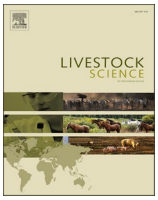
Livestock Science 311 (2026) 106000

Contents lists available at ScienceDirect

Livestock Science

journal homepage: www.elsevier.com/locate/livsci



Expected performance of selection for uniformity of birth weight in real populations of guinea pigs

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HIGHLIGHTS

- Birth weight uniformity can be achieved under low number of repeated records.
- Fitting litter effect in the model does not affect the breeding values accuracy.
- The differences in accuracy between statistical approaches were negligible.

ARTICLE INFO

Keywords:
Uniformity
Guinea pig
Limited records
Simulation
Heteroscedastic models

ABSTRACT

The guinea pig is a species of significant economic and nutritional importance, especially in the Andean region of South America. Measuring within-litter variability of birth weight (BW) is a challenge in this species because there are few records per litter. The objective of this study was to evaluate the performance of heteroscedastic models under realistic pedigree structures through simulation, as well as to determine the potential of selection for uniformity of within-litter BW in guinea pig populations. Real pedigree and BW data from three guinea pig populations (P1, P2, and UNH) were analyzed. BW data were simulated based on prior estimates of variance components and by maintaining the actual mating scheme. Parameter estimation was performed by fitting a complete model (with litter effect) and an incomplete model (without litter effect) under Frequentist and Bayesian approaches. The results showed that the heteroscedastic model allows for a reasonable estimation of the variance components and prediction of genetic values. In population P1, which had greater pedigree depth and a larger number of records, the results were more consistent compared to populations P2 and UNH. Comparing the complete and incomplete models, the accuracy of the genetic values for the residual variance were similar. After five generations of selection, a reduction in BW variability is expected. Overall, despite their low litter size, our results suggest that selection for uniformity of BW in guinea pig populations is potentially viable, but its efficiency is contingent upon a sound pedigree structure and a sufficient number of records.

1. Introduction

The guinea pig is a rodent native primarily to certain Andean regions of South America. Because it has a short reproductive cycle and is easy to manage, this species is highly valued, making it a useful resource for meat production. The main producers and consumers of guinea pig meat are countries such as Peru, Ecuador, Bolivia, and Colombia (Donoso et al., 2025). According to the Ministerio de Desarrollo Agrario y

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https://doi.org/10.1016/j.livsci.2026.106000
Received 11 May 2026; Received in revised form 21 June 2026; Accepted 23 June 2026
Available online 24 June 2026

Riego (2023), in 2021, Peru produced just over 25 million guinea pigs, with annual consumption nearing 22 tons.

Although guinea pigs have been widely used as laboratory animals (Padilla-Carlin et al., 2008) and a considerable amount of information has been generated regarding their biology, management, and care (Grădinaru and Popa, 2025), this knowledge has limited utility in addressing the practical and economic challenges associated with meat production in family and farm breeding systems. Birth weight (BW) in guinea pigs is a trait of interest because it is believed to be related to neonatal survival and the subsequent growth of the offspring. In this context, selection for uniformity within-litter BW could help improve production efficiency, as it has been shown to be associated with reduced management and production costs in the livestock industry (Hennessy, 2005). Furthermore, in prolific species, it has been linked to reduced mortality and to the animals' robustness and resilience to environmental challenges (Formoso-Rafferty et al., 2019, 2020, 2023).

To address the genetic control of residual variance, an appropriate statistical model capable of exploring it is necessary. SanCristobal-Gaudy et al. (1998) proposed a heteroscedastic model that allows for the adjustment of not only genetic effects on the mean of the trait but also on the residual variance, thereby opening up the possibility of selecting for uniformity. Although the use of these models provided favorable results in species with relatively large litter sizes (Formoso-Rafferty et al., 2016; Sell-Kubiak et al., 2025), their performance regarding BW variability in species with low litter sizes, such as guinea pigs, has not yet been evaluated in real populations. Because addressing variability requires repeated measurements, and only a single BW record is available for each animal, variability must be addressed by assigning the BW records to the mother (Pun et al., 2013). Nevertheless, the low number of observations per litter in guinea pigs would still pose challenges when evaluating the variability and performance of the model. Under these conditions, the variance estimate would be less accurate, and it would be difficult to distinguish between the genetic and environmental effects acting on the residual variance. This could compromise the estimation of variance components (Felleki et al., 2012), the accuracy of predicted additive genetic values affecting residual variance, and consequently, selection efficiency for uniformity.

Despite the potential of heteroscedastic models in uniformity selection, their practical application may face several challenges. The estimation of parameters affecting residual variance is typically less accurate than that of parameters affecting the mean of the trait, and its accuracy may depend largely on population size, pedigree depth, and the number of available records (Madsen et al., 2021; Rojas et al., 2026). In this context, simulation studies that account for the actual mating scheme observed in the pedigree, thereby mimicking the real structure of populations, constitute a valuable tool for evaluating the performance of heteroscedastic models under different real scenarios of interest, allowing for the analysis of the bias and precision of estimators in a context closer to reality. Furthermore, these studies allow for the comparison of Frequentist and Bayesian methods. Among the most commonly used models for addressing uniformity that could be compared are Double Hierarchical Generalized Linear Models (Rönnegård et al., 2010; Felleki et al., 2012), which are based on the theory of Lee and Nelder. (2006), and Bayesian hierarchical models (Sorensen and Waagepetersen, 2003).

