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Improving Accuracy of Genetic Evaluation of Survival Traits in Quail by Including Dominance Effect in the Random Regression Threshold Model

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Abstract

Survival is an important economic trait that can enhance production and profits while reducing breeding costs. Therefore, it is crucial to consider this trait in breeding programs, which require knowledge of the (co)variance components of traits. This study aimed to compare various random regression threshold models and determine the most suitable model for estimating the variance components of survival traits in Japanese quail. The survival trait at different ages was defined as code one (bird alive at considered age) and code zero (bird dead at considered age) as binary traits. In total, survival records of 5956 birds born from 709 cocks and 825 hens between ages one and 45 days with a recording interval of 5 were used. Different random regression threshold models varying in the number of effects and order of Legendre polynomials were compared, and the best model was selected using the logarithm of the likelihood (LogL), Bayesian Information Criterion (BIC), and Akaike Information Criterion (AIC). The results showed that the model containing direct additive genetic (4^{th} order), maternal genetic (2^{nd} order), permanent environment of the bird (5^{th} order), and dominance (1^{st} order) was the most suitable model. An increasing trend was observed for direct additive genetic variance with age, whereas the remaining variance components exhibited a declining trend. Heritability for survival traits at different ages ranged from 0.041 to 0.200. The ratio of maternal genetic, permanent environment of the bird, and dominance variances to phenotypic variance of survival traits was higher at early ages but decreased in later ages. The lowest and highest direct genetic correlations were estimated as 0.536 (between survival at hatch and up to 45 days of age) and 0.979 (between survival up to 15 and up to 20 days of age), respectively. Considering the estimated heritability and genetic correlation for survival up to 30 days of age and survival traits at later ages, this trait can be recommended as a practical and effective selection criterion for improving overall survival in breeding programs.

Introduction

In recent years, the increase in population and food demands have led to significant growth in the poultry industry. This increase was a response to people's need to meet their protein requirements (Garcia *et al*., 2007). Quail, one of the smallest animal species, was first domesticated as a songbird in the 11^{th} century. This bird is bred for both meat and egg production. In recent years, it has also been utilized as a laboratory animal model for scientific research due to its remarkable characteristics (Minvielle, 1998).

Survival on farms can have a significant impact on the net profit of breeding units and is one of the most critical issues that has been gaining increasing attention (Mc Cullough & Delorenzo, 1996). Improving farm survival can lead to reduced costs related to breeding and purchasing replacement animals, while also potentially increasing overall

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production (Van Raden & Wiggans, 1995). In recent decades, performance traits have become a focal point in breeding programs due to their economic significance. These traits are those that can enhance net income by lowering input costs. Longevity is a key performance trait that is taken into consideration in livestock breeding. Many performance traits exhibit a non-normal phenotypic distribution and can often be analyzed as threshold traits (Damgaard & Korsgaard, 2006). The phenotypic expression of these traits often falls into two categories, and occasionally more than two. Because they are not normally distributed, simple regression and variance analysis are inappropriate for such data. Consequently, threshold models are the preferred method for estimating genetic parameters in these traits (Kaps & Lamberson, 2004; Jamdar & Eskandarinasab, 2014).

In a study on turkey survival traits using a multi-trait animal model in paternal and maternal lines, it was reported that the heritability of survival up to 3 weeks in both lines was less than 5%. The heritability of survival from 3 to 23 weeks in both lines was found to be in the range of 0.12 to 0.14. Additionally, it was noted that the two survival traits were not genetically correlated and were independent traits. Therefore, any selection to improve survival would only affect the specific life stage under selection (Quinton *et al*., 2011). In another study, survival traits and production traits (egg weight and weekly weight gain) in Japanese quail were studied using a linear-threshold model. The heritability range for survival traits in various weeks ranged from 0.138 to 0.399 (Saghi *et al*., 2022). The heritability range of survival using different repeatability models has been reported to be 0.14 to 0.93 for laying hens (Brinker *et al*., 2015) and 0.02 to 0.1 for inbred laying hen lines (Ellen *et al*., 2008).

Accurate knowledge of (co)variance components and genetic parameters is a key requirement for both livestock breeding and designing breed- specific selection programs (Mostret *et al*., 2006). Random regression models are used to analyze traits with repeated observations over time, such as milk production, body weight, wool production, sperm production and quality in males, and reproductive traits in females (Schaeffer, 2004). In these models, there are no assumptions of constant variances or correlation of records over time (Meyer, 2005). Using a random regression model allows the researcher to examine changes in genetic variance over time and select individuals based on the pattern of these changes (Schaeffer, 2004). Using random regression models in genetic analysis compared to animal models has advantages, including: no need to adjust records to obtain weight at a specific age, the ability to consider specific environmental effects for each day of recording in statistical analysis (Meyer, 2001), predicting breeding value and selecting animals at young ages, reducing the generation interval, increasing the accuracy of estimating genetic parameters, and predicting breeding value due to the increase in the number of records per animal compared to the animal model (Swalve, 1998; Farhangfar *et al*., 2001).

By considering the dates of body weight recording and the presence or absence of the bird during recording, we can treat the survival trait as a binary trait. Because the survival trait was recorded at various times, and analyzing traits with repeated observations over time is possible using random regression models, this study aimed to compare different random regression models and to select the most suitable model for estimating the variance components of the survival traits in Japanese quail.

