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An evaluation of maternal influences on growth traits: the Zandi sheep breed of Iran as an example

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ABSTRACT

An animal model was used to estimate direct and maternal genetic parameters for birth weight (BW), weaning weight (WW), 9-month weight (W9) and yearling weight (YW) for a population of Zandi sheep. The magnitude of estimates of these parameters was used to evaluate the importance of direct and maternal influences on body weight at various stages of Zandi lambs' life. Results confirmed the potential maternal influences to change pattern of body weight's heritability with age. Maternal influences were significant for early growth traits. The importance of maternal influences diminished with age, although for W9 and YW those effects did not disappear completely. In contrast to variation due to maternal effects, the variance of direct effects increased from birth to a year of age. Estimates of maternal breeding values averaged by year of birth decreased throughout the experiment for both BW and WW. It was concluded that for more precise designing selection programs and, in consequence, increasing efficiency of selection, inclusion of maternal effects as well as direct-maternal genetic covariance into the model, especially for early growth traits, is necessary.

KEY WORDS: animal model, maternal effects, body weight, heritability, sheep

INTRODUCTION

Most livestock are mammals with long periods of maternal dependence, so that an offspring's phenotype is determined not only by its own genotype and the random environmental conditions it experiences during development, but

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also by the environment provided by its parents. The influence of the mother on her offspring has been apparent since the beginning of animal husbandry. Many erroneous ideas have been handed down over the years, particularly with regard to maternal impressions. For example, one of the earliest recorded statements is the belief that effects due to events which the mother was subjected to during mating or pregnancy are transmitted to the foetus as maternal influences and affect pre- and post-natal phenotypes of the offspring (Legates, 1972). Now, maternal effects can be described as any contribution of a mother that affects the phenotypic expression of her offspring. The mother's milk production, health status, size, intrauterine environments, and mothering ability are all common components which are controlled by her genotype and associated environmental factors (Maniatis and Pollott, 2003). Therefore, maternal effects are divided in to genetic and environmental components. However, for the offspring, maternal effects are considered to be environmental. So, there are indirect genetic (heritable maternal effects) and environmental effects (Szwaczkowski et al., 2006). Before the 1990s, due to computational limitations and other problems in estimating maternal components (Willham, 1980), for most studies of growth, maternal effects were ignored from the analyses and only direct effects considered (see e.g., Atkins, 1986). With increasing computing power and availability of REML algorithms for analyses to fit an animal model has been simplified estimation of (co)variance components due to maternal effects (Meyer, 1997). Hence, during the last decade, most estimates of (co)variance components have been obtained for various sheep breeds using an animal model incorporating maternal effects (Snyman et al., 1995; Van Vleck et al., 2003; Ekiz, 2004; Szwaczkowski et al., 2006; Miraei-Ashtiani et al., 2007). These studies have shown the biases that are introduced by using the simple direct additive genetic animal model and the importance of modeling maternal inheritance in order to obtain accurate estimates of (co)variance components. However, in most studies, estimates of genetic parameters due to maternal effects have generally been restricted to traits describing growth till weaning.

The aims of the present paper were to investigate the importance of direct and maternal effects on body weight at different ages of Zandi lambs and to develop a suitable model for the data set used.

MATERIAL AND METHODS

Data and management

Data and pedigree information on Zandi sheep collected at the Breeding Station of Zandi sheep over the period from 1987 to 2005 were used in this research. The station is situated in Khojir national park between Tehran and Abali at 35°45′E and 51°40′N, 1547 m above see level. Only pedigree information was recorded prior to 1990. In the experiment, maiden ewes were exposed to rams at about 18 months of age and kept in the flock until death or the apparent infertility. Rams were used for 3 or 4 breeding years and kept separated from ewes, except in the mating season. In the mating season (commenced in August), initially artificial insemination (AI) was performed, but animals that did not conceive by AI were allocated to natural service. In the latter case, each group of the ewes (detected in oestrus) was allotted to one fertile ram in a separate mating pen. At birth, lambs were weighed, tagged, sexed, and identified to their parents. Birth date was also recorded. During the suckling period, lambs were kept indoors and allowed to nurse their mothers twice a day. The suckling stage lasted for 90 days on average. Animals were kept on natural pasture during the spring, summer and autumn seasons and indoors during the winter. Selection was based on weaning weight and, to some extent, body conformation.

The traits analysed were birth weight (BW), weaning weight (WW), body weight at 9 months of age (W9) and yearling weight (YW). Age at weighing was used as a covariate to account the differences in age at each time of weighing. Characteristics of the data used in the analyses are given in Table 1.

