Genotype and protein level interaction in growth traits of meat-type quail through reaction norm models

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ABSTRACT. One possible strategy to optimize breeding programmes in terms of feed costs is selecting animals based on their genetic performance over protein levels (PL). A genotype and environment (G×E) interaction in which the gradual environmental changes are represented by the respective PL is such a strategy. Reaction norm models (RNM) are suitable to perform these analyses, since they enable to evaluate genetic differences among animals as well as variance components and heritability estimates over PL. The aim of the study was to investigate the G and PL interaction in two meat-type quail lines (UFV1 and UFV2) for their body weight at day 28 (BW28) and 35 (BW35) of age by using RNM. Diets were composed in order to have different PL (22, 23, 24, 25, 26, 27, 28 and 29%) but the same metabolizable energy (2900 kcal) by keeping constant amino acids:lysine ratio for animal performance. The data set contained 970 and 410 animals from UFV1 and UFV2 lines, respectively. Several RNM (with different Legendre polynomial orders and residual variance classes) were compared *via* Akaike (AIC) and Schwarz Bayesian (BIC) information criteria. The RNM outperformed (lower AIC and BIC values) the traditional model disregarding G×E and suggested G×PL interaction for BW28 and BW35. The observed moderate-to-high heritabilities increased over PL, thus proving the existence of G×PL for growth traits in meat-type quail.

Introduction

The term meat-type quail (*Coturnix coturnix coturnix*) is often used to differentiate from the term Japanese quail (*Coturnix coturnix japonica*) describing species widely used for egg production (Silva et al., 2013). Regardless the quail production approach (meat or egg), these animals are an economic animal model for breeding research (Alkan et al., 2010) due to the small body size (a large number of birds can be kept in a limited space) and short generation interval.

In poultry breeding, understanding the genetics of traits that are affected by environmental change is important, as this will allow to assess the adaptive potential of these traits (Gienapp et al., 2017). The main part (about 70%) of total cost in livestock production is feed (Caetano et al., 2017), with the protein being the most expensive diet component. One possible strategy to optimize breeding programmes

might be selecting animals for their genetic performance over different protein levels (PL) in the diet. This strategy can be performed through the regression of the genetic values in function of PL. This characterizes genotype and environment interaction (G×E), in which gradual environmental changes are represented by the respective PL.

Among methodologies used in this kind of analysis are random regression reaction norm models (RNM) (Kolmodin et al., 2002; Calus and Veerkamp, 2003) which allow to evaluate genetic differences among animals as well as between variance components and heritability on different environmental levels. According to Husby et al. (2015), the heritability in poultry populations is not necessarily constant across environments. Thus, models that are able to accommodate this feature are essentially useful for the modern poultry breeding. The RNM have been generally used to study G×E interaction for disease resistance in other species, such as chicken (Kause et al., 2012), dairy (Calus et al., 2006) and beef (Mota et al., 2016) cattle. However, to our knowledge, studies on trait growth performance under different nutritional levels are still scarce, mainly for meat quail.

The aim of the study was to investigate the G×PL interaction in two meat-type quail lines with two different body weights on day 28 and 35 of age by using RNM. It was hypothesised that low-potential individuals benefit substantially less in favourable conditions than their high-potential counterparts. Thus, the main objective of the present study was to examine whether changing the PL in the diet affect genetic differences between animals.

Material and methods

All animal procedures were approved by the Animal Care and Use Committee of the Animal Science Department from Federal University of Viçosa (Brazil) (No. 73/2014-CEUAP). Data used in this study were from an experiment carried out in 2014 and supported by the UFV Breeding Programme for Meat Quail.

Two lines of quails (UFV1 and UFV2) originated from two different farms in Brazil were used in the study. The animals (970 birds from UFV1 and 410 from UFV2) were selected according to high body weight. The average weight and meat yield indicated that these strains are suitable for meat production (Silva et al., 2013).

Eggs were collected during 10, incubated for 14, and placed in hatcheries for 3 days, in total 17 days before hatch. During this time, birds were identified for pedigree information, then were randomized and allocated to 24 screen pens (1.0 m × 0.8 m) of

20 animals in each (10 animals from UFV1 and 10 from UFV2). The pens were equipped with wood shavings as litter substrate. Animals have *ad libitum* access to feed and water. In the first 14 days, dish-type feeders and pressure cup drinkers were used and starting from day 15 they were replaced by tubular feeders and automatic nipple drinkers. Diets were formulated according to NRC requirements (1994) and composed to have different PL (22, 23, 24, 25, 26, 27, 28 and 29%) and fixed metabolizable energy (2900 kcal). The NRC assumes 24% as the optimal PL for quail. So, the constant amino acids:lysine ratio for animal performance was maintained.