Materials and Methods

Population and management

The animal care and experimental procedures in the present study were conducted according to Iranian Council for Animal Care guidelines and had its protocol approved by the Research Animal Ethics Committee of the University of Zabol (AEUOZ-2012-BR). The data used in the present study were collected from 5,956 chicks (5008 females and 948 males) born from 709 cocks and 825 hens from a random-bred population of Japanese quails over 6 generations at the Special Domestic Animals Institute, Research Institute of Zabol, Zabol, Iran. The number of records was uniform across all age groups, with each group consisting of 5,956 observations. Table 1 shows the pedigree structure of the studied population.

Table 1: The pedigree structure of the studied population

Bird	number
Birds in total	6216
Inbreds in total	294
Cocks in total	709
Hens in total	825
Average full-sib family size	6.57
Maximum full-sib family size	36
Minimum full-sib family size	2
Birds with known cock	93
Birds with known hens	157
Birds with known cock and hens	4894
Average pedigree completeness index	87.71

The chicks were reared in groups until they were 45 days of age and then randomly distributed (in pairs of one male and one female) in cages equipped for mating and producing fertile eggs. Between days 70 and 80 of parental age, fertilized eggs from each cage were identified according to their breeding pairs, numbered, disinfected, and stored at 12–16°C and 70% relative humidity prior to incubation. Each generation comprised two consecutive hatches, conducted at 5-day intervals. In the first week, the brooding room temperature was considered at 35°C and then progressively decreased to 20–25°C during the following weeks. All birds were fed a standard growth diet (at 1-45 d) and laying diet (after 45 d) during the experimental period. The selection and mating system among birds in all generations was random. All birds had ad libitum access to food and water throughout the experiment.

Traits

Based on the body weight of birds recorded every 5 days from hatch to 45 days of age, survival traits at different ages were obtained as follows: if the bird was alive at the weighing date, it was coded as 1 (alive), and otherwise it was coded as 0 (dead). Survival status was coded cumulatively: once a bird was recorded as dead, it was considered deceased for all subsequent time points. Therefore, survival at hatch (S_1), hatch to 5 (S_5), 10 (S_{10}), 15 (S_{15}), 20 (S_{20}), 25 (S_{25}), 30 (S_{30}), 35 (S_{35}), 40 (S_{40}), and 45 (S_{45}) days of age were obtained as binary traits. The frequency of alive and dead birds at different ages is presented in Table 2.

Table 2: Frequency of alive and dead birds at different ages

Age (days)	Total records	Frequency of alive	Frequency of dead
1	5956	5956	0
5	5956	4770	1186
10	5956	3933	2023
15	5956	3223	2733
20	5956	3100	2856
25	5956	2894	3062
30	5956	2776	3180
35	5956	2677	3279
40	5956	2588	3368
45	5956	2292	3664

Statistical analysis

In this study, a threshold model was employed to analyze binary survival traits. We assumed that the observed outcome (y) for each bird followed a Bernoulli distribution (alive = 1, dead = 0). Furthermore, we assumed that each bird possesses an underlying latent liability (U_i) for survival. Birds with liabilities exceeding the threshold (t) were observed as alive (y=1), whereas those with liabilities below the threshold were observed as dead (y=0). After editing, the data were analyzed using the following random regression threshold model:

$$y_{ijk} = S_i + GH_j + \sum_{k=0}^{k_a-1} a_{ik}\emptyset_k(a_{ijk}) + \sum_{k=0}^{k_m-1} m_{mk}\emptyset_k(a_{ijk}) + \sum_{k=0}^{k_{pe}-1} pe_{ik}\emptyset_k(a_{ijk}) + \sum_{k=0}^{k_d-1} d_{ik}\emptyset_k(a_{ijk}) + e_{ijk}$$

Where y_{ijk} is the underlying variable; $S_i$is the ith sex of chicks; GH_j is the jth generation-hatch; a_{ik}, pe_{ik}, d_{ik} and m_{mk} are random regression coefficients for the kth-order polynomial of the direct additive genetic, permanent environment of the bird, and dominance of chick i, maternal genetic of hen m, respectively; e_{ijk} is the residual effect; $\emptyset_k$ is the kth Legendre polynomial of age; k_a, k_m, k_{pe}, and k_d are the order of fit for direct additive genetic, maternal genetic, permanent environment of the bird, and dominance, respectively; a_{ijk} is the standardized age in the range of -1 to +1, which is calculated as follows:

$$a_{ijk} = -1 + \frac{2(t - t_{min})}{t_{max} - t_{min}}$$

Where t is the days of recording, t_{min} and t_{max} are the minimum and maximum days of recording.

Model selection

Various models were applied to the data, which differed in terms of the type of random effects included in the model and the order of Legendre polynomial fit used for these effects. Given that the residual variance in a threshold model is not identifiable and is typically fixed to 1 (Vazquez *et al*., 2009). Therefore, in all models, the residual effects were considered homogeneous. The optimal order of Legendre polynomials for each effect was determined through a stepwise forward selection procedure. Initially, the model that only included the permanent

environmental of the bird random effect was fitted with varying order of fit (1 to 6) until reaching the appropriate model (5th order). Subsequently, other effects such as the direct additive genetic (1 to 5), maternal genetic (1 to 3), and dominance (1 to 2) were added to the previous model with the appropriate order of fit, respectively. Model convergence was evaluated using the log-likelihood change, gradient norm ($<1\times10^{-8}$), and step size tolerance, with a maximum of 100 iterations. The appropriate model was selected based on the logarithm of likelihood value (LogL), Bayesian Information Criterion (BIC), and Akaike Information Criterion (AIC). This selection required a higher logarithm of likelihood value (LogL) and lower values for both the BIC and AIC. The BIC and AIC were calculated as follows:

AIC=-2 log (L) + 2p

BIC= -2 log (L) + p log(n)

Where log (L), p, and n represent the log-likelihood value, number of parameters, and number of observations, respectively. The number of parameters was also calculated using the following Equation:

P=k(k+1)/2

Where k represents the order of fit for the Legendre polynomial for random effects (Kirkpatrick *et al*., 1990).

