



Investigating age-related changes in variability of body weight in sheep

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ABSTRACT

'Variance compounding' and 'compensatory growth' in growth curve of Zandi sheep were investigated through monitoring ontogenetic changes in causal components of phenotypic variability of body mass from birth until one year of age. To do this, phenotypic variance and its casual components were estimated for body weight taken at different ages in male and female lambs separately by REML procedure fitting a multi-trait animal model. Estimates of standardized variance components showed greater genetic and environmental differences among animals for traits related to early growth. In addition, results indicated that sexual puberty can act to growth compensation as phenotypic, additive genetics and residual coefficient of variations minimized at about sexual puberty. Latter result provided evidence that body weight measured around sexual puberty is not a suitable selection criterion for improving body weight as it experienced low additive genetic variation. In most studied growth phases, compensatory growth was predominant and only in the period between 9 and 12 months of age, in which an accelerated growth occurred, variance compounding process was observed.

1. Introduction

Complex phenotypes such as body weight are multifactorial traits, determined by an interaction between environmental and genetic factors (Wilson and Réale, 2006; Cornes et al., 2007). Hence, many studies have investigated the role of genes and environment in the variability of body weight. These quantitative genetic studies have shown that development of body weight occurs through the actions of many genes that act differentially during ontogeny, i.e., as an individual grew, heritable component of phenotypic variation may also show ontogenetic variation. Therefore, age-specific weights might differ in additive genetic variation and, hence, in potential rates of response to selection (Riska et al., 1984; Cheverud et al., 1996; Wilson and Réale, 2006). Changes in causal variance components during ontogeny are controlled by several processes. Among them, 'variance compounding' and 'compensatory growth' has been the subject of several studies (Riska et al., 1984; Ali et al., 2003; Wilson and Réale, 2006). Variance compounding is explained by cumulative effects of allelic variants which lead to variance compounding over ontogeny (Atchley and Zhu, 1997). Contemporary growth which also called 'targeted growth' (Riska et al., 1984) defined as the tendency of growth trajectories to converge on a reduced range of phenotypes. Compensatory growth has also been defined as any growth that reduces the variance in the system (Atchley, 1984) or as the negative correlation between the growths of a trait in successive time intervals (Riska et al., 1984).

In this study, growth data from an experimental population of Zandi sheep was used to test for variance compounding and contemporary growth processes by analyzing patterns of age-related changes in phenotypic variance and its casual components.

2. Material and methods

2.1. Data

In the late-1980s, an experimental population of Zandi sheep was established in the Khojir national park between Tehran and Abali at 35°45'E and 51°40'N, 1547 m above mean sea level. Climatically, this location has temperate summers and cold winters with an average rainfall of approximately 300 mm/yr. The aim was to establish a nucleus source for improving other flocks in the region. The founder animals (with unknown pedigrees) were purchased from various sheep farms in the region of the breeding station. Since 1991 the sheep have been the subject of individual level study, with animals tagged and monitored throughout their lifetime. There was one breeding season commenced in August, with lambing commenced in January. Coat colour is black in new-born, but gradually changes with age in a way that adult animals are found in black, light-brown, and gray. Body weight records of tagged individuals have been monitored since 1991 through regular censuses taken five times a year which provided an opportunity to quantify heritable and non-heritable components of

Abbreviation: BW, birth weight (BW); W3, 3-month weight (W3); W6, 6-month weight (W6); W9, 9-month weight (W9); W12, 12-month weight (W12); CV, coefficient of variation; P1, growth rate from birth to 3 months of age; P2, growth rate from 3 to 6 months of age; P3, growth rate from 6 to 9 months of age; P4, growth rate from 9 to 12 months of age
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phenotypic variation of body weight.

2.2. Studied traits

Data included birth weight (BW), 3-month weight (weaning weight, W3), 6-month weight (W6), 9-month weight (W9) and 12-month weight (W12). In order to account for the differences among animals with different ages, weaning weight was adjusted to 90 days of age by adding 90 times the pre-weaning average daily gain to birth weight. Adjusted 6-month weight (W6), 9-month weight (W9) and 12-month weight (W12) were obtained by adding t times the post-weaning daily gain to weaning weight, where t is the number of days in the period. The increases in weight for the different growth phases, namely from birth to 3 months of age, from 3 to 6 months of age, from 6 to 9 months of age and from 9 to 12 months of age were used for calculations of growth rates (P1, P2, P3 and P4), as total gain divided by the number of days in the period.

2.3. Statistical analysis

In order to be able to obtain reliable estimates of genetic parameters, an individual's phenotype should be 'corrected' for known sources of non-genetic variation (fixed effects) such as year of birth, birth type, sex, and etc. Inclusion of fixed effects is used to protect against downward bias in heritability estimates. To identify fixed effects, least square analyses were conducted using the GLM procedure (SAS, 2004) with a model including fixed effects of year of birth, age of dam at lambing, sex of lambs and type of birth. All these fixed effects were significant ($p < 0.05$) for all traits and were included in the linear animal models.