Table 1. Characteristics of the data set

Item	Trait[a]			
	BW	WW	W9	YW
Number of records	5111	4056	1942	1501
Number of animals	5645	4520	2426	1980
Number of sires with progeny	165	170	149	145
Number of grandsires with progeny	127	132	108	97
Number of dams with progeny	1372	1312	955	839
Number of granddams with progeny	805	674	455	392
Number of sires with own record	130	143	99	83
Number of dams with own record	914	912	508	424
Number of sire-offspring record pairs	3475	3200	1221	849
Number of dam-offspring record pairs	3271	2716	979	711
Average number of progeny per sire	25.83	22.25	12.43	9.54
Average number of progeny per dam	3.79	3.06	2.02	1.77
Mean, kg	4.12	20.72	32.22	34.12
SD, kg	0.72	4.33	5.78	6.59
CV, %	14.50	15.87	11.75	12.98

[a] BW - birth weight; WW - weaning weight; W9 - body weight at 9 months of age; YW - yearling weight

Statistical analysis

The fixed part of the models included birth year (15 years), season of birth (winter and spring), sex (male and female), type of birth (single, twin and triplet) and age of dam at lambing (2-10 years old). Least square analyses using the GLM procedure of SAS (2004) showed that all these fixed effects were significant ($P<0.05$) for all traits. These effects then were included in the linear mixed models. The same fixed effects were used for models with different random effects. A series of six single-trait linear animal models were considered that differed in the (co)variance components fitted to assess the importance of maternal effects. The models expanded from a simple animal model (Model 1) to a comprehensive maternal effects model (Model 6). The random models used are summarized in Table 2. Depending on the model fitted, direct additive genetic variance (σ^2_a), maternal permanent environmental variance (σ^2_c), maternal additive genetic variance (σ^2_m), covariance between direct and maternal genetic effects ($\sigma_{a,m}$), residual variance (σ^2_e), phenotypic variance (σ^2_p), direct heritability (h^2), maternal heritability (m^2), the ratio of maternal permanent environmental variance to phenotypic variance (c^2), and correlation between direct and maternal genetic effects (r_{am}) were estimated, accordingly.

Table 2. (Co)variance components fitted to models used in the analyses

Model	(Co) variances fitted[a]
1	$\sigma^2_a + \sigma^2_e$
2	$\sigma^2_a + \sigma^2_c + \sigma^2_e$
3	$\sigma^2_a + \sigma^2_m + \sigma^2_e$
4	$\sigma^2_a + \sigma^2_m + \sigma_{a,m} + \sigma^2_e$
5	$\sigma^2_a + \sigma^2_c + \sigma^2_m + \sigma^2_e$
6	$\sigma^2_a + \sigma^2_c + \sigma^2_m + \sigma_{a,m} + \sigma^2_e$

[a] σ^2_a - direct additive genetic variance; σ^2_c - maternal permanent environmental variance; σ^2_m - maternal additive genetic variance; $\sigma_{a,m}$ - direct-maternal additive genetic covariance; σ^2_e - residual variance

Estimates of (co)variance components, and log likelihoods values, were obtained using a derivative-free REML algorithm as implemented in the DFREML program (Meyer, 2001). In fitting the models, the Simplex procedure was employed to locate the maximum of the log likelihood (log L). Convergence was considered to have been reached when the variance of function values (-2 log L) in the Simplex was less than 10^{-8}. Standard errors were obtained for the estimated parameters from a part of the DFREML program.

The information criterion (AIC) of Akaike (1977) was computed to rank the models according to their power to fit the data. The criterion for model *i* is defined as $AIC_i = -2 \log L_i + 2$ (number of independently estimated parameters_i), which $\log L_i$ denoting maximum of the likelihood of model *i*. The model yielding the smallest AIC fits the data best.

Estimates of maternal breeding values were obtained with Best Linear Unbiased Prediction (BLUP) method based on a two-trait animal model for the traits which significantly influenced by maternal effects (BW and WW). Means for estimated maternal breeding values of the animals by year of birth were calculated to evaluate the maternal genetic trends.

RESULTS

Estimates of genetic parameters for each pair of traits (related to early and later stages of lambs' life) obtained *via* the six models with corresponding AIC value for each analysis are summarized in Tables 3 and 4, respectively. For all traits, estimates of direct heritability were influenced by the statistical model. With the simple animal model (Model 1), h^2 estimates were overestimate; but when maternal effects were included in the models, estimates of h^2 decreased, especially for BW and WW. For BW and WW models 5 and 4, respectively, had lowest AIC. Latter result shows that maternal effects on body weight early in life are significant. The inclusion

Table 3. Genetic parameters [a] ± SE for birth weight (BW) and weaning weight (WW)

