{bmatrix}' G \begin{bmatrix} 1 \\ t_1 \end{bmatrix} \quad (2)$$

where $\begin{bmatrix} 1 \\ t_1 \end{bmatrix}$ is the vector containing the covariates of the additive random regression coefficients a_{int_i} and a_{slp_i} at recording time t_1, and $G = \begin{bmatrix} \sigma^2_{a_{int}} & \sigma_{a_{int},a_{slp}} \\ \sigma_{a_{int},a_{slp}} & \sigma^2_{a_{slp}} \end{bmatrix}$ is the matrix of genetic covariance estimates between the two additive genetic random regression coefficients. Equation (2) can be explicitly stated algebraically as:

$$\sigma^2_{a_{t_1}} = \sigma^2_{a_{int}} + 2\, t_1\, \sigma_{a_{int},\, a_{slp}} + {t_1}^2\, \sigma^2_{a_{slp}} \quad (2b)$$

Similarly,

$$\sigma^2_{p_{t_1}} = \begin{bmatrix} 1 \\ t_1 \end{bmatrix}' P \begin{bmatrix} 1 \\ t_1 \end{bmatrix} \quad (3)$$

where $P = \begin{bmatrix} \sigma^2_{p_{int}} & \sigma_{p_{int},p_{slp}} \\ \sigma_{p_{int},a_{slp}} & \sigma^2_{p_{slp}} \end{bmatrix}$ is the matrix of permanent environment covariance estimates between the two permanent environment random regression coefficients p_{int_i} and p_{slp_i}. Equation (3) can be explicitly stated algebraically as:

$$\sigma^2_{p_{t_1}} = \sigma^2_{p_{int}} + 2\, t_1\, \sigma_{p_{int},\, p_{slp}} + {t_1}^2\, \sigma^2_{p_{slp}} \quad (3b)$$

$$\sigma_{a_{t_1},a_{t_2}} = \begin{bmatrix} 1 \\ t_1 \end{bmatrix}' G \begin{bmatrix} 1 \\ t_2 \end{bmatrix} = \sigma^2_{a_{int}} + (t_1 + t_2)\, \sigma_{a_{int},a_{slp}} + t_1 t_2\, \sigma^2_{a_{slp}} \quad (4)$$

$$\sigma_{p_{t_1},p_{t_2}} = \begin{bmatrix} 1 \\ t_1 \end{bmatrix}' P \begin{bmatrix} 1 \\ t_2 \end{bmatrix} = \sigma^2_{p_{int}} + (t_1 + t_2)\, \sigma_{p_{int},p_{slp}} + t_1 t_2\, \sigma^2_{p_{slp}} \quad (5)$$

Using these measures of variance and covariance, the heritability of traits at various points and the genetic correlation between points along the gradient *t* were computed as follows:

$$h^2_{t_1} = \frac{\sigma^2_{a_{t_1}}}{\sigma^2_{a_{t_1}} + \sigma^2_{p_{t_1}} + \sigma^2_{e_{t_1}}} \quad (6)$$

with $\sigma^2_{e_{t_1}}$ the residual variance of the trait at point t_1.

$$r_{g_{t_1,t_2}} = \frac{\sigma_{a_{t_1},a_{t_2}}}{\sqrt{\sigma^2_{a_{t_1}} \sigma^2_{a_{t_2}}}} \quad (7)$$

Significance of the different correlations were tested using the method described in [43].

Production level at the start of period under study

In particular, equation (6) was applied at t_1=70 weeks of age, to calculate the heritability of the production level at the start of the period under study (h^2_{P70}).

Overall persistence weeks of age after 70 weeks of age

The overall persistence (OP) for a trait X was assessed through the average weekly evolution of the trait from 70 weeks of age to the end of the period under study t_{max} (90 weeks of age for RFI and DBWV and 92 weeks of age for the others traits), i.e. as

$$(X_{t_{max}} - X_{t_{70}}) \big/ (t_{max} - t_{70}) \quad (8)$$

Therefore, the genetic variance of OP was calculated as in [44]:

$$\sigma^2_{a_{OP}} = \frac{1}{(t_{max}-t_{70})^2}\left(\begin{bmatrix}1\\t_{max}\end{bmatrix}-\begin{bmatrix}1\\t_{70}\end{bmatrix}\right)' G\left(\begin{bmatrix}1\\t_{max}\end{bmatrix}-\begin{bmatrix}1\\t_{70}\end{bmatrix}\right) \quad (9)$$

Equation (9) can be simplified as :

$$\sigma^2_{a_{OP}} = \frac{1}{(t_{max}-t_{70})^2}\left(\begin{bmatrix}0\\t_{max}-t_{70}\end{bmatrix}\right)' G\left(\begin{bmatrix}0\\t_{max}-t_{70}\end{bmatrix}\right) = \sigma^2_{a_{slp}} \quad (9b)$$

Similarly, the permanent environment variance of OP was calculated as :

$$\sigma^2_{p_{OP}} = \sigma^2_{p_{slp}} \quad (10)$$

The residual variance of OP was calculated as:

$$\sigma^2_{e_{OP}} = \frac{1}{(t_{max}-t_{70})^2}\left(\sigma^2_{e_{t_{max}}}+\sigma^2_{e_{70}} - 2\sigma_{e_{70},e_{t_{max}}}\right) = \frac{1}{(t_{max}-t_{70})^2}\left(\sigma^2_{e_{t_{max}}}+\sigma^2_{e_{70}}\right) \quad (11)$$

under the same assumption as ASREML of no residual covariance between the phenotypes at 70 weeks of age and t_{max}. It can be assumed, however, that if the residual covariance were not zero, it would be positive, as the environmental effects included in the residual would likely affect measurements between 70 and 92 weeks in the same direction. The consequence could be an overestimation of $\sigma^2_{e_{OP}}$, and therefore perhaps a slight underestimation of h^2_{OP} calculated as:

$$h^2_{OP} = \frac{\sigma^2_{a_{OP}}}{\sigma^2_{a_{OP}}+\sigma^2_{p_{OP}}+\sigma^2_{e_{OP}}} = \frac{\sigma^2_{a_{slp}}}{\sigma^2_{a_{slp}}+\sigma^2_{p_{slp}}+\frac{1}{(t_{max}-t_{70})^2}(\sigma^2_{e_{t_{max}}}+\sigma^2_{e_{70}})} \quad (12)$$

Finally, the genetic correlations between the slope a_{slp} and the intercept a_{int} of the linear function modelling the additive genetic effect was calculated as:

$$r_{a_{int},a_{slp}} = \frac{\sigma_{a_{int},a_{slp}}}{\sqrt{\sigma^2_{a_{int}}\sigma^2_{a_{slp}}}} \quad (13)$$

with $\sigma^2_{a_{int}}$, $\sigma^2_{a_{slp}}$ and $\sigma_{a_{int},a_{slp}}$ being the genetic (co)variance estimates for the two additive genetic random regression coefficients a_{int} and a_{slp} .

Multivariate analysis

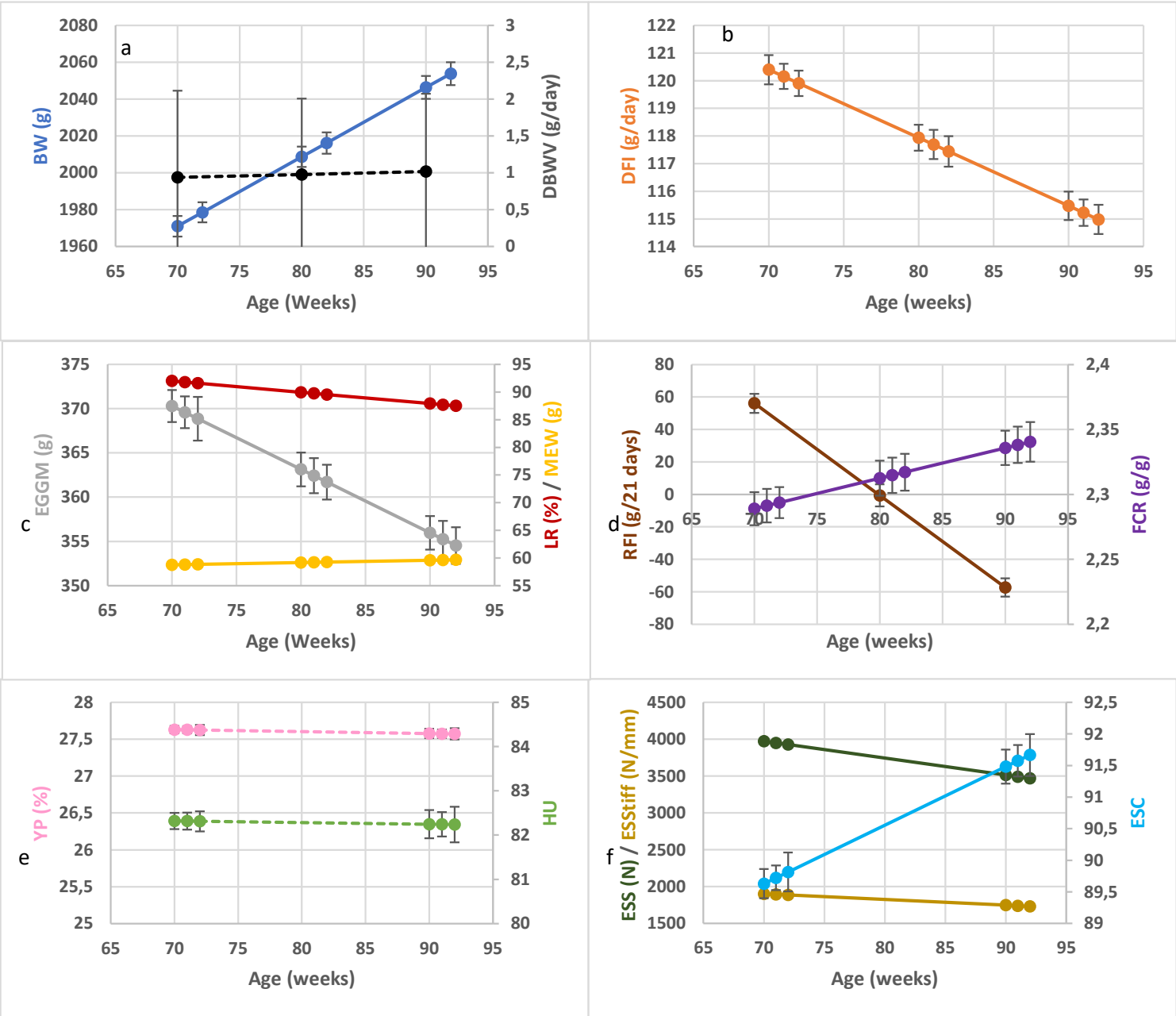
To understand the relationship between the persistence of various traits and pinpoint distinctive persistence clusters among the analysed hens, we used the *FactoMineR* package in R [44] on individual estimated breeding values (EBV) for intercept and slope for the analysed traits (i.e. the random regression coefficient estimates for intercept ($\hat{a}_{int_i}$) and slope ($\hat{a}_{slp_i}$)). We used the *PCA* function in *FactoMineR* package in R [44], to identify pattern of association between the EBV for the slope and intercept. To identify distinct persistence clusters, we used the *HCPC* function on the PCA coordinates of each hen persistence. We determined four persistence clusters based on a combination of inertia gain (more than 5% of the total inertia) and the number of animals within each cluster. The significance of the difference between groups has been tested by student tests, with a correction by False Discovery Rate applied to the obtained p values.