Animals were individually weighted at days 1, 7, 14, 21, 28 and 35 of age. However, only body weights at days 28 (BW_{28}) and 35 (BW_{35}) were taken into account since they normally constitute the basic selection criteria in breeding programmes.

The RNM were implemented under random regression framework by combining second (linear) and third (quadratic) orders of Legendre polynomials to describe the average and additive genetic curves, respectively. In addition, two assumptions were considered for residual variances: homogeneity and heterogeneity (different number of residual variance classes). A general notation to represent all tested Legendre models is: LEGαγ_δ, where α and γ correspond to polynomial order for the average and additive genetic effects, respectively. The δ represents the number of residual variance classes: one (homogeneity, i.e. the same variance for all PL), two (22–25% and 26–29% of PL), three (22–24%, 25–27%, and 28–29% of PL), four (22–23%, 24–25%, 26–27%, and 28–29% of PL) and eight (one variance for each PL).

The following RNM was fitted separately for each line:

$$y_{ijkl} = s_k + h_l + \sum_{m=0}^{M} \beta_m \phi_{ijm} + \sum_{m=0}^{M} a_{im} \phi_{ijm} + e_{ijkl} \qquad (1)$$

where: y_{ijkl} – phenotypic (BW_{28} or BW_{35}) record for animal i (i = 1,2,..,N) submitted to the protein level j (j = 1,2,..,8) within sex k (s_k, k = 1,2) and hatching l (h_l, l = 1,2), β_m – average regression coefficient of order m (m = 0,1,..,M), a_{im} – random regression coefficient of order m for additive genetic effect of animal i, ϕ_{ijm} – m^{th} Legendre polynomial for PL j from animal i, e_{ijkl} – residual term $e_{ijkl} \sim N(0, \sigma^2_{e_n})$, being n = 1,2,..,N the number of residual variance classes (by assuming heterogeneity of residual variances). Random regression models with Legendre polynomials have been chosen to have better convergence properties as the regressions are orthogonal, being probably the easiest to calculate and utilize, as presented in detail by Schaeffer (2004).

In matrix notation, model (1) is described as follows:

$$y = X\beta + Za + e \qquad (2)$$

where: y – vector of phenotypic records, assumed as $\beta, a, G, \sigma^2_{e_n} \sim N\left(X\beta + Za, I\sigma^2_{e_n}\right)$, β – vector of fixed effects (average coefficients, sex and hatching), a – vector of additive genetic coefficients, assumed as: |a| G, A~N (0,G⊗A). Here, A – relationship matrix among animals, and G – additive genetic variance-covariance matrix between additive genetic coefficients.

The predicted additive genetic effect of animal in PL j ($\hat{u}_{ij}$), and the genetic variance ($\hat{\sigma}^2_{u_j}$) and heritability ($\hat{h}^2_j$) estimates for the studied traits in each level j of PL are given, respectively by:

$$\hat{u}_{ij} = K'_j \hat{a}_i, \ \hat{\sigma}^2_{u_j} = K'_j \hat{G} K_j \ \text{and} \ \hat{h}^2_j = \hat{\sigma}^2_{u_j}/(\hat{\sigma}^2_{u_j} + \sigma^2_{e_n}) \quad (3)$$

where: $K'_j = \begin{bmatrix} \phi_{ij1} & \phi_{ij2} & \cdots & \phi_{ijM} \end{bmatrix}$.

Several RNM, with different Legendre polynomial orders and residual variance classes, were compared *via* Akaike (AIC) and Schwarz Bayesian (BIC) information criteria. To infer upon the presence of G×E, the RNM were also compared with the traditional animal model (disregarding G×E). The variance components, genetic parameter and reaction norm estimates were calculated by using the best fit RNM for each trait within each line. All models were fitted through REML (restricted maximum likelihood) *via* WOMBAT (Meyer, 2007) software. The used codes and data sets are available by contacting authors.

Results

For BW$_{28}$, the average value (in g), standard deviation, minimum and maximum for the UFV1 line were 210.06, 29.67, 81.00 and 315.06, respectively, whereas for UFV2 lines these values were 213.01, 28.52, 78.00, 358.17, respectively. In case of BW$_{35}$, data on the UFV1 were 248.81, 31.61, 109.01 and 397.68, respectively; for UFV2 – 255.65, 31.17, 104.01 and 396.67, respectively. Although higher BW$_{28}$ and BW$_{35}$ were for UFV2 than for UFV1, the high magnitude of the estimated standard deviation avoid exploiting possible significant difference between them.

