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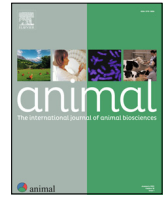
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Egg production in nests and nesting behaviour: genetic correlations with egg quality and BW for laying hens on the floor



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ABSTRACT

In laying hen production, cage-free housing is growing rapidly to provide living conditions that meet hens' needs. Unlike cages, this housing requires nests for automatic collection of eggs, as eggs laid outside nests must be collected by hand. Selecting hens for nest-related traits, such as egg production in nests and nesting behaviour, could help meet the requirements of cage-free housing. However, genetic correlations between these traits and major traits of breeding programmes, such as egg quality or BW, are poorly known. In addition, the genetic determinism of major traits has rarely been studied under cage-free conditions. The objective of the present study was to estimate the heritability of egg quality and BW measured on the floor and their genetic correlations with nest-related traits. Egg production in nests was based on the laying rate in nests, laying rhythm (clutch number and mean oviposition time), and nest acceptance. Nesting behaviour was based on nest preference (mean distance between nests used for laying) and mean laying duration (time spent in the nest for laying). Nest-related traits were recorded from 24 to 64 weeks of age. BW and egg quality were measured at 50 and 55 weeks of age, respectively. Nest-related traits and identification of the eggs laid by each hen (for individual measurements of egg quality) were obtained using individual electronic nests used by hens raised in groups and on the floor. The phenotypes of 1 455 Rhode Island Red and 1 538 White Leghorn hens were analysed. Heritability coefficients and genetic correlations were estimated using a multi-trait animal model for each line. Heritability estimates for egg quality and BW were moderate to high for both lines (0.17–0.74). Overall, weak genetic correlations were estimated between nest-related traits and egg quality or BW for both lines. However, strong and antagonistic genetic correlations were estimated between eggshell strength and laying rate in the nests (−0.46 to −0.42) or laying rhythm (+0.46 to +0.68) for both lines. Several moderate-to-strong genetic correlations were found for White Leghorn between nest-related traits and egg weight, eggshell shape, albumen height, and BW. This study shows that nest-related traits can be used to select hens better adapted to cage-free housing without degrading overall egg quality and BW. It also shows that some traits, like the eggshell strength, must be carefully monitored if these new traits are included in breeding goals. These results must now be confirmed for other populations and larger datasets.

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Implications

Developing cage-free housing for egg production requires reconsidering breeding goals for laying hens. Unlike in cage housing, hens must use nests for laying because eggs laid outside them must be collected by hand, which is laborious and time-consuming. New traits related to nest use are useful for selecting hens that are more adapted to cage-free housing. This study investigated genetic relationships between nest-related traits and the major traits selected in layers (i.e. egg quality and BW). Under-

standing these relationships is important for optimising new breeding goals that include these nest-related traits.

Introduction

In European Union, one of the main changes in the egg-production sector is changes in housing systems, with a gradual abandonment of cages followed by the development of a wide variety of cage-free housing, such as barn, free-range, and organic housing (Gautron et al., 2021). Breeders must adapt hens to the housing, especially in large flocks, and to using nests for laying. Eggs laid in nests can be automatically collected, while eggs laid

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outside them (i.e. floor eggs) must be collected by hand, which is laborious and time-consuming. However, individual cages are currently the main environment for selection, which does not adequately reflect the rearing conditions of commercial hens (Leenstra et al., 2016). Including nest-related traits in breeding programmes is important to meet the requirements of rearing conditions in cage-free housing.

Nest-related traits can be obtained using individual electronic nests that can perform high-throughput phenotyping of individual hens raised in large groups. Several nest-related traits have been suggested to improve egg production and nesting behaviour in cage-free housing (Icken et al., 2012; Bécot et al., 2021; 2023). These traits include the laying rate in nests, laying rhythm (clutch number and oviposition time), nest acceptance, nest preference, and laying duration (i.e. time spent in the nest for laying). All of these traits are heritable, which provides opportunities for selective breeding. Including these traits in selection programmes requires assessing their genetic correlations with the major traits selected in layers, such as egg quality and BW. However, they have rarely been studied in the literature, except for hens in cage housing (Yoo et al., 1988; Akbas et al., 2002; Wolc et al., 2010).