Genetic parameter estimation

The variance-covariance functions of the random effects of survival traits for each age pair were calculated based on the suggestions of Meyer & Hill (1997). The variance-covariance matrix for the direct additive genetic effect was calculated as follows:

$$\widehat{\boldsymbol{G}} = \emptyset \boldsymbol{K} \acute{\emptyset}$$

Where $\widehat{\boldsymbol{G}}$ is a variance-covariance matrix for the direct additive genetic effect with rank t*t, where t is the number of age classes studied; $\emptyset$ is a matrix with rank t*k of Legendre polynomials with order of fit k; $\acute{\emptyset}$ is the transpose of $\emptyset$ the matrix; **K** is the variance-covariance matrix for the random regression coefficients of the direct additive genetic effect. For other random effects, only the variance-covariance matrix was substituted with the random regression coefficients of that effect. The covariance structure for direct additive genetic effects was assumed to follow a multivariate normal distribution with covariance matrix $\mathbf{G}_a=\mathbf{K}_a\otimes\mathbf{A}$, where **A** is the numerator relationship matrix, and $\mathbf{K}_a$ is the covariance matrix of the regression coefficients. Similarly, maternal genetic effects were modelled as $\mathbf{G}_m=\mathbf{K}_m\otimes\mathbf{A}$. The permanent environmental effects of birds were assumed to be independently distributed with covariance matrix $\mathbf{P}=\mathbf{K}_{pe}\otimes\mathbf{I}$, where **I** is an identity matrix. For the dominance effects, the covariance structure was specified as $\mathbf{D}=\mathbf{K}_d\otimes\mathbf{D}_{dom}$ where $\mathbf{D}_{dom}$ is the dominance relationship matrix. All random effects were fitted using Legendre polynomials as basic functions.

Phenotypic variance for each age point and between two age points was obtained by summing the variance-covariance of all random effects. Subsequently, heritability for each age (h_j^2), and broad- sense heritability (H_j^2) were calculated using variance-covariance matrices as follows:

$$h_j^2 = \frac{V_{Aj}}{V_{Pj}}$$

$$\mathrm{H_j^2} = \frac{\mathrm{V_{Aj}} + \mathrm{V_{dj}}}{\mathrm{V_{pj}}}$$

Where V_{Aj}, $\mathrm{V_{dj}}$, and V_{Pj} are the direct additive genetic variance in the diagonal of $\hat{G}$ matrix at age j, dominance variance in the diagonal of $\hat{\mathrm{d}}$ matrix at age j and phenotypic variance at age j, respectively. Using the $\hat{G}$ matrix, the genetic correlation (r_g) between traits was computed as follows:

$$r_g = \frac{Cov(A_i, A_j)}{\sqrt{V_{Ai} * V_{Aj}}}$$

Where $Cov(A_i, A_j)$ shows additive genetic covariance of $\hat{G}$ matrix between two ages i and j; V_{Ai} and V_{Aj} are the additive genetic variance at ages i and j, respectively (Tongsiri *et al*., 2020).

Software

Data editing was performed using FoxPro software. The nadiv package (Wolak, 2012) of R software was utilized to estimate the inverse dominance matrix. Echidna software (Gilmour, 2018) was employed to analyze random regression models.

Results

Log-likelihood (LogL), BIC, and AIC values for the 16 fitted threshold random regression models are presented in Table 3. These models varied in the number of random effects and the order of fit for these effects. The first six models only considered the effect of the permanent environment of the bird with different orders of fit. As the order of fit increased, there was an improvement in the values of LogL, BIC, and AIC up to order 5. However, there was no favorable trend when increasing the order of fit from 5 to 6 for the permanent environment of the bird. Therefore, the additive genetic effect was included in the model with a 5th order for the permanent environment of the bird. As the order of fit for the direct additive genetic effect increased, a favorable trend was noted for the LogL, BIC, and AIC. However, this trend was only observed up to a 4th order. Beyond an order of fit of 4, the LogL value decreased, and the values of the BIC and AIC increased.

