GROWTH CURVE OF QUAILS BY BAYESIAN INFERENCE

Bayesian hierarchical model for comparison of different nonlinear function and genetic parameter estimates of meat quails

Ariane Gonçalves Gotuzzo*[1]; Miriam Piles†; Raquel Pillon Della-Flora*; Jerusa Martins Germano*; Janaina Scaglioni Reis*; Darilene Ursula Tyska*; Nelson José Laurino Dionello*

*Federal University of Pelotas, Faculty of Agronomy Eliseu Maciel, Department of Animal Science, PO Box 354, 96010-900 Pelotas, RS, Brazil; † Institute of Agro-food Research and Tecnology, Unidad de Cunicultura, Caldes de Montbui, 68140, Spain.

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[1] Corresponding author: arianegotuzzo@gmail.com , phone +55 53 981360874, Federal University of Pelotas, Faculty of Agronomy Eliseu Maciel, Department of Animal Science, PO Box 354, 96010-900 Pelotas, RS, Brazil.

ABSTRACT

This work aims to compare different nonlinear functions to describe the growth curve of European quails and to estimate growth curve parameters, (co)variance components and genetic and systematic effects that affected the curve using a hierarchical Bayesian model that allows joint estimation. Three different models were fitted in the first stage (Gompertz, Logístic and von Bertalanffy). The analyzed data set had 45,965 records of 6,838 meat quails selected by higher body weight at 42 d of age for 15 successive generations, weighed at birth, 7, 14, 21, 28, 35 and 42 d of age. Comparisons of the overall goodness of fit were based on deviance information criterion (DIC) and mean square error (MSE). Gelfand's check function compared the models at different points of the growth curve. In the second stage, the systematic (sex and generation) and genetic effects were considered in an animal model. Random samples of the *a posteriori* distributions were obtained by Metropolis-Hastings and Gibbs sampling algorithms. The Gompertz function presented lower DIC and better adjustment at different ages and was defined as the best fit. The heritabilities of *A*, *b* and *k* parameters were moderate (0.32, 0.29 and 0.18 respectively). The genetics correlations were: *A* and *b* (0.25), *A* and *k* (-0.50) and *b* and *k* (0.03). The samples of the posterior marginal distributions for the differences between the estimates of the parameters of the Gompertz model, for generation, *A*, *b*, *k*, age at inflexion point (*APOI*) and weight at inflexion point (*WPOI*) showed differences in relation to sex, the females are heavier, *A*, *WPOI* and *APOI* for females was also higher. Concluding that the selection by 15 generations altered the growth curve, leaving the quails heavier and with greater weight and age at the point of inflection of the curve, decreased precocity and increased the birth weight. The curve parameters could be used in a selection index, despite the difficulty in selecting quails with higher rate of growth and body weight.

Key words: meat quail, growth curve, Gibbs sampling, Bayesian

INTRODUCTION

The growth curves can describe the growth process in terms of few parameters with biological interpretation (Varona et al., 1999; Blasco et al., 2003), and the biological interpretability includes ability to rank correctly individuals or populations for important biological characteristics, which are required in selection programs mainly for growth rate, maturing rate or mature size (Fitzhugh, Jr., 1976).

The nonlinear models have been developed in order to correlate the weight-age data (Garnero et al., 2005) and have been found to be adequate to describe growth curves of several animals (Garnero et al., 2005; Mazzini et al., 2005). In poultry, the most widely used growth funtions are Gompertz, Logistic, and von Bertalanffy models with three parameters (Braccini et al., 1996; Akbaz and Oguz, 1998; Narinç et al., 2017). The biological meaning of the parameters are: ***A*** is the adult weight or theoretical maximum weight, ***b*** is parameter of scale, degree of maturation at birth and ***k*** is growth measure, influences the rate of growth or the rate of gain.

Specifically in quail, Du Preez and Sales (1997) used the Gompertz function to describe the growth of the European quail and to quantify differences between males and females in growth parameters and some indexes derived from them; Akbas and Oguz (1998) compared three nonlinear growth functions (Gompertz, von Bertalanffy and Logistic) in terms of goodness of fit to Japanese quail data and also estimated genetic and environmental effects on growth curve parameters, in this case the Gompertz function showed the best performance. Sezer and Tarhan (2005) compared the growth characteristics and growth curve parameters of three meat-type lines of Japanese quail using the Richards function. However, Drummod et al. (2013) comparing the Brody, von Bertalanffy, Gompertz, Logistic and Richards functions found that only Richards could be considered not adequate to model growth in meat quails.