The genetic determinism of egg quality and BW have been widely studied for cage housing (e.g. Zhang et al., 2005; Blanco et al., 2014; Wolc et al., 2014; Picard Druet et al., 2020) but rarely for cage-free housing (Icken et al., 2013; Bédère et al., 2022). The genotype-by-housing interaction for these traits seems weak but has rarely been studied (Leenstra et al., 2016). Bédère et al. (2022) found no interaction between genotype and housing (cage or cage-free) for egg quality or BW. They estimated strong genetic correlations between a given trait measured in the two types of housing, but they were low enough to suggest possible re-ranking of the best candidates depending on the housing. Weaker genetic correlations between the number of eggs in cage vs. cage-free housing have been estimated at peak egg production, suggesting a genotype-by-housing interaction for this trait (Icken et al., 2012). Relationships between egg production and other major traits of breeding programmes could thus differ depending on the housing, and must be investigated for cage-free housing.

This study had two objectives: (1) estimate heritability coefficients of egg-quality traits and BW for hens raised in cage-free housing and (2) estimate genetic correlations between these traits and nest-related traits (egg production in nests and nesting behaviour) under cage-free conditions.

Material and methods

Hens and housing

Hens and data came from the *nucleus* of the Novogen breeding company (Plédran, France). The two pure lines studied were from the breeds Rhode Island Red (RIR, brown eggshell) and White Leghorn (WL, white eggshell). Both were selected for the number of eggs, egg quality, BW, and behaviours such as reduced feather pecking. The population included hens from three batches hatched from 2018 to 2020 (Table 1). Hens were raised together from hatching to 17 weeks of age on the floor in a barn. They were then

raised in floor housing composed of several pens, one per line, until 64 weeks of age. Roosters were raised with the hens (approximately one for every 10 hens). The floor pens were equipped with individual electronic nests (20 cm wide × 40 cm long × 27 cm high) developed by Novogen. The nests were overlaid in two rows (total of 80–120 nests, depending on the batch; Table 1). The floor pens included perches and a living area with free access to feed and water. In total, 1 455 RIR and 1 538 WL hens were phenotyped. At 64 weeks of age, hens selected by the company were transferred to individual cages. In this housing, breeding hens for the next generation were inseminated with selected roosters, allowing the monitoring of the pedigree. On average, the genetic structure of the two populations was from 10 hens per sire and three hens per dam that were raised on the floor. The known pedigree used to estimate the variance components came from seven (3 613 hens) and six (3 284 hens) generations of RIR and WL, respectively.

Acquisition of egg production and nesting behaviour

The individual electronic nests' recorded egg production and nesting behaviour using radio-frequency identification. Hens were individually identified by a transponder tagged on one leg. The system recorded which nest the hen chose and when it entered and exited it. Oviposition time, and thus egg production, was recorded by an egg sensor located behind each nest.

Data were collected daily from 24 to 64 weeks of age after the hens had adapted to the floor housing for about 7 weeks. For the 2018–2019 batch of RIR, data after 58 weeks of age were excluded due to an infection that strongly decreased production. In total, 279 582 and 350 940 nest visits with oviposition were kept for analyses for RIR and WL, respectively.

Acquisition of BW and egg quality

A scale was used to measure BW at 50 weeks of age. Eggs were collected on two consecutive days at about 55 weeks of age. To measure egg quality at the individual scale, an egg-collection system behind each nest stored eggs by oviposition time, which enabled us to know which hen had laid which egg. Eggs were excluded if their order of laying could not be accurately determined (15 and 32 eggs for RIR and WL, respectively) or they could not be attributed to a specific hen (e.g. when the nest did not detect a hen's transponder correctly; 29 and 106 eggs for RIR and WL, respectively). Data for 2 112 and 2 468 eggs for RIR and WL, respectively, were kept for analyses.

Egg quality was measured by the Zootests company (Ploufragan, France). Egg-quality traits were named according to the Animal Trait Ontology for Livestock (ATOL, 2022). Five traits were studied: egg weight (EW), eggshell colour (ESC), eggshell strength (ESS), eggshell shape index (ESshape), and albumen height (AH). A scale was used to measure EW (in g). ESC was calculated from three parameters of the eggshell – L^* (black/white contrast), a^* (green/red contrast), and b^* (blue/yellow contrast) – measured with a chromameter as: $ESC = 100 - (L^* - a^* - b^*)$. ESS (in N) was measured with a compression machine to assess the static stiffness of the shell. The egg was compressed between two flat plates

Table 1
Characteristics of the laying hen batches studied.