Results

Population average trajectories through time

The population average trajectories between 70 and 92 weeks of age, calculated as $\hat{\mu} + \hat{\beta}_1 t_j$ (with $\hat{\mu}$ and $\hat{\beta}_1$ being, respectively the estimates for μ and β_1 in model (1)), differed among traits (Figure 2). More specifically, persistence was observed for DBWV, HU, and YP, as their slopes were close to 0. Increasing trends with age were observed for BW, MEW, FCR and ESC as shown the positive slopes observed. On the other hand, significantly negative slopes were observed for the remaining traits

Fig. 2: Population average trajectories for BW and DBWV (a), DFI (b), EGGM, EW and LR (c), FCR and RFI (d), HU and YP (e), ESS and ESStiff and ESC (f). Coloured lines represent the mean trait, vertical black lines the standard error. Whole lines represent the traits where the slope is significantly different form 0. Dotted lines represent traits with the slope not significantly different from 0.



Genetic variances estimates for the intercept and slope of the random regression and heritabilities estimate for the production level at the start and the overall persistence

The genetic variance estimates of the slope term (σ^2aslp) were not significantly different from 0 for MEW and ESC. For the other traits, both the intercept and slope terms were significantly different from 0, as detailed in Table 1. For numerous traits, the genetic covariance between the two terms of the regression was non-significant. Among the significant ones, negative covariance between the slope and the intercept was identified for DBWV, RFI, EGGM, and ESS, resulting in negative correlations between these parameters. Conversely, the covariance between the slope and intercept for HU was positive, leading to a positive correlation between them.

Heritabilities estimated at the start of the analysed period (P70) were significantly different form 0 for all traits and ranged from 0.12, for DBWV, to 0.45, for BW. The heritability of the overall trait persistence (OP) was not significantly different from zero for MEW and ESC. For the other traits it was significant and ranged from 0.05 for ESS_{tiff} to 0.62 for RFI. For most traits, the h^2_{OP} was smaller than the $h^2_{P70,}$ while for RFI and DBWV it was notably larger.

Table 1 Variance components and heritability estimates for the intercept and the slope of studied characters and heritability estimates.

Traits	Genetic variance component estimates for the intercept and the slope				Heritabilities	
	σ^2_{aint}*	σ^2_{aslp}*	$\sigma_{aint,aslp}$*	$r_{aint,aslp}$*	h^2_{P70}*	h^2_{OP}*
BW	13810 ± 2842	2.95 ± 1.37	39.3 ± 46.20[1]	0.19 ± 0.23[1]	0.45 ± 0.08	0.08 ± 0.04
DBWV	1.59 ± 0.59	0.0136 ± 0.00	-0.14 ± 0.04	-0.97 ± 0.04	0.12 ± 0.04	0.20 ± 0.06
LR	16 ± 4.60	0.035 ± 0.01	-0.22 ± 0.19[1]	-0.30 ± 0.22[1]	0.14 ± 0.04	0.09 ± 0.03
MEW	7.0 ± 1.60	0.00024 ± 0.00[1]	0.003 ± 0.024[1]	0.07 ± 0.61[1]	0.35 ± 0.07	0.01 ± 0.02[1]
EGGM	837 ± 196	0.45 ± 0.19	-13.4 ± 5.30	-0.69 ± 0.17	0.27 ± 0.06	0.05 ± 0.02
DFI	48 ± 13	0.16 ± 0.04	-0.70 ± 0.60[1]	-0.26 ± 0.19[1]	0.17 ± 0.04	0.18 ± 0.04
FCR	0.02 ± 0.01	0.00002 ± 0.00	-0.0004 ± 0.00[1]	-0.59 ± 0.20[1]	0.13 ± 0.04	0.04 ± 0.02
RFI	14736 ± 3395	71.23 ± 11.52	-745.5 ± 173.8	-0.73 ± 0.08	0.43 ± 0.08	0.62 ± 0.08
HU	17.0 ± 3.8	0.05 ± 0.01	0.30 ± 0.20	0.34 ± 0.15	0.29 ± 0.06	0.23 ± 0.05
YP	1.60 ± 0.30	0.0008 ± 0.00	-0.004 ± 0.01[1]	-0.11 ± 0.19[1]	0.41 ± 0.07	0.12 ± 0.04
ESS	99963 ± 28643	131.92 ± 45.18	-2349.5 ± 936.1	-0.65 ± 0.15	0.19 ± 0.05	0.09 ± 0.03
ESStiff	23038 ± 5647	10.86 ± 5.19	-72.3 ± 129[1]	-0.14 ± 0.24[1]	0.25 ± 0.05	0.05 ± 0.02
ESC	25.40 ± 5.80	0.003 ± 0.00[1]	-0.14 ± 0.11[1]	-0.53 ± 0.34[1]	0.28 ± 0.06	0.01 ± 0.02[1]

[1]: Values with this superscript are not significantly different from 0

*: σ^2_{aint} and σ^2_{aslp} are the variance estimates for the intercept and slope terms of the additive genetic effect, $\sigma_{aint, aslp}$ is the covariance, $r_{aint, aslp}$ is the genetic correlation between the intercept and slope of the additive genetic effect, h^2_{P70} is the trait heritability at the start of the recording period (70 weeks of age) and the h^2_{OP} is the heritability of the overall trait persistence.

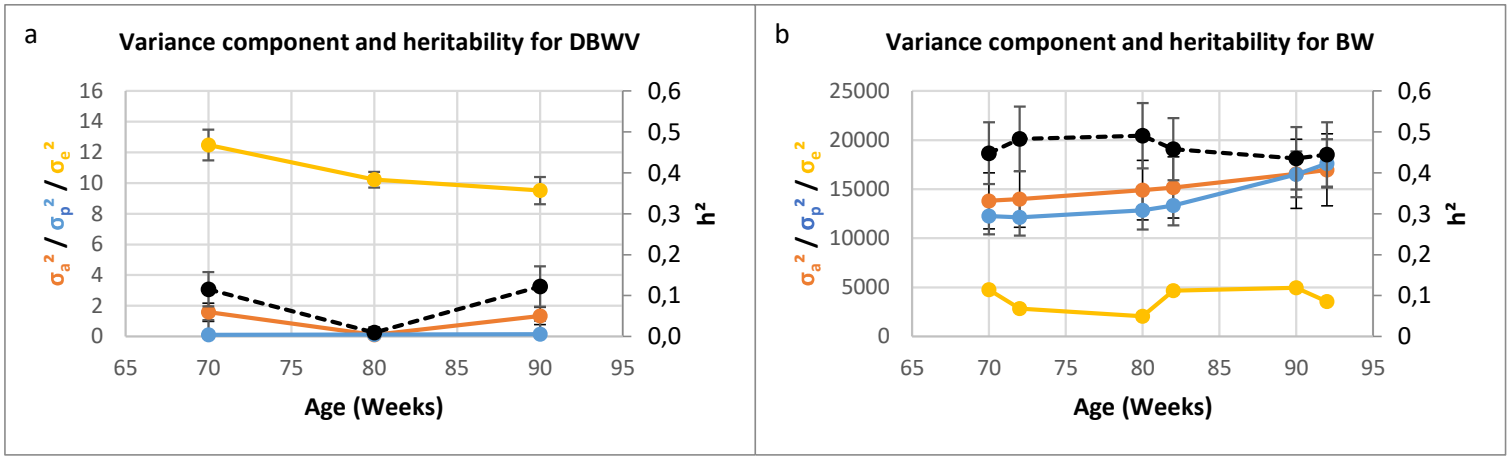
Trait genetic parameter estimation at different ages

Variance component and heritability estimates are represented in Figures 3 to 6 and data are summarised in Supplementary table 2.

For DBWV we found relatively modest heritabilities at 70 and 90 weeks of age (~0.12 (± 0.05)). At 80 weeks, the absence of significant genetic variance led to a heritability not significantly different from zero (Figure 3a). The permanent environment variance remained consistently low, while residual variance remained notably high across the entire period. In contrast, for BW a distinct variance pattern emerged, characterised by consistently low

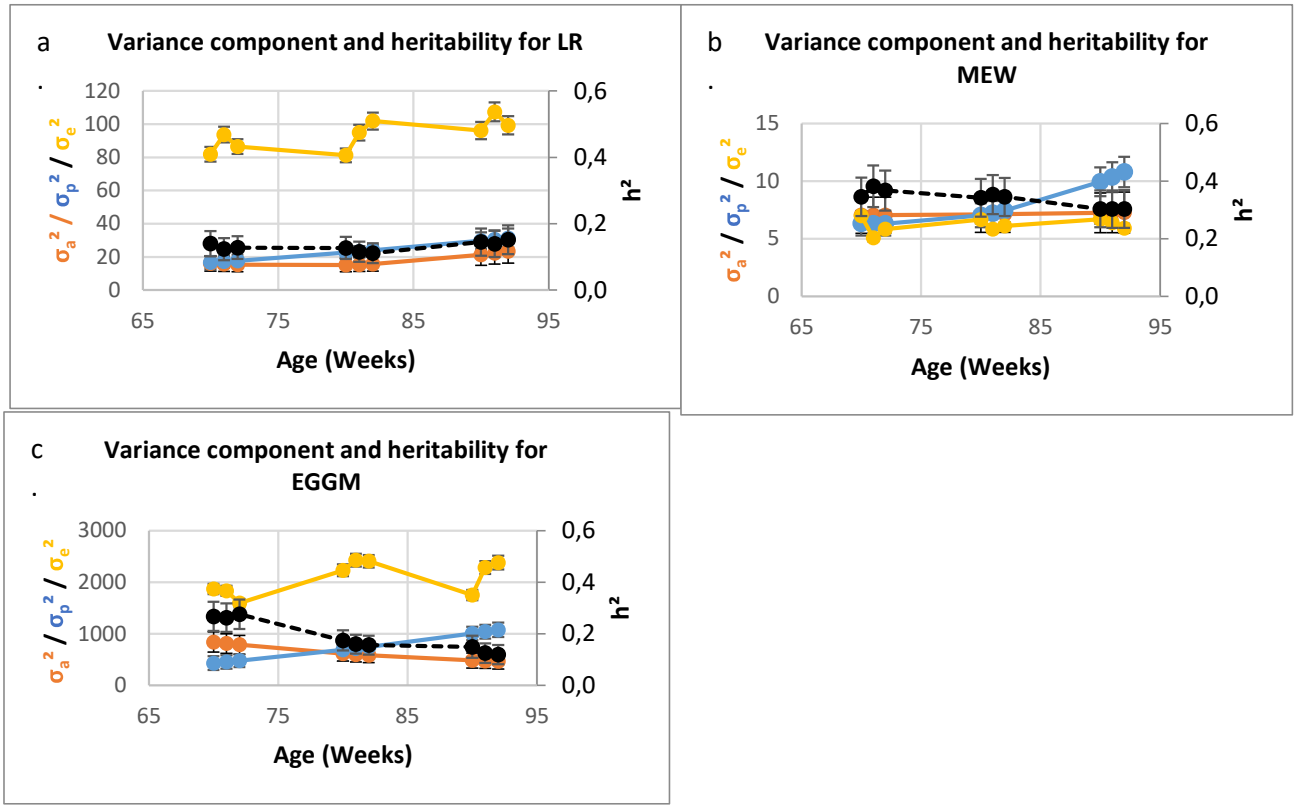
residual variance, and increasing genetic and permanent environmental variances over time. The heritability values across ages remained relatively stable, ranging between 0.45 and 0.50 (Figure 3b).