The best models (lower AIC and BIC values; Table 1) for BW$_{28}$ in UFV1 and UFV2 were called, respectively as LEG22_1 and LEG32_2, whereas for BW$_{35}$, LEG32_1 best fit for both lines. For all traits and lines, the RNM outperformed the tradi-

Table 1. Akaike (AIC) and Schwarz Bayesian (BIC) information criteria for different reaction norm models for body weight at 28 (BW$_{28}$) and 35 (BW$_{35}$) days of age in two meat-type quail lines (UFV1 and UFV2)

Line	Trait	Model*	AIC	BIC
UFV1	BW$_{28}$	Traditional	6630.82	6650.55
		LEG22_1	6625.88	6645.09
		LEG23_1	6629.45	6663.58
		LEG32_1	6626.96	6646.42
		LEG33_1	6630.20	6664.27
		LEG22_2	6627.85	6652.19
		LEG22_3	6626.21	6645.99
		LEG22_4	6625.34	6659.41
		LEG22_8	6631.14	6684.69
	BW$_{35}$	Traditional	7285.14	7314.89
		LEG22_1	7287.67	7307.16
		LEG23_1	7289.59	7323.69
		LEG32_1	7284.18	7303.67
		LEG33_1	7286.12	7320.22
		LEG32_2	7285.52	7309.87
		LEG32_3	7286.29	7315.52
		LEG32_4	7287.56	7321.66
		LEG32_8	7291.39	7344.97
UFV2	BW$_{28}$	Traditional	2843.45	2851.46
		LEG22_1	2804.20	2820.21
		LEG23_1	2805.54	2833.57
		LEG32_1	2803.17	2819.17
		LEG33_1	2804.67	2832.68
		LEG32_2	2797.79	2817.79
		LEG32_3	2803.95	2827.96
		LEG32_4	2801.66	2829.87
		LEG32_8	2804.82	2848.83
	BW$_{35}$	Traditional	3171.53	3179.53
		LEG22_1	3117.37	3133.37
		LEG23_1	3119.61	3147.62
		LEG32_1	3114.40	3130.39
		LEG33_1	3117.18	3145.17
		LEG32_2	3115.88	3135.87
		LEG32_3	3118.16	3142.15
		LEG32_4	3117.58	3145.58
		LEG32_8	3117.35	3161.34

* traditional – disregarding genotype by protein level interaction; LEGαγ_δ – α and γ correspond to polynomial orders for the average and additive genetic effects, respectively. The δ term is the number of residual variance classes

tional animal model. Additionally, the genetic effect over PL was modelled as linear regression, and the heterogeneity of residual variance was noticed only for BW$_{28}$ in UFV2 line.

The phenotypic, genetic and residual variances were similar for BW$_{35}$ in both lines and for BW$_{28}$ in UFV1 (Figure 1). Such finding is connected with an
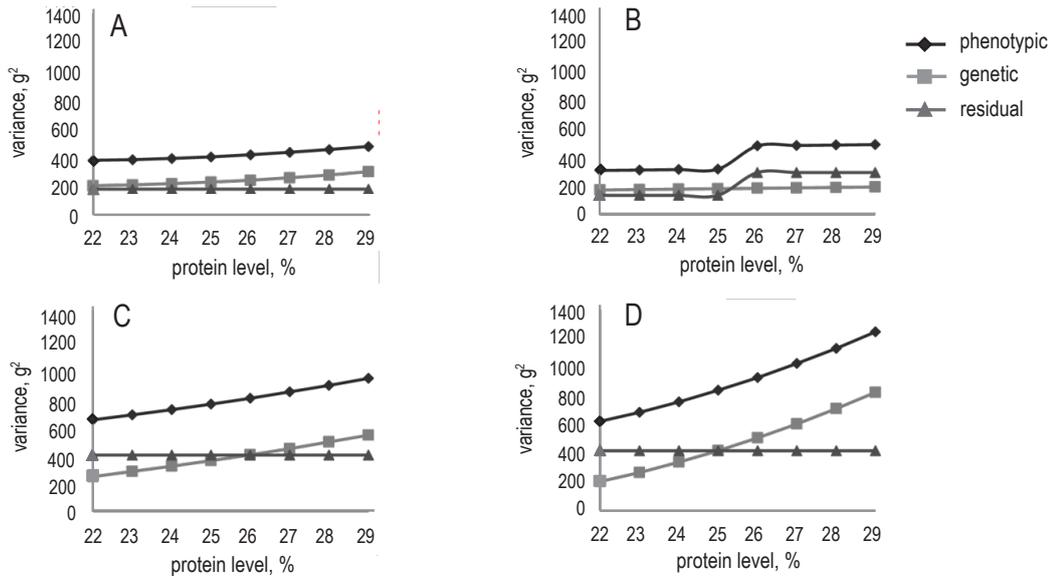
Figure 1. Variance component estimates for body weight at day 28 in UFV1 (A) and UFV2 (B) lines; and at day 35 in in UFV1 (C) and UFV2 (D) lines
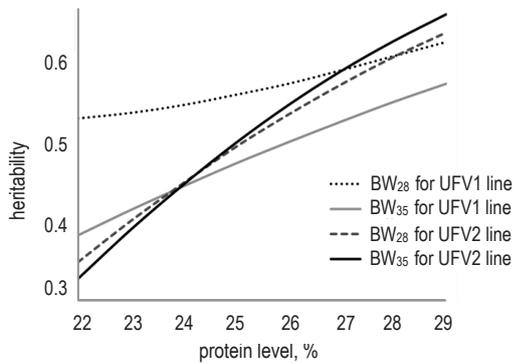