Characteristic	Rhode Island Red hens			White Leghorn hens		
	2018–2019	2019–2020	2020–2021	2018–2019	2019–2020	2020–2021
Batch year						
Hens housed	455	552	570	513	598	607
Density (hens/nest)	4.55	4.60	4.75	6.41	4.98	5.06
Hens analysed	401	522	532	471	509	558

moving at a constant speed, and ESS was the maximum force recorded before the shell fractured. ESShape was calculated as a function of egg diameter (i.e. the short length of the egg, in mm) and EW: $ESShape = (diameter/10)/(EW/10^{1/3})$. AH (in mm) was measured using a tripod micrometer (Wilgus and VanWagenen, 1936). ESShape and AH were not recorded for the 2018–2019 batch.

To identify outliers, egg-quality traits were adjusted for significant environmental effects ($P < 0.05$): egg-laying date, waiting time between laying and measurement (for EW and AH only), and the permanent environmental effect of the hen. Then, measurements were considered outliers and removed when adjusted data exceeded four phenotypic SDs from the mean (<0.7% of data for all traits).

Traits

Egg production in nests was based on the laying rate in the nests (LRN), laying rhythm: clutch number (CN) and mean oviposition time (MOT), and nest acceptance for laying (NAL). LRN equalled the number of eggs laid in the nests divided by the number of days alive during the recording period, multiplied by 100. CN equalled the number of pauses + 1. LRN and CN were studied for hens with $LRN \geq 50\%$. See Bécot et al. (2021) for more details on procedures used to calculate these traits. The mean time of entry (i.e. time after the lights were turned on) for nest visits with oviposition (Supplementary Table S1) was used to study MOT because it was more accurate than oviposition time and strongly correlated with it (Bécot et al., 2021). However, phenotypes for MOT were compared to those in the literature (Table 2). NAL assessed the ability of hens to lay eggs in nests: $LRN < 50\%$ or $\geq 50\%$ were assigned the value of 0 or 1, respectively.

Nest preference and laying duration (i.e. nesting behaviour) were based on the mean distance between nests used for laying (MDN) and the mean laying duration (MLD), respectively. MDN was the mean of the horizontal distances, as a number of nests that separated the nests used for laying for two consecutive days. MLD was the mean time spent in the nests used for laying (i.e. the time of exiting the nest minus the time of entering the nest). See Bécot et al. (2023) for more details on the calculation of these traits. MOT, MDN, and MLD were calculated for hens with at least 10 records. All traits were studied for hens that survived for at least half of the recording period (Table 1).

Table 2
Summary statistics of the analysed traits in hens.

Trait	Rhode Island Red hens					White Leghorn hens				
	n	Mean	SD	Min	Max	n	Mean	SD	Min	Max
LRN (%)	1 178	91.67	9.31	50.58	100.00	1 420	88.21	8.84	50.54	98.57
CN	1 178	4.50	4.19	1.00	32.00	1 420	7.56	5.63	1.00	41.00
MOT (hh:mm)	1 243	02:50	01:13	00:05	07:11	1 473	03:46	00:59	00:27	06:38
MDN (nests)	1 235	7.78	3.21	1.07	23.61	1 471	9.57	3.35	2.43	22.38
MLD (min)	1 242	41	18	11	113	1 474	59	24	10	156
EW (g)	1 104	62.32	4.37	49.00	78.00	1 337	64.24	4.47	50.25	84.00
ESC	1 103	81.31	9.55	34.15	99.70	1 335	5.10	1.33	2.10	12.59
ESS (10^{-2} N)	1 036	3 822	774	1 045	6 238	1 242	3 507	730	645	5 630
ESShape (mm/g)	732	1.11	0.01	1.06	1.16	891	1.09	0.01	1.04	1.15
AH (mm)	783	6.64	1.00	3.70	10.00	963	5.95	1.00	2.00	9.70
BW (g)	1 411	1 923	183	1 162	2 762	1 479	1 666	143	1 125	2 300
	n	0	1			n	0	1		
NAL (%)	1 455	19.04	80.96			1 538	7.67	92.33		

Abbreviations: LRN = laying rate in the nests; CN = clutch number; MOT = mean oviposition time; MDN = mean distance between nests used for laying; MLD = mean laying duration; EW = egg weight; ESC = eggshell colour; ESS = eggshell strength; ESShape = eggshell shape index; AH = albumen height; NAL = nest acceptance for laying (0 for hens with $LRN < 50\%$, 1 otherwise).