To our knowledge, there are no studies that address the genetic control of residual variance of BW in real populations of guinea pigs. The primary objective of this study was to evaluate the performance of the heteroscedastic model proposed by SanCristobal-Gaudy et al. (1998) under realistic guinea pig population structures by comparing complete and incomplete model specifications and Frequentist and Bayesian approaches through simulation. As a secondary objective, we assessed the potential of selection for uniformity of within-litter BW in three real guinea pig populations.

Table 1
Description of the pedigree and performance datasets for the guinea pig populations P1, P2, and UNH.

	P1	P2	UNH
Number of records	6881	2058	1426
Number of mothers with records	2302	1110	335
Mean number of parities	1.00	1.00	1.50
Number of animals	9170	3347	1639
Number of founders	164	1289	212
Number of animals with both parents known	8431	2058	1353
Number of animals with only one known parent	575	0	74
Maximum number of equivalent generations	13.38	2.75	3
Effective population size via individual increase in inbreeding	73.64	-	91.33
Effective population size via individual increase in coancestry	52.83	-	74.63

2. Material and methods

2.1. Field data

In this study, data from three different guinea pig populations (P1, P2, and UNH) were used. Populations P1 and P2 belong to the Instituto Veterinario de Investigaciones Tropicales y de Altura (IVITA) in Peru. Line P1 is based on the Peru genetic line developed by the Instituto Nacional de Innovación Agraria (INIA), while line P2 was created by IVITA. Line P1 was selected for growth rate, and line P2 for feed conversion rate. Further details on the characteristics of these two populations can be found in Cedano-Castro et al. (2020). The UNH population, on the other hand, is a native population belonging to a guinea pig genetic improvement program at the Universidad Nacional de Huancavelica (UNH) in Peru. A description of the BW records and pedigree for each population is shown in Table 1. Population P1 consisted of a total of 9170 individuals, while populations P2 and UNH consisted of a total of 3347 and 1639 individuals, respectively. In addition, descriptive pedigree parameters such as effective population size via individual increase in inbreeding (Gutiérrez et al., 2009) and via increase in coancestry (Cervantes et al., 2011) were calculated for populations P1 and UNH. These parameters were computed using the program ENDOG v4.8 (Gutiérrez and Goyache, 2005). For the P2 population, it was not possible to calculate these parameters due to the lack of a sufficient number of generations for this population. The maximum number of equivalent generations for populations P1, P2, and UNH was 13.78, 2.75, and 3, respectively. It should be noted that at least two generations are needed for inbreeding to occur, and matings for P2 were managed to prevent it.

2.2. Simulated data

The BW data were simulated considering the actual mating scheme observed in the pedigree, such that the simulation mimicked the actual structure of the three populations evaluated. For all individuals with records, phenotypes were simulated according to the heteroscedastic model (HE) proposed by SanCristobal-Gaudy et al. (1998). Under this model, it is assumed that the residual variance is heterogeneous and partially under genetic control. Thus, the following model was used:

$$y_i = x_i'b + z_i'u + w_i'c + exp\left(\frac{1}{2}\left(x_i'b^* + z_i'u^* + w_i'c^*\right)\right)\varepsilon_i$$

where y_i is the *i th* observed value of the response variable; the asterisk (*) denotes the parameters affecting the residual variance; b and b^* are the vectors of systematic effects associated with the categorical variables according to each guinea pig population, as described above; u and u^* are the vectors of additive genetic effects; c and c^* are the vectors of litter effects; $\mathbf{x}_i'$, $\mathbf{z}_i'$ and $\mathbf{w}_i'$ are the incidence vectors associated with the systematic, additive genetic, and litter effects, respectively; ε_i is an unscaled residual, such that $\varepsilon_i \sim N(0,1)$. Under this model, the random vectors

corresponding to the additive genetic and litter effects followed a normal distribution given by:

$$\begin{pmatrix} u \\ u^* \\ c \\ c^* \end{pmatrix} \Big| \sigma_u^2, \sigma_{u^*}^2, \sigma_c^2, \sigma_{c^*}^2, \rho \sim N\left(\begin{pmatrix} 0 \\ 0 \\ 0 \\ 0 \end{pmatrix}, \begin{pmatrix} A\sigma_u^2 & A\rho\sigma_u\sigma_{u^*} & 0 & 0 \\ A\rho\sigma_u\sigma_{u^*} & A\sigma_{u^*}^2 & 0 & 0 \\ 0 & 0 & I\sigma_c^2 & 0 \\ 0 & 0 & 0 & I\sigma_{c^*}^2 \end{pmatrix} \right),$$

where $\boldsymbol{A}$ is the numerator relationship matrix (Wright, 1922) and $\boldsymbol{I}$ is the identity matrix; σ_u^2 and $\sigma_{u^*}^2$ are the genetic variances affecting the mean of the trait and its residual variance, respectively; σ_c^2 and $\sigma_{c^*}^2$ are the litter variances affecting the mean of the trait and its residual variance, respectively; ρ is the correlation coefficient between the additive genetic effects affecting the mean and the residual variance.