The traditional method for estimating genetic parameters of growth curves consists of two steps: in the first step, the parameters are estimate for each animal; in a second step, the genetic and environmental effects that act on these parameters are predicted and variance components estimated. Thus, the error of adjustment of the first step is not taken into account in the estimation of the (co)variance components and in the prediction of the genetic values. In addition, animals with few records cannot be included in the analysis because of problems of convergence of the iterative process to estimate the growth curve parameters (Forni et al., 2007).

Varona et al. (1997) proposed an alternative method, where a Bayesian hierarchical model was implemented to jointly estimate the parameters of the growth curves and their (co)variance components. The estimation procedure uses individual records and information from relatives and from animals that were under the same systematic effects. The parameters can be estimated with greater accuracy and adjustment errors are considered in the estimation of (co)variance components. The hierarchical model allows the prediction of differences between levels of systematic effects on curve parameters, thus making it possible to quantify differences between sexes or selected generations.

The objective of this work was to use the bayesian hierarchical methodology to compare different nonlinear functions, estimating jointly the posterior distribution of growth curve parameters, (co)variance components, and genetic and environmental effects in European quail.

MATERIALS AND METHODS

Animals and Data

Data come from meat quails of both sexes selected for body weight at 42 d of age from year 2007 to 2014, distributed in 15 generations were used. Animals belonged to the breeding program of the Federal University of Pelotas, Department of Animal Science, Faculty of Agronomy Eliseu Maciel, located in Capão do Leão, Rio Grande do Sul state, Brazil.

Animals were reared in the Laboratory of Zootechnical Teaching and Experimentation Professor Renato Peixoto (LEEZO). Quails were housed in rice husks bed until 42 d of age, receiving water and food "ad libitum". The starter diet (1 to 21 d) contained 25% CP and 2,900 kcal/kg of ME and grower diet (22 to 35 d) the diet contained 20% CP and 3,050 kcal/kg of ME. Daily lighting was 16 h during all period. At 21 d of age, they were sexed and, at 42 d, they were housed individually in cages. Quails were weighed once a week after hatching until they were 42 d old. After the beginning of the posture, the 120-130 heaviest females and the 60-70 heaviest males were mated in the proportion of one male to two females (except at first generation, where 160 females and 110 males were selected), for a period of 13 d. The hatching eggs were identified by the female number and collected. The incubation period was 18 d, and at birth the quail was identified with a number in the leg. In preliminary analysis outliers were removed, 2% of data. For each age in weeks and generation, body weight records outside the interval defined by Q1-1.5 * (Q3-Q1) and Q3 + 1.5 * (Q3 -Q1), with Q1 being equal to the first quartile and Q3 being equal to the third quartile, were removed. The final data set contained 45,965 weights of 6,838 birds and the relationship matrix was constructed with information from 15 generations of selection plus the base population, i.e. a total of 7,118 birds (Table 1).

Models

A Bayesian analysis was performed by using the hierarchical model described by Varona et al. (1997), Blasco et al. (2003) and Forni et al. (2007). The individual growth trajectories were described by a nonlinear function and it was assumed that each parameter had genetic and environmental components described in a mixed linear model.

In the first stage of the hierarchy, three different nonlinear models were tested to verify which was the one that best described the average growth curve of the birds. The evaluated growth functions were: Gompertz, $Y_{ij} = A_i e^{-b_i e^{-k_i t_{ij}}} + \mathcal{E}_{ij}$ (Laird, 1965); Logístic, $Y_{ij} = A_i(1 - b_i e^{-k_i t_{ij}})^{-1} + \mathcal{E}_{ij}$ (Nelder, 1961); and von Bertalanffy, $Y_{ij} = A_i\left(1 - b_i e^{-k_i t_{ij}}\right)^3 + \mathcal{E}_{ij}$ (von Bertalanffy, 1957), where Y_{ij} is the body weight of animal ith at age jth; A_i, the asymptotic weight of animal ith when t tends to infinity, that is, this parameter is interpreted as body weight at adulthood; b_i is an integration constant related to the initial weights of the bird ith, with no direct biological interpretation. The value of b is established by the initial values of Y and t; k_i is interpreted as the maturation rate, which should be understood as the change of weight in relation to weight at maturity, that is, as an indicator of the speed with which the animal ith approaches its adult size; $\mathcal{E}_{ij}$ is the associated random error of animal ith at each weighing time jth, considered to be independent between individuals and normally distributed. Residual standard deviation was considered to be constant throughout the growth trajectory.