Nest-related traits were calculated with data recorded between 24 and 64 weeks of age. BW and egg quality were recorded, respectively, at 50 and 55 weeks of age.

Six major traits selected in layers were studied: BW and five egg-quality traits (i.e. EW, ESC, ESS, ESShape, and AH). Egg quality was based on the mean of the records per hen (one egg or two). Summary statistics of the analysed traits are shown in Table 2.

Estimation of genetic parameters

The traits with a non-normal distribution (all except the binary trait NAL, EW, AH, and BW) were normalised to avoid overestimating the residual variance. To facilitate model convergence, all traits except NAL were scaled with a mean of 0.00 and a variance of 1.00. All traits were analysed as continuous variables.

Variance and covariance components were estimated for each line individually (RIR or WL) using the following multi-trait animal model (Henderson, 1975):

$$\begin{bmatrix} y_1 \\ y_2 \\ \vdots \\ y_{12} \end{bmatrix} = \begin{bmatrix} 1_1 \\ 1_2 \\ \vdots \\ 1_{12} \end{bmatrix} + \begin{bmatrix} X_1 & 0 & \dots & 0 \\ 0 & \ddots & & \vdots \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \dots & X_{12} \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \\ \vdots \\ b_{12} \end{bmatrix} + \begin{bmatrix} Z_1 & 0 & \dots & 0 \\ 0 & \ddots & & \vdots \\ \vdots & \vdots & \ddots & \vdots \\ 0 & 0 & \dots & Z_{12} \end{bmatrix} \begin{bmatrix} a_1 \\ a_2 \\ \vdots \\ a_{12} \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \\ \vdots \\ e_{12} \end{bmatrix}$$

where y_i is the vector of observations for the trait $i = LRN, CN, MOT, NAL, MDN, MLD, EW, ESC, ESS, ESShape, AH, \text{ or } BW$. 1_i is the vector of the phenotypic mean for the trait i . X_i and b_i are the incidence matrix and vector, respectively, for the trait i related to the fixed effect of the hen's hatch date. Z_i and a_i are the incidence matrix and vector, respectively, for the trait i related to the random additive genetic effect. e_i is the vector of the random residual effect for the trait i . a_i and e_i are assumed to follow normal distributions and covariance matrices:

$$\sigma^2 \begin{bmatrix} a_1 \\ a_2 \\ \vdots \\ a_{12} \end{bmatrix} = \begin{bmatrix} \sigma_{a1}^2 & \sigma_{a1,a2} & \dots & \sigma_{a1,a12} \\ \sigma_{a2,a1} & \ddots & & \vdots \\ \vdots & \vdots & \ddots & \vdots \\ \sigma_{a12,a1} & \sigma_{a12,a2} & \dots & \sigma_{a12}^2 \end{bmatrix} \otimes \mathbf{A}$$

$$\sigma^2 \begin{bmatrix} e_1 \\ e_2 \\ \vdots \\ e_{12} \end{bmatrix} = \begin{bmatrix} \sigma_{e1}^2 & \sigma_{e1,e2} & \dots & \sigma_{e1,e12} \\ \sigma_{e2,e1} & \ddots & & \vdots \\ \vdots & \vdots & \ddots & \vdots \\ \sigma_{e12,e1} & \sigma_{e12,e2} & \dots & \sigma_{e12}^2 \end{bmatrix} \otimes \mathbf{I}$$

where σ_{ai}^2 is the variance of additive genetic effects for the trait i , $\sigma_{ai,aj}$ is the additive genetic covariance between traits i and j , and \mathbf{A} is the additive genetic relationship matrix based on pedigree. σ_{ei}^2 is the residual variance for the trait i , $\sigma_{ei,ej}$ is the residual covariance between traits i and j , and \mathbf{I} is the identity matrix.

Phenotypic correlations (r_p) were calculated as follows (Falconer and Mackay, 1996):

$$r_p = h_i h_j r_a + e_i e_j r_e$$

where \mathbf{h} and \mathbf{e} are, respectively, the square root of the heritability and the square root of the proportion of residual variance of traits i and j . r_a and r_e are, respectively, the additive genetic and residual correlations between traits i and j .

Software

Quality control of the data and calculation of traits were performed with R software (R Core Team, 2022). Traits were normalised with the R package bestNormalize (Peterson and Cavanaugh, 2019). Variance components and SE were estimated with the REMLF90 and AIREMLF90 programs, respectively (Misztal et al., 2002).