The values of the systematic effects ($\boldsymbol{b}$ and $\boldsymbol{b}^*$) included in the model were the posterior marginal mean estimates of those effects, which were obtained after performing a Bayesian analysis of the real data from populations P1, P2, and UNH separately. The variance components and genetic correlations for the actual populations could only be estimated using an incomplete model, without litter effect. Therefore, because the complete model did not converge for the real datasets, the simulation scenarios were parameterized using estimates obtained from the incomplete model (Table 2). Therefore, the simulated scenarios should not be interpreted as exact representations of the true populations, but rather as plausible sensitivity scenarios reflecting the available information structure of each population. Thus, the values of the variance components were distributed in proportions of 0%, 25%, 50%, 75%, and 100% of the genetic variance. The genetic correlation between the mean of the trait and its residual variance was kept constant across all scenarios for each population. For each defined scenario, 10 replicas were simulated.

The additive genetic values ($\boldsymbol{u}$ and $\boldsymbol{u}^*$) of the founder individuals were simulated from a normal distribution $N(0,1)$ and scaled by their corresponding genetic standard deviations. For subsequent generations, the additive genetic values for individuals with both parents known were simulated as the average of the additive genetic values of the father and mother plus a random Mendelian sampling value simulated from a normal distribution $N(0,1)$ and scaled by $\sqrt{0.5}$ times the corresponding genetic standard deviation. For individuals with only one known parent, additive genetic values were simulated as one-half of the known parent's additive genetic value plus a random Mendelian sampling value simulated from a normal distribution $N(0,1)$ and scaled by $\sqrt{0.75}$ times the corresponding genetic standard deviation.

Table 2
Values of simulated parameters for the three guinea pig populations.

Population	Parameter				
	σ_u^2	$\sigma_{u^*}^2$	ρ	σ_c^2	$\sigma_{c^*}^2$
P1	0	0.00	−0.19	400	0.20
	100	0.05	−0.19	300	0.15
	200	0.10	−0.19	200	0.10
	300	0.15	−0.19	100	0.05
	400	0.20	−0.19	0	0.00
P2	0	0.00	0.12	400	0.40
	100	0.10	0.12	300	0.30
	200	0.20	0.12	200	0.20
	300	0.30	0.12	100	0.10
	400	0.40	0.12	0	0.00
UNH	0	0.00	0.21	300	0.50
	75	0.13	0.21	225	0.38
	150	0.25	0.21	150	0.25
	225	0.38	0.21	75	0.13
	300	0.50	0.21	0	0.00

σ_u^2: genetic variance of the trait; $\sigma_{u^*}^2$: genetic variance affecting residual variance; ρ: genetic correlation between the mean of the trait and its residual variance; σ_c^2: litter variance of the trait; $\sigma_{c^*}^2$: litter variance affecting the residual variance.

2.3. Analysis of field and simulated data

The variance components using field data were estimated considering the HE model described above, but in this case the litter effect was not included (incomplete model) because the full model (with litter effect) did not provide results for any of the three populations studied. The systematic effect vectors ($\boldsymbol{b}$ and $\boldsymbol{b}^*$) differed from one population to another. Thus, population P1 included the systematic effects of sex (2 levels), group (6 levels), and litter size (6 levels). For population P2, the model included the systematic effects of year (8 levels), litter size (6 levels), group (6 levels), and season (2 levels). Finally, for population UNH, the systematic effects were sex (2 levels), month-year (29 levels), litter size (7 levels), and number of parities (6 levels). The systematic effect of group was established because both populations P1 and P2 were managed in separate groups, with each group consisting of eight males and 32 females, as described in Cedano-Castro et al. (2020).

The parameters estimated under the HE model were the genetic variance affecting the mean, the genetic variance affecting the residual variance, the genetic correlation, and the genetic coefficient of variation (GCV_e). This last was approximated by taking the square root of the genetic variance affecting the residual variance $\left(\sqrt{\sigma_{u^*}^2}\right)$ (Mulder et al., 2007). The posterior marginal distributions of these parameters were approximated using the GSEVM software (Ibáñez-Escriche et al., 2010). The statistical inferences were based on the overlapping of the high posterior density intervals at a 95% probability ($HPD_{95\%}$). It was considered one million iterations, with a burn-in of 100,000 and a sampling interval of 200, such that a total of 4500 samples were used to make the inferences. The convergence of the chains was evaluated using Geweke's criterion (Geweke, 1992), available in the boa package (Smith, 2007) of the R software (R core team, 2025), and by graphical inspection.

The simulated data for the three guinea pig populations were also analyzed using the HE model described above. Additive genetic values and variance components were estimated by fitting a complete model and an incomplete model under a Frequentist and Bayesian approach. Estimation under the Frequentist approach was performed by fitting a double hierarchical generalized linear model (DHGLM) using the AsReml software (Gilmour et al., 2015), while under the Bayesian approach, the same software used to analyze the field data was employed. The Pearson correlation coefficient between true and predicted genetic values was calculated to obtain the prediction accuracy in each replicate. The expected genetic response for BW uniformity was calculated as $\Delta u^* = exp\left(-i * r_{(u^*,\hat{u}^*)} * \sigma_{u^*}\right)$, where i is the selection intensity, assumed to be equal to 1.10, $r_{(u^*,\hat{u}^*)}$ is the accuracy of the additive genetic values for the residual variance, and σ_{u^*} is the additive genetic deviation affecting the residual variance. The means and standard errors of the estimates of the variance components and accuracies were calculated, taking into account the 10 replicates of each simulated scenario. Inferences regarding the differences between the estimates were made by examining the virtual confidence intervals for each parameter, defined as the mean ± 1.96 times the corresponding standard errors. In this case, virtual confidence intervals were used because, in the Frequentist approach, unlike the Bayesian approach, the distribution of the parameter itself is not known, but rather that of the parameter estimator.