Trait-model	Parameter					
	h^2	m^2	c^2	r_{am}	h_t^2	AIC[b]
BW						
M1	0.33 ± 0.04	-	-	-	0.33	983.07
M2	0.19 ± 0.04	-	0.15 ± 0.02	-	0.19	916.05
M3	0.11 ± 0.04	0.18 ± 0.02	-	-	0.20	900.05
M4	0.12 ± 0.04	0.20 ± 0.03	-	-0.18	0.18	901.03
M5	0.11 ± 0.04	0.12 ± 0.02	0.07 ± 0.02	–	0.17	893.83
M6	0.13 ± 0.04	0.14 ± 0.02	0.07 ± 0.02	-0.21	0.15	895.03
WW						
M1	0.16 ± 0.04	-	-	-	0.16	11242.22
M2	0.14 ± 0.04	-	0.03 ± 0.02	-	0.14	11241.39
M3	0.11 ± 0.04	0.05 ± 0.02	-	-	0.16	11237.10
M4	0.08 ± 0.04	0.02 ± 0.02	-	0.99	0.15	11235.92
M5	0.10 ± 0.05	0.05 ± 0.02	0.00 ± 0.01	-	0.13	11239.13
M6	0.08 ± 0.05	0.04 ± 0.02	0.00 ± 0.01	0.51	0.15	11239.34

[a] h^2 - direct heritability; m^2 - maternal heritability; c^2 - maternal permanent environmental variance as proportion of phenotypic variance; r_{am} - direct-maternal genetic correlation; h_t^2 - total heritability

[b] AIC - Akaike's information criterion

Table 4. Genetic parameters[a] ± SE for 9-month weight (W9) and yearling weight (YW)

Trait-model	Parameter					
	h^2	m^2	c^2	r_{am}	h_t^2	AIC[b]
W9						
M1	0.22 ± 0.07	-	-	-	0.22	4777.72
M2	0.19 ± 0.08	-	0.05 ± 0.05	-	0.19	4778.86
M3	0.18 ± 0.08	0.05 ± 0.04	-	-	0.20	4778.57
M4	0.21 ± 0.08	0.06 ± 0.04	-	-0.25	0.19	4780.36
M5	0.18 ± 0.08	0.03 ± 0.05	0.02 ± 0.05	–	0.19	4780.41
M6	0.20 ± 0.08	0.05 ± 0.05	0.02 ± 0.05	-0.27	0.18	4782.21
YW						
M1	0.26 ± 0.09	-	-	-	0.26	3662.52
M2	0.24 ± 0.09	-	0.08 ± 0.07	-	0.24	3662.94
M3	0.21 ± 0.10	0.07 ± 0.05	-	-	0.24	3663.19
M4	0.24 ± 0.10	0.09 ± 0.05	-	-0.22	0.23	3665.09
M5	0.22 ± 0.10	0.03 ± 0.07	0.06 ± 0.08	-	0.24	3664.69
M6	0.24 ± 0.10	0.05 ± 0.07	0.06 ± 0.08	-0.22	0.23	3666.64

[a] h^2 - direct heritability; m^2 - maternal heritability; c^2 - maternal permanent environmental variance as proportion of phenotypic variance; r_{am} - direct-maternal genetic correlation; h_t^2 - total heritability

[b] AIC, Akaike's information criterion

of maternal genetic effects in the model (Model 3), led to a greater decrease in direct heritability than when maternal permanent environmental effects were in the model (Model 2). Hence, the maternal genetic influence of the dam was determined to be the most important maternal effect. At birth, maternal heritability (m^2) was greater than direct heritability (0.12 vs 0.11, Model 5), diminished to 0.02 for weaning weight (Model 4). Likewise, the importance of maternal permanent environmental effects (c^2) decreased with age at weighing. Fitting the direct-maternal genetic covariance in the models (Models 4 and 6, respectively) resulted to negative estimates of direct-maternal genetic correlation (r_{am}) for BW and positive estimates for WW. For W9 and YW, although maternal effects were present, but as clearly demonstrated by AIC values, those effects did not significantly increase the likelihood over that for a simple animal model. On the other hand, sampling errors of direct heritability increased when maternal effects were estimated for W9 and YW. These effects, therefore, should not be included if they have no significant influence on the interested trait.

DISCUSSION

Numerous studies have investigated the importance of maternal effects for various mammalian species. For livestock species such as sheep, where there is variation in litter size and suckling period is substantial, maternal effects would be more important than for cattle or swine (Bradford, 1972). As AIC values clearly indicate, maternal effects are important for BW and WW. For W9 and YW maternal effects did not disappear completely, although they were not significant. This may be due to carry-over effects from weaning weight. Such carry-over of maternal effects beyond weaning are biologically sensible; particularly when lamb growth to weaning is restricted by low dam milk production either due to high litter size or seasonal constraints on feed (Bradford, 1972; Snyman et al., 1995).