In the second stage of the hierarchical model the following three-trait animal model described the genetic and environmental effects on parameters of the growth functions:

$$\boldsymbol{\theta} = \boldsymbol{X\beta} + \mathbf{Zu} + \mathbf{e},$$

where, $\boldsymbol{\theta}$ is a vector with the parameters *A*, *b* and *k* for all individuals; $\boldsymbol{\beta}$ is the vector of systematic effects (sex and generation); $\mathbf{u}$ is the vector of additive genetic effects; $\boldsymbol{X}$ and $\boldsymbol{Z}$ are the corresponding incidence matrices linking growth function parameters to systematic and additive genetic effects, respectively. Thus,

$$f(\boldsymbol{A}, \boldsymbol{b}, \boldsymbol{k} \mid \boldsymbol{u}_A, \boldsymbol{u}_b, \boldsymbol{u}_k, \boldsymbol{\beta}_A, \boldsymbol{\beta}_b, \boldsymbol{\beta}_k, \boldsymbol{R}, \boldsymbol{G}) = N \begin{bmatrix} \boldsymbol{X\beta}_A + \mathbf{Zu}_A & \\ \boldsymbol{X\beta}_b + \mathbf{Zu}_b, & \boldsymbol{R} \otimes \boldsymbol{I}_N \\ \boldsymbol{X\beta}_k + \mathbf{Zu}_k & \end{bmatrix}$$

where, $\boldsymbol{u}_A, \boldsymbol{u}_b, \boldsymbol{u}_k$ are the vectors of breeding values for all the animals in the pedigree for parameters *A*, *b* and *k*, respectively. $\boldsymbol{\beta}_A, \boldsymbol{\beta}_b, \boldsymbol{\beta}_k$ are the vectors of systematic effects for parameters *A*, *b* and *k*, respectively. $\boldsymbol{I}$ is an identity matrix and $\boldsymbol{N}$ is the number of animals with data. **R** and **G** are the 3 x 3 matrices of systematic and genetic (co)variance components for the growth curve parameters. **X** and **Z** are the common to all parameters incidence matrices linking *A*, *b* and *k* with the systematic and genetic effects, respectively. The residual effects were considered independent between individuals and normally distributed. The residual covariance between parameters of the same individual was considered differ from zero.

The prior distribution for additive genetic effects followed a multivariate normal distribution.

$f(\boldsymbol{u}_A, \boldsymbol{u}_b, \boldsymbol{u}_k | \boldsymbol{G}) = N(\boldsymbol{0}, \boldsymbol{A} \otimes \boldsymbol{G})$, where **A** is the relationship matrix.

Prior distributions of σ_ε^2, and elements of **R** and **G** were considered to be uniform.

Statistical analysis

The marginal posterior distributions of the variables of interest were approximated using the Gibbs sampler algorithm. Conditional distributions of the model parameters can be found in Blasco et al. (2003). In addition, marginal posterior distributions of age at inflexion point (***APOI***) and weight at inflexion point (***WPOI***) were computed from samples of the growth function parameters according to the expressions showed in Table 2.

Single chains of 100,000 iterations were run for all the analyses. The first 10,000 iterations of each chain were discarded, and samples of the parameters of interest were saved every 10 iterations. The number of discarded samples was, in all cases, much larger than the required burn-in determined by Raftery and Lewis (1992) and Geweke (1992) procedures. The sampling variance of the chains was obtained by computing Monte Carlo standard errors (Geyer, 1992). The "boa" package of R was used to assess convergence and to estimate summary statistics of marginal posterior distributions.

The samples from marginal posterior distributions for the differences between the parameters estimates *A*, *b*, *k*, *APOI* and *WPOI* for sex (male and female) and for generation (first and last) were obtained with the intention to verify statistical significance by **HPD** (high posterior density interval at a 95% probability). If the zero value is contained within this range, it is concluded that the parameters of the two populations involved in the contrast are statistically the same.

Goodness of fit

The overall goodness of fit was checked by computing the mean square error (**MSE**) and the deviance information criterion (**DIC**) proposed by Spiegelhalter et al. (2002). Models with a smaller DIC should be favored since indicate a better fit and a smaller degree of complexity. More details can be found in Forni et al. (2009).