3. Results

Mean estimates of the posterior marginal distributions of the variance components and genetic parameters obtained for the three actual guinea pig populations are shown in Table 3. The genetic variance of the trait showed a wide overlapping of $HPD_{95\%}$ between populations P1 and

Table 3
Mean estimates of the posterior marginal distributions of variance components and genetic parameters for the guinea pig populations P1, P2, and UNH.

	Population					
	P1		P2		UNH	
Parameter	Estimate ± SD	$HPD_{95\%}$	Estimate ± SD	$HPD_{95\%}$	Estimate ± SD	$HPD_{95\%}$
σ^2_u	397.83 ± 21.04	356.78: 438.55	401.51 ± 29.07	346.33: 460.99	314.97 ± 45.62	233.10: 414.32
$\sigma^2_{u^*}$	0.20 ± 0.04	0.13: 0.28	0.44 ± 0.10	0.27: 0.64	0.50 ± 0.12	0.29: 0.77
ρ	−0.19 ± 0.08	−0.34: −0.04	0.12 ± 0.10	−0.07: 0.30	0.20 ± 0.14	−0.07: 0.47
GCV_e	0.45 ± 0.04	0.36: 0.52	0.66 ± 0.07	0.52: 0.81	0.70 ± 0.09	0.54: 0.88

σ^2_u: genetic variance of the trait; $\sigma^2_{u^*}$: genetic variance affecting residual variance; ρ: genetic correlation between the mean of the trait and its residual variance; GCV_e: coefficient of genetic variation of the residual variance; SD: standard deviation of the posterior marginal distribution; $HPD_{95\%}$: high posterior density interval at a 95% probability.

P2, while population UNH had a lower estimate and a higher $HPD_{95\%}$. In contrast, the estimate of the genetic variance affecting the residual variance was lower in population P1 compared to populations P2 and UNH. The estimate of the genetic correlation was negative and statistically different from zero in population P1, whereas in populations P2 and UNH the intervals included zero. The coefficient of genetic variation was lower in the population P1 compared to the populations P2 and UNH.

Mean estimates of variance components, genetic correlations, and accuracies obtained for the complete and incomplete models under the Frequentist and Bayesian approaches for the different scenarios evaluated in populations P1, P2, and UNH are shown in Tables 4–6, respectively. The standard errors associated with the mean estimates for populations P1, P2, and UNH are shown in Supplementary Tables S1, S2, and S3, respectively. The performance of the heteroscedastic model varied across populations, model specifications, and statistical approaches (Tables 4–6). Overall, population P1 showed the highest number of converged replicates across scenarios, whereas P2 consistently exhibited the lowest convergence rates. Population UNH displayed intermediate values. Across populations, convergence was generally lower for the complete model than for the incomplete model, regardless of the estimation approach.

Estimates of variance components showed different levels of agreement with the simulated values among populations. In general, estimates obtained in P1 were closer to the simulated parameters than those obtained in P2 and UNH. Differences between the complete and

Table 4
True values (in bold) and mean estimates of variance components, genetic correlations, and accuracies obtained under Frequentist (Freq) and Bayesian (Bayes) approaches for population P1.

	Complete model							
	n	σ^2_u	$\sigma^2_{u^*}$	ρ	σ^2_c	$\sigma^2_{c^*}$	$r_{(u,\hat{u})}$	$r_{(u^*,\hat{u}^*)}$
True		**0.00**	**0.00**	**−0.19**	**400.00**	**0.20**		
Freq	5	14.25	0.05	0.02	386.28	0.05	-	-
Bayes	0	-	-	-	-	-	-	-
True		**100**	**0.05**	**−0.19**	**300.00**	**0.15**		
Freq	9	94.29	0.07	−0.15	307.99	0.03	0.57	0.35
Bayes	0	-	-	-	-	-	-	-
True		**200.00**	**0.10**	**−0.19**	**200.00**	**0.10**		
Freq	10	195.87	0.12	−0.26	208.83	0.01	0.72	0.47
Bayes	6	210.68	0.11	−0.30	196.24	0.12	0.71	0.49
True		**300.00**	**0.15**	**−0.19**	**100.00**	**0.05**		
Freq	10	315.50	0.13	−0.14	103.31	0.00	0.83	0.52
Bayes	8	311.31	0.16	−0.12	98.35	0.06	0.82	0.53
True		**400.00**	**0.20**	**−0.19**	**0.00**	**0.00**		
Freq	10	410.19	0.14	−0.25	2.67	0.00	0.91	0.55
Bayes	9	382.29	0.16	−0.23	12.02	0.06	0.91	0.56
	Incomplete model							
	n	σ^2_u	$\sigma^2_{u^*}$	ρ	σ^2_c	$\sigma^2_{c^*}$	$r_{(u,\hat{u})}$	$r_{(u^*,\hat{u}^*)}$
True		**0.00**	**0.00**	**−0.19**				
Freq	10	741.58	0.08	0.02			-	-
Bayes	10	712.04	0.17	0.02			-	-
True		**100.00**	**0.05**	**−0.19**				
Freq	10	656.36	0.09	−0.04			0.49	0.34
Bayes	10	632.86	0.18	−0.04			0.48	0.32
True		**200.00**	**0.10**	**−0.19**				
Freq	10	572.15	0.12	−0.21			0.67	0.46
Bayes	10	549.76	0.20	−0.14			0.67	0.46
True		**300.00**	**0.15**	**−0.19**				
Freq	10	499.00	0.13	−0.13			0.81	0.52
Bayes	10	478.57	0.20	−0.10			0.81	0.51
True		**400.00**	**0.20**	**−0.19**				
Freq	10	414.88	0.14	−0.25			0.91	0.55
Bayes	10	401.21	0.20	−0.20			0.91	0.56