Results

Heritability estimated for nest-related traits, BW, and egg quality

Most heritability estimates were moderate to high for traits of egg production in nests and nesting behaviour (Table 3). They ranged from 0.28 to 0.65 for RIR, except for LRN and NAL (0.15 for both). They ranged from 0.34 to 0.74 for WL, except for LRN and NAL (about 0.15 for both). Heritability estimates for egg-quality traits were similar for the two lines: high for EW and ESshape (0.39–0.46) but lower for ESS (0.16–0.24). They differed, however, between RIR and WL for ESC (0.37 and 0.17, respectively), AH (0.40 and 0.23, respectively), and BW (0.48 and 0.74, respectively).

Genetic correlations with egg production in nests

Genetic correlations between egg production in nests (LRN, CN, MOT, and NAL) and egg-quality traits and BW were estimated for RIR (Table 4) and WL (Table 5). Those between egg production in

Table 3
Heritability estimated for nest-related traits, egg quality, and BW in hens.

Trait	Rhode Island Red hens	White Leghorn hens
LRN	0.15 (0.04)	0.16 (0.03)
CN	0.40 (0.04)	0.42 (0.03)
MOT	0.65 (0.04)	0.56 (0.04)
NAL	0.15 (0.04)	0.14 (0.04)
MDN	0.28 (0.04)	0.34 (0.04)
MLD	0.57 (0.07)	0.74 (0.07)
EW	0.45 (0.07)	0.46 (0.07)
ESC	0.37 (0.07)	0.17 (0.05)
ESS	0.24 (0.06)	0.16 (0.04)
ESshape	0.45 (0.09)	0.39 (0.07)
AH	0.40 (0.08)	0.23 (0.06)
BW	0.48 (0.07)	0.74 (0.07)

Abbreviations: LRN = laying rate in the nests; CN = clutch number; MOT = mean oviposition time; MDN = mean distance between nests used for laying; MLD = mean laying duration; NAL = nest acceptance for laying; EW = egg weight; ESC = eggshell colour; ESS = eggshell strength; ESshape = eggshell shape index; AH = albumen height.

SE are in brackets. Nest-related traits were calculated with data recorded between 24 and 64 weeks of age. BW and egg quality were recorded, respectively, at 50 and 55 weeks of age.

nests and EW were weak or not significantly different from zero for RIR (−0.21 to −0.09). They were moderate for WL (negative with LRN (−0.29) and positive with CN (+0.25) and MOT (+0.22)), but weak with NAL (−0.17).

Genetic correlations were negative and strong between LRN and ESS for RIR (−0.46) and WL (−0.42). For both lines, they were positive and strong between both CN and MOT with ESS (+0.46 to +0.68), while phenotypic correlations were weaker (+0.15 to +0.20). The genetic correlation was positive and strong between NAL and ESS for RIR (+0.64) but not significantly different from zero for WL.

Genetic correlations were weak or not significantly different from zero between egg production in nests and the traits ESC, ESshape, AH, and BW for RIR. They were also weak or not significantly different from zero for WL, except between CN and ESshape (−0.26), MOT and AH (+0.36), and NAL and AH (−0.49). Overall, phenotypic correlations were similar to or weaker than the genetic correlations.

Genetic correlations with nesting behaviour

Genetic correlations between nesting behaviour (MDN and MLD) and egg quality or BW were estimated for RIR (Table 4) and WL (Table 5). Genetic correlations with MDN were weak or not significantly different from zero for both lines (−0.26 to +0.12), except for ESshape (−0.41) and BW (−0.30) for WL. They were weak with MLD for both lines (−0.14 to +0.19). Genetic correlations between nest-related traits and major traits of breeding programmes (egg quality and BW) are given in Supplementary Tables S2 and S3, respectively.