The goodness of fit at different points of the growth trajectory was evaluated as it is described by Blasco et al. (2003). A predictive density was estimated for each record. The observed values (***yr***) were compared with their prediction (***Yr***) obtained by using all other records. If the model is adequate, the *yr* is a sample from its predictive distribution. We applied the checking functions proposed by Gelman et al (1992) to assess the probability of a *Yr* being lower than the observed one. When the *Yr* is lower than that observed one (*yr*), a checking g function is equal to one unit, when the *Yr* is greater than or equal to the *yr*, g is zero.

g = 1 if $Yr < yr$;

g = 0 if $Yr \geq yr$;

The average of these expectations at each point of the longitudinal trajectory shows the goodness of fit in different parts of it. If the model fits the data correctly, $E(g|\mathbf{y}_{-r})$ should be close to 0.5, so an overall fit quality criterion is the average of these expectations for all individuals at each point of the growth curve. A graph with these averages computed at each time of the longitudinal trajectory shows whether the fit is good along the curve, or if there are parts of the curve that fit better than others. This technique has the advantage of being free of scale effect. The expectation of the checking function $E(g|\mathbf{y}_{-r})$ is calculated using Monte Carlo Markov Chain (MCMC) method (see Forni et al. 2009 for a detailed description of the algorithm).

RESULTS AND DISCUSSION

The Bayesian procedure applied here, based on a hierarchical mixed model, provide estimates of the growth curve parameters for each animal taking into account individual information and information from relatives and other animals affected by the same systematic effects. Thus, the chance of having incorrect parameters estimates due to a lack of individual information is minimized (Varona et al., 1997). In addition, growth parameters are estimated taking into account the uncertainty on variance components and systematic and random effects of the model, unlike the two-step procedure (Denise and Brinks, 1985).

No lack of convergence was detected for any chain by visual inspection of sample trace plots, indicating that sampling processes were appropriate. As expected, heritabilities and genetic correlations showed the highest correlation between consecutive samples. However, the Monte Carlo standard error (**MCse**) was still low (lower than 12% of the posterior mean). The MCse is the error produced by the size of the sample and the lower its value, the better the algorithm performance to approximate the exact response, a larger sample size equals the lower MCse (Blasco, 2017).

Overall goodness of fit was evaluated for comparing models using the deviance information criterion (DIC) proposed by Spiegelhalter et al. (2002). A smaller DIC value indicates a better fit and a smaller degree of complexity. The Gompertz growth function was the one that lead to a smaller DIC value followed by Logistic and von Bertalanffy models, respectively (Table 3). On the other hand, the smallest MSE value was obtained with the von Bertalanffy function and the biggest with the Gompertz function. The MSE can strongly depend on the fitting at the last part of the trajectory due to scale effects. However, looking at the goodness of fit at different points of the longitudinal trajectory using the check function proposed by Gelfand et al. (1992), we observed that the probability of a predicted value being bigger or smaller than the observed values was smaller for the Gompertz and the von Bertalanffy growth functions than for the Logistic model.

The mean of the expected check function proposed by Gelfand et al. (1992) was computed at each point of the longitudinal trajectory (i.e. at each time point). The closer the mean in each point is to 0.5 the better the fit. Values over 0.5 indicate a greater probability of having predictions smaller than the observed values whereas values under

0.5 indicate a greater probability of obtaining predictions bigger than the true record. According to our results (Figure 1), none of the models overestimated the initial weights. The Logistic model underestimated the initial weight and also at seven and 28 d of age, overestimating at 14, 21 and 42 d of age. The von Bertalanffy model underestimated or overestimated to a lesser extent at all ages when it was compared to the Logistic model, but did not generally achieve better fit than Gompertz function, which showed the best fit at any time of the trajectory.

The results of analysis indicated que Gompertz model is the most appropriate to describe growth pattern in this population of meat quails. This result is in agreement with those reported by other authors using different methodologies such as: Akbas and Oguz (1998) using the generalized least squares, Rossi and Santos (2014) adopting a Bayesian procedure with skew-normal errors for female and skew-t for males, Narinç et al. (2010) with the NLIN procedure of SAS software and Firat et al. (2016) with a two-step Bayesian procedure. However, it disagrees with results obtained by Shoukry et al. (2015) and Kaplan and Gurcan (2016) with using NLIN procedure of SAS software. Therefore, results regarding mean values of growth function parameters, variance components and heritabilities refer only to the ones obtained with the Gompertz growth function.

The Table 4 shows means, standard deviations and Monte Carlo standard error of the marginal posterior distributions of parameters of each growth function for all animals with records. The MCse values were around or lower than 1% of the posterior mean. They are larger values than those obtained by Firat et al. (2016). However, those authors used a two-step Bayesian procedure instead of a hierarchical Bayesian model, ignoring uncertainty on estimates of growth curve parameters when they estimate variance components and systematic and random effects of the model. Estimates of A, b and k were close to those reported by Drumond et al. (2013) in meat quail, which were estimated by

Gauss Newton algorithm using the NLIN procedure of SAS. More work was done with nonlinear modeling of Japanese quails (Akbas and Oguz, 1998; Narinç et al., 2010; Rossi and Santos, 2014; Shoukry et al., 2015). However, none of these studies had such a high number of individuals and records than here.