Fig. 3: Variance component and heritability for DBWV (a) and BW (b). Orange lines represent the additive genetic variances (σ_a^2), blue lines the permanent environment variances (σ_p^2), yellow line the residual variances (σ_e^2), dotted black line the heritability (h^2) and vertical black lines the standard error.



The heritability estimates for LR, were overall low (0.13 ± 0.03) and relatively stable across ages. The permanent environmental variance was higher than the genetic variance, particularly from 80 weeks onwards, and the residual variance was high throughout the period (Figure 4a). For MEW, a low but steady decrease in heritabilities was observed. Genetic and residual variances were overall stable, while, permanent environment variance increased after 81 weeks of age (Figure 4b). For EGGM a decrease of heritability was observed with age passing from 0.27 at 70 weeks of age to 0.12 at 92 weeks of age (Figure 4.c). Genetic variance was higher than the permanent environment variance up to 80 weeks of age, when the trend was inverted; the residual variance was high throughout the period. .

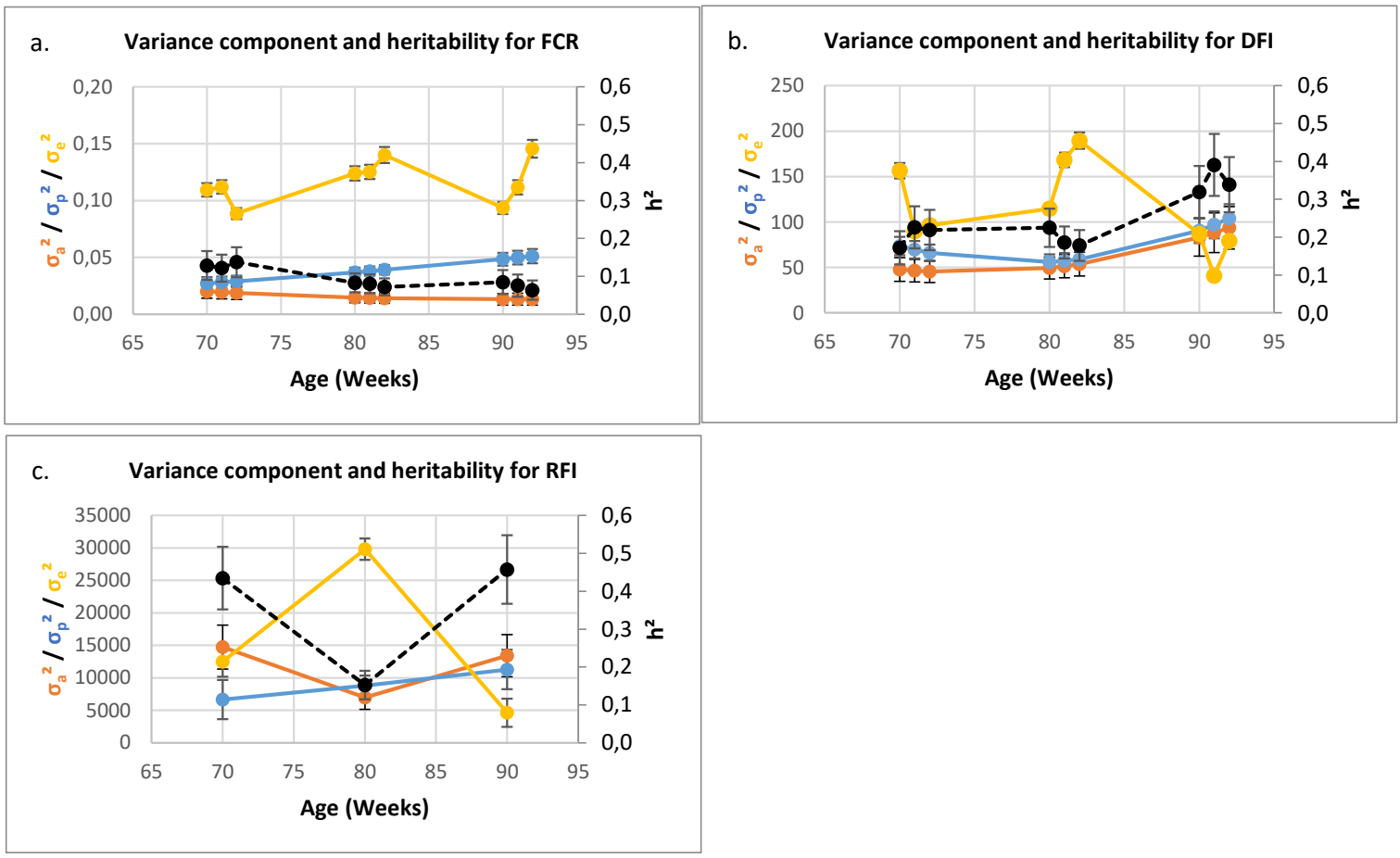
Fig. 4: Variance component and heritability for LR (a), MEW (b) and EGGM (c). Orange lines represent the additive genetic variances (σ_a^2), blue lines the permanent environment variances (σ_p^2), yellow line the residual variances (σ_e^2), dotted black line the heritability (h^2) and vertical black lines the standard error.



Feed-related traits presented high residual variance, particularly over the 80-82 period. The heritability of FCR showed a decline with advancing age, passing from 0.13 at 70 weeks of age to 0.06 at 92 weeks of age (Figure 5a). Throughout this period, genetic variance presented a decreasing trend, while the permanent environment variance showed an increasing one. The heritability of DFI remained stable between 71 and 80 weeks of age, experienced a dropped between 81 and 82 wk, followed by an increase during the 90-92 week period. Conversely, the residual variance displayed an opposite pattern, peaking between 81 and 82 weeks of age before declining in the 90-92 week period. Both genetic and the permanent environment variances increased during the period 82 and 92 week period. The pattern of variance components for RFI indicate similar patterns at 70 and 90 weeks of age with heritability

estimates round 0.45 and low residual variance. An inversed pattern was observed at 80 weeks with low heritability and high residual variance surpassing genetic variances (Figure 5c).

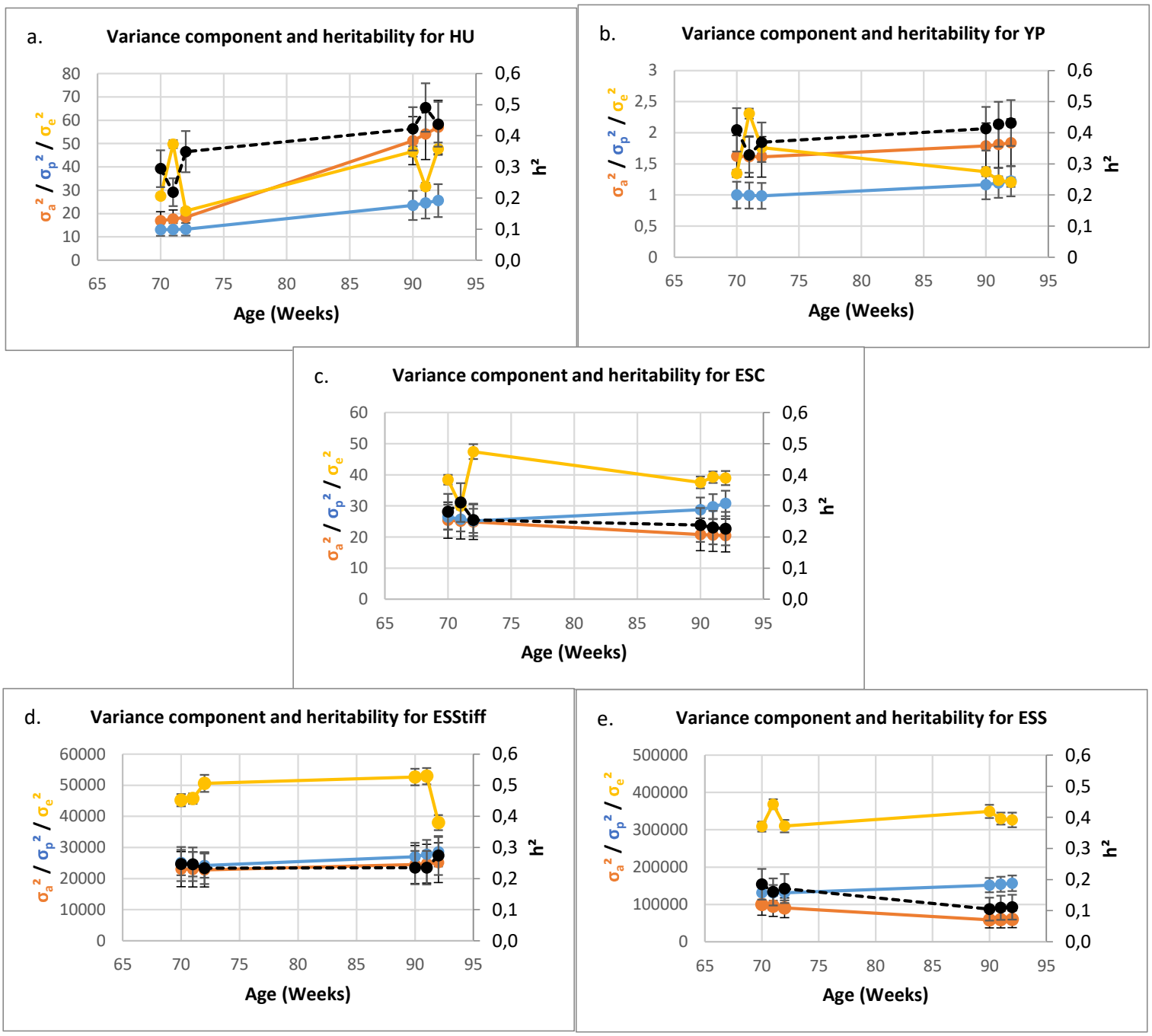
Fig. 5: Variance component and heritability for FCR (a), DFI (b) and RFI (c). Orange lines represent the additive genetic variances (σ_a^2), blue lines the permanent environment variances (σ_p^2), yellow line the residual variances (σ_e^2), dotted black line the heritability (h^2) and vertical black lines the standard error.



