Using a linear-threshold model to investigate the genetic relationship between survival and productive traits in Japanese quail

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ABSTRACT
The main goal of breeding programmes is to maximise the genetic improvement of the economic traits of farm animals. Beside the economic traits, the birds’ survival has directly influenced on the economic gain. Therefore, this study aimed to investigate the genetic relationship between survival and productive traits in Japanese quail. A total of 1854 records were collected during four generations from 2017 to 2019 in Khorasan Razavi Agricultural Research and Training Centre (KRARTC). Data were used to estimate the genetic correlations among quail survival (S) with egg weight (EW) and body weight gain (BWG) traits. Linear-threshold model was used to estimate (co)variance components, and genetic parameters of traits via the Gibbs sampling method. The heritability of EW was 0.04, and the heritability estimates for survival at different ages ranged from 0.138 to 0.399 in joint analysis with EW. The highest negative genetic correlation between EW and S0–14 (i.e. survival up to 14 d) was obtained as −0.704. The highest and lowest heritability of weight gain traits for BWG0–7 and BWG7–14 were 0.583 and 0.116, respectively. The analyses of BWG traits with survival at different ages revealed that the genetic correlations ranged from 0.015 (between BWG0–7 and S0–14) to 0.638 (between BWG0–7 and S0–7). This study showed that the genetic selection for survival at different ages could be effective. On the other hand, selection for BWG0–7 could also indirectly improve the survival in quails because of the positive and high genetic correlation between BWG0–7 with S0–7.

HIGHLIGHTS
- Genetic improvement of production traits in quail may lead to reduced survival in quail. Studies regarding on the survival of quail were yet not carried out.
- Heritability of the survival at different ages showed that genetic selection for this trait could improve the survival.
- Survival at different ages had a negative genetic correlation with egg weight (EW), and body weight gain (BWG) traits after 21 d of old.

Introduction
The beginning of breeding programmes in quails has lasted for more than three decades and considerable progression has been attained in terms of product quantity. Despite the development of quail breeding, maximising quality and quail performance have received less attention. Compared with other commercial poultry species, some attributes, such as short generation interval, higher egg production rate, small body size, fast growth, early puberty and lower feed intake have been considered as the most attractive characteristics to select the quail as the animal models in breeding programmes (Okamoto et al. 1989). Maximising quail productivity is the main goal of breeding programmes for industry. On the other hand, the industrial productivity is a function of performance and reproductive traits while the mortality is the most important limiting factor. A lot of genetic and environmental factors may affect the mortality, in which the most effective elements are the genetic capacity of the bird, genetic abnormalities, the plan of population management and nutrition. So far, several studies have investigated the reasons of mortality and factors
affecting the rate of these parameters in the poultry industry. It was reported that environmental factors have the profound impacts on the growth rate and mortality of quail chicks in early days post-hatch (Aggrey and Marks 2002).

In the study on quail Coturnix c. coturnix in two regions of Italy, the average of annual mortality rate ranged from 69 to 73% (Puigcerver 1992), however, other experiments on liabat three research stations of Florida resulted in 54% mortality rate on average for both sexes per year (Pollock et al. 1989).

By definition, survival has been mentioned as the opposite of mortality. Survival in the population is the most critical issues in the breeding farms that calls more attention by scientists. Survival significantly affects the net profit of breeding farms, and increasing the population survival reduces production costs. Usually, longevity in the bovine species is evaluated not on the basis of the spontaneous animal death, but on the culling choice following a reduction in production and/or functional performance (Van Raden and Wiggans 1995; McCullough and DeLorenzo 1996).

The recording of bird survival in the farm is the difficult task and it conveniently may be recorded after culling of the animals. Therefore, the use of correlated traits with survival which are easy to record could be applicable to extend the bird’s survival. Body weight (BW) and egg weight (EW) are traits that have been studied extensively and their heritability and genetic correlations have been reported in many studies. Therefore, knowledge of the genetic correlations between BW and EW with survival can be effective in improving survival by using indirect selection.

The body weight gain (BWG) and EW are the continuous traits that can be used in the best linear unbiased prediction (BLUP) methodology to predict breeding values for those traits with normal distribution. In contrast, the survival is the discontinuous traits (i.e. discrete) and (co)-variance components of discontinuous traits, such as survival could be estimated by threshold methods (Giansola and Foulley 1983; Hagger and Hofer 1990). Evaluating both continuous and threshold traits simultaneously resulted in high accuracy of selection, especially for the threshold traits (Riggio et al. 2005; Cloete et al. 2009; Hatcher et al. 2010).

