

Estimates of the genetic parameters of turkey body weight using random regression analysis

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(Received 18 August 2010; Accepted 31 March 2011; First published online 3 June 2011)

Random regression (RR) analysis has been recommended to estimate the genetic parameters of longitudinal data. The objective of this study was to evaluate the growth of turkeys using RR models. Data were collected from 957 turkeys and included 15 478 individual body weight recorded during the first week of life and between weeks 2 and 32 by 2-week intervals. To take into account the repeated measurements of weight for each animal, a specific overall growth curve was modelled using a cubic smoothing spline. Animal deviation to this curve was also modelled using an RR function. All data were analysed with the ASRemI package. The results showed an increase in heritability estimates over the trajectory and peaked at 0.60 around 20 to 32 weeks of age. Genetic correlations showed that turkeys could be selected at earlier time points, at 12 weeks of age, in order to increase the growth rate. In general, genetic correlation estimates were higher among adjacent ages, decreasing markedly with the increase of distance between ages. Negative genetic correlations were observed between ages.

Keywords: repeated measurements, growth, heritability, smoothing spline function

Implications

The results obtained show that the growth trait is highly heritable in turkeys, and that birds can be selected for the growth trait as early as 12 weeks of age; it is also shown that random regression (RR) models are interesting models for studying such longitudinal data. Until now, in turkey only egg production has been analysed using RR, and as very limited information is currently available on turkey growth it could be interesting to use RR to study live body weight (BW). Furthermore, the use of RR maximises the costeffectiveness of selection because it provides an opportunity to identify the optimum points for recording. Although BW is one of the important traits, breeding objectives should include all important traits. Consequently, before constructing a selection index for BW, there is a need to evaluate the genetic correlations between BW and the other traits under selection, that is, there is possibly a negative genetic correlation between growth and reproductive traits.

Introduction

To increase the profitability of producers, the main selection objective for most genetic programmes of turkeys is to produce

birds that have high body weight (BW) at slaughtering (20 to 24 weeks of age). BW and its variation over time are affected by many processes and determined by various effects of genes depending on the age of individuals. Consequently, the genetic evaluation for growth trait can be based on the live weights measured at different standard ages during the growth period. Increases in the number of weights recorded per animal do not allow for the use of a multiple-trait (MT) model to analyse the traits because of the high number of parameters to estimate. Several models can be used to take into account the correlations between the different repeated measurements over time performed on the same animal but with a reduction of the number of parameters to be estimated: the structured antedependence model, which defines the observation at time t as a function of the previous observation (Jaffrezic et al., 2004); the character process model, which focuses on modelling the covariance functions themselves (Pletcher and Geyer, 1999); and the RR model, which attempts to model the shapes of the functions of time for each component of the phenotype (mean, genetic additive value, permanent environment; Henderson, 1982). The RR has been considered by several authors as the most appropriate model for studying repeated measurements (Van Der Werf et al., 1998). At present, it has been widely used for genetic estimations of longitudinal

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data in various species, for example in dairy cattle (DeGroot *et al.*, 2007), rainbow trout (McKay *et al.*, 2002), pigs (Huisman *et al.*, 2002) and sheep (Huisman *et al.*, 2002; Molina *et al.*, 2007). In birds, the use of RR to estimate the genetic parameters of the growth trait is much more limited (Banos *et al.*, 2006; Tholon and Queiroz, 2006; Kranis *et al.*, 2007). Consequently, the objective of this study was to investigate the use of RR for the genetic analysis of BW in turkeys to estimate the relevant genetic parameters throughout the growth period.

Material and methods

Animal management

This study was based on a research turkey population. Animals were bred at the breeding station of indigenous turkeys located at Tatar, East Azerbaijan. After hatching, at 1-week of age, turkey chicks were allocated to four groups based on the colour of feathers (contemporary group). These groups included white, pied, black and golden colours. All birds were fed *ad libitum* until 2 months of age. Water was freely available to the chicks. Birds were kept in closed barns with concrete floors and controlled lighting (16 h/day). From 2 months to 32 weeks of age, birds were kept in individual cages. The dietary recommendation based on National Research Council (1994) was adjusted. Individual cages had hand-feeding supplies and nipple-water suppliers. Birds did not undergo a vaccination programme as the Tatar research station is located in an isolated region. The environmental temperature was maintained at 30°C to 32°C during the first week, and then was decreased gradually with the age of the birds at the rate of 3°C/week. From 12 weeks of age, the temperature was kept constant at 14°C to 17°C. The average survival rate for birds was approximately 88% at 32 weeks. Phenotypic evolution of the weight with age and mean weight by sex and contemporary group are given in Table 1.