In terms of egg quality-related traits, both HU and YP exhibited an overall increase in heritability with age, and a genetic variance that was higher than the permanent environment and residual variances at 90 weeks of age (Figure 6a and Figure 6b). Eggshell quality traits

presented similar pattern of variance components, characterized by elevated residual variances and relatively low genetic variances. For ESC and ESS the heritability declined with age (Figure 6c and 6e), whereas for ESStiff, it remained relatively constant (Figure 6d).

Fig. 6: Variance component and heritability for HU (a), YP (b). ESC (c), ESStiff (d) and ESS (e). Orange lines represent the additive genetic variances (σ_a^2), blue lines the permanent environment variances (σ_p^2), yellow line the residual variances (σ_e^2), dotted black line the heritability (h^2) and vertical black lines the standard error.



Most genetic correlations for traits recorded at one week interval within each of the 3 recording periods were close to 1 (supplementary Figure 1).Therefore, in Table 2, we reported only the genetic correlation between traits recorded at 70, 80 and 90 weeks of age. For most traits, we observed a good degree of consistency in genetic effects between ages. This was not the case for DBWV that presented genetic correlations not significantly different from 0 in the comparison 70x80 and 80x90 and a strong negative genetic correlation in the comparison 70x90. A reduced genetic correlation at the 70 x 90 wk comparison is observed for LR, DFI and ESS and for RFI it was not significantly different from 0.

Table 2. Genetic correlations (± SE) between traits measured at different ages

Traits	70x80	80x90	70x90
BW	0.99 ± 0.01	0.99 ± 0.01	0.97 ± 0.02
DBWV	0.41 ± 0.45[1]	0.11 ± 0.57[1]	-0.86 ± 0.18
LR	0.89 ± 0.04	0.92 ± 0.04	0.63 ± 0.13
EW	1.00 ± 0.00	1.00 ± 0.00	0.99 ± 0.02
EGGM	0.98 ± 0.01	0.97 ± 0.02	0.9 ± 0.06
DFI	0.84 ± 0.05	0.91 ± 0.03	0.53 ± 0.13
FCR	0.95 ± 0.03	0.93 ± 0.04	0.77 ± 0.13
RFI	0.72 ± 0.08	0.69 ± 0.09	-0.01 ± 0.15[1]
HU	0.91 ± 0.03	0.97 ± 0.01	0.79 ± 0.06
YP	0.97 ± 0.01	0.98 ± 0.01	0.91 ± 0.03
ESS	0.94 ± 0.03	0.9 ± 0.05	0.69 ± 0.13
ESStiff	0.98 ± 0.01	0.98 ± 0.01	0.91 ± 0.05
ESC	1.00 ± 0.01	0.99 ± 0.01	0.98 ± 0.03

[1]: Values with this superscript are not significantly different from 0

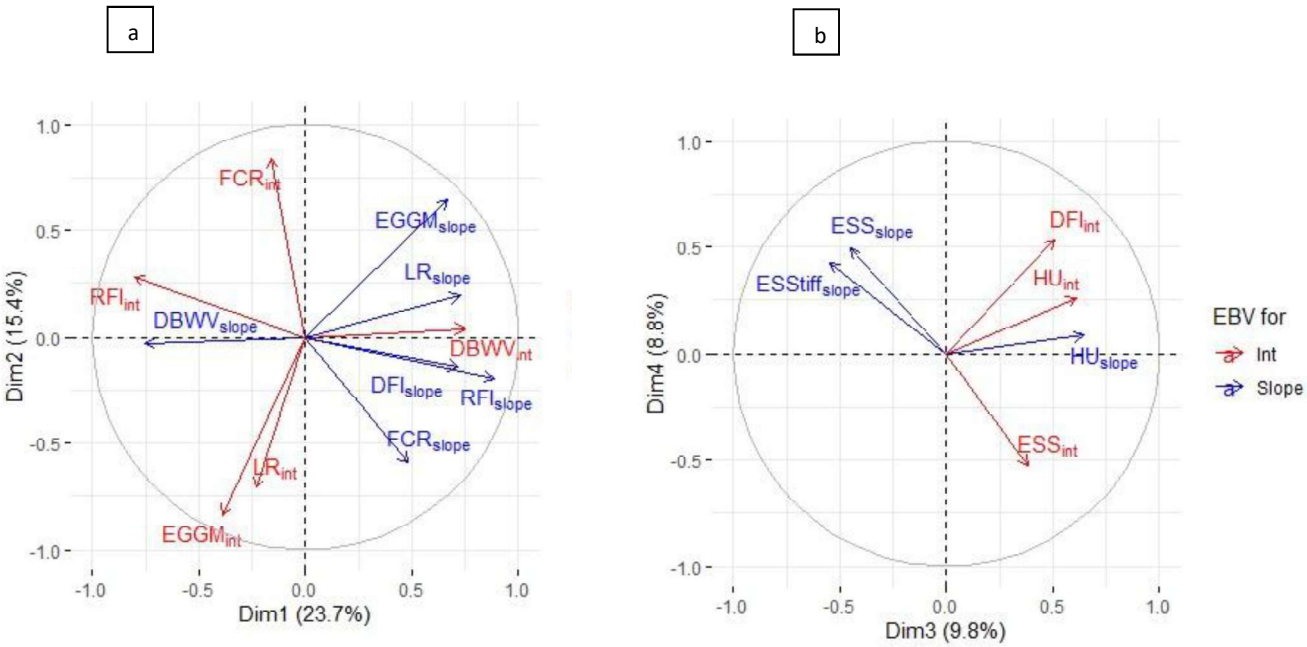
Principal component analysis and hierarchical clustering of individual breeding value estimated from the trait intercept and slope

The principal component was performed using the EBV estimated for each trait's intercept and slope but for clarity reasons, only traits having the strongest contribution to the principal components (PC) (cos^2 value above 0.5 with one of the different PC) were shown in Figure 7.

The first PC captured 23.7% of the variability and separated animals based on the EBV for the intercept and slope of DBWV and RFI, and the slopes of LR, EGGM and DFI. The second PC contributed to 15.4% of the variance and separated animals based on the EBV of the intercept of FCR, LR, and EGGM.

The third PC explained 9.8% of the variance, and separated animals based on the EBV of the intercept and slope of HU, the intercept of DFI and the slope of ESStiff . Finally, the fourth PC, explained 8.8% of the variance and separated animals based on the intercept and the slope of ESS .

Fig. 7: Correlation circles of PC1 and 2 (a) and of PC3 and 4 (b). Blue and red arrows represent the EBV of the slope and intercept of the traits, respectively.



The hierarchical clustering analysis allowed to identify four distinct clusters: cluster 1 included 247 animals, cluster 2 included 265 animals, cluster 3 included 350 animals, and cluster 4 included 135 animals. The cluster dendogram is presented in Figure 8a and the cluster mean EBV values for the intercept and slope of each trait are provided in the Table 3.

The projection of the four clusters on the first and second PC showed that the first axis primarily separated cluster 1 and 2 from the cluster 3 and 4, while the second mainly separated cluster 1 and 4 from clusters 2 and 3 (Figure 8b). The subsequent PC axes did not provide clear separation between clusters and were consequently not shown.

Fig. 8: Hierarchical clustering (a) and projection of the different clusters on the first and second principal components (b)

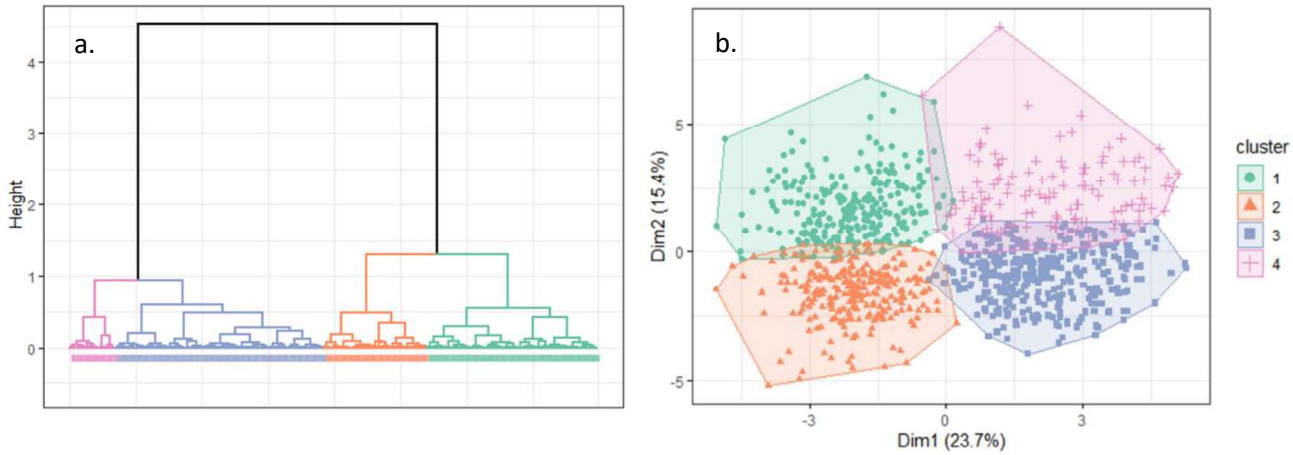


Table 3: Mean (± SE) estimated breeding values of the slope and intercept for the analysed traits, calculated from each of the 4 cluster groups identified by HPCP analysis