The most of the genetic improvement studies have focussed on the number of early eggs, BW and growth traits at fixed ages (Kaplan et al. 2016, Finco et al. 2016; Mohammadi-TighSiah et al. 2018; Gotuzzo et al. 2019; Ozsoy 2019a, 2019c) Aggrey and Marks (2002) evaluated the risk factors with the occurrence of mortality in divergently selected lines and controls of Japanese quail. To our knowledge, there are no studies regarding the estimation of survival variance components in quail and this study is the first report on this topic. Although there are few reports on the correlation of BWG and other traits including feed conversion ratio in the chickens (N’Dri et al. 2006), feed residual in the chickens (Aggrey et al. 2010), feed conversion ratio in Pekin duck (Zhang et al. 2017) and humoral immunity in quail (Mohammadi-TighSiah et al. 2018), there is no report on the correlation between BWG and survival in quail. Therefore, this study aimed to analyse survival and its relationship with EW and BWG from hatch to 42 d in Japanese quail, considering the time range for survival trait using linear-threshold model via Gibbs sampling method.

**Material and methods**

A total of 1854 records related to the 3916 birds from the mating of 243 sires and 243 dams were collected in four generations from 2017 to 2019 by the Khorasan Razavi Agricultural Research and Training Centre (KRARTC). The parents (one male and one female) were reared in the individual breeder cages (30 × 30 × 30 cm). The produced eggs from each cage were numbered separately and kept in the separate combs at 15°C and 70% humidity until incubation. The produced eggs were transferred to the incubator at 5 or 7 d intervals. On hatching day, all quail chicks were identified by wing bands and the hatching weight was recorded. BW of the birds was recorded by a digital scale (accuracy of 0.01 g) in a seven days period till 42 d of age. The BWGs were calculated as the average growth performance of the birds in a 7 d period. A 20h light programme was applied from the hatch to the end of the experiment. Diets were formulated based on the recommendations of the National

| Trait | Mean | SD | Minimum | Maximum |
|-------|------|----|---------|---------|
| EW    | 12.91| 1.35| 7.16    | 16.91   |
| BWG7  | 2.78 | 0.80| 0.56    | 7.02    |
| BWG14 | 3.87 | 1.29| 0.10    | 10.71   |
| BWG21 | 4.88 | 2.04| 0.33    | 12.31   |
| BWG28 | 5.27 | 1.67| 0.10    | 14.64   |
| BWG35 | 5.87 | 1.97| 0.02    | 14.51   |
| BWG42 | 4.04 | 1.90| 0.14    | 12.77   |

EW, BWG and S are egg weight, body weight gain and the birds’ survival, respectively; indices show the age range.
Table 2. Variance components and heritability ± standard deviation of survival and egg weight traits.

| Traits     | $\sigma^2_a$     | $\sigma^2_e$     | $\sigma^2_r$     | $h^2$      |
|------------|------------------|------------------|------------------|------------|
| EW         | 0.372 ± 0.199    | 8.884 ± 0.355    | 9.256 ± 0.323    | 0.040 ± 0.021 |
| S0–7       | 0.663 ± 0.403    | 1                | 1.663 ± 0.462    | 0.399 ± 0.148 |
| S0–14      | 0.472 ± 0.479    | 1                | 1.472 ± 0.479    | 0.321 ± 0.110 |
| S0–21      | 0.471 ± 0.260    | 1                | 1.471 ± 0.266    | 0.320 ± 0.110 |
| S0–28      | 0.160 ± 0.084    | 1                | 1.160 ± 0.095    | 0.138 ± 0.062 |
| S0–35      | 0.208 ± 0.084    | 1                | 1.208 ± 0.095    | 0.172 ± 0.059 |
| S0–42      | 0.429 ± 0.134    | 1                | 1.429 ± 0.139    | 0.300 ± 0.068 |

$\sigma^2_a$: additive genetic variance; $\sigma^2_e$: residual variance; $\sigma^2_r$: phenotypic variance; $h^2$: heritability; EW and S are egg weight and the birds’ survival, respectively; indices show the age range.

Table 3. Genetic correlation of egg weight with the birds’ survival at different ages.

| EW with | Genetic correlation | Standard deviation |
|---------|---------------------|--------------------|
| S0–7    | 0.087               | 0.215              |
| S0–14   | −0.704              | 0.269              |
| S0–21   | −0.672              | 0.269              |
| S0–28   | −0.099              | 0.102              |
| S0–35   | −0.336              | 0.320              |
| S0–42   | −0.602              | 0.232              |

EW and S are egg weight and the birds’ survival, respectively; indices show the age range.