σ^2_u: genetic variance of the trait; $\sigma^2_{u^*}$: genetic variance affecting residual variance; ρ: genetic correlation between the mean of the trait and its residual variance; σ^2_c: litter variance of the trait; $\sigma^2_{c^*}$: litter variance affecting the residual variance; $r_{(u,\hat{u})}$: accuracy of genetic values for the trait; $r_{(u^*,\hat{u}^*)}$: accuracy of the genetic values for the residual variance; n: number of replicas that converged.

Table 5
True values (in bold) and mean estimates of variance components, genetic correlations, and accuracies obtained under Frequentist (Freq) and Bayesian (Bayes) approaches for population P2.

	Complete model							
	n	σ^2_u	$\sigma^2_{u^*}$	ρ	σ^2_c	$\sigma^2_{c^*}$	$r_{(u,\hat{u})}$	$r_{(u^*,\hat{u}^*)}$
True		**0.00**	**0.00**	**0.12**	**400.00**	**0.40**		
Freq	3	315.57	0.09	0.17	91.17	0.00	-	-
Bayes	1	269.57	0.23	−0.09	158.58	0.22	-	-
True		**100.00**	**0.10**	**0.12**	**300.00**	**0.30**		
Freq	4	314.65	0.08	−0.02	88.56	0.00	0.40	0.12
Bayes	0	-	-	-	-	-	-	-
True		**200.00**	**0.20**	**0.12**	**200.00**	**0.20**		
Freq	1	232.85	0.01	−0.82	141.67	0.00	0.55	−0.05
Bayes	0	-	-	-	-	-	-	-
True		**300.00**	**0.30**	**0.12**	**100.00**	**0.10**		
Freq	1	442.82	0.17	0.03	0.00	0.00	0.70	0.30
Bayes	0	-	-	-	-	-	-	-
True		**400.00**	**0.40**	**0.12**	**0.00**	**0.00**		
Freq	2	413.13	0.09	0.38	0.00	0.00	0.81	0.27
Bayes	0	-	-	-	-	-	-	-
	Incomplete model							
	n	σ^2_u	$\sigma^2_{u^*}$	ρ	σ^2_c	$\sigma^2_{c^*}$	$r_{(u,\hat{u})}$	$r_{(u^*,\hat{u}^*)}$
True		**0.00**	**0.00**	**0.12**				
Freq	4	400.12	0.14	−0.06			-	-
Bayes	9	413.90	0.42	0.01			-	-
True		**100.00**	**0.10**	**0.12**				
Freq	4	408.36	0.10	0.19			0.40	0.13
Bayes	10	412.25	0.39	0.01			0.40	0.17
True		**200.00**	**0.20**	**0.12**				
Freq	3	400.87	0.08	0.05			0.59	0.13
Bayes	8	410.94	0.36	0.02			0.58	0.23
True		**300.00**	**0.30**	**0.12**				
Freq	5	399.32	0.11	−0.05			0.70	0.22
Bayes	10	407.95	0.40	0.07			0.70	0.31
True		**400.00**	**0.40**	**0.12**				
Freq	5	411.63	0.09	0.38			0.81	0.27
Bayes	10	404.98	0.35	0.13			0.80	0.35

σ^2_u: genetic variance of the trait; $\sigma^2_{u^*}$: genetic variance affecting residual variance; ρ: genetic correlation between the mean of the trait and its residual variance; σ^2_c: litter variance of the trait; $\sigma^2_{c^*}$: litter variance affecting the residual variance; $r_{(u,\hat{u})}$: accuracy of genetic values for the trait; $r_{(u^*,\hat{u}^*)}$: accuracy of the genetic values for the residual variance; n: number of replicas that converged.

incomplete models were observed for several variance components, particularly those associated with the partitioning of genetic and environmental sources of variation. Similar trends were observed under both Frequentist and Bayesian approaches, although the magnitude of the estimates varied among scenarios. Breeding value accuracies for residual variance were obtained for both model specifications and estimation approaches. Across the converged scenarios, accuracies were of similar magnitude under the complete and incomplete models. This pattern was observed in the three populations, although the number of successful replicates available for comparison varied among scenarios. Comparable trends were also observed for the Frequentist and Bayesian analyses.

The expected proportions of residual and phenotypic variances for the different scenarios evaluated in the three guinea pig populations are shown in Table 7. In population P1, the response ranged from −0.28 to −0.08, indicating a progressive reduction in residual variance. After one generation of selection, the expected proportion of residual variance could decrease between 92% and 76%, while phenotypic variance could decrease between 97% and 90%. After five generations, the reduction could be more pronounced, with residual and phenotypic variances reaching proportions between 67% and 25% and between 87% and 70%, respectively. In population P2, the response ranged from −0.22 to −0.05. After one generation, residual variance could decrease to values between 95% and 85%, while phenotypic variance could range between 98% and 92%. After five generations, the reduction could be more pronounced, with residual variance values between 77% and 34% and phenotypic variance values between 90% and 71%. Population UNH showed the highest expected response to selection. Phenotypic variance in this population could be reduced by up to 66% after five generations of selection.