When comparing the estimates of the growth function parameters with the ones reported in other studies carried out in quail, it can be observed that the values of *A*, *b* and *k* show the same trends. Despite the letter used to represent the parameters of the different growth functions are the same, they do not have the same biological meaning. The *A* parameter is the only parameter comparable across models. It represents the asymptotic body weight and presented highest value in von Bertalanffy followed by Gompertz and finally Logistic function. (Akbas and Oguz, 1998; Narinç et al., 2010; Drumond et al., 2013; Shoukry et al., 2015; Firat et al., 2016; Kaplan and Gurcan, 2016).

Our line of quails has been selected for body weight at 42 d of age for 15 generations. It is not possible to assess the correlated response to selection in the parameters of the growth function (i.e. the effect of selection on the growth pattern) because the systematic effect of batch is completely confounded with the genetic effects in each generation (there was just one batch per generation) and we do not have an unselected control population. Therefore, in Figure 2 we show the mean of the phenotypic values of males and females at each generation to show the evolution over time of growth curve parameters which is due to genetic and environmental effects. The estimated *A*, *APOI* and *WPOI* have increased mainly in the generations 13 and 14 of selection, whereas the *k* has decreased in both males and females (Figure 2). Blasco et al. (2003) and Piles et al. (2008) using the same methodology to estimate phenotypic and genetic parameters of the Gompertz function reported that, as a consequence the selection for growth rate at fattening, there was an increase in the asymptotic weight but no change in *b* and *k* parameters in their rabbit population.

The results concerning the significance of the contrasts related to the comparison of the first and last generation for the parameters *A, b, k, APOI* and *WPOI* were showed at Table 5. These results were obtained by inference in the samples of the marginal distribution *a posteriori* of each parameter. All HPD for the differences between the parameters of the first and last generations did not contain zero, thus confirming that there were differences in the values for *A*, *b*, *k*, *WPOI* and *APOI* related to generation. The quails in the last generation were 17% heavier for *A* and *WPOI*, *k* was 15.9% lower, *APOI* was 12.6% higher and *b* was 7.8% lower than in first generation.

In the case of quails, females are heavier than males (Akbas and Oguz, 1998). This result was also observed in our work (Figure 2). It can be observed that for the parameters that the females presented greater values than the males (*A*, *APOI* and *WPOI)*, the results presented in Table 5 for the contrasts by sex effect were significant. Thus, the females are heavier adult and at inflexion point, and reach the age at the inflection point after males. For *k* and *b* the results not showed difference by sex.

In Japanese quails for age at the inflexion point, Akbas and Oguz (1998) found 18.74 and 21.22 d of age for males and females respectively, and Raji et al. (2014) reported age at the inflexion point of 17.36 d for males and 20.37 d for females, both authors using the Gompertz function. Aggrey (2009) applying the Logistic model with nonlinear mixed effects in Japanese quail showed age at the inflexion point for females of 22.26 d and for males of 17.5 d. For age at the inflexion point, the values were similar to the mean of the results found here, however for the weight at the inflexion point the results in this study were greater than of other researches cited, that ranged of 48.82 g to

89.90 g. These results are expected due the difference between meat quails and Japanese quails and also differences selected populations by different criteria.

The heritabilities of the growth function parameters were moderate (Table 6), indicating that one can expect to obtain some response to selection based on parameters *A*, *b* and *k* of the growth curve, even if slow and limited. The highest heritability was for the *A* (0.32) and the lowest for the *k* parameter (0.18). Our estimates are similar from the ones reported by Akbas and Oguz (1998) also in quails, but the standard errors of the heritabilities estimates in that study were quite high.

Using the same methodology of our study, Mignon-Grasteau et al. (2000) obtained higher values of heritability in chickens than those found here (0.54, 0.43 and 0.60 for adult weight, degree of maturation at birth and maturity rate, respectively) for meat quails. In a previous analysis of the same data set, Mignon-Grasteau et al. (1999) obtained slightly lower heritability values using REML methodology. Authors attributed those differences in heritabilities to differences between models (including or not maternal effects) and methodology (using or not information from relatives).

Genetic correlation between *A* and *b* parameters was low and positive (0.25), it was null between *b* and *k* parameters (0.03), and moderate to high and negative between *A* and *k* parameters (-0.50) (Table 7). Mignon-Grasteau et al. (2000) also obtained a moderate and negative genetic correlation between *A* and *k* parameters of the Gompertz function in chickens. They explain that a high and negative correlation can be expected between *A* and *k* parameters due to a rapid decrease in growth rate after inflection point, resulting in a lower asymptotic body weight. Santoro et al. (2005) indicated that the expected genetic correlation between asymptotic weight and maturity rate would be negative, since heavier animals would tend to have a lower maturation rate than lighter animals. Mignon-Grasteau et al. (2000) also found a positive genetic correlation between

A and *b* parameters but it was much higher than the one observed in our study (0.75). In addition, unlike our results, they found a moderate and negative genetic correlation between *b* and *k* parameters (-0.40).