Table 3: The orders of Legendre polynomials and model selection criteria for various fitted threshold random regression models

Model	K_a	K_m	K_{pe}	K_d	Number of parameters	Log-Likelihood	AIC	BIC
1			1		3	-12076.41	142944.17	142969.81
2			2		6	-12007.29	142834.29	142885.57
3			3		10	-11887.27	142643.97	142729.44
4			4		15	-11726.29	142387.45	142515.64
5			5		21	-10941.05	141219.05	141398.53
6			6		28	-11083.44	141243.93	141583.24
7	1		5		24	-10475.50	140668.17	140873.28
8	2		5		27	-10214.58	140465.14	140695.89
9	3		5		31	-9893.76	140366.50	140631.44
10	4		5		36	-9649.32	140347.33	140655.01
11	5		5		21	-10473.64	140795.37	140974.84
12	4	1	5		39	-9942.22	140430.41	140763.72
13	4	2	5		42	-9542.34	140250.71	140609.66
14	4	3	5		46	-9945.48	140709.04	141102.18
15	**4**	**2**	**5**	**1**	**45**	**-8940.16**	**140023.75**	**140408.34**
16	4	2	5	2	48	-9088.90	140015.09	140425.32

Order of fit for direct additive genetics (K_a), maternal genetics (K_m), permanent environment of the bird (K_{pe}), and dominance (K_d)

Adding maternal genetic effect to the model containing the direct additive genetic effect (4th order) and the permanent environment of the bird (5th order) increased the LogL value and decreased the values of BIC and AIC. This favorable trend was observed only when increasing the order of fit from one to two for the maternal genetic effect. Finally, the dominance effect was added to the model as another random effect; however, a favorable trend in the LogL, BIC and AIC values was only observed with a 1st order for dominance, along with other random effects with a suitable order. When the order of fit for dominance was increased to two, the LogL values decreased, although there was no observed increasing trend for the AIC, but the BIC increased. Based on the BIC and LogL, which both showed an unfavorable trend, it can be concluded that an order of fit 1 is suitable for the dominance effect. Therefore, after considering these criteria, model 15 was selected as the most appropriate model for estimating variance components and genetic parameters of survival traits at different ages of quail. This model includes the effects of direct additive genetic (4th order), maternal genetics (2nd order), permanent environment of the bird (5th order), and dominance (1st order).

Table 4 shows the estimated variance components for the random effects on survival traits at various ages. The direct additive genetic variance for survival traits was found to be lower at early ages compared to later ages. As age increased, there was an observed increasing trend for direct additive genetic variance. The lowest and highest direct additive genetic variances were estimated for survival at hatch and hatch to 45 days of age, respectively. The amount of maternal genetic variance for survival traits was estimated to be higher than the amount of direct additive genetic variance at 1 and 5 days of age. However, at later ages, the amount of maternal genetic variance was lower than the amount of direct additive genetic variance. It can be observed that the amount of maternal genetic variance for survival traits decreased with increasing bird age, reaching its lowest value at 45 days of age. Therefore, it can be concluded that maternal genetics had the most significant effect on bird survival at younger ages, while at older ages the maternal genetic effect on survival traits was lower.

The permanent environment of bird and dominance variances were estimated to be lower than maternal genetic and direct additive genetic variances at all ages. The dominance variance of the survival traits at different ages was also lower than the permanent environment of bird variance. However, a decreasing trend was observed with age in both the dominance and permanent environment of bird variances. The highest amount of variance was found in young ages, especially at one day old, while the lowest amount was estimated for the survival trait up to 45 days old.

The direct heritability, ratio of maternal genetic, permanent environment of bird and dominance variance to phenotypic variance, repeatability, and broad- sense heritability for survival traits of the studied population are provided in Table 5. The direct heritability value for survival at hatch (0.041) was estimated to be lower than for other survival traits at different ages. However, as age increased, the direct heritability value also increased. Until the age of 20 days, the direct heritability value for survival traits remained less than 10%, but it increased at later ages. The highest direct heritability value for the survival

trait was estimated at 45 days of age, reaching 20%. Therefore, it can be concluded that the contribution of direct additive genetic effects on survival traits at early ages was minimal, and genetic selection for these traits in the short term may not yield desirable results.

Table 4: The estimated direct additive genetic (V_a), maternal genetic (V_m), permanent environment of the bird (V_{pe}), dominance (V_d), residual (V_e), and phenotypic (V_p) variance for survival traits at various ages

Trait	V_a	V_m	V_{pe}	V_d	V_e	V_p
S_1	0.048	0.079	0.049	0.010	1	1.187
S_5	0.057	0.059	0.031	0.009	1	1.156
S_{10}	0.074	0.048	0.027	0.005	1	1.154
S_{15}	0.096	0.037	0.026	0.004	1	1.163
S_{20}	0.107	0.029	0.024	0.003	1	1.164
S_{25}	0.148	0.028	0.018	0.004	1	1.198
S_{30}	0.175	0.020	0.008	0.003	1	1.206
S_{35}	0.172	0.019	0.007	0.003	1	1.200
S_{40}	0.217	0.015	0.006	0.002	1	1.240
S_{45}	0.252	0.011	0.004	0.0016	1	1.268

S1-S45 are survival at hatch (1d), and hatch to 5, 10, 15, 20, 25, 30, 35, 40, and 45 days of age

Table 5: Direct heritability (h2), ratio of maternal genetic variance to phenotypic variance (m2), ratio of permanent environment of the bird variance to phenotypic variance (p2), ratio of dominance variance to phenotypic variance (d2), repeatability (r) and broad- sense heritability (H2) of survival traits

Trait	h^2	m^2	p^2	d^2	r	H^2
S_1	0.041	0.067	0.041	0.008	0.082	0.049
S_5	0.049	0.051	0.027	0.007	0.076	0.057
S_{10}	0.064	0.041	0.023	0.004	0.087	0.068
S_{15}	0.082	0.032	0.023	0.004	0.105	0.086
S_{20}	0.092	0.025	0.021	0.003	0.113	0.095
S_{25}	0.123	0.024	0.015	0.003	0.138	0.126
S_{30}	0.145	0.016	0.006	0.003	0.151	0.148
S_{35}	0.143	0.016	0.006	0.002	0.148	0.146
S_{40}	0.175	0.012	0.004	0.002	0.179	0.177
S_{45}	0.200	0.008	0.003	0.001	0.202	0.200