4. Discussion

Guinea pig populations are characterized by a low number of BW records within-litter. This could compromise the estimation of variance components (Felleki et al., 2012; Pun et al., 2013), the accuracy of predicted additive genetic values that affect residual variance, and consequently the efficiency of selection for uniformity. Furthermore, field data from guinea pig populations are limited, which typically prevents the fitting of a complete model (with litter effect), thus making it impossible to differentiate the genetic and environmental effects acting on residual variance and raising interest in knowing the consequences of fitting an incomplete model (without litter effect). Thus, our study aimed to evaluate, through simulation, the performance of the HE model developed by SanCristobal-Gaudy et al. (1998) by fitting both a complete and an incomplete model to data from three guinea pig populations (P1, P2, and UNH) and comparing Frequentist and Bayesian statistical approaches. We analyzed the model's ability to estimate parameters and the accuracy of predicted genetic values for residual variance. This last was analyzed to assess the feasibility of selecting for uniformity of BW in guinea pigs, given that such selection has been shown to benefit welfare and robustness in similar species such as mice (Formoso-Rafferty et al., 2019, 2020, 2022; Formoso-Rafferty et al.,

Table 6
True values (in bold) and mean estimates of variance components, genetic correlations, and accuracies obtained under Frequentist (Freq) and Bayesian (Bayes) approaches for population UNH.

	Complete model							
	n	σ^2_u	$\sigma^2_{u^*}$	ρ	σ^2_c	$\sigma^2_{c^*}$	$r_{(u,\hat{u})}$	$r_{(u^*,\hat{u}^*)}$
True		**0.00**	**0.00**	**0.21**	**300.00**	**0.50**		
Freq	0	-	-	-	-	-	-	-
Bayes	0	-	-	-	-	-	-	-
True		**75.00**	**0.13**	**0.21**	**225.00**	**0.38**		
Freq	3	71.10	0.23	0.09	222.16	0.00	0.50	0.44
Bayes	0	-	-	-	-	-	-	-
True		**150.00**	**0.25**	**0.21**	**150.00**	**0.25**		
Freq	4	178.03	0.24	0.23	139.29	0.00	0.66	0.52
Bayes	0	-	-	-	-	-	-	-
True		**225.00**	**0.38**	**0.21**	**75.00**	**0.13**		
Freq	6	273.53	0.30	0.15	28.24	0.01	0.76	0.55
Bayes	6	234.44	0.39	0.19	66.57	0.23	0.69	0.55
True		**300.00**	**0.50**	**0.21**	**0.00**	**0.00**		
Freq	7	286.12	0.34	0.27	0.00	0.00	0.84	0.63
Bayes	9	297.32	0.42	0.23	15.70	0.14	0.74	0.61
	Incomplete model							
	n	σ^2_u	$\sigma^2_{u^*}$	ρ	σ^2_c	$\sigma^2_{c^*}$	$r_{(u,\hat{u})}$	$r_{(u^*,\hat{u}^*)}$
True		**0.00**	**0.00**	**0.21**				
Freq	9	201.77	0.11	0.01			-	-
Bayes	8	220.95	0.27	0.04			-	-
True		**75.00**	**0.13**	**0.21**				
Freq	6	212.81	0.17	0.14			0.48	0.37
Bayes	8	240.73	0.35	0.02			0.47	0.38
True		**150.00**	**0.25**	**0.21**				
Freq	7	250.90	0.22	0.22			0.65	0.51
Bayes	10	261.23	0.33	0.15			0.60	0.47
True		**225.00**	**0.38**	**0.21**				
Freq	8	282.12	0.31	0.14			0.75	0.55
Bayes	10	282.22	0.46	0.15			0.72	0.54
True		**300.00**	**0.50**	**0.21**				
Freq	5	287.33	0.37	0.31			0.84	0.62
Bayes	10	314.33	0.50	0.21			0.81	0.64

σ^2_u: genetic variance of the trait; $\sigma^2_{u^*}$: genetic variance affecting residual variance; ρ: genetic correlation between the mean of the trait and its residual variance; σ^2_c: litter variance of the trait; $\sigma^2_{c^*}$: litter variance affecting the residual variance; $r_{(u,\hat{u})}$: accuracy of genetic values for the trait; $r_{(u^*,\hat{u}^*)}$: accuracy of the genetic values for the residual variance; n: number of replicas that converged.

2023; El-ouazizi et al., 2023) and rabbits (García et al., 2018; Garreau et al., 2008; Blasco et al., 2017; Agea et al., 2020). It should be noted that this paper is the first study to address the genetic control of residual variance of BW in real guinea pig populations.

Some differences in estimates of variance components and genetic parameters were observed from the analysis of the actual datasets from the guinea pig populations studied. The overlapping of $HDP_{95\%}$ for the genetic variance of the trait between populations P1 and P2 suggest that there are no significant differences in this parameter between these two populations. This is likely because both populations were raised under the same environmental conditions, as they belong to the same location where the data were collected. On the other hand, the greater uncertainty observed for the UNH population is likely due to the smaller number of records available for this population. The additive genetic variance affecting the residual variance is a parameter that does not depend on the scale of the trait, and its square root approximately represents the coefficient of genetic variation (GCV_e) of the residual variance (Hill and Mulder, 2010). In a review study, Iung et al. (2020) found that GCV_e values ranged from 0 to 0.86. In the present study, the GCV_e value was lower in population P1 (0.45±0.04) and similar for P2 (0.66±0.07) and UNH (0.70±0.09), indicating that selection for uniformity of BW using predicted genetic values under the HE model could be viable in guinea pig populations but the standard deviations of the posterior marginal distribution of this parameter prevent definitive conclusions from being drawn in this regard.