Phenotypic correlations were low and positive between *A* and *b* parameters and between *b* and *k* parameters but high and negative between *A* and *k* parameters (Table 7). Those results differ from the ones obtained by Akbas and Oguz (1998) in Japanese quails who found a very high and positive correlation between *b* and *k* parameters (0.99), and low and negative correlation between *A* and b (-0.16). However, the phenotypic correlation between *b* and *k* was high and negative (-0.63) as in our study. The phenotypic correlations between Gompertz function parameters estimated by Drumond et al. (2013) in meat quails were high and negative between *A* and *b* (-0.60) and between *A* and *k* (-0.95), whereas it was high and positive between *b* and *k* (0.78).

In conclusion, Gompetz growth function is adequate to establish mean growth patterns in our population of meat quails. The parameter *A*, and consequently *APOI* and *WPOI* have increased over time from the first generation of selection, whereas *k* has decreased. The heritability of growth curve parameters is moderate, therefore selection for one or more of them in an index could be feasible. However, because of the negative and moderate to high genetic correlation between *A* and *k* it could be difficult or not possible to obtain animals with high (*k*) growth rate without decreasing (*A*) adult weight.

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Table 1. Summary of weights data of European quail per generation

Generation	No. of records	No. of animals	No. of sires	No. of dams
1	3,628	535	109	151
2	4,000	587	57	94
3	5,832	870	70	129
4	2,439	367	58	86
5	3,941	586	38	63
6	1,686	251	47	61
7	3,621	535	44	70
8	1,952	293	61	92
9	2,310	337	52	82
10	2,052	311	54	86
11	3,417	500	67	96
12	2,463	374	52	79
13	2,868	428	51	83
14	3,256	494	61	94
15	2,500	370	51	79
Totals	45,965	6,838	872	1,345

Table 2. Age (*APOI*) and weight (*WPOI*) at inflexion point in Gompertz, Logistic and von Bertalanffy functions

Growth functions	*APOI*	*WPOI*
Gompertz	$\ln(b)/k$	A/e
Logistic	$-\ln(1/b)/k$	$A/2$
von Bertalanfy	$\ln(3b)/k$	$8A/27$

Table 3. Goodness of fit of growth function of European quails

Growth functions	DIC	MSE	$E(g\|y_r)$
Gompertz	342496.00	1.99	0.495
Logistic	356754.10	1.74	0.457
von Bertalanffy	386464.70	0.53	0.494

Table 4. Estimating growth curve parameters for meat quails

Growth function	Trait	Mean	SD[1]	MCse[2]
Gompertz	A	361.29	61.12	5.41
	b	3.86	0.22	0.02
	k	0.073	0.011	0.001
Logistic	A	309.89	41.29	3.39
	b	17.34	1.83	0.22
	k	0.130	0.013	0.001
von Bertalanffy	A	450.48	88.12	10.6
	b	0.76	0.021	0.002
	k	0.044	0.008	0.001

[1] SD = posterior standard deviation.

[2] MCse = Monte Carlo SE.

Table 5. Mean of the systemic effects of parameters *A, b, k, APOI* and *WPOI,* high posterior density interval at a 95% probability (HPD) and Monte Carlo SE

Trait[1]	Sex effect[2]			Trait	Generation effect[3]		
	Mean	HPD	MCse		Mean	HPD	MCse
A	-15,73	**-18.55; -12.91**	0.01	*A*	50.30	**29.33; 70.64**	0.60
b	-0.019	-0.041; 0.0024	0.00008	*b*	-0.32	**-0.42; -0.20**	0.002
k	0.00061	-0.00006; 0.0013	0.000003	*k*	-0.013	**-0.017; -0.009**	0.0001
APOI	-0.24	**-0.39; -0.09**	0.004	*WPOI*	18.50	**10.79; 25.99**	0.22
WPOI	-5.78	**-6.82; -4.74**	0.0006	*APOI*	2.18	**1.22; 3.17**	0.03

(MCse)

[1] *A* = asymptotic weight of animal; *b* = degree of maturation at birth; *k* = maturation rate; *APOI* = age at inflexion point; *WPOI* = weight at inflexion point.