In this research, the equations and assumptions have been based on an extension of the equations for a multivariate threshold-linear animal model by Varona et al. (1999). THRGIBBS3F90 program was used to simultaneously fit a threshold model for the survival and a linear model for EW and BWG traits. A single chain of 2,000,000 samples with a burnt-in of the first 200,000 samples and a sampling interval of 100 were generated. Every 100th samples were stored to estimate the posterior mean and posterior standard deviation using POSTGIBBSF90 (Misztal et al. 2002).

Result and discussion

Genetic parameters for EW and survival

The variance components and heritability of survival and EW traits are shown in Table 2. The heritability of EW in the studied population was estimated 0.040, which indicates that genetic selection for this trait in the short term cannot cause genetic improvement, and environmental effects must be considered to improve this trait. EW depends on diet, age at first egg, BW, age, genotype and lighting programme. In fact, any condition that reduces feed intake resulted in EW reduction. Heritability of EW in Japanese quail was reported in the range of 0.25–0.59 (Khaldari et al. 2010; Daikwo et al. 2013; Momoh et al. 2014) that was higher than the result of this study. The heritability of EW in both native chickens of Urmia and Fars was reported as 0.01, which was lower than our finding (Aghazadeh Bokat et al. 2014). Ghorbani et al. (2013)
Ideal eggs for hatching and proper EW lead to the production of chickens with suitable body conditions, and this suitable physical condition of the chicken probably reduce the mortality rate of chickens in the first weeks. On the other hand, the survival may be affected by the pre-hatch physical conditions, so that a low correlation between EW and survival at the first week of age was found in this study (Table 3). In fact, there was no expectation of a significant association between EW and survival in older ages. However, the results of this study confirm the relationship between EW and survival from post-hatching up to the 6th week of age, and despite the changes, this effect seems to continue until the end of 6 weeks. The genetic correlation between EW and survival at different ages is negative after the first week. The negative correlations decreased from the second to fourth week and increased again after the fourth week. This trend of change remains a question in this study. Some of these changes might be related to the physiological transition of the bird to the maturity and development of genital tract between the second and fourth week. In this case, the selection for EW could be against the survival due to the negative correlations and vice versa.

A positive and almost moderate genetic correlation (in the range of 0.1–0.58) between EW and BW traits was observed in Japanese quails and some poultry species (Ojo et al. 2010; Ozsoy and Aktan 2011; Kamani 2019). Selection for higher EW in three strains of Tswana chickens improved the egg quality traits (Kgwatala et al. 2016). The high correlation in these studies indicates that the BW and EW may be controlled by many similar genes.

There are few studies on EW and its association with mortality. Skoglund et al. (1952) observed that post-hatching chicks from small eggs tended to die but did not find a significant difference in mortality caused by EW. Other studies also found no association between EW and mortality in broiler chickens (Skoglund and Tomhave 1949; Wiley 1950). To our knowledge, there were no reports of genetic and phenotypic correlations between EW and survivalability.

**Genetic parameters for BWG and survival**

The variance components and heritability of survival and BWG traits obtained by the multivariate analysis (Table 4). The highest heritability was estimated for BWG0-7 (0.583) and followed by BWG14-21, BWG31-35, BWG28-35 and BWG35-42 and BWG7-14. The corresponding values of heritability were 0.583, 0.116, 0.257, 0.583, 0.116, 0.257.