Traits	EBV	Cluster 1	Cluster 2	Cluster 3	Cluster 4
BW	Intercept	25.37 ± 5.66^{b}	-21.35 ± 5.53^{a}	13.5 ± 4.62^{b}	-39.5 ± 6.44^{a}
	Slope	0.53 ± 0.05^{c}	0.12 ± 0.04^{b}	-0.31 ± 0.04^{a}	-0.41 ± 0.08^{a}
DBWV	Intercept	-0.48 ± 0.03^{b}	-0.62 ± 0.03^{a}	0.61 ± 0.03^{d}	0.53 ± 0.06^{c}
	Slope	0.0478 ± 0.00^{c}	0.0571 ± 0.00^{d}	-0.0582 ± 0.00^{a}	-0.0487 ± 0.01^{b}
LR	Intercept	-1.16 ± 0.14^{b}	1.94 ± 0.1^{d}	0.52 ± 0.09^{c}	-3.03 ± 0.2^{a}
	Slope	-0.053 ± 0.01^{b}	-0.105 ± 0.00^{a}	0.07 ± 0.01^{c}	0.122 ± 0.01^{d}
EW	Intercept	-0.46 ± 0.12^{a}	0.35 ± 0.11^{b}	0.39 ± 0.10^{b}	-0.85 ± 0.17^{a}
	Slope	-	-	-	-
EGGM	Intercept	-7.8 ± 1.07^{b}	17.91 ± 0.81^{d}	2.68 ± 0.68^{c}	-27.81 ± 1.45^{a}
	Slope	-	-0.4 ± 0.01^{a}	0.11 ± 0.01^{b}	0.54 ± 0.03^{c}
DFI	Intercept	0.86 ± 0.29^{b}	-	-	-2.66 ± 0.36^{a}
	Slope	-0.2 ± 0.01^{a}	-0.15 ± 0.01^{b}	0.2 ± 0.01^{d}	0.15 ± 0.02^{c}
FCR	Intercept	0.0766 ± 0.00^{d}	-0.0511 ± 0.00^{a}	-0.0382 ± 0.00^{b}	0.0591 ± 0.00^{c}
	Slope	-0.0022 ± 0.00^{a}	-	0.0014 ± 0.00^{b}	-
RFI	Intercept	94.84 ± 4.32^{d}	39.2 ± 4.01^{c}	-82.39 ± 3.79^{a}	-36.87 ± 6.5^{b}
	Slope	-7.91 ± 2.65^{a}	-5.06 ± 2.68^{b}	7.42 ± 2.77^{d}	5.17 ± 3.94^{c}
HU	Intercept	-	-0.79 ± 0.21^{a}	-	1.07 ± 0.21^{b}
	Slope	0.01 ± 0.01^{b}	-0.06 ± 0.01^{a}	0.01 ± 0.01^{b}	0.08 ± 0.01^{c}
YP	Intercept	0.5 ± 0.05^{b}	-0.45 ± 0.05^{a}	-	-
	Slope	-0.007 ± 0.00^{b}	-0.0114 ± 0.00^{a}	0.0083 ± 0.00^{c}	0.0137 ± 0.00^{d}
ESS	Intercept	117.29 ± 11.06^{c}	-	-105.27 ± 8.41^{a}	60.24 ± 17.61^{b}
	Slope	-3.62 ± 0.38^{a}	-3.11 ± 0.33^{b}	4.88 ± 0.27^{c}	-
ESStiff	Intercept	58.05 ± 6.52^{c}	-36.43 ± 5.93^{a}	-24.09 ± 4.76^{a}	27.74 ± 8.65^{b}
	Slope	-0.29 ± 0.09^{a}	-	0.41 ± 0.08^{b}	-0.64 ± 0.16^{a}
ESC	Intercept	1.1 ± 0.23^{b}	-0.58 ± 0.22^{a}	-	-
	Slope	-	-	-	-
Number of animals		247	265	350	135

^{a,b,c,d} : Within a line, value with same superscript are not significantly different
-: Value not different from 0

Cluster 1 animals are characterized primarily by their growth, having above-average EBVs for the intercept and slope of BW and the slope of DBWV. This results in them being the heaviest animals over the entire observation period. However, their potential for laying traits is less promising, with negative EBVs for the intercept of laying traits and a faster-than-average deterioration over time, as indicated by then negative EBV for the slope of LR.

Despite starting with better-than-average quality traits, the decline is more pronounced, with positive EBVs for the intercept and negative EBVs for the slope of most quality traits. Finally, their decline in DFI is stronger than average, leading to an improvement in efficiency compared to their above-average start.

Cluster 2 animals, on the other hand, are primarily defined by their egg production potential, evident in positive EBVs for the intercept of laying traits. However, this potential undergoes a considerably stronger-than-average decline over time, impacting both quantity and quality of egg production, reflected in mainly negative EBVs for the slope of egg production and quality traits. Despite this decline in production, there is a stronger-than-average reduction in DFI, maintaining better FCR from the start and improving the above-average RFI over the period.

Cluster 3 comprises animals initially efficient but experiencing a decline in efficiency over time. This loss is mainly attributed to higher EBVs for the slope of DFI compared to EGGM, coupled with lower-than-average EBVs for the slope of BW and DBWV, leading to the deterioration of both FCR and RFI. Interestingly, this loss in efficiency seems to positively impact egg quality, with positive EBVs for the slope and, thus, a slower decline rate compared to the broader population.

Cluster 4 groups animals with the least deterioration in laying capacity over the production period, evidenced by the strongest EBVs for the slope of LR and EGGM among the four clusters. However, these animals start with the worst laying potential. Despite an above-average egg quality at the beginning, it declines fairly over time. They exhibit fair

efficiency at the start but with a slower-than-average decline in DFI, coupled with lower-than-average growth, resulting in a deterioration of their RFI over the period.

Discussion

In this study, we investigated the persistence, defined as the capacity to maintain the level of a trait over time, of egg production, egg quality, body weight, and feed efficiency traits during the advanced production stages in laying chickens, spanning from 70 to 92 weeks of age. Our aim was then to better understand the genetic determinants of the hen's aptitude to longer production careers and identify opportunities for selecting hens with improved persistence.

Phenotypic evolution as a function of age

The observed decrease in laying rate with age aligns with previous studies, including those that analysed laying rate at different ages (raw data) [16, 18, 45] and others that like us, employed random regression techniques [20, 46–48]. However, laying rate is not the sole crucial criterion in egg production. Achieving a high egg mass with superior egg quality is equally fundamental, especially within the context of extending the production period [6].

In adequation to previous literature, we observed an increased in egg weight at later production stages [2, 45, 49]. However, on the 22 weeks of measure, that represents an increasing of barely 1.6%, reflecting the successful selection strategy on egg weight stability applied on this parental line.

Different aging trajectories were observed for egg quality traits. The HU remained stable as already observed previously in aging hens [50]. The YP also remained stable over time, in accordance with what already found in commercial lines [2, 49], but in opposition of what described in a leghorn line [51]. Finally, shell resistance decreased with age as shown by the decreasing of ESS and ESStiff, in agreement with the known increased eggshell fragility in aging hens [52, 53]. The absence of shell weight and mineral composition measures in our dataset prevents us from verifying whether the increased fragility of the shell stems from a decreased shell proportion, diminished calcium composition, or alterations in the shell's structural integrity [53].

Most studies that investigated persistence in hens, mainly focused on laying rate or egg quality [54, 55]. In this study, we explored the persistence of a broader range of traits, including feed intake and feed efficiency related traits. To our knowledge, the persistence of feed efficiency has never been explored for ages beyond 70 weeks of age. The FCR and RFI presented different trajectories: an increasing for FCR, while a decrease over time was observed for RFI. This difference can be justified considering that these two metrics give different perspectives on the animal's efficiency, as stated above. The observed FCR increasing may be due to a stronger decrease in egg production than in DFI, resulting in a loss of efficiency over time. Conversely, the declining RFI between 70 and 92 weeks can mainly be due to a generalised reduction in DFI not mirrored by large changes in the predicted feed intake, due to the small increase in BW mitigating the decrease in EGGM.

Despite a decline in feed intake throughout the period, we observed a steady positive body weight variation over time, as well as a large variability, which can reflect variations in lipid storage among animals. Indeed, increase in body weight is often attributed to the accumulation of abdominal fat, which is linked to physiological factors mirroring metabolic and hormonal changes [56]. Increased abdominal fat was also observed in our study, where a larger abdominal

fat proportion was observed in birds at 90 weeks of age compared to those analysed at 70 weeks (2.4% versus 3.4%, $p < 0.05$, data not shown).

Kinetics of genetic architecture over time

The estimation of the genetic parameters for egg and feed efficiency related traits revealed different trends in variance components and heritability estimates. Overall, we obtained low heritability values for LR over the period, which resulted from a high residual variance across the period and a permanent environmental variance higher than the genetic one. A similar pattern was observed for EGGM, while the decrease of heritability for MEW at the end of the production period was due to an increase of the permanent environmental variance. For egg production traits, the heritability estimates fell often below those reported in the literature for earlier periods [3, 57–61]. This may be a reflection of the intense selection applied to these traits before 70 weeks of age [6] that may lead to an erosion of the available genetic variability at later ages, with a consequent increased role of non-genetic factors. This is in line with what observed in the literature, at least for egg production traits [20]. However, it is worth mentioning that heritability being a population parameter, is dependent on several factors such as the models used, the methods applied to estimate genetic effects [25] as well as the genetic background of the population, environmental conditions, and management practices, therefore comparison between studies may not be always pertinent. In line with other studies, strong genetic correlations were observed for egg production traits at almost all time points [62, 63], suggesting that the genetic determinism is rather the same throughout the extended production period.

The scattered pattern of heritability estimates for DFI that decreased at 81 wk for then increase again at 90 wk is the result of a high residual variance particularly around 80 weeks of

age, followed by a drastic reduction at later stages. Heritability estimates for DFI in the literature diverge considerably across studies and genotypes, ranging from 0.20-026 and in a reciprocal cross between White Leghorns and Dongxiang blue-shelled chickens cross [64] to 0.46 in an experimental brown-egg pure line layer population [65]. The heritabilities we obtained at different ages were closer to the lower literature estimates in the 70-82 periods and to the upper literature estimates in the 90-91 periods. The RFI heritability estimates at 70 and 90 week of age were higher than what proposed previously earlier on different layer populations [37, 64] , but it was aligned with what observed in meat-chickens [66]. Fewer heritability estimates are available in the literature for FCR in egg-type chickens, but we found that heritability around 70 weeks were close to what is already observed [64]. For feed efficient related traits and DFI, residual variance was greater at 80 weeks of age, indicating a stronger environmental effect than that observed at other ages. The higher overall variability (genetics plus permanent environment plus residual variances), may reflect a change in the animal environment we are not aware of, as no anomalies were recorded during the period. Alternatively, it could reflect a sort of animal adaptive response to an extended production, potentially influenced by the animals' genetic background, as evidenced by the increased heritability observed after 90 weeks of age for RFI and DFI , and low genetic correlations between those traits at 70 and 90 weeks of age.