[2] Sex effect = mean of male (*A, b, k, APOI* and *WPOI*) - mean of female (*A, b, k, APOI* and *WPOI*).

[3] Generation effect = mean of first (*A, b, k, APOI* and *WPOI*) - mean of last (*A, b, k, APOI* and *WPOI*).

Table 6. Marginal posterior distributions of variance components of Gompertz growth curve parameters for meat quails

Trait[1]	Genetic variance			Trait	Phenotypic variance		
	Mean	HPD[2]	MCse[3]		Mean	HPD	MCse
A	875.5	663.8; 1100.1	4.8	*A*	2685.1	2529.8; 2838.6	1.9
b	0.011	0.007; 0.016	0.00006	*b*	0.038	0.039; 0.042	0.00004
k	0.00002	0.00001; 0.00003	0.0000001	*k*	0.00011	0.00010; 0.00012	0.00000004

Trait	Residual variance			Trait	Heritability		
	Mean	HPD	MCse		Mean	HPD	MCse
A	1809.7	1640.8; 1981.7	3.0	*A*	0.32	0.26; 0.40	0.002
b	0.027	0.023; 0.031	0.00003	*b*	0.29	0.20; 0.39	0.001
k	0.00009	0.00008; 0.00010	0.00000009	*k*	0.18	0.12; 0.24	0.001

[1] A = asymptotic weight of animal; b = degree of maturation at birth; k = maturation rate.

[2] HPD = High posterior density interval at a 95% probability.

[3] MCse = Monte Carlo SE.

Table 7. Marginal posterior distributions of correlation between Gompertz growth curve parameters of meat quails

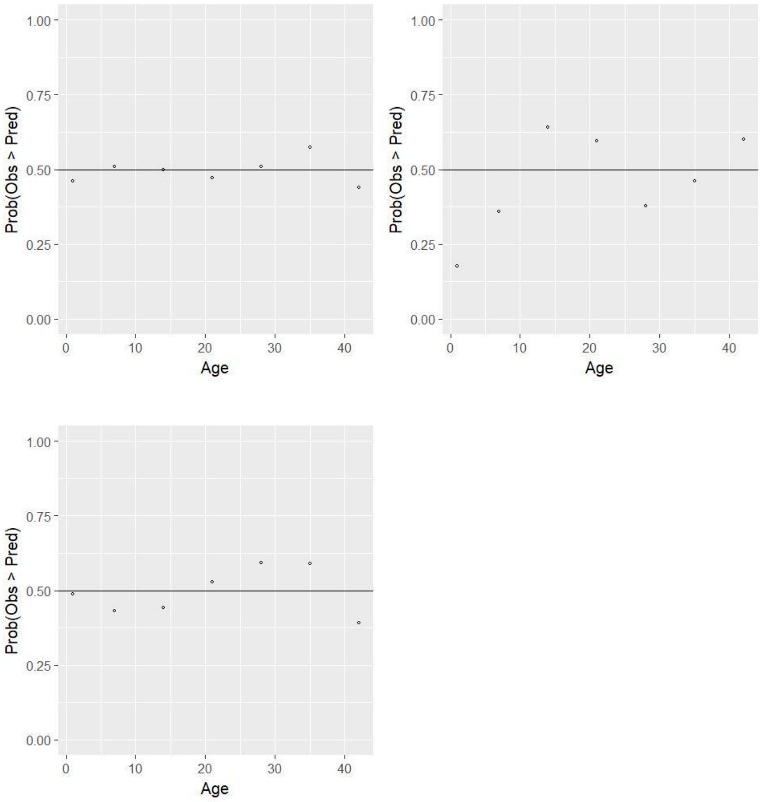
	Genetic correlation				Phenotypic correlation		
Trait[1]	Mean	HPD[2]	MCse[3]	Trait	Mean	HPD	MCse
A, b	0.25	0.05; 0.45	0.003	A, b	0.10	0.03; 0.17	0.0006
A, k	-0.50	-0.63; -0.35	0.002	A, k	-0.72	-0.74; -0.69	0.0002
b, k	0.03	-0.24; 0.27	0.004	b, k	0.26	0.20; 0.32	0.0004

	Residual correlation		
Trait	Mean	HPD	MCse
A, b	0.04	-0.05; 0.13	0.0007
A, k	-0.80	-0.82; -0.77	0.0002
b, k	0.34	0.26; 0.42	0.0006

[1] A = asymptotic weight of animal; b = degree of maturation at birth; k = maturation rate.