Discussion

Heritability estimates for BW and egg quality on the floor: moderate to high overall

The heritability estimates for BW and egg quality are consistent with those in the literature for hens in cages. The high heritability estimated for BW is widely reported in the literature, but only for hens in individual cages. For example, Wolc et al. (2010) estimated a heritability of 0.42 for a RIR line, while Yoo et al. (1988) reported a mean heritability of 0.74 for a WL line. Picard Druet et al. (2020) reported similar heritability for egg-quality traits for the same RIR line, but for older hens raised in individual cages (60–80 weeks of age). Differences in heritability estimates for AH (0.40 and 0.23 for RIR and WL, respectively) were also reported by Blanco et al. (2014), with higher coefficients for a RIR line (0.64 and 0.69) than for a WL line (0.28 and 0.32). Few studies have been conducted for cage-free housing. To our knowledge, no heritability estimates for BW or egg quality have been reported for other populations in cage-free housing, except for EW, but with a high variability in the estimates (Icken et al., 2013). The moderate-to-high heritability estimates for egg quality in the present study confirm that egg quality can be measured accurately at the individual scale for cage-free housing. Egg quality could be improved by selective breeding in these housing conditions. This opens up interesting prospects for maintaining breeding populations in a floor breeding system that is more respectful of animal welfare.

Genetic correlations with egg production in nests: generally weak, or strong and antagonistic with eggshell strength

Genetic correlations between egg production in nests (LRN, CN, MOT, and NAL) and BW or egg quality were generally weak. The weak genetic correlations between egg production in nests and

Table 4
Genetic (r_g) and phenotypic (r_p) correlations estimated between nest-related traits and egg quality or BW for Rhode Island Red hens.

Trait	Item	EW	ESC	ESS	ESshape	AH	BW
LRN	r_g	-0.09 (0.18)	-0.02 (0.19)	-0.46 (0.21)	-0.03 (0.19)	0.09 (0.20)	0.09 (0.16)
	r_p	0.02 (0.03)	0.02 (0.03)	-0.05 (0.03)	0.00 (0.04)	0.02 (0.04)	0.16 (0.03)
CN	r_g	-0.14 (0.11)	-0.03 (0.13)	0.68 (0.12)	0.03 (0.13)	-0.07 (0.14)	-0.13 (0.12)
	r_p	-0.04 (0.03)	0.01 (0.03)	0.19 (0.03)	-0.06 (0.04)	-0.06 (0.04)	-0.10 (0.03)
MOT	r_g	-0.14 (0.11)	0.02 (0.12)	0.46 (0.13)	0.08 (0.11)	-0.13 (0.12)	-0.04 (0.11)
	r_p	-0.09 (0.03)	-0.01 (0.03)	0.17 (0.03)	0.00 (0.04)	-0.06 (0.04)	-0.06 (0.03)
NAL	r_g	-0.21 (0.19)	-0.20 (0.19)	0.64 (0.18)	0.13 (0.20)	-0.11 (0.22)	0.00 (0.18)
	r_p	0.03 (0.04)	-0.06 (0.04)	0.14 (0.04)	0.05 (0.05)	-0.12 (0.05)	0.11 (0.03)
MDN	r_g	-0.10 (0.13)	-0.25 (0.14)	0.12 (0.15)	-0.07 (0.17)	-0.04 (0.17)	-0.14 (0.14)
	r_p	-0.02 (0.03)	-0.02 (0.03)	0.02 (0.03)	-0.02 (0.04)	0.05 (0.04)	-0.10 (0.03)
MLD	r_g	0.12 (0.12)	-0.14 (0.13)	0.04 (0.15)	0.02 (0.15)	0.16 (0.15)	0.05 (0.12)
	r_p	0.06 (0.03)	0.04 (0.03)	0.03 (0.03)	-0.03 (0.04)	0.01 (0.04)	0.07 (0.03)

Abbreviations: LRN = laying rate in the nests; CN = clutch number; MOT = mean oviposition time; NAL = nest acceptance for laying; MDN = mean distance between nests used for laying; MLD = mean laying duration; EW = egg weight; ESC = eggshell colour; ESS = eggshell strength; ESshape = eggshell shape index; AH = albumen height. SE are in brackets. Nest-related traits were calculated with data recorded between 24 and 64 weeks of age. BW and egg quality were recorded, respectively, at 50 and 55 weeks of age.

Table 5
Genetic (r_g) and phenotypic (r_p) correlations estimated between nest-related traits and egg quality or BW for White Leghorn hens.