The low heritabilities of DBWV primarily arise from the important residual variance, overshadowing the low genetic variance. This pattern has been consistent since the early stages, evident from findings in laying hens as early as 8 weeks of age [67]. In contrast, the residual variance for BW remains consistently low, and the elevated heritability is primarily attributed to a genetic and permanent variances that remain relatively stable. This trait's heritability estimates align with observations in laying hens, regardless of age and genotype, both at early

age [68], during their production life [61, 69] and at the end of their production phase [70, 71]. The stability of the genetic determinism for BW and the low, even negligible, one for DBWV during this elongated period of production are expected. For BW, a cross between a broiler and White Leghorn lines has revealed age-dependent differential expression of QTL [72]. Extensive evidence supports the persistence of the majority of QTL identified at 24 weeks throughout the animals' entire lifespan. Furthermore, the study reveals that the sparse QTL discovered for the weight changes after 48 weeks, in comparison to earlier stages, are exclusively correlated with fatness post the production peak. This correlation elucidates the significant contribution of residual variance to variability and the markedly diminished role of genetic factors in later stages we found for DBWV. Our results underscore that the expression of genes implicated in growth, despite their low impact on the variability, exhibit modification over the extended production period, potentially yielding opposing effects post the hypothesized adaptation period.

The heritability dynamics of egg quality traits are primarily driven by genetic variance over an extended period of production. In the context of eggshell quality traits, non-genetic variance tends to remain relatively stable, with genetic variance often playing a less prominent yet crucial role in shaping heritability dynamics. Consequently, heritability values for eggshell quality traits are positioned at the lower end of the spectra reported in the literature, ranging from 0.10 to 0.48 for ESS, 0.2 to 0.49 for ESStiff, and 0.17 to 0.46 for ESC, depending of the strain and period of measure [61, 62, 73–76]. These lower heritabilities suggest that, over the extended production period, gene expression related to eggshell traits becomes less influential, and quality becomes more reliant on external factors impacting the animals before or during this period. This aligns with studies indicating that the primary source of variability in eggshell quality of old laying hens is linked to the health and aging of endometrial cells. The observed decrease in genetic variance for ESS in our case may be attributed to a decline in the expression

of genes involved in the regeneration of these cells [77]. There is also evidence of a shift in the type of protein present in the ultrastructure of the eggshell as laying hens age. This alteration contributes to the development of a more fragile ultrastructure over time, leading to the observed decreasing in ESS [77]. This aligns with the genetic correlation of 0.7 found for ESS, indicating a modification in the expression of genes coding for ultrastructure proteins with age. Regarding egg inside quality, it is noteworthy that genetic variance at 90 weeks surpasses other variances, suggesting that genetic factors play a more substantial role in trait variability at old age. This is particularly evident for HU, where genetic variance triples from 70 to 90 weeks. This increase in genetic variance may be attributed to the growing diversity of proteins found in egg white as animals age [78], leading to more variable interactions among proteins and subsequently increased variability in the properties of egg white, including HU.

Genetic improvement of trait persistence

When variance components were estimated for the intercept and the slope, we observed that the later was null for MEW and ESC, while we observed a strong genetic variance for the intercept. This suggests that the kinetic of the egg weight depends entirely from early performances and cannot be improved at these later stages. Therefore, to select for persistence at advanced laying stages for this trait, it may be necessary to consider the entire production period. For the other traits, feasibility of a selection on the persistence was assessed by the calculating the heritability of OP. What we observed for most traits is a rather high heritability for the P70 compared to OP, certainly due to the applied selection for egg production, effectively mitigating the effects of age and reducing the variation in performance towards the end of the traditional laying period (60 weeks of age) [6]. This means that selecting to improve the slope will be more challenging than selecting to improve the intercept.

While for most traits' selection on the slope, will not impact the intercept, for some it will. For some trait it will be beneficial, as for HU the strong positive genetic correlation between the intercept and the slope supports the idea that selection to improve albumen quality at earlier stages will persist at later stages. For some other traits, like EGGM, the negative genetic correlation between the intercept and the slope implies that selecting for a better slope, will not be without consequences at earlier stages, reducing the EGGM, mainly by decreasing the LR, due to the observed preferential genetic association observed between the slope of those two traits.

Concerning the feed related traits, selecting for the persistence of RFI will be beneficial and easily feasible, due to the high heritability of OP. Improving the persistence by selecting a more positive slope will lead to lower intercept values and, thus, animals that will have a better and more persistent RFI. This is not the case for FCR, where there is no correlation between the intercept and the slope, indicating the presence of multiple possible trajectories for a given intercept value. The contrasted results for these two feed efficient related metrics may be expected as they provide distinct perspectives on how efficiently birds convert feed into egg mass with FCR representing a ratio between production and intake, while RFI reflecting more body changes in energy requirements independent of the level of production [79].

The observed increase in BW from 70 weeks of age onwards may be due to the accumulation of abdominal fat [56, 72], which may indicate, when associated to a reduced egg production, an excess of energy intake. Our analysis suggests that potential strategies to mitigate body weight gain, whether through selective breeding on the intercept or the slope, face significant challenges. Firstly, the low heritabilities observed for DBWV indicate a limited influence of genetic factors, raising concerns about the efficiency of selection on either the slope or the intercept. Secondly, the strong negative genetic correlation between DBWV intercept and slope suggest that persistence and starting value may be governed by the same genetic

factors but with opposing impacts on them. Moreover, estimation of response to selection either by targeting the starting point or the persistence, led to a DBWV that remain unchanged at averagely 0.9g/day throughout the whole extended period of production, with either a stronger fattening at the start or end of the period depending of the strategy.

Lastly, for egg shell stiffness and yolk percentage evolution at later production stages, we observed the possibility to improve persistence without impacting the starting value, due to a lack of covariation between intercept and slope. On the contrary improving the persistence of ESS, despite a low genetic determinism of OP, is possible. However, selecting to reach a persistent ESS over the whole elongated will lead to 10.2% more fragile eggs at 70 weeks, certainly due to also more fragile eggs before, for only a 2.8% gain at 92 weeks.

PCA analysis and hierarchical clustering analysis

The PCA provides insight into the relationship between the slope and intercept of analysed traits. The correlation circle of the PCA confirmed the correlation between the slope and intercept for FCR, DBWV, and HU. Interestingly, the PCA analysis allowed to observe a relation between DBWV intercept with egg production traits. This may underline that higher positive DBWV at 70 weeks of age may contribute to maintaining egg production by maintain the laying rate. Egg production demands a steady supply of energy and nutrients, and the body composition of laying hens not only influences early-stage egg production but also exerts an impact on later production [80]. A relation was also observed between the intercept of DBWV and the slope of RFI, indicating that animals with larger body gains at start are less efficient in the long term, mostly due to a tendency to increase feed intake as previously observed [64]. The relation between the intercept and slope of FCR and EGGM and the slopes of FCR and DFI highlights the fact that the feed efficiency at start may be driven by the EGGM solely but

the temporal evolution of the efficiency may be impacted by the evolution of DFI and nearly not by the one of EGGM, implying that a selection to improve the feed efficiency persistence by increasing the production may not be the interesting.

The clustering analysis allowed to highlight the structure existing in the population and revealed distinct response patterns concerning the extension of the production period. It also revealed the individual persistence qualities of animals and the fact that improving persistence for several traits will necessarily require compromising on breeding goals. Among these responses, some exhibit potential for enhancing feed efficiency during this timeframe. This focus is particularly crucial as the environmental impact of egg production is predominantly linked to feed production [5, 81]. Choosing inefficient animals during this period contradicts the objective pursued by extending the production period. The first selectable group is represented by animals from cluster 3, displaying a better than mean FCR at the start of the period due to higher egg production and a medium DFI. Despite being more efficient than the average for the entire period, animals in this group show a less substantial decrease in egg production and a persistent DFI of around 120g/day throughout. This implies a higher environmental impact and increased feed costs compared to other groups. However, their less pronounced decrease in EGGM may result in decreased primary production costs per kilogram of egg produced, making them economically advantageous but less ecologically favourable. The second strategy involves selecting animals from cluster 2, characterized by robust initial production and a moderate feed intake that decreases throughout the period. However, these animals also exhibit compromised egg quality, both internally and externally, resulting in more fragile eggs throughout the extended production period. While the egg quality impact needs consideration, by its link to farmer revenue, the main advantage lies in the consistently higher egg production of these animals, coupled with a stronger decrease in DFI compared to other

clusters. Opting for these animals could effectively reduce the environmental impact attributable to feed production.

Conclusion

The current study aimed to gain a better understanding of the persistence capacity of hens for a broad range of traits, including egg production, quality and feed efficiency related traits, at advanced production periods, from 70 to 92 weeks of age. The findings suggested that although animals showed a gradual decrease in laying rate and egg production over time, it may be possible to genetically improve egg production persistence, but may be challenging due to the low genetic variances, and may impact efficiency and egg quality on the elongated period of production but also on previous period. This observed decreasing in egg production is however not met with an equal decreasing in feed intake leading to a slight deterioration in feed efficiency. The estimation of genetic parameter at different ages revealed high genetic correlations between traits across different ages, indicating consistent genetic influence on a given trait across different life times. The PCA clustering analysis on estimated breeding values for intercept and slope traits highlighted the existence of distinctive response patterns associated with extending the production period, underlying the existence of compromises among traits. Selecting for enhanced persistence across multiple traits will inevitably require making compromising with respect to breeding goals.

Abbreviations

a*: Redness of the eggshell in chromameter readings; a_{int}: Random additive genetic effect for the intercept of the random regression; a_{slp}: Random additive genetic effect for the regression coefficient for slope of the random regression; b*: Yellowness of the eggshell in chromameter readings; β_1: Fixed regression coefficient on the time period between the day of egg lay and the day of quality measurement; β_2: Fixed regression coefficient for the slope on the age in weeks; BW: Body Weight; DBWV: Daily Body Weight Variation;DFI: Daily Feed Intake; DOB: Date of Birth; EBV: Estimated Breeding Values; EggLaid: Number of Eggs Laid; EGGM: Egg Mass; e_{ijkl}: Random residual effect; ENVT55wk: Rearing system before 55 weeks; ESC: Eggshell Color; ESS: Eggshell Breaking Strength; ESStiff: Eggshell Stiffness; EW: Egg Weight; FCR: Feed Conversion Ratio; FI: Feed Intake; HCPC: Hierarchical Clustering on Principal Components; HU: Haugh Unit; L*: Lightness of the eggshell in chromameter readings; LR: Laying Rate; MEW: Mean Egg Weight; OP : Overall Persistence; P70 : Production level at start; p_{int}: Random permanent environment effect for the intercept of the random regression; p_{slp}: Random permanent environment effect for the regression coefficient for slope of the random regression; PC: Principal Component; PCA: Principal Component Analysis; PFI: Predicted Feed Intake; PosCage: Individual cage location in the barn during the period of measure; REML: Restricted Maximum Likelihood; RFI: Residual Feed Intake; RRM: Random Regression Models; TimeRM: Time between the day of egg lay and the day of quality measurement; WFI: Weekly Feed Intake; YP: Yolk Percentage

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Authors ’contributions

TB, SL, and TZ conceived the project and secured funding and QB, NB, TZ, TT and PL refined the project and advised on statistical analyses. TB managed animal production and organised phenotype collection. QB performed the statistical analysis and QB and TZ wrote the manuscript. NB, and TT contributed useful comments and suggestions on the manuscript draft. All authors read and approved the final manuscript.