Another parameter of interest is the genetic correlation between the mean of the trait and its residual variance. The differences in estimates of genetic correlation among the populations studied are likely due to the varying amounts of data available for each population, and a vast amount of data is typically required to accurately estimate this parameter. This correlation was negative and statistically different from zero for the P1 population (−0.19 ± 0.08), which would indicate a favorable scenario in which selection on the mean would lead to a reduction in residual variance, thereby favoring the production of more uniform animals. In contrast, in populations P2 and UNH, the estimated genetic correlation would prevent a clear determination of the direction of the correlated response, as the $HPD_{95\%}$ for this parameter included zero. Large differences in estimates of genetic correlation have been reported in the literature (Hill and Mulder, 2010; Iung et al., 2020). However, Tatliyer et al. (2019) observed that the scale effect leads to reported positive genetic correlations and that the sign may vary depending of the type of trait, with positive correlations most frequently obtained for traits related to individual weight or milk production and negative correlations for reproductive traits. Specifically for BW, genetic correlations of 0.34 were reported in a selection experiment for environmental variability in mice (Formoso-Rafferty et al., 2018), ranging from 0.15 to 0.59 in pigs (Sell-Kubiak et al., 2025), 0.39 in sheep (Sae-Lim et al., 2018), and 0.44 in beef cattle (Fina et al., 2013).

The results of the simulation study suggest that the heteroscedastic model was able to recover several of the simulated parameters under some scenarios, although the degree of recovery depended strongly on pedigree structure, the amount of available information, and the model specification. Therefore, the results should be interpreted primarily as descriptive evidence of model behavior under the evaluated conditions rather than as proof of consistent parameter recovery across all scenarios. Furthermore, in the interpretation, it should be considered that the simulation scenarios defined for the complete model were based on estimates obtained from the fit of the incomplete model for the three guinea pig populations studied. In general, the differences observed between populations were mainly due to pedigree depth, generations of records, and the number of repeated records for each dam, among other factors. All of these factors are crucial to the accuracy with which the model parameter estimates are obtained.

The genetic variance affecting the mean of the trait was estimated with greater stability in population P1 than in populations P2 and UNH. In population P1, where the pedigree had a maximum of about 13 equivalent generations and the number of records was the highest among the populations, the estimates obtained under the complete

Table 7
Expected proportions of residual and phenotypic variances after one and five generations of selection for uniformity of BW in three guinea pig populations.

				One generation		Five generations	
Population	σ_{u^*}	$r_{(u^*,\hat{u}^*)}$	Δu^*	σ^2_e	σ^2_p	σ^2_e	σ^2_p
P1	0.22	0.33	−0.08	92%	97%	67%	87%
	0.32	0.46	−0.16	85%	94%	45%	78%
	0.39	0.52	−0.22	80%	92%	33%	73%
	0.45	0.56	−0.28	76%	90%	25%	70%
P2	0.32	0.15	−0.05	95%	98%	77%	90%
	0.45	0.18	−0.09	92%	96%	64%	84%
	0.55	0.27	−0.16	85%	93%	44%	76%
	0.63	0.31	−0.22	81%	92%	34%	71%
UNH	0.36	0.38	−0.15	86%	95%	47%	80%
	0.50	0.49	−0.27	76%	91%	26%	73%
	0.62	0.55	−0.37	69%	89%	15%	69%
	0.71	0.63	−0.49	61%	86%	9%	66%

σ_{u^*}: additive genetic deviation of the trait; $\rho_{(u^*,\hat{u}^*)}$; accuracy of the genetic values for the residual variance; Δu^*: Responses to selection assuming a selection intensity of 1.10; σ^2_e: proportion of residual variance; σ^2_p; proportion of phenotypic variance.

model fit were close to the simulated value. In population P2, the estimates were considerably more unstable and showed significant deviations in several scenarios, especially in the complete model. This is likely due to the poor pedigree available for this population, which had a higher number of founders relative to its population size. In this context, Clément et al. (2001) also found biased estimates of variance components when the pedigree was insufficient. On the other hand, Jensen et al. (1991) found unbiased estimates when all relationship information was utilized. Although the UNH population was the smallest, it showed moderate performance, which may be due to the informative pedigree and a higher average number of parturitions compared to the other populations. The estimates of the genetic variance affecting the mean for population UNH were reasonably close to the simulated values, although with slightly larger deviations than in population P1. When the incomplete model was fitted, the genetic variance of the trait was overestimated in all three populations, as expected, since in such cases the genetic variance typically absorbs part of the litter variance (Sell-Kubiak et al., 2025). In P1, the overestimation was particularly high, even exceeding the sum of the two variance components, which could be due to the simulated negative genetic correlation for this population. However, in the UNH population, with a genetic correlation of 0.21, the overestimation was somewhat lower, while in P2, where very few replicates converged, the estimates were more unstable.