Figure 2. Heritability estimates for body weight at day 28 (BW28) and 35 (BW35) in UFV1 and UFV2 lines

increase of genetic and phenotypic variances over PL, whereas residual variance tends to remain constant. The genetic variance for BW_{28} in UFV2 line tended to be constant over PL, thus the behaviour of the phenotypic variances followed directly the behaviour of residual variance components (assumed as heterogeneous in this case).

In UFV1, the heritability estimates for BW_{28} (0.56–0.63) were higher than for BW_{35} (0.38–0.58) (Figure 2). Regarding UFV2, due to heterogeneity of residual variance assumed by the best fit model, the heritability estimates for BW_{28} (0.56–0.57) were higher than for BW_{35} (0.33–0.50) over from 22 to 25% PL. These results has changed with PL between 23 and 29%, in which the heritability estimates varied from 0.39 to 0.40, and from 0.55 to 0.63 for BW_{35} and BW_{28}, respectively.

The reaction norms were plotted in Figure 3. A sample of 25 animals were taken from each scenario (traits and lines). For BW_{28} in UFV2 (Figure 3B), the genetic values tended to be constant over the
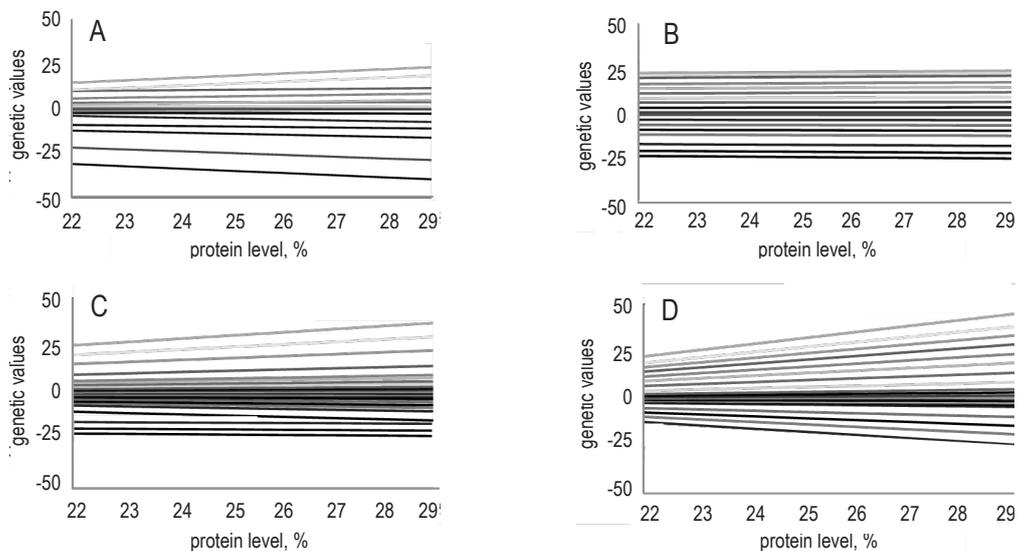

Figure 3. Reaction norms for a sample of 25 animals for body weight at day 28 in UFV1 (A) and UFV2 (B) lines; and at day 35 in UFV1 (C) and UFV2 (D) lines

studied PL. On the other hand, mainly for BW_{35} in UFV2 (Figure 3D), changes in genetic values according to PL were noticeable; however there are no re-ranking, but only a scaling effect between the best and worse animals in each PL.