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Availability of data and materials

The datasets used in the study are available from the corresponding author on request.

Ethics approval and consent to participate

Consent for publication

Not applicable

Competing interests

The authors declare that they have no competing interests

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Figure titles

Fig. 1 : Summary of the data used in the study.

Fig. 2: Population average trajectories for BW and DBWV (a), DFI (b), EGGM, EW and LR (c), FCR and RFI (d), HU and YP (e), ESS and ESStiff and ESC (f). Coloured lines represent the mean trait, vertical black lines the standard error. Whole lines represent the traits where the slope is significantly different form 0. Dotted lines represent traits with the slope not significantly different from 0.

Fig. 3: Variance component and heritability for DBWV (a) and BW (b). Orange lines represent the additive genetic variances (σ_a^2), blue lines the permanent environment variances (σ_p^2), yellow line the residual variances (σ_e^2), dotted black line the heritability (h^2) and vertical black lines the standard error.

Fig. 4: Variance component and heritability for LR (a), MEW (b) and EGGM (c). Orange lines represent the additive genetic variances (σ_a^2), blue lines the permanent environment variances (σ_p^2), yellow line the residual variances (σ_e^2), dotted black line the heritability (h^2) and vertical black lines the standard error.

Fig. 5: Variance component and heritability for FCR (a), DFI (b) and RFI (c). Orange lines represent the additive genetic variances (σ_a^2), blue lines the permanent environment variances (σ_p^2), yellow line the residual variances (σ_e^2), dotted black line the heritability (h^2) and vertical black lines the standard error.

Fig. 6: Variance component and heritability for HU (a), YP (b). ESC (c), ESStiff (d) and ESS (e). Orange lines represent the additive genetic variances (σ_a^2), blue lines the permanent environment variances (σ_p^2), yellow line the residual variances (σ_e^2), dotted black line the heritability (h^2) and vertical black lines the standard error.

Fig. 7: Correlation circles of PC1 and 2 (a) and of PC3 and 4 (b). Blue and red arrows represent the EBV of the slope and intercept of the traits, respectively.

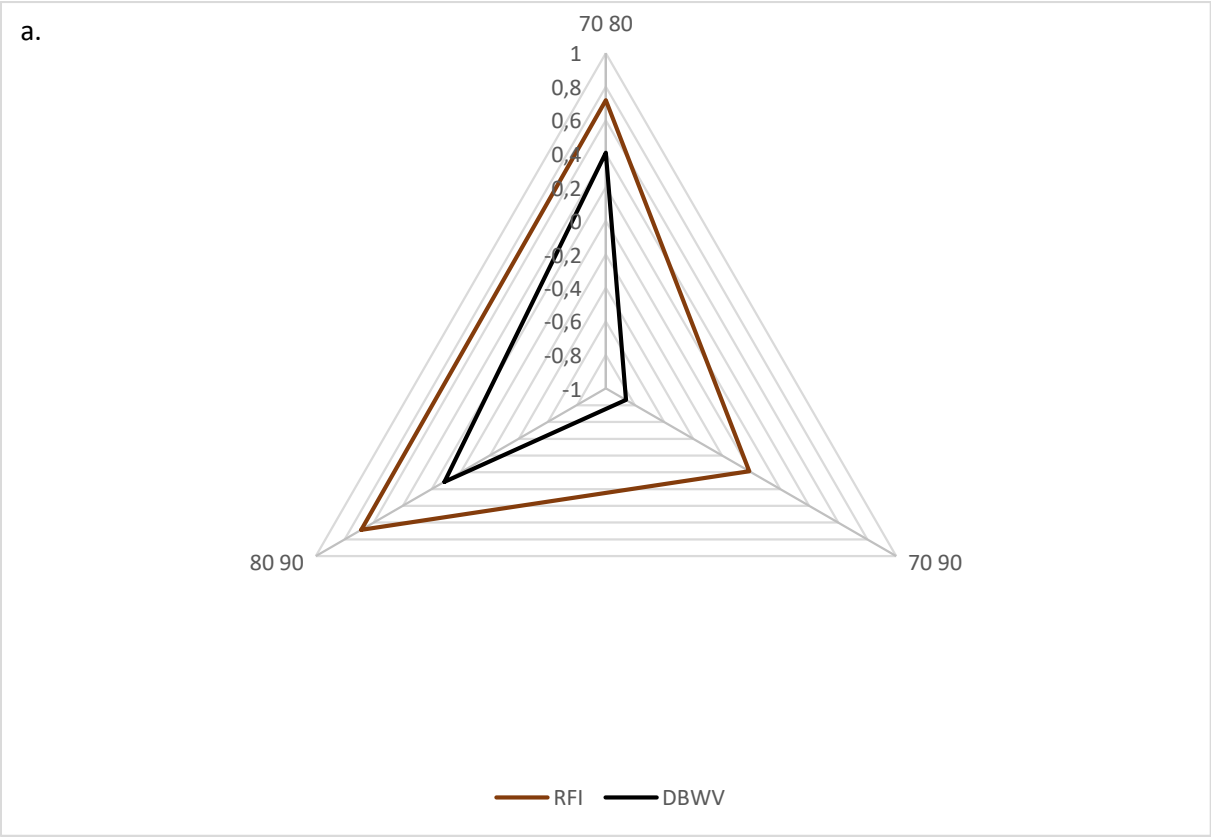
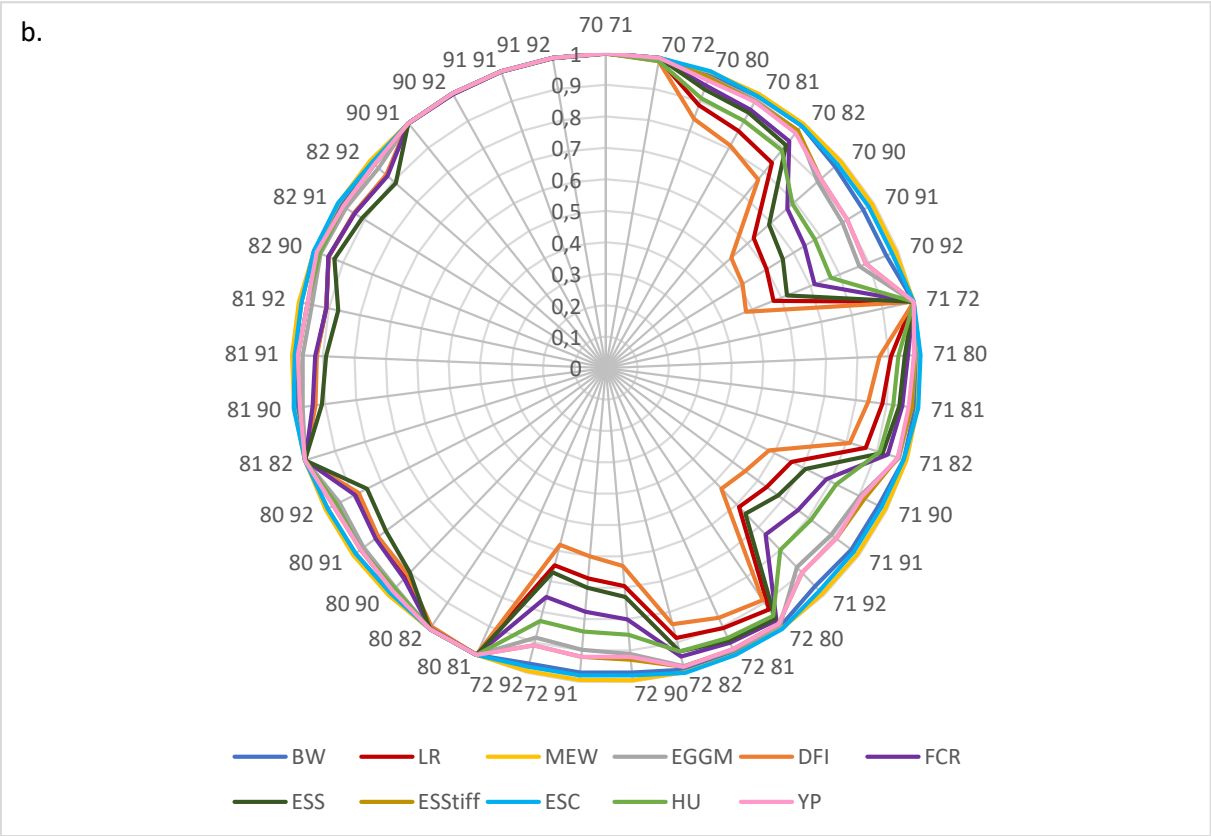
Fig. 8: Hierarchical clustering (a) and projection of the different clusters on the first and second principal components (b)

Supplementary table 1 : Variance estimates for the intercept (σ_{p^2int}) and slope terms (σ_{p^2slp}) of the permanent environment effect, the covariance ($\sigma_{pint,\ pslp}$), the correlation between the intercept and slope of the permanent environment effect ($r_{pint,pslp}$).