Genetic analysis

The pedigree consisted of 1520 individuals. Data consisted of 15 478 individual BW from 957 turkeys recorded at the first week of life and between weeks 2 and 32 by 2-week intervals. Before weighing, birds were fasted off feed for 4 to 5 h. All birds were weighed at appropriate weeks based on their hatching date. Two hatching dates accounted for all the birds of the population. In a first step of the analysis, the least square means method with the GLM procedure (SAS version 9.1, SAS institute Inc., Cary, NC, USA) was used to select the fixed effects affecting growth traits. The effects of age \times sex and contemporary group were significant (P < 0.01). In a second step of the analysis, five models including the selected fixed effects and genetic effects were compared to determine which was the most appropriate for studying growth traits. In all models, the sex-specific pattern of animal growth over time was modelled using a cubic smoothing spline with

Table 1	Number of	records,	mean	and s.d.	for	Turkey	body	weight	at
each we	ek. sex and	contemp	orarv	aroup le	vels				

	Age (weeks)	п	Mean (g)	s.d. (g)
Week	1	957	54.89	4.942
	2	957	113.92	23.614
	4	956	215.92	57.912
	6	958	366.15	114.442
	8	955	560.54	160.819
	10	957	863.31	239.578
	12	957	1227.94	324.254
	14	954	1569.83	392.198
	16	954	1914.31	459.952
	18	874	2254.97	534.069
	20	863	2491.25	667.306
	22	856	2723.66	770.261
	24	858	2960.59	877.287
	26	858	3201.05	981.010
	28	856	3439.97	1076.799
	30	854	3703.82	1183.143
	32	854	3956.26	1278.705
Sex	Group			
Male	White	700	1877.95	1515.958
Male	Pied	2699	2345.67	1867.100
Male	Black	2001	2007.08	1688.834
Male	Golden	1946	2115.77	1679.110
Female	White	983	1369.12	957.232
Female	Pied	2690	1569.20	1089.672
Female	Black	2548	1431.97	1051.630
Female	Golden	1911	1470.38	995.217

knots at the first week of life and then 2-week intervals from weeks 2 to 32. Models differ in the way genetic and permanent environmental effects are included. The first four models are all sub-models of the following global model:

$$y = Xeta + Z_s s + Z_u u + Wp + arepsilon_{(ext{qlobalmodel})}$$

where \boldsymbol{y} is the vector of observations, $\boldsymbol{\beta}$ is the vector of fixed effect (contemporary group) with the incidence matrix \boldsymbol{X} , \boldsymbol{s} is the vector of female (\boldsymbol{s}_f) and male (\boldsymbol{s}_m) overall spline parameters with length 2 × 15 and covariance matrix $\begin{bmatrix} \sigma_{2m}^2 & 0 \\ 0 & \sigma_{2f}^2 \end{bmatrix}$ with the incidence matrix $\boldsymbol{Z}_{\boldsymbol{s}}$, \boldsymbol{u} is the vector of direct genetic intercept (\boldsymbol{u}_1) and slope (\boldsymbol{u}_2) breeding value parameters for each animal in the pedigree with covariance matrix $\begin{bmatrix} \sigma_{2m}^2 & \sigma_{2m}^2 \\ \sigma_{1m}^2 & \sigma_{2m}^2 \end{bmatrix} \otimes \boldsymbol{A}$ and incidence matrix $\boldsymbol{Z}_{\boldsymbol{u}}$ where \boldsymbol{A} is the relationship matrix and \otimes represents the Kronecker product, \boldsymbol{p} is the vector of permanent environmental intercept (\boldsymbol{p}_1) and slope (\boldsymbol{p}_2) with covariance matrix $\begin{bmatrix} \sigma_{p1p2}^2 & \sigma_{p2}^2 \\ \sigma_{p1}^2 & \sigma_{p2}^2 \end{bmatrix}$ with the incidence matrix \boldsymbol{W} . $\boldsymbol{\varepsilon} \sim$

 $N(0, I \sigma_{\varepsilon}^2)$ is the vector of homogeneous random iid residuals.