**Table 4. Variance components and heritability of survival and body weight gain traits.**

| Trait            | $\sigma^2_e$ | $\sigma^2_r$ | $\sigma^2_p$ | $h^2$ |
|------------------|-------------|--------------|--------------|-------|
| BWG$_{0-7}$      | 0.296 ± 0.029 | 0.212 ± 0.017 | 0.508 ± 0.022 | 0.583 ± 0.040 |
| $S_{0-7}$        | 0.703 ± 0.356 | 1             | 1.703 ± 0.426 | 0.413 ± 0.045 |
| $S_{0-14}$       | 0.414 ± 0.409 | 1             | 1.414 ± 0.409 | 0.293 ± 0.041 |
| $S_{21-28}$      | 0.421 ± 0.258 | 1             | 1.421 ± 0.258 | 0.296 ± 0.115 |
| $S_{28-35}$      | 0.154 ± 0.083 | 1             | 1.154 ± 0.083 | 0.133 ± 0.062 |
| $S_{35-42}$      | 0.210 ± 0.086 | 1             | 1.210 ± 0.086 | 0.173 ± 0.059 |
| $S_{42-7}$       | 0.449 ± 0.139 | 1             | 1.449 ± 0.140 | 0.310 ± 0.068 |
| BWG$_{7-14}$     | 0.103 ± 0.034 | 0.787 ± 0.038 | 0.890 ± 0.033 | 0.116 ± 0.036 |
| $S_{0-14}$       | 0.426 ± 0.320 | 1             | 1.426 ± 0.320 | 0.299 ± 0.108 |
| $S_{21-28}$      | 0.429 ± 0.253 | 1             | 1.429 ± 0.253 | 0.300 ± 0.114 |
| $S_{28-35}$      | 0.144 ± 0.083 | 1             | 1.144 ± 0.083 | 0.126 ± 0.064 |
| $S_{35-42}$      | 0.210 ± 0.089 | 1             | 1.210 ± 0.089 | 0.174 ± 0.062 |
| $S_{42-7}$       | 0.424 ± 0.137 | 1             | 1.424 ± 0.137 | 0.298 ± 0.070 |
| BWG$_{14-21}$    | 0.423 ± 0.089 | 1.220 ± 0.074 | 1.643 ± 0.067 | 0.257 ± 0.048 |
| $S_{0-21}$       | 0.406 ± 0.253 | 1             | 1.406 ± 0.253 | 0.289 ± 0.115 |
| $S_{28-35}$      | 0.163 ± 0.089 | 1             | 1.163 ± 0.089 | 0.140 ± 0.065 |
| $S_{35-42}$      | 0.220 ± 0.094 | 1             | 1.220 ± 0.094 | 0.180 ± 0.064 |
| $S_{42-7}$       | 0.456 ± 0.144 | 1             | 1.456 ± 0.144 | 0.313 ± 0.070 |
| BWG$_{21-28}$    | 0.484 ± 0.179 | 2.346 ± 0.158 | 2.830 ± 0.125 | 0.171 ± 0.059 |
| $S_{0-28}$       | 0.146 ± 0.085 | 1             | 1.146 ± 0.085 | 0.127 ± 0.064 |
| $S_{35-42}$      | 0.219 ± 0.091 | 1             | 1.219 ± 0.091 | 0.180 ± 0.062 |
| $S_{42-7}$       | 0.447 ± 0.142 | 1             | 1.447 ± 0.142 | 0.309 ± 0.070 |
| BWG$_{28-35}$    | 0.380 ± 0.142 | 2.364 ± 0.145 | 2.744 ± 0.121 | 0.138 ± 0.049 |
| $S_{0-35}$       | 0.222 ± 0.089 | 1             | 1.222 ± 0.089 | 0.181 ± 0.060 |
| $S_{35-42}$      | 0.460 ± 0.138 | 1             | 1.460 ± 0.138 | 0.315 ± 0.068 |
| BWG$_{35-42}$    | 0.430 ± 0.286 | 3.087 ± 0.260 | 3.517 ± 0.189 | 0.122 ± 0.077 |
| $S_{42-7}$       | 0.447 ± 0.138 | 1             | 1.447 ± 0.138 | 0.309 ± 0.068 |

$\sigma^2_e$: additive genetic variance; $\sigma^2_r$: residual variance; $\sigma^2_p$: phenotypic variance; $h^2$: heritability; BWG and S are body weight gain and the birds’ survival, respectively; indices show the age range.

reported that the heritability of the first and peak EW in Fars native chickens were 0.33 and 0.64, respectively.

In the joint analysis of EW and survival, the heritability of survival at different ages is presented in Table 2. The lowest and highest heritability were estimated for $S_{0-28} (0.138)$ and $S_{0-7} (0.399)$, respectively, suggesting that genetic selection for mentioned traits at different age categories, especially for early days post-hatching ($S_{0-7}$), could be the effective tool.