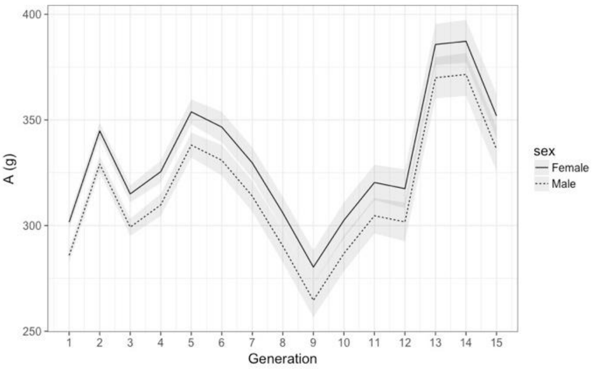
[2] HPD = High posterior density interval at a 95% probability.

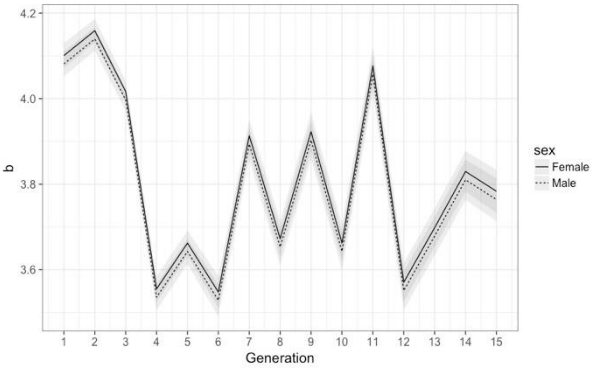
[3] MCse = Monte Carlo SE**.**



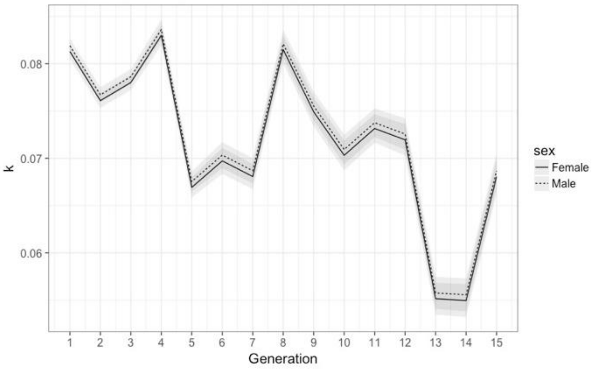
(a) (b) (c)

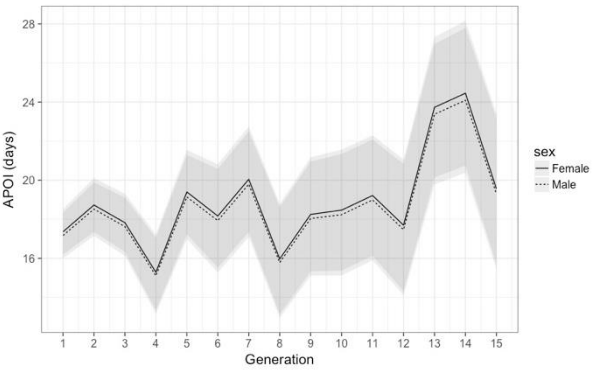
Figure 1. Mean expectations of the Gelfand's check function $E(g|\mathbf{y}_{-r})$ for Gompertz (a), Logistic (b) and von Bertalanffy (c) growth curve for European quails


A (g)
400
350
300
250
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
Generation
sex
Female
Male

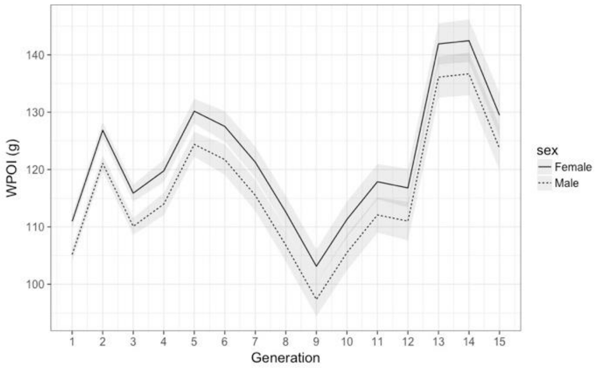

b
4.2
4.0
3.8
3.6
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
Generation
sex
Female
Male

(a) (b)


k
0.08
0.07
0.06
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
Generation
sex
Female
Male


APOI (days)
28
24
20
16
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
Generation
sex
Female
Male

(c) (d)



(e)

Figure 2. Posterior means and standard deviation (shadow) for *A* (a), *b* (b) and *k* (c), *APOI* (d) and *WPOI* (e) parameters of the Gompertz curve by sex and generation