Trait	Item	EW	ESC	ESS	ESshape	AH	BW
LRN	r_g	-0.29 (0.12)	-0.15 (0.17)	-0.42 (0.17)	0.03 (0.15)	-0.18 (0.16)	0.02 (0.11)
	r_p	-0.10 (0.03)	-0.04 (0.03)	-0.08 (0.03)	0.00 (0.03)	0.00 (0.03)	0.07 (0.03)
CN	r_g	0.25 (0.08)	0.15 (0.14)	0.64 (0.11)	-0.26 (0.10)	0.03 (0.13)	0.00 (0.09)
	r_p	0.09 (0.03)	0.04 (0.03)	0.20 (0.03)	-0.08 (0.04)	-0.01 (0.03)	-0.06 (0.03)
MOT	r_g	0.22 (0.10)	0.14 (0.12)	0.55 (0.12)	-0.23 (0.12)	0.36 (0.12)	0.13 (0.09)
	r_p	0.03 (0.03)	0.00 (0.03)	0.15 (0.03)	-0.04 (0.04)	0.10 (0.03)	-0.03 (0.03)
NAL	r_g	-0.17 (0.17)	-0.17 (0.21)	0.25 (0.20)	0.33 (0.19)	-0.49 (0.19)	-0.19 (0.15)
	r_p	-0.07 (0.03)	-0.04 (0.03)	0.01 (0.04)	-0.02 (0.04)	-0.13 (0.04)	0.01 (0.03)
MDN	r_g	0.06 (0.12)	-0.01 (0.16)	0.00 (0.16)	-0.41 (0.13)	-0.26 (0.16)	-0.30 (0.11)
	r_p	-0.03 (0.03)	0.04 (0.03)	0.01 (0.03)	-0.05 (0.03)	-0.02 (0.04)	-0.09 (0.03)
MLD	r_g	0.08 (0.10)	-0.05 (0.15)	0.08 (0.14)	0.17 (0.12)	0.19 (0.14)	0.02 (0.09)
	r_p	0.02 (0.03)	0.03 (0.03)	0.06 (0.03)	0.06 (0.04)	-0.01 (0.03)	-0.04 (0.03)

Abbreviations: LRN = laying rate in the nests; CN = clutch number; MOT = mean oviposition time; NAL = nest acceptance for laying; MDN = mean distance between nests used for laying; MLD = mean laying duration; EW = egg weight; ESC = eggshell colour; ESS = eggshell strength; ESshape = eggshell shape index; AH = albumen height. SE are in brackets. Nest-related traits were calculated with data recorded between 24 and 64 weeks of age. BW and egg quality were recorded, respectively, at 50 and 55 weeks of age.

EW for RIR are consistent with the results for cage housing. Wolc et al. (2010) found weak genetic correlations between EW and egg production (number of eggs up to 64 weeks of age) or laying rhythm (clutch traits and mean oviposition interval) ranging from -0.16 to +0.04. For WL, the genetic correlation was estimated to be negative between LRN and EW (-0.29) and positive between laying rhythm and EW (+0.22 and +0.25). These results are consistent with those of Yoo et al. (1988), who observed that WL raised in individual cages had genetic correlations that were negative between egg production and EW (-0.62 to -0.28) and positive between MOT and EW (+0.20). Lillpers and Wilhelmson (1993) estimated more variable correlations between MOT and EW (-0.54 to +0.08), depending on the population studied. We also calculated a negative but weak phenotypic correlation between oviposition time and EW, which was recorded daily for three weeks for the 2018–2019 flock (-0.22 and -0.17 for RIR and WL, respectively; data not shown). However, genetic correlations estimated with these data had a low accuracy (SE > 0.25), probably due to the low number of individuals (<400). Long-term selection for clutch length (strongly correlated with CN) was conducted for 16 generations of two dwarf brown-egg layer lines in individual cages (Chen and Tixier-Boichard, 2003). This study estimated negative genetic correlations between clutch length and EW (-0.29 to -0.16), with a slight decrease in EW over generations (-0.127 or -0.071 g per generation according to the line). Relationships between egg production in nests and EW seem weak but not null, given the present results and the literature on cage systems, which suggests that potential negative effects on EW must be monitored if these traits are selected.

The negative genetic correlations between LRN and ESS (antagonistic) are consistent with the results for egg production and eggshell quality in cage housing. For example, negative genetic correlations were reported between the number of eggs and egg-specific gravity (-0.25 to -0.10; Yoo et al., 1988) or dynamic stiffness of the eggshell (-0.36 and -0.19; Dunn et al., 2005). The strong and positive genetic correlations estimated between laying rhythm and ESS indicate that decreasing CN and MOT through selection (to increase egg production) will decrease ESS, which is undesirable for breeders. Positive but weaker genetic correlations were reported between MOT and egg-specific gravity (+0.23; Yoo et al., 1988). Oviposition time influences eggshell quality, as reviewed by Ketta and Tümová (2016), but its potential effects on ESS are not fully known (Tümová et al., 2017). The genetic correlations estimated in the present study were stronger than the phenotypic correlations. This could be due to the strong influence of a few genes, which is not consistent with the assumptions of the additive model used. However, these antagonistic correlations between ESS and LRN or laying rhythm need to be monitored, whereas the positive and strong correlation with NAL (+0.64) for RIR is favourable.