S1-S45 are survival at hatch (1d), and hatch to 5, 10, 15, 20, 25, 30, 35, 40, and 45 days of age

The ratio of maternal genetic variance to phenotypic variance for survival traits ranged from 0.008 to 0.067. The highest values were observed at early ages, especially at one and 5 day of age. However, as age increased, the ratio decreased so that it reached less than one percent for survival up to 45 days of age. The significant contribution of maternal genetics at early ages may be one reason for the low amount of direct additive genetics at these ages. The ratio of the permanent environmental variance of birds to phenotypic variance also followed a similar trend to the ratio of maternal genetics to phenotypic variance. The impact of this effect on early traits was substantial, but its influence decreased as the birds aged. For survival traits, the ratio of permanent environmental variance of birds to phenotypic variance was higher than one percent up to 25 days of age, but for older dropped to less than one percent. The ratio of dominance variance to phenotypic variance for survival traits was estimated to be less than one percent at all ages. The highest and lowest values were at 1 and 45 days of age, respectively, with a decreasing trend observed as age increased. Although these effects have a smaller contribution, according to the model selection criteria in Table 3, they were found to be effective on survival traits. To obtain accurate genetic parameters from the direct additive genetic effects of survival traits, it is important to consider these effects (dominance, permanent environment of the bird, and maternal genetics) in genetic evaluation models. Ignoring these effects in the model can result in their contribution being absorbed into the additive or residual genetic variance, leading to inaccurate estimation of genetic parameters. The range of repeatability and broad-sense heritability for survival traits at different ages was 0.082-0.202 and 0.049-0.200, respectively. Although the repeatability of traits was not high, especially at ages less than 20 days, the repeatability for survival at ages older than 20 days was higher than 10%.

Figure 1 shows the direct additive genetic correlations between survival traits at various ages. The direct genetic correlation between survival at hatching day and from hatch to 5 days of age was estimated to be over 90%. However, the direct

genetic correlation of survival traits at hatching day with other traits at older ages exhibited a decreasing trend with increasing age intervals. For instance, the direct genetic correlation between survival at hatching and hatch to 45 days of age decreased to 0.536.

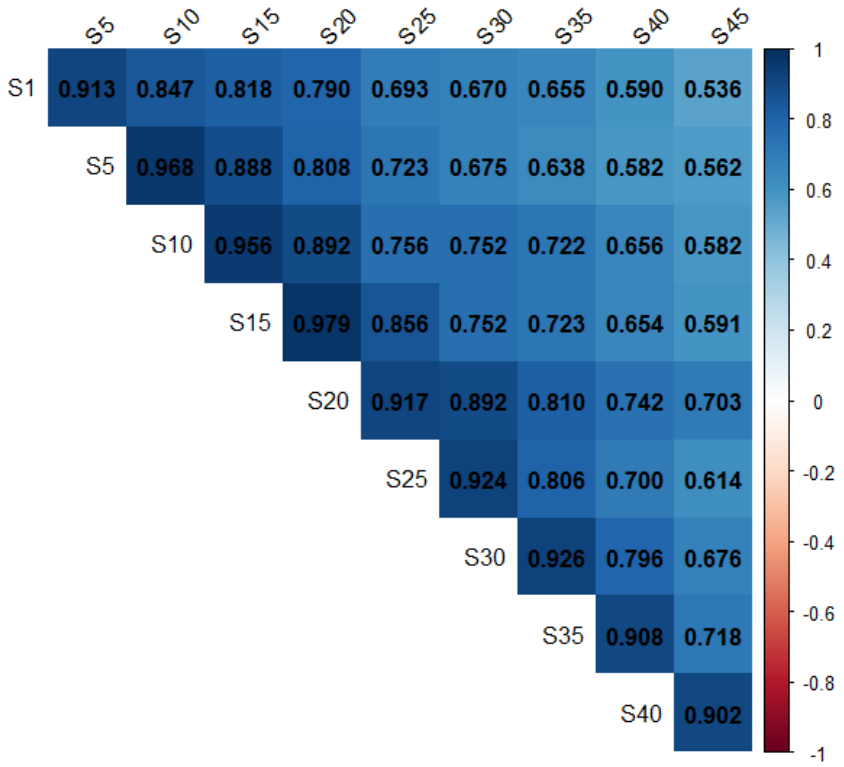


Figure 1. Direct genetic correlations between survival traits (S_1-S_{45} are survival at hatch (1d), and hatch to 5, 10, 15, 20, 25, 30, 35, 40, and 45 days of age) at different ages. Red and blue color gradients represent positive and negative correlation coefficients, respectively. The intensity of the color (redder or bluer) reflects the magnitude of the correlation, while lighter/whiter areas indicate values closer to zero.

The correlation of survival from hatch to 5 days of age with other traits at older ages was found to be higher than the direct genetic correlation of survival at hatch with other traits. However, a similar decreasing trend was observed with increasing age intervals between traits for direct genetic correlations. The highest direct genetic correlation value among all correlations was obtained for survival from hatch to 15 and hatch to 20 days of age, with a value of 0.979. After 20 days of age, the correlation between traits was consistently higher than 60%, with high correlation values estimated for traits with a small age interval and the lowest for survival traits with a large age interval. A high and positive correlation between traits indicates that genetic selection for one trait to improve it is expected also to improve other traits that have a high direct genetic correlation. Therefore, selecting for survival at an early age should also result in improvements for survival at an older age.