Discussion

The results obtained in the present study (Table 1) favour RNM over the traditional animal model (disregarding G×E). Also, it can be treated as first example of genotype and PL interaction for the studied traits. Other relevant point is the choice of Legendre polynomial of second order to describe the genetic effects for all traits and also lines. This linear behaviour of genetic values over different PL was indicated. In other random regression models, such applications in animal breeding as lactation and growth curves, higher polynomial order can be used to capture the complexity of curve trajectories (Schaeffer, 2004). However, assuming the PL range as in the present study, it is expected that genetic values will behave like straight lines over them. Maybe, in the presence of very low and/or very high PL, high order polynomials would be selected to describe the genetic effects over these levels.

In the most of cases (BW_{28} in UFV1 and BW_{35} in both lines), models assuming homogeneity of variance (Table 1) presented better results (lower AIC and BIC values). In lactation and growth curve studies, models approaching heterogeneity of residual variance generally outperformed models assuming constant residual variance (Schaeffer, 2004). This is due to the well-known time effect over these physiological features. However, there are no reports about this heterogeneity in studies related to G×E focused in nutritional levels as environment gradient.

Regardless the UFV line, the amount of variances accounted for BW_{35} was higher than for BW_{28} for both lines (Figure 1), and this is mainly due to scale effect, since observed values for BW_{35} are naturally higher than BW_{28}. An additional source of body weight variation in advanced ages (e.g., 35 days) is the physiological difference between animals as sexual maturity for female and competitive behaviour for male. The increment of body weight variances over ages has already been reported in meat-type quail by Akbas et al. (2004) and Gonçalves et al. (2012). The increase of the genetic variance over PL suggests the presence of G×E for BW_{28} in UFV1 line and BW_{35} in both

lines. However, for BW_{28} in UFV2 line, this variance was almost constant and over the PL.

The moderate-to-high heritability estimates (Figure 2) for body weights indicated the potential of these traits for breeding programmes. These estimates were partially higher than previous estimates reported in Japanese quail (Varkoohi et al., 2010); and partially similar to the results obtained by Silva et al. (2013) in meat-type quail. However, in the latter, different PL had not been considered for the genetic parameter estimation. In this context, the reports of Husby et al. (2015) approaching that the heritability in poultry populations is not necessarily constant across environments can be partially proved by the results of the present study. Additionally, all heritability estimates reported in the present study were estimated under a single trait random regression framework. It is believed that more reliable results can be obtained through multi-trait approach, especially by using recursive models as proposed by Beck et al. (2016) in an F2 cross of Japanese quail.

Thus, it is thought that the advantage of BW_{28} would be the selection period reduction, consequently leading to breeding programme reduction costs (feed and management). In general, the heritability estimates increased over the considered PL; however, this was less evident for BW_{28} in UFV2. This increase is directly related to the increase of the previously mentioned genetic variance, since the residual variance tends to be constant over the PL in the diet (except BW_{28} in UFV2). The environment improvement tends to highlight the genetic potential of animals under selection processes due to favourable conditions associated with genes expression (Falconer and Mackay, 1996). In this context, it is necessary to evaluate if the increase in genetic gain due to higher heritability estimates offset the increase in costs due to high PL.

The reaction norms mainly for BW_{35} suggest that low-potential individuals (low genetic value) benefit substantially less in favourable conditions than their high-potential counterparts. The genetic differences are more pronounced in high PL in the diet due to the increase of the genetic variance.

It should be also emphasised that in the present study only polynomial models were used to describe reaction norms. However, when using very low and very high PL as environmental gradient, some kind of nonlinear behaviour e.g., plateau, can be selected as the best model. So, the non-linear theory presented by Streit et al. (2012) can be adapted to accommodate reaction norms modelling.

Conclusions

The reaction norm models outperformed the traditional model suggesting genotype by protein level (PL) interaction for the studied traits (body weight at day 28 and 35). The observed moderate-to-high heritabilities increased over PL, thus proving the existence of interaction of genotype and PL for these traits in meat-type quail. However, it is necessary to evaluate if the increase in the genetic gain due to the increase in the heritability is offset or not by the increase in costs due to high PL.

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