The genetic variance affecting residual variance also showed differences among populations. In P1, the estimates of this parameter were generally around the simulated values, indicating greater model stability when a deep pedigree and a larger number of records are available. At UNH, the estimates were slightly more variable but maintained a trend of approaching the simulated values. In contrast, in the few convergent replicates, greater deviations were observed in P2, which could suggest that the estimate of the genetic variance affecting the residual variance is sensitive to the amount of available information. When the number of repeated observations is too small, or even a single record per animal, there may not be sufficient information to fit a model with random effects for both the mean and the residual variance (Felleki et al., 2012; Mulder et al., 2013). The genetic correlation between the mean and the residual variance also exhibited different patterns across populations. In the P1 and UNH populations, estimates tended to approach the simulated value, although with greater variation between replicates in UNH. In P2, however, estimates were more unstable and, in some cases, reached extreme values.

The litter variances affecting the mean and residual variance showed relatively consistent patterns across populations when the complete model was fitted. Specifically, considering the replicates that have converged, the litter variance affecting the residual variance appears to be underestimated in all three populations under the Frequentist approach. In this context, Rojas et al. (2026) also reported, under the Frequentist approach, underestimated estimates of this parameter when the mean litter size was low, and observed that such estimates only approximated the true value when a higher litter size was simulated, whereas the Bayesian approach provided estimates close to the true value even in scenarios with low litter sizes. On the other hand, under the incomplete model, the litter components were redistributed toward genetic variance, confirming the importance of including litter effects in prolific species to avoid overestimating variance components. Under the incomplete model, the Bayesian approach appears to perform better than the Frequentist approach, as it converged and provided results in most of the simulated scenarios for the P2 and UNH populations.

A consistent descriptive pattern across the evaluated scenarios was that breeding value accuracies for residual variance were similar under the complete and incomplete models. However, this observation should be interpreted cautiously because several scenarios showed low convergence rates, particularly for the complete model. Therefore, the results do not demonstrate equivalence between model specifications, but rather suggest that, under the simulated conditions considered here, breeding value prediction may be less sensitive to the omission of litter effects than variance component estimation. In contrast, the partitioning of variance components was clearly affected by model specification. This could be because accuracy depends primarily on the available information structure, such as the number of observations for the individual and their relatives, rather than on the partitioning of the genetic and litter components. The two models fitted used the same mating scheme for each population, and therefore the difference resides in the partitioning of the variances and not in the available information. Therefore, although biased estimates of variance components were found in some cases, the accuracy of the genetic values for residual variance could be maintained. This implies that omitting the litter effect could affect the quality of the model parameter estimates, but not the accuracy of the additive genetic values. On the other hand, it was observed that, under both approaches, the complete model tended to fail more when the genetic variance of the trait became increasingly smaller relative to the sum of the genetic and litter components, suggesting that the magnitude of the true genetic variance in real guinea pig populations might be small. Furthermore, although similar accuracies were obtained with both models, the incomplete model tended to fail much less than the complete model when a higher genetic variance was simulated by both the Frequentist and Bayesian approaches.

On the other hand, our results show that selection aimed at reducing the residual variance in BW could lead to a progressive decrease in the variability of this trait. The response to negative selection observed in all evaluated scenarios indicates that selection favors individuals associated with lower sensitivity to microenvironmental effects, which would lead to greater uniformity in BW within litters. Another interesting aspect is the cumulative effect of selection across generations. While reductions in residual variance were moderate after one generation, selection over five generations produced more evident reductions. Therefore, reducing BW variability could help improve litters' uniformity, which would facilitate production management. Furthermore, in guinea pig production systems, where the BW of offspring is associated with survival, greater uniformity could translate into production and economic benefits. Overall, our results suggest that genetic selection aimed at reducing residual variance could be a viable strategy for improving BW uniformity in guinea pig production systems.

4.1. Limitations

The results of this study should be interpreted considering several methodological constraints. The simulation scenarios were parameterized using estimates obtained from the incomplete model because the complete model failed to converge for the real datasets. Consequently, the evaluated scenarios should be regarded as plausible representations of the populations rather than exact descriptions of their underlying genetic architecture. In addition, convergence difficulties were observed in several simulation scenarios, particularly when fitting the complete model, which reduced the number of successful replicates available for comparison and limited the strength of the inferences that can be drawn from some results. On the other hand, although the populations studied allowed the evaluation of a range of realistic conditions, caution is warranted when extrapolating the findings to other populations with different structures or management systems. Despite these limitations, the study provides useful insights into the behavior of heteroscedastic models under the data conditions commonly encountered in guinea pig breeding programs.

5. Conclusions

The heteroscedastic model was able to recover simulated parameters with varying success depending on pedigree depth, amount of information, and model specification. Although omitting litter effects altered variance partitioning, the accuracy of the genetic values for both the mean and the residual variance was similar regardless of whether the litter effect was included. Favorable responses were expected for

uniformity of BW. These results suggest that selection for within-litter BW uniformity may be feasible in guinea pig populations with pedigree depth and data availability comparable to population P1. However, further studies using larger datasets and alternative parameterizations are required before generalizing these findings.

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

During the revision process, the authors used DeepL to improve the style and grammar of individual sentences, making the text more concise. The authors then reviewed and edited the content as needed. The authors took full responsibility for the content of the publication.

Ethics approval

No ethical statement was required in these studies.

Funding

This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Finance Code 001. This study was conducted within the framework of project PID2023–149012OB-I00, funded by the Spanish Ministry of Science, Innovation, and Universities.

CRediT authorship contribution statement

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Declaration of competing interest

The authors declare that they have no financial conflicts of interest or personal relationships that could have influenced the work presented in this article.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.livsci.2026.106000.

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