Maternal genetic correlation values between traits were lower at most ages than the direct genetic correlation between them (Figure 2), so that the maternal genetic correlation between survival at hatching day and survival from hatch to 40 and 45 days of age had low and negative values. Similar to the direct genetic correlation, as the distance between traits increased, maternal genetic correlations between traits also showed a decreasing trend. Maternal genetic correlation values between traits were higher at older ages than at younger ages. Although maternal genetic correlations were less than 50% between traits before 15 days of age, they were higher than 50% at 15 days and beyond. The highest maternal genetic correlation value was 0.922 between survival from hatch to 20 and hatch to 25 days of age, while the lowest value was -0.020 between survival at hatch and hatch to 45 days of age. These results indicate that maternal genes affecting survival traits are consistent at most ages.

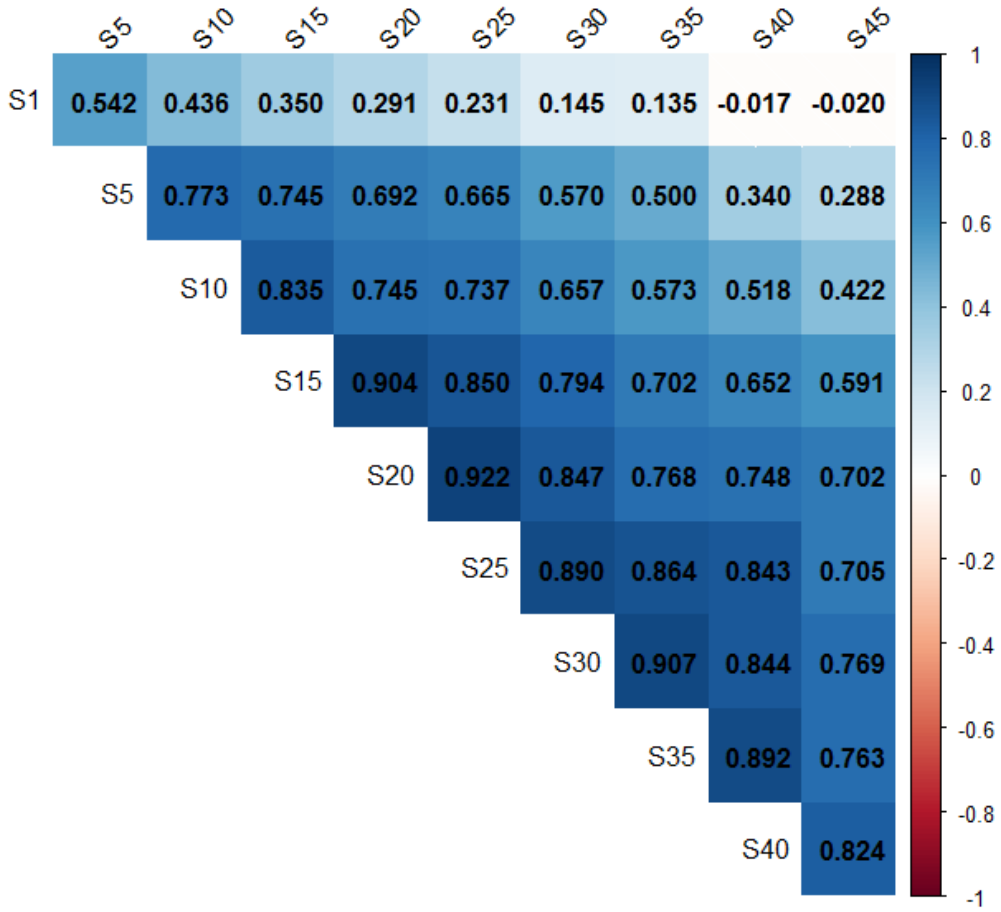


Figure 2. Maternal genetic correlations between survival traits (S_1-S_{45} are survival at hatch (1d), and hatch to 5, 10, 15, 20, 25, 30, 35, 40, and 45 days of age) at different ages. Red and blue color gradients represent positive and negative correlation coefficients, respectively. The intensity of the color (redder or bluer) reflects the magnitude of the correlation, while lighter/whiter areas indicate values closer to zero.

Discussion

In a study on survival in pigs at different calvings, researchers observed an unfavorable trend in the deviation information criterion (DIC) when adding the degree of fit for permanent environment and direct additive genetics, consequently from two to the next. Thus, 2nd order was utilized for the analysis of survival traits involving the two aforementioned effects (Plaengkaeo *et al*., 2020). Asefi *et al.* (2020) reported a favorable trend in the AIC when adding random effects to the survival analysis in Moghani sheep. They stated that direct additive genetic, maternal genetic, maternal permanent environmental, and common litter effects all contributed significantly to the observed survival variation in this breed. In a separate investigation on Moghani sheep, the suitable model was one that incorporated both maternal permanent environmental and direct additive genetic effects (Ghavi Hossein-Zadeh *et al*., 2018). Additionally, it was noted that the impact of maternal genetics and direct additive genetic effects on the survival traits of sheep lambs up to weaning was significant, while the effects of the permanent environment were deemed insignificant (Everett-Hincks *et al*., 2014).