Traits	Variance component estimates for the intercept and the slope			
	σ_{p^2int}	σ_{p^2slp}	$\sigma_{pint,slp}$	$r_{pInt,slp}$
BW	12256 ± 1865	-47.9 ± 37.80	15 ± 2.00	-0.11 ± 0.09
DBWV	11.38 ± 0.95	0.1 ± 0.05	0.0009 ± 0.00	0.96 ± 1.00
LR	16.6 ± 3.9	0.27 ± 0.18	0.006 ± 0.01	0.86 ± 1.00
MEW	6.3 ± 1.1	-0.021 ± 0.02	0.01108 ± 0.00	-0.08 ± 0.09
EGGM	428 ± 133	11.4 ± 4.4	0.3 ± 0.25	1.00 ± 0.78
DFI	74 ± 10	-2.2 ± 0.5	0.26 ± 0.03	-0.50 ± 0.08
FCR	0.03 ± 0.01	0.0004 ± 0.00	0.00001 ± 0.00	0.84 ± 0.94
RFI	6654 ± 3011	100.4 ± 152.2	2 ± 12	0.99 ± 1.00
HU	13 ± 3	0.03 ± 0.11	0.02 ± 0.01	0.05 ± 0.19
YP	1.0 ± 0.2	-0.005 ± 0.005	0.0009 ± 0.00	-0.16 ± 0.16
ESS	131346 ± 21818	-166.4 ± 756.6	67.21 ± 41.49	-0.06 ± 0.24
ESStiff	25123 ± 4065	-267.6 ± 119.5	31.53 ± 6.42	-0.30 ± 0.11
ESC	26.4 ± 4.1	-0.34 ± 0.1	0.04 ± 0.00	-0.33 ± 0.09

Supplementary table 2 : Variance and heritability estimates for the different ages

Traits	Ages (weeks)								
	70	71	72	80	81	82	90	91	92
					Genetic variances				
BW	13810 ± 2843	13891 ± 2849	13979 ± 2857	14891 ± 3034	15031 ± 3070	15178 ± 3108	16562 ± 3523	16762 ± 3588	16968 ± 3656
DBWV		1.59 ± 0.59			0.1 ± 0.14			1.34 ± 0.56	
LR	16 ± 4.6	15.6 ± 4.4	15.2 ± 4.3	15.1 ± 4.1	15.4 ± 4.2	15.7 ± 4.4	21.3 ± 6.3	22.3 ± 6.7	23.3 ± 7.1
MEW	7 ± 1.6	7 ± 1.6	7.1 ± 1.6	7.1 ± 1.6	7.1 ± 1.6	7.1 ± 1.6	7.3 ± 1.7	7.3 ± 1.8	7.3 ± 1.8
EGGM	837 ± 196	811 ± 189	786 ± 183	614 ± 147	597 ± 145	581 ± 143	482 ± 146	473 ± 148	466 ± 151
DFI	47.7 ± 13	46.5 ± 12.5	45.5 ± 12.1	49.5 ± 12.2	51.4 ± 12.6	53.7 ± 13.2	83.2 ± 20.6	88.3 ± 21.9	93.7 ± 23.3
FCR	0.02 ± 0.006	0.019 ± 0.006	0.019 ± 0.006	0.015 ± 0.005	0.014 ± 0.004	0.014 ± 0.004	0.013 ± 0.005	0.013 ± 0.005	0.013 ± 0.005
RFI		14736 ± 3394			6949 ± 1794			13407 ± 3259	
HU	17 ± 3.8	17.6 ± 3.9	18.4 ± 4.1	28.7 ± 5.8	30.5 ± 6.2	32.4 ± 6.5	51.2 ± 10.3	54.1 ± 10.9	57 ± 11.5
YP	1.62 ± 0.33	1.62 ± 0.33	1.61 ± 0.33	1.62 ± 0.32	1.63 ± 0.32	1.64 ± 0.33	1.79 ± 0.37	1.81 ± 0.37	1.84 ± 0.38
ESS	99963 ± 28678	95396 ± 27421	91093 ± 26256	66164 ± 20255	64235 ± 19928	62570 ± 19695	58748 ± 21250	59457 ± 21865	60430 ± 22572
ESStiff	23038 ± 5652	22905 ± 5568	22793 ± 5496	22679 ± 5320	22762 ± 5349	22868 ± 5389	24491 ± 6109	24791 ± 6248	25114 ± 6397
ESC	25.4 ± 5.8	25.1 ± 5.7	24.8 ± 5.6	22.8 ± 5.2	22.6 ± 5.1	22.4 ± 5.1	20.8 ± 5.2	20.6 ± 5.2	20.5 ± 5.3
					Permanent environment variances				
BW	12256 ± 1867	12176 ± 1862	12126 ± 1860	12840 ± 1953	13069 ± 1979	13328 ± 2007	16511 ± 2339	17048 ± 2394	17616 ± 2452
DBWV		0.11 ± 0.96			0.13 ± 0.28			0.16 ± 0.87	
LR	16.6 ± 3.9	17.1 ± 3.7	17.7 ± 3.6	22.6 ± 3.2	23.3 ± 3.2	23.9 ± 3.3	29.8 ± 5	30.6 ± 5.3	31.4 ± 5.6
MEW	6.3 ± 1.1	6.3 ± 1	6.3 ± 1	7 ± 1	7.2 ± 1.1	7.4 ± 1.1	9.9 ± 1.2	10.4 ± 1.3	10.8 ± 1.3
EGGM	428 ± 133	451 ± 128	474 ± 124	686 ± 105	715 ± 105	744 ± 105	1004 ± 128	1039 ± 133	1075 ± 139
DFI	73.6 ± 10	69.5 ± 9.5	66 ± 9.1	56.1 ± 8.3	57.2 ± 8.6	58.8 ± 8.9	90.6 ± 13.8	96.9 ± 14.7	103.8 ± 15.7
FCR	0.027 ± 0.005	0.028 ± 0.005	0.029 ± 0.005	0.037 ± 0.004	0.038 ± 0.004	0.039 ± 0.004	0.048 ± 0.006	0.05 ± 0.006	0.051 ± 0.006
RFI		6654 ± 3017			8816 ± 1522			11286 ± 3025	
HU	13.1 ± 2.7	13.2 ± 2.7	13.3 ± 2.7	16 ± 3.6	16.5 ± 3.8	17.1 ± 4	23.5 ± 6.3	24.5 ± 6.7	25.6 ± 7
YP	1 ± 0.21	0.99 ± 0.21	0.98 ± 0.21	0.99 ± 0.2	1 ± 0.2	1.01 ± 0.2	1.17 ± 0.23	1.19 ± 0.24	1.22 ± 0.25
ESS	131350 ± 21834	131080 ± 20907	130950 ± 20063	134740 ± 16345	135820 ± 16261	137030 ± 16260	151570 ± 19272	154000 ± 20022	156550 ± 20854
ESStiff	25123 ± 4063	24619 ± 3966	24179 ± 3881	22925 ± 3655	23052 ± 3682	23242 ± 3720	27033 ± 4456	27790 ± 4603	28611 ± 4761
ESC	26.4 ± 4.1	25.7 ± 4	25.2 ± 3.9	23.6 ± 3.5	23.7 ± 3.5	24 ± 3.5	28.8 ± 3.9	29.8 ± 4	30.8 ± 4.1

					Residual Variances				
BW	4763 ± 298		2835 ± 206	2067 ± 153		4654 ± 241	4968 ± 298		3572 ± 282
DBWV		12.48 ± 1			10.22 ± 0.51			9.51 ± 0.88	
LR	81.8 ± 4.4	93.7 ± 4.8	86.4 ± 4.4	81.2 ± 4.1	94.9 ± 4.8	101.8 ± 5.1	96.1 ± 5.2	107.4 ± 5.7	99.3 ± 5.5
MEW	7 ± 0.4	5.1 ± 0.3	5.8 ± 0.3	6.7 ± 0.3	5.8 ± 0.3	6.1 ± 0.3	6.7 ± 0.4	6.4 ± 0.4	5.9 ± 0.4
EGGM	1868 ± 101	1832 ± 97	1593 ± 86	2231 ± 113	2428 ± 122	2407 ± 121	1748 ± 100	2285 ± 125	2381 ± 131
DFI	156.4 ± 8.5	90.1 ± 5.5	96.5 ± 5.6	114.6 ± 5.7	168.3 ± 8	189.4 ± 9	87 ± 4.7	40.8 ± 3.1	79.2 ± 4.7
FCR	0.109 ± 0.006	0.112 ± 0.006	0.089 ± 0.005	0.124 ± 0.006	0.125 ± 0.006	0.14 ± 0.007	0.094 ± 0.005	0.112 ± 0.006	0.146 ± 0.008
RFI		12514 ± 2339			29819 ± 1653			4621 ± 2169	
HU	27.5 ± 1.2	49.8 ± 1.7	21.1 ± 1.2				46.6 ± 2.2	31.6 ± 1.5	47.8 ± 2.7
YP	1.34 ± 0.06	2.31 ± 0.08	1.76 ± 0.09				1.37 ± 0.07	1.24 ± 0.06	1.21 ± 0.08
ESS	308649 ± 13414	368380 ± 13333	309921 ± 16725				349216 ± 17339	329777 ± 15893	326398 ± 19866
ESStiff	45201 ± 1965	45715 ± 1698	50575 ± 2746				52614 ± 2669	52915 ± 2604	37976 ± 2413
ESC	38.4 ± 1.6	29.9 ± 1.1	47.4 ± 2.4				37.6 ± 1.8	39.3 ± 1.8	39 ± 2.3
					Heritabilities				
BW	0.45 ± 0.08		0.48 ± 0.08	0.49 ± 0.08		0.46 ± 0.08	0.44 ± 0.08		0.44 ± 0.08
DBWV		0.12 ± 0.04			0.01 ± 0.01			0.12 ± 0.05	
LR	0.14 ± 0.04	0.12 ± 0.03	0.13 ± 0.03	0.13 ± 0.03	0.12 ± 0.03	0.11 ± 0.03	0.14 ± 0.04	0.14 ± 0.04	0.15 ± 0.04
MEW	0.35 ± 0.07	0.38 ± 0.07	0.37 ± 0.07	0.34 ± 0.07	0.35 ± 0.07	0.35 ± 0.07	0.3 ± 0.06	0.3 ± 0.06	0.3 ± 0.07
EGGM	0.27 ± 0.06	0.26 ± 0.06	0.28 ± 0.06	0.17 ± 0.04	0.16 ± 0.04	0.16 ± 0.04	0.15 ± 0.04	0.12 ± 0.04	0.12 ± 0.04
DFI	0.17 ± 0.04	0.23 ± 0.06	0.22 ± 0.05	0.22 ± 0.05	0.19 ± 0.04	0.18 ± 0.04	0.32 ± 0.07	0.39 ± 0.08	0.34 ± 0.07
FCR	0.13 ± 0.04	0.12 ± 0.04	0.14 ± 0.04	0.08 ± 0.03	0.08 ± 0.02	0.07 ± 0.02	0.08 ± 0.03	0.08 ± 0.03	0.06 ± 0.03
RFI		0.43 ± 0.08			0.15 ± 0.04			0.46 ± 0.09	
HU	0.29 ± 0.06	0.22 ± 0.04	0.35 ± 0.07				0.42 ± 0.07	0.49 ± 0.08	0.44 ± 0.07
YP	0.41 ± 0.07	0.33 ± 0.06	0.37 ± 0.06				0.41 ± 0.07	0.43 ± 0.07	0.43 ± 0.07
ESS	0.19 ± 0.05	0.16 ± 0.04	0.17 ± 0.05				0.11 ± 0.04	0.11 ± 0.04	0.11 ± 0.04
ESStiff	0.25 ± 0.05	0.25 ± 0.05	0.23 ± 0.05				0.24 ± 0.05	0.24 ± 0.05	0.27 ± 0.06
ESC	0.28 ± 0.06	0.31 ± 0.06	0.25 ± 0.05				0.24 ± 0.05	0.23 ± 0.05	0.23 ± 0.05

Supplementary Figure 1: Genetic correlations between different ages of the three studied periods for DBWV and RFI (a) and the remaining traits (b).