Model 1 is a simple repeatability model, in which the global model includes the following constraints: $\sigma_{u2}^2 =$

 $\sigma_{u1u2} = \sigma_{p2}^2 = \sigma_{p1p2} = 0.$ Model 2 only considers the slope for the direct genetic effect, that is, the global model with the following con-

straints: $\sigma_{p_2}^2 = \sigma_{p_1p_2} = 0$. Model 3 only considers the slope for the permanent effect, that is, the global model with the following constraints: $\sigma_{u2}^2 = \sigma_{u1u2} = 0.$

Model 4 is the global model.

To take into account the hypothetical influence of maternal effects on growth during the first weeks of life, model 5 included the maternal genetic effects in the global model over the 12 first weeks of life: $y = X\beta + Z_s s + Z_s s$ $Z_u u + Wp + Z_m m + \varepsilon$, where notations are the same as in the global model and *m* is the vector of maternal genetic effect: m1 for the 0 to 12-week period and m2 for the 12 to 32-week period with variance $\begin{bmatrix} \sigma^2_{m1} & 0\\ 0 & 0 \end{bmatrix} \otimes A$, Z_m is the corresponding incidence matrix.

We also tried to fit three other models, all derived from the global model, considering a quadratic form for the permanent effect, direct genetic effect or both. None of these models reached convergence.

All data were analysed using the ASReml package version 2.0 (Gilmour et al., 2006).

Nested models were compared using the likelihood-ratio tests (only models 2 and 3 were not nested).

Heritability was estimated at each age as follows:

heritability was estimated at each age as follows. $h^2 = \sigma_n^2 / \sigma_d^2$ with $\sigma_n^2 = \sigma_{u_1}^2 + 2age \times \sigma_{u_1u2} + age^2 \sigma_{u_2}^2$ and $\sigma_d^2 = \sigma_n^2 + \sigma_\epsilon^2 + \sigma_{p_1}^2 + 2age \times \sigma_{p_1p_2} + age^2 \sigma_{p_2}^2$ for models 1 to 4 and model 5 after 12 weeks and $\sigma_d^2 =$ $\sigma_n^2 + \sigma_\epsilon^2 + \sigma_{p_1}^2 + 2age \times \sigma_{p_1p_2} + age^2 \sigma_{p_2}^2 + \sigma_{m_1}^2$ for model 5 during the 0 to 12-week period.

Approximate standard errors of heritability and genetic correlations were estimated using inverse of the average information matrix in Asreml.

Furthermore, to compare the results obtained with the RR models, BW at some ages were analysed using an MT model. The weight analysed included five blocks of multivariate traits as follows: block 1 - weeks 1, 2, 4, 6, 8 and 10; block 2 – weeks 8, 10, 12 and 16; block 3 – weeks 16, 18, 20, 22 and 24; block 4 – weeks 22, 24, 26, 28, 30 and 32; and block 5 (MT) - weeks 1, 2, 6, 16, 20 and 32. The direct additive genetic effect was included as the random effect, and the contemporary group and sex as fixed effects at each age. Models with more than six traits failed to converge.

Results and discussion

Model comparison indicated that the most parsimonious model that best fits the data is model 4 (Table 2). The fit improves significantly at each step from models 1 to 4, (models 1, 2 and 4 or models 1, 3 and 4, as models 2 and 3 were not nested). In contrast, the likelihood did not improve from models 4 to 5, indicating that there are no significant maternal effects. The relative influence of maternal effects is generally moderate in poultry. In turkeys, environmental maternal effects represented < 5.2% to 8% of the total variance of BW at 12 and 16 weeks of age, depending on the strains tested (Chapuis et al., 1996). This result, in addition to the particularities of our pedigree (65% of the 334 dams were of unknown parents), may explain why we were not able to evidence any maternal effects. In our study, efforts to fit a polynomial guadratic led to failure to converge. Convergence problems while estimating variance components with RR have been mentioned previously (Anang et al., 2002).

Heritability

The estimates of heritability obtained with the global model are presented in Figure 1. Heritability increased over the trajectory and peaked at 0.60 around 20 to 32 weeks of age. The same trend (increasing heritability with age) has been reported in other bird species (Muscovy duck (Hu et al., 1999); partridges (Tholon and Queiroz, 2006)) and in mammals (wild ungulate; Wilson et al., 2005). Nevertheless, the comparison of these results with those obtained with



Figure 1 Estimation of the heritability of turkey body weight performed week by week using random regression (RR) models and multiple-trait models (ages in weeks: block 1 - 1, 2, 4, 6, 8 and 10 weeks; block 2 - 8, 10, 12, 14 and 16 weeks; block 3 – 16, 18, 20, 22 and 24 weeks; block 4 – 22, 24, 26, 28, 30 and 32 weeks; and block 5 – 1, 2, 6, 16, 20 and 32 weeks).