Genetic correlations were weak between egg production in nests and the traits ESC, ESshape, and AH for the two lines, implying that it can be selected without degrading these egg-quality traits. However, for WL, the moderate genetic correlations between CN and ESshape (-0.26) or MOT and AH (+0.36) were antagonistic, as was the strong genetic correlation between NAL and AH (-0.49).

The weak genetic correlations between egg production in nests and BW are consistent with those between BW and egg production

or laying rhythm (CN and MOT) for RIR lines in individual cages (Akbas et al., 2002; Wolc et al., 2010). For WL, Yoo et al. (1988) estimated no genetic correlation between MOT and BW and a negative correlation between egg production and BW (−0.29 to −0.42), which was not observed in the present study.

To our knowledge, this is the first study that shows genetic correlations between egg production in nests and BW or egg quality in a cage-free system. Overall, the results are similar to those of studies of egg production in cage systems. Additional studies with longitudinal data on egg quality could help to better understand the genetic relationships between these traits (mainly EW or ESS) and oviposition time.

Generally weak genetic correlations with nesting behaviour

Traits for nest preference and laying duration generally had weak genetic correlations with BW and egg quality for the two lines. This suggests the potential to select these traits without degrading the major traits of breeding programmes. However, negative and moderate or strong correlations between MDN and BW (−0.30) or ESShape (−0.41), respectively, were found for WL. The WL hens that lay their eggs in nests far from each other have a genetic trend for a lower BW and to lay pointier eggs. To our knowledge, the literature does not mention relationships between nesting behaviour and BW or egg quality. Other behaviours, such as feeding behaviour, have been genetically correlated with production or quality traits (Canario et al., 2013). Genetic correlations between nesting behaviour and the major traits of breeding programmes must now be confirmed for other populations and larger datasets.

Conclusion

This study estimated the heritability of BW and egg quality for hens raised in groups on the floor. Heritability estimates were generally moderate to high. This suggests that electronic nests can be used to measure accurately egg quality at the individual scale and on the floor. Electronic nests could be an alternative to the individual cages currently used to record egg quality in selection nuclei. This study also estimated genetic correlations between nest-related traits and BW or egg quality. Genetic correlations were generally weak for the two lines studied. However, strong and antagonistic genetic correlations were estimated between egg production in nests and ESS, indicating that improving egg production in nests via selection could decrease the ESS. For WL, several moderate-to-strong genetic correlations were estimated with egg quality (e.g. between egg production in nests and EW), which requires monitoring. These results are promising for selecting hens that are better adapted to cage-free housing by recording phenotypes under conditions that are more similar to those of commercial farms and monitoring genetic relationships between nest-related traits and the major traits of breeding programmes.

Supplementary material

Supplementary material to this article can be found online at <https://doi.org/10.1016/j.animal.2023.100958>.

Ethics approval

All data were registered as part of the commercial and selection activities of Novogen (Plédran, France). The animals used in the study were thus not considered to be experimental animals as defined by European Union Directive 2010/63 and subsequent national application texts. Consequently, we did not seek ethical

review or approval of this study regarding the use of experimental animals. All animals were raised in compliance with national regulations on livestock production and according to procedures approved by the French Veterinary Services.

Data and model availability statement

The data that support the findings of this study were used under license from Novogen because they are not publicly available; however, the data can be provided upon reasonable request to Novogen.

Declaration of Generative AI and AI-assisted technologies in the writing process

The authors did not use any artificial intelligence-assisted technologies in the writing process.

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Author contributions

All authors contributed to conceptualisation of the study. **AF** and **TB** supervised animal management and production. **LB** analysed the data and wrote the original draft. **NB** and **PLR** proofread the manuscript. All authors read and approved the final manuscript.

Declaration of interest

LB, NB, and PLR declare that they have no competing interests. AF and TB are employed by Novogen, a laying hen breeding company. The data are of commercial interest for Novogen, but this interest did not influence the results in this article. There are no patents, products in development, or marketed products associated with this research to declare.

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