In order to estimate (co)variance components, an animal model was used. The animal model is a form of mixed model which partitions each individual animal's phenotype for a given trait into a linear sum of different fixed and random effects. As random effects for all traits studied, direct additive genetic, maternal genetic and residual effects were included. By including only one of the maternal effects in the model, most of the maternal variation would be accounted for. In matrix notation this model was specified as:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Z}_1\mathbf{a} + \mathbf{Z}_2\mathbf{m} + \mathbf{e},$$

where \mathbf{y} is the vector of phenotypic observations for each trait and \mathbf{b} is the vector of fixed effects as evidenced by GLM with association matrix \mathbf{X} . \mathbf{Z}_1 and \mathbf{Z}_2 are the design matrices for the direct additive genetic effects and maternal genetic effects, respectively. The vector \mathbf{a} contains the direct additive genetic effects for each individual (a_i) having mean of zero and a variance of V_A . This is estimated from the variance-covariance matrix of additive genetic effects (\mathbf{G}) which is equal to AV_A , where A is the additive numerator relationship matrix containing the individual elements $A_{ij} = 2\Theta_{ij}$, and Θ_{ij} is the coefficient of co-ancestry between individuals i and j obtained from the pedigree structure. Maternal genetic variance (σ_m^2) was estimated by including \mathbf{m} , the vectors of maternal genetic effects. The variance-covariance matrix of maternal genetic effects is specified as AV_M such that estimating V_M uses the relationship matrix in the same way as the additive genetic effect. \mathbf{e} was fitted as the vector of residual errors (corresponding to temporary environment effects) with variance of V_E . The additive genetic effects were related to individual records with the corresponding incidence matrix \mathbf{Z}_1 . Total phenotypic variance (V_P) was estimated as the sum of all (co)variance components. Estimates of heritability (h^2) were calculated as the ratio of the additive genetic variance to the total phenotypic variance.

(Co)variance components and heritability coefficients were estimated using a multi-trait Restricted Maximum Likelihood (REML) animal model fitting a derivative-free (DF) algorithm as implemented in the WOMBAT software package of Meyer (2006), with analyses performed separately for males and females.

Table 1
Characteristics of the data structure^a.

Trait	Males			Females		
	N	\bar{X}	SD	N	\bar{X}	SD
BW (kg)	2401	4.25	0.79	2467	4.01	0.68
W3 (kg)	1741	20.34	4.25	1782	18.94	3.67
W6 (kg)	955	32.48	5.58	1107	29.81	4.87
W9 (kg)	664	34.45	5.44	875	30.82	5.70
W12 (kg)	513	38.24	6.54	698	31.29	5.50
P1 (gr/day)	1741	178	45	1782	166	38
P2 (gr/day)	955	130	47	1107	117	42
P3 (gr/day)	587	8	51	762	4	49
P4 (gr/day)	424	53	54	550	27	44

^a BW: birth weight, W3: 3-month weight, W6: 6-month weight, W9: 9-month weight, W12: 12-month weight, P1: growth rate from birth to 3 months of age, P2: growth rate from 3 to 6 months of age, P3: growth rate from 6 to 9 months of age, P4: growth rate from 9 to 12 months of age.

As variance often increases with the square of the mean, scale effects may limit the efficacy of directly comparing the magnitudes of (co)variance components across ages, in particular for body weight since the phenotypic mean increases as animals age. For such comparisons, coefficients of variation are therefore more appropriate than are the non-standardized variance components (Houle, 1992; Kruuk et al., 2000). To calculate a trait's CV_A , we need to know two things: its mean (on a true ratio scale), and its additive genetic variance. Using these parameters additive coefficient of variation (CV_A) is calculated as $CV_A = 100 \times \sqrt{V_A}/\bar{x}$, where V_A is the additive genetic variance and \bar{x} is the sample mean. Thus a CV_A is a mean-standardized index of genetic variance in a trait. In a more abstract manner, a trait's CV_A reflects the amount of genetic variance that currently exists in the trait, not relative to the environmental variance that affects the trait (as in a heritability estimate), but relative to the trait's current average value (Miller and Penke, 2007).

3. Results

The characteristics of the data used in the analyses are shown in Table 1. As it was expected, males were heavier than females at all the ages. The differences between body weight of male and female lambs increases with age because male lambs gained more weights than female lambs during all the growth phases. However, the growth pattern was similar in males and females in a way that maximum growth rate was observed during 0–3 months of age. Afterwards, growth rate diminished by 30% during P2, sharply decreased during P3, and then recovered during P4.

Least square means for growth traits are shown in Table 2. The results showed that the sex of lamb, birth type, age of dam and year of birth had significant effect on all traits studied ($p < 0.01$).

Estimates of (co)variance components and coefficients of variations are presented in Table 3. In both males and females estimates of V_A , V_E and V_P increased from birth to 6 months of age when they started to decline up until 9-month and subsequently increased during P4. In contrast, in both the sexes, results showed a decreasing trend for CV_A , CV_E and CV_P up to 9 months of age, and an increasing trend from 9 to 12 months of age.

Phenotypic correlations between growth rates in different growth phases are listed in Table 4. In males, phenotypic correlation ranged from 0.00 (P1–P4) to -0.133 (P1–P2) and in females, phenotypic correlation was between -0.048 (P1–P4) to -0.157 (P1–P3).

4. Discussion

The significant effect of sex of lambs on traits related to growth has been reported by Réale and Boussès (1999), Dass et al. (2004), Yilmaz

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