In a study of survival traits in a crossbred population of quail, it was reported that the effect of maternal permanent environment was significant only for cumulative survival up to 5 days of age and not significant for survival at later ages. Additionally, the effect of maternal genetics was found to be effective on survival up to 25 days of age. After 25 days, only the direct additive genetic effect was reported to be significant (Faraji-Arough *et al.*, 2023).

While the pedigree structure in this study provided sufficient information for estimating dominance variance, some degree of confounding among additive, maternal, permanent environmental, and dominance effects may persist. Specifically, maternal or permanent environmental effects can be partially confounded with dominance, necessitating their inclusion as random effects within the model. Furthermore, pedigree-based methods may overestimate dominance variation, particularly in

hierarchical mating designs where dominance and maternal effects are prone to confounding. To mitigate these issues, a stepwise model selection procedure was employed and included all relevant random effects (additive, maternal, permanent environmental, and dominance) simultaneously in the final model. The significant improvement in model fit observed upon the inclusion of dominance (Table 3) demonstrates that dominance exerts a substantial effect on these traits. Nevertheless, these estimates should be interpreted with caution, and future studies using genomic data could help disentangle these effects more accurately.

To the best of our knowledge, there are few survival studies in birds that utilize random regression models. Most survival analyses involve animal models, primarily focusing on animals like sheep and cattle. However, the trend observed in the model selection criteria in our study has also been noted in the study of body weight traits in quail and broiler poultry. For example, increasing the order of fit from two to three for the direct additive genetic and the permanent environment of the bird resulted in undesirable trends in the values of the goodness of fit criteria for analyzing body weight traits in four lines of chickens raised in an open system. Subsequently, increasing the order of fit from three to six in the models caused convergence issues (Rovadoscki *et al*., 2016). In another study, a regression model with order of fit three and four, respectively, for the direct additive genetic and the permanent environment of the bird was chosen as the appropriate model for studying body weight traits in native Mazandaran chickens (Naderi *et al*., 2019). Similar to the current study, an enhancement in model selection criteria was observed by increasing the order of fit to 3 for the direct additive genetic and the permanent environment of the bird in regression models during a study of body weight traits in Japanese quail (Karami *et al*., 2017).

With increasing age, an increasing trend was reported in the direct additive genetic variance of survival traits in white shrimp (Ren *et al*., 2022), which was similar to the results of our study. However, the permanent environment of bird variance exhibited an opposite trend compared to our findings. In Dutch cattle, direct additive genetic variance for survival traits at various ages also increased with age, so that the highest variance was reported for older age groups (Van Pelt *et al*., 2015).

Consistent with our observations, an increase in the direct additive genetic variance of body weight has also been documented in commercial broiler chickens (Tuan Chu *et al*., 2020), Japanese quail (Resende *et al*., 2005), crossbred chicks from 2 to 10 weeks (Begli *et al*., 2016), free-range chickens (Rovadoscki *et al*., 2016.), crossbred quail populations from 1 to 45 days of age (Ebrahimi *et al*., 2019), and native Thai chicken populations from 1 to 168 days of age (Tongsiri *et al*., 2020). It has been reported that rapid selection response can be achieved with an additive model in the short term. However, further genetic improvement can be achieved by including non-additive genetic effects in the model (Fuerst *et al*., 1997). The exclusion of non-additive genetic effects from genetic evaluation models can be largely attributed to two factors: the general expectation that such effects are insignificant for quantitative traits, and the lack of practical estimation methods (Rye & Mao, 1998).

In a study on quail survival, researchers analyzed this trait as a threshold alongside production traits. The range of direct heritability for quail survival in different weeks was reported to be between 0.126 and 0.413 (Saghi *et al*., 2022). The highest heritabilities were associated with survival in the first two weeks, while the lowest were linked to survival in the middle stage of growth. The use of a model that only includes direct additive genetic effect and does not consider maternal genetic effect, the permanent environment of the bird, and other random effects in this study may have led to an overestimation of survival heritability in the first weeks. However, many reports related to the study by Saghi *et al.* (2022) showed higher results than those found in our present study. The range of direct heritability of survival traits in a crossbred population of quail was estimated to be 0.250-0.386 in different weeks, and no clear trend for heritability with increasing age was observed (Faraji-Arough *et al*., 2023), which differs from the results of our study. The reason for this difference could be attributed to variations in study populations, models, and analysis methods.

The direct heritability of survival time under heat stress conditions in Japanese quail, based on full-sib relationships, has been reported to range from 0.13 to 0.53 (Bowen & Washburn, 1984). This range is higher than the results of the present study, although some estimates did align with our findings. In a study of survival traits in maternal and paternal lines of turkeys (Quinton *et al*., 2011), the direct heritability of survival up to 3 weeks was reported as 0.02 for maternal lines and 0.04 for paternal lines. These values were lower than the results of our study. However, the direct heritability of survival from 3 to 33 weeks for maternal and paternal lines was estimated at 0.12 and 0.14, respectively, which was similar to our findings.

In a study on survival in laying hen lines, direct heritability for survival was found to be 0.07, 0.10 and 0.02 for W1, WB and WF lines, respectively (Ellen *et al*., 2008). In a similar study on different laying hen lines and crosses, survival direct heritability ranged from 0.03 to 0.26 (Ellen & Bijma, 2019). Additionally, a study on survival of white laying hen crosses (Peeters *et al*., 2012) and brown laying hen lines (Alemu *et al*., 2016) reported a range

of 0.1-0.22 for estimated survival heritability, which aligns with the range found in the present study.