 Table 2 LogL and LRT comparing different models with model 4

Model		-2 imes LogL	LRT [*]
1	Simple repeatability model	-15 717.4	2077.38
2	Slope for the direct genetic effect	-17 676.52	118.26
3	Slope for the permanent effect	-17 371.04	423.74
4 (global model)	Slopes for genetic and permanent effects	-17 794.78	
5	Model 4 + maternal effect	-17 794.86	0.08

LogL = log likelihood values; LRT = likelihood-ratio test.

value of the LRT in comparison with model 4.

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MT models suggest that the heritabilities found at the lowest ages (<10 weeks) with the RR are underestimated and therefore this trend should be overestimated. In fact, the heritabilities obtained at 10 weeks were in the same range with the two types of models, whereas they were much lower (on average three times less) with the RR than with the MT (block 5) model before 10 weeks. However, none of the MT models used the overall data set to estimate parameters. It should be noted that the standard errors for heritability estimates were lower for the first part of the trajectory and higher towards the end of the trajectory than those published by Fischer et al. (2004a). The published estimates for the heritability of BW in turkeys did not cover the period after 24 weeks of age. For example, Nestor et al. (1967) summarised heritability estimates of BW as ranging from 0.36 to 0.42 in the different age groups from 0 to 24 weeks of age. Case et al. (2010) reported values of 0.35 ± 0.02 for the heritability of BW at 15 weeks with the bivariate method. Chapuis et al. (1996) reported heritability estimates of 0.77 for female BW and 0.68 for male BW at 16 weeks of age. In the study by Nestor et al. (2006), the realised heritability of 16-week BW was 0.202, 0.130 and 0.166 for males, females and both sexes, respectively, during the last generations of selection. In addition, in other bird species such as chickens and Muscovy ducks, heritability of growth traits appears to be moderate or high (Mignon-Grasteau et al., 1998). However, lower estimates of heritability were obtained with RR for the early ages of European quail, that is, 0.018, 0.001 and 0.012 at 1, 7 and 14 weeks of age, respectively (Dionello et al., 2006). Therefore, they did not recommend the selection of European quail for BW during the first 3 months of age.

Correlations

Phenotypic and genetic correlation estimates for BW from 1 to 32 weeks of age by RR and MT (block 5) are presented in Figures 2, 3 and 4, respectively. Standard errors for these estimates with RR are shown in Table 3. In general, genetic and phenotypic correlation estimates were higher between adjacent ages, and decreased markedly with the increase of distance between ages. These results indicate that all growth measurements for ages over 12 weeks correspond to the same trait (correlations of >0.99 in all cases). This trait is different from the growth traits at younger ages. Traits in younger ages also differ from each other, especially at the lowest ages (for instance, the correlation between growth traits at 2 and 4 weeks is 0.70). In other studies, it has been shown that the genetic control of weight at initial ages is different from that observed at later ages (Fischer et al., 2004b; Wilson et al., 2005; Szwaczkowski et al., 2007; Costa et al., 2008; El Faro et al., 2008; Oliveira et al., 2010). The genetic correlations of BW measured between 14 and 24 weeks estimated with the multivariate method were 0.89 and 0.97 in US and UK turkey populations, respectively (Kranis et al., 2006). These values are slightly lower than the one reported in this study (0.99 \pm 0.002; Figure 3). Kranis et al. (2006) concluded that as the genetic correlations of



Figure 2 Phenotypic correlation estimates for turkey body weight as a function of age from 1 to 32 weeks of age using random regression models.



Figure 3 Genetic correlation estimates for turkey body weight as a function of age from 1 to 32 weeks of age using random regression models.

turkey BW were all close to 1, it is possible to select for BW at as early as 14 weeks of age. However, our current data are in support of selection for BW even earlier at 12 weeks of age. As shown in Figure 3, negative genetic correlations were observed between 1 and >8 weeks of age, as well as between 2 and >12 weeks of age. The presence of negative additive genetic covariance between early-age and later BW

traits is a little surprising, especially as the correlations obtained with the MT model between the same age groups are low but not negative (Figure 4) and no such results have been reported elsewhere. This result maybe due to the constraints of the RR, which can induce bias in the estimation as it seems to be the case for genetic variances at early ages. Similar issues have been reported when other traits are studied (test-day milk yield) using the RR (El Faro *et al.*, 2008).