The genetic correlation between EW and survival at different ages is shown in Table 3. All genetic correlations between EW with survival had the negative values, except for $S_{0-7}$. The highest genetic correlation was estimated between EW and $S_{0-14} (-0.704)$, while the lowest value was found between EW and $S_{0-7} (0.087)$. Negative estimations of genetic correlation indicate that an increase in one traits will lead to decrease in another trait and a portion of additive variance is in common between the two traits was done as antagonistic. The survival at different ages may be influenced by different genes, resulting in low response to direct selection. The improvement in survival could be achieved through the management strategies and selection based on direct breeding values without consideration of non-genetic factors affecting the survivability in quail.
vival, the heritability of BWG0 and S with BWG14 and BWG14–21 were the highest heritabilities among all studied traits. After 21 d of age, the heritability of BWG and the birds’ survival were decreased. Decreased heritability of BWGs and the birds’ survival after 21 d and low genetic correlation between 21 and 28 d weight gain with S0–28 indicate the fourth week of life is a stressful period and sensitive to quails. The development of the female reproductive system has a direct effect on BW in females, and the increase in weight varies depending on the environmental and genetic conditions of the female could be reasons for this issue. A few factors may contribute to the decline in heritability during the 4th week of age, including sexing, removing surplus chicks (e.g. resulting in small size of population), transferring the chicks to the cage. The chicks in the cage faced with the new spatial and feeding conditions and variation in habituation depends on genotypes. Overall, variation in the estimation of genetic parameters of BW traits could be affected by management systems, nutritional and environmental conditions and incredibly random effects (i.e. chick sample) in the model.

Despite controlling environmental conditions during the incubation period, such as humidity, temperature and ventilation, variation in BW decreases on hatch day. However, environmental variance of the population increases with increasing age and reaches to the highest value at slaughter, resulting in raising the heritability of the BWG0–21 (Daikwo et al. 2013; Ebrahimi et al. 2019). Moreover, the maternal variance such as egg size could increase the heritability of hatch BW before egg production (Aggrey and Cheng 1992).

The genetic correlation of BWG with survival at different ages is shown in Table 5. The highest genetic correlation was estimated between BWG0–7 with S0–7 (0.638), and the lowest value was attributed to the BWG28–35 with S0–14 (0.015). All correlations were negative except for genetic correlations between BWG0–7 and BWG7–14 with survival. The genetic correlation between BWG0–7 with survival ranged from 0.015 to 0.638. The high value of the positive genetic correlation between BWG0–7 with S0–7 indicates that the selection for BWG in the first week of age could improve the survival. In addition, the genetic correlation between BWG7–14 with the survival ranged from 0.148 to 0.362, in which the highest values were attributed to the BWG7–14 and S0–35 (0.355) and S0–42 (0.362).

Table 5. Genetic correlation of daily weight gain with the birds’ survival at different ages.

| First trait | Second trait | Genetic correlation | Standard deviation |
|------------|--------------|---------------------|--------------------|
| BWG0–7     | S0–7         | 0.638               | 0.399              |
| BWG0–14    | S0–14        | 0.015               | 0.013              |
| BWG0–21    | S0–21        | 0.034               | 0.014              |
| BWG0–28    | S0–28        | 0.031               | 0.048              |
| BWG0–35    | S0–35        | 0.039               | 0.014              |
| BWG7–14    | S0–14        | 0.148               | 0.079              |
| BWG7–21    | S0–21        | 0.155               | 0.107              |
| BWG7–28    | S0–28        | 0.344               | 0.322              |
| BWG7–35    | S0–35        | 0.355               | 0.229              |
| BWG14–21   | S0–21        | 0.342               | 0.225              |
| BWG14–28   | S0–28        | 0.058               | 0.099              |
| BWG21–28   | S0–28        | 0.027               | 0.045              |
| BWG28–35   | S0–35        | 0.087               | 0.033              |
| BWG28–42   | S0–42        | 0.139               | 0.162              |
| BWG35–42   | S0–42        | 0.235               | 0.183              |

BWG and S are body weight gain and the birds’ survival, respectively; indices show the age range.
ascites, including low temperature, feeding high-energy diets and increasing feed intake with pelleted diets. Ascites are the metabolic disorder that could be resulted in low survivability (Moghadam et al. 2005).

Conclusion

Very low heritability of EW in the studied population indicates that short-term genetic selection for this trait may not be effective on the genetic improvement. Negative estimates of the genetic correlation between EW and survival showed that the transfer of EW genes is different from that of survival genes and selection performed for EW could reduce the survival. Heritability of the survival at different ages showed that genetic selection for this trait at early days post-hatching (i.e. S0–2) could improve the survival. A short-term genetic selection for BWG traits would not applicable to improve the BWG because of low heritability.

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Ethical approval

Animal handling and experimental procedures of the study were approved by the Research Animal Committee of the Research Institute at the University of Zabol, Zabol, Iran.

Disclosure statement

We agree that this article is original, is not being considered for publication elsewhere, and it is approved by all authors. There is no conflict of interest.

Data availability statement

The data that support the findings of this study are available from the corresponding author, [Mohammad Rokouei], upon reasonable request.

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