In this study, maternal genetics had a significant impact on all traits. In contrast, Faraji-Arough *et al*. (2023) found that maternal genetics influenced cumulative survival up to 20 days of age in a crossbred population of quail. The ratio of maternal genetic variance to phenotypic variance in Faraji-Arough *et al*. (2023) ranged from 0.064 to 0.111, which was higher than the range observed in our study. In our study, we found that the influence of maternal genetics on survival traits decreased as the age of birds increased. This trend is consistent with previous research on native Iranian chickens (Jasouri *et al*., 2017) and quail (Mota *et al*., 2018), which also showed a decrease in the contribution of maternal genetic effects with increasing bird age for body weights.

The ratio of maternal environment of bird variance to the phenotypic variance for survival up to 5 days of age in a crossbred population of quail has been reported to be 0.021, which was not significant for survival at later ages (Faraji-Arough *et al*., 2023). This ratio was numerically lower than the estimates of the present study. In a survival study in turkeys, the ratio of common environmental variance to the phenotypic variance for survival up to 3 weeks of age for the maternal and paternal lines was 0.05 and 0.01, respectively. For survival from 3 to 33 weeks, this ratio was reported to be 0.42 and 0.37, respectively, for the maternal and paternal lines. These results differ from the results of the present study (Quinton *et al*., 2011).

In this study, the contribution of dominance effects to phenotypic variance was less than one percent for survival traits. Although there are no reports of dominance effects on survival, some studies have reported its effect on other traits. The dominance effect for body weight traits in a crossbred population of quail aged 5 to 30 days was significant, with its contribution to phenotypic variance reported to be about two percent (Ebrahimi *et al*., 2019), which was higher than the results of the present study. In another study on the crossbred population of quail, the ratio of dominance variance to phenotypic variance for body weight gain traits before 25 days of age was significant and reported to be about 2 percent (Faraji-Arough *et al*., 2022). The reported value for the contribution of dominance effect for fertility traits of native Thai chickens (0.049-0.145) (Mookporm *et al*., 2021) was higher than the value obtained in the present study.

Variation in heritability estimates for survival traits can be explained by multiple factors, such as genotype-by-environment interactions in response to stressors, selection, environmental conditions, non-genetic influences, and *negative associations* between health traits and social behavior (Merilä & Sheldon, 1999; Ellen *et al*., 2008; Faraji-Arough *et al*., 2023). The results of the present study demonstrate that genetic parameters for traits can vary at different ages. This variation is likely influenced by changes in the expression of key genes, as well as factors such as hormones, physiological and environmental conditions (Karami *et al*., 2017)

In a study on pig survival, Plaengkaeo *et al.* (2020) reported direct genetic correlations of survival traits in different litters ranging from 0.27 to 0.99. A high genetic correlation was observed between survival traits in white-leg shrimp, particularly for traits with a short age interval. This correlation decreased as the age interval increased, which aligns with the findings of the present study (Ren *et al*., 2022). Although the range of genetic correlations for survival traits in a fish species varied between -0.18 and 0.31 (Wang *et al*., 2010), similar to the findings of the present study, genetic correlations decreased with increasing age intervals. Additionally, genetic correlations between traits were higher for older ages than for younger ages. The genetic correlations between survival traits at different ages in Dutch cattle have been reported to range from 0.25 to 0.99, which aligns with the results of the current study (Van Pelt *et al*., 2015).

A similar trend of increasing genetic correlation between traits has been observed in other poultry species, where the age interval between traits decreases. For example, a positive and high genetic correlation between body weights at close weeks has also been reported for Thai native chickens (Tongsiri *et al.,* 2020). In another study on body weight traits in quail, high correlations were found between body weight traits at similar ages (Akbas *et al.*, 2004). Previous findings in Thai native chickens demonstrate that the direct genetic correlation for body weight was higher than the maternal genetic correlation (Tongsiri *et al*., 2020), which was similar to the findings of the present study. High correlations between traits indicate that the age of selection for traits can be reduced compared to the target age in breeding programs with little loss in selection accuracy (Tuan Chu *et al*., 2019).

Conclusion

Based on the model selection criteria, the threshold random regression model that includes the effects of direct additive genetics (4^{th} order), maternal genetics (2^{nd} order), permanent environment of the bird (5^{th} order) and dominance (1^{st} order) was chosen as the appropriate model for the genetic evaluation of survival traits in quail. The amount of direct additive genetic variance increased with age, while the amount of maternal genetic variance, permanent environment of the bird, and dominance variance showed a decreasing trend with age. Survival traits before 25 days of age had low heritability, while survival traits after 25 days of age had moderate heritability. This

suggests that at early ages, a significant portion of the survival phenotypic variance is influenced by other random effects. The direct and maternal genetic correlation values between survival traits at early ages were found to be lower than those at later ages. Additionally, both correlations decreased as the age interval between survival traits increased. Given the estimated heritability (h^2 = 0.145) and genetic correlations (rg = 0.676, Fig 1) for survival from hatch to 30 days of age and traits at later ages, this trait can be recommended as a practical and effective selection criterion for improving overall survival in Japanese quail breeding programs.

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