In other species, RR has been used to estimate the genetic parameters of growth and egg production in quail (Akbas



Figure 4 Genetic correlation estimates for turkey body weight using the multi-trait model with six traits at 1, 2, 6, 16, 20 and 32 weeks of age.

Genetic parameters of turkeys by random regression

et al., 2004; Dionello et al., 2006), laying hens (Anang et al., 2002) and broiler chicken (Banos et al., 2006; Wolc et al., 2009). Kranis et al. (2007) fitted RR for egg production in turkeys and illustrated that the use of RR for genetic analysis offered greater accuracy for prediction. Other published studies used a more traditional approach to modelling the repeated records of BW over time in turkeys (Nestor et al., 2000: Kranis et al., 2006: Nestor et al., 2008). The advantages of RR over traditional approaches include the ability to allow for easy interpolation between the ages at which recordings occurred, accurate prediction of selection responses and more efficient use of the data (Kirkpatrick and Heckman, 1989; Albuquerque and Meyer, 2001). Misztal (2006) compared MT and RR models and concluded that RR was more accurate than repeatability or MT models. Huisman et al. (2002) obtained better results with RR in comparison with the traditional multivariate model. Fischer et al. (2004b) proposed that RR could be a good alternative to MT genetic analysis. Kranis et al. (2007) compared genetic parameter estimates using RR and MT models for egg production in turkeys and concluded that both models were equally effective to describe the dynamics of genetic variance over time. Nevertheless, as mentioned previously, the multivariate animal model showed convergence problems when more than six traits were included. However, our aim was not to perform an extensive comparison of the MT and RR methods.

In conclusion, in order to increase the growth rate of turkeys, birds could be selected at an earlier time point than the previously published 14 weeks of age. In other words, BW measurements up to 12 weeks of age would be sufficient for growth trait. This study investigated the use of RR for the genetic analysis of BW in turkeys. The RR models for BW in turkeys allow reasonable adjustment of data and an efficient use of available information. During the selection process of meat turkeys, it should be considered that growth at early

Table 3 Standard error of genetic correlations (above diagonal) and of phenotypic correlations (below diagonal) using random regression model

Week	1	2	4	6	8	10	12	14	16	18	20	22	24	26	28	30	32
1		0.02	0.12	0.14	0.13	0.12	0.11	0.11	0.10	0.10	0.10	0.10	0.09	0.09	0.09	0.09	0.09
2	< 0.01		0.07	0.11	0.12	0.12	0.12	0.12	0.12	0.12	0.12	0.12	0.12	0.12	0.12	0.12	0.12
4	< 0.01	< 0.01		0.03	0.05	0.07	0.08	0.09	0.10	0.10	0.10	0.10	0.11	0.11	0.11	0.11	0.11
6	0.01	0.01	< 0.01		0.01	0.02	0.02	0.03	0.03	0.04	0.04	0.04	0.04	0.04	0.04	0.05	0.05
8	0.02	0.01	0.01	< 0.01		< 0.01	0.01	0.01	0.01	0.01	0.01	0.02	0.02	0.02	0.02	0.02	0.02
10	0.02	0.02	0.01	< 0.01	< 0.01		< 0.01	< 0.01	< 0.01	< 0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
12	0.02	0.02	0.01	0.01	< 0.01	< 0.01		< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01
14	0.02	0.02	0.01	0.01	< 0.01	< 0.01	< 0.01		< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01
16	0.02	0.02	0.02	0.01	< 0.01	< 0.01	< 0.01	< 0.01		< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01
18	0.03	0.02	0.02	0.01	0.01	< 0.01	< 0.01	< 0.01	< 0.01		< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01
20	0.02	0.02	0.02	0.01	0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01		< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01
22	0.02	0.02	0.02	0.01	0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01		< 0.01	< 0.01	< 0.01	< 0.01	< 0.01
24	0.08	0.02	0.02	0.01	0.01	0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01		< 0.01	< 0.01	< 0.01	< 0.01
26	0.02	0.02	0.02	0.01	0.01	0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01		< 0.01	< 0.01	< 0.01
28	0.02	0.02	0.02	0.01	0.01	0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01		< 0.01	< 0.01
30	0.02	0.02	0.02	0.01	0.01	0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01		< 0.01
32	0.02	0.02	0.02	0.01	0.01	0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	< 0.01	

ages is under the genetic control of different genes when compared with growth at older ages.

Acknowledgement

SAR thanks A. Gilmour for his help in the construction of the primary model for analysis. The authors are grateful to the anonymous reviewers for their helpful comments.

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