In the absence of maternal effects, estimates of heritability were 0.33, 0.16, 0.22 and 0.26 for BW, WW, W9 and YW, respectively. This shows that in case of body weight the genetic control diminishes with age. Dobek et al. (2004) reported similar findings. The general paucity of literature on the subject of estimates of heritability for models including or not including maternal effects in sheep over a similar range of ages makes comparisons difficult. Bosso et al. (2007) studied the growth traits in Djallonke sheep and with analyses not including maternal effects reported heritability estimates of 0.50, 0.43 and 0.30 for body weight at birth, 120 and 360 days of age, respectively. In addition, while a study by Dobek et al. (2004), also ignoring maternal effects, resulted in heritability estimates of 0.31 and 0.28 for birth weight and body weight at four weeks of age for a population of pure and crossbreeding lambs, Szwaczkowski et al. (2006) who worked on the population studied by Dobek et al. (2004), of course with a larger data set, for analyses that contained maternal effects, reported direct heritability estimates of 0.21 and 0.22 for body weight at similar ages. Moreover, Bahreini-Behzadi et al. (2007) studied the importance of direct and maternal effects on body weight at different ages of Kermani sheep and with a model not including maternal effects reported heritability estimates of 0.62, 0.59, 0.66, 0.41 and 0.27 for birth weigh, weaning weight, 6-month weight, 9-month weight and yearling weight, respectively; while when maternal effects were considered, those estimates reduced to 0.10, 0.22, 0.09, 0.13 and 0.14, respectively. These reports provide evidence that disregarding maternal effects when they are actually present will cause to an upward bias in estimates of direct heritability because estimated additive genetic variance will capture at least part of the maternal variation.

When maternal effects are included in the analyses and so that maternal components of variance can be separated from the direct component, a new parameter which has been called "direct heritability" can be extracted. In that case direct heritability increased with age. All else being equal, maternal effects will change the general pattern of body weight's heritability with age when they allowed being presence in the analyses.

The genetic basis to maternal effects has been frequently estimated in domestic species (see e.g., Meyer, 1997; Van Vleck et al., 2003; Szwaczkowski et al., 2006).

Maternal genetic effects arise from allelic differences between individual mothers at loci influencing offspring phenotype, and are themselves a heritable component of phenotypic variance (Wolf et al., 1998). Maternal heritability was highest at birth and comparable with direct heritability, but decreased with age and for W9 and YW was small in comparison with direct heritability. With respect to the magnitude of maternal heritability, Miraei-Ashtiani et al. (2007) reported a surprisingly greater estimate of m^2 for birth weight (0.65) compared with the estimates for weaning weight (0.08) and body weight at 6 months of age (0.11). In the current study, the low estimate of maternal heritability for WW may be due to pre-weaning feed conditions. Lambs receiving limited supplies of ewe's milk may be encouraged to start eating creep feed earlier. In such a situation, the importance of milk yield of dams would decrease more rapidly when lambs were offered a high quality pasture (in the spring) or grass hay and concentrate (in the winter). This presumably would lead to a smaller estimate of maternal heritability at weaning.

Where maternal genetic effects are present, the potential response to selection might better be expressed by "total heritability" (h_t^2) defined as the ratio of the sum ($\sigma_a^2 + 0.5\sigma_m^2 + 1.5\sigma_{a,m}$) to phenotypic variance (Willham, 1972). Since maternal genetic effects are heritable, the h_t^2 of weight may be somewhat higher than the estimates of direct heritability reported, unless the direct-maternal genetic covariance is large and negative. Total heritability has the intuitive interpretation of describing total potential response to selection, replacing direct heritability when maternal genetic effects are present (Wilson et al., 2005). Presence of maternal genetic variance would increase the total heritability and hence the potential response to selection. Therefore, as a result, phenotypic response to selection may be accelerated by maternal genetic effects, but can also be dampened, if there is negative covariance between direct and maternal genetic effects (Wolf et al., 1998). At a mechanistic level such a negative covariance might occur through pleiotropy, for example if a gene has a positive effect on an offspring trait but a negative effect on maternal performance for that trait (Wilson et al., 2005).

Estimates of maternal breeding values, as an indication of maternal performance, averaged by year of birth for BW and WW are shown in Figure 1. For both BW and WW, means of estimates of maternal breeding value by year of birth decreased over time. Young and Legates (1965) and Legates (1972) reported that if the correlation between direct and maternal genetic effects is negative, maternal performance may decline under continuous selection for growth to the extent that pre-weaning viability and growth may be retarded. Such retardation, if extreme, would not likely be offset by compensatory growth during a later period despite the presence of genes for rapid growth. From a genetic analysis on growth traits of beef cattle, Vesely and Robison (1971) showed that selection effectiveness for body weight at 205 days was reduced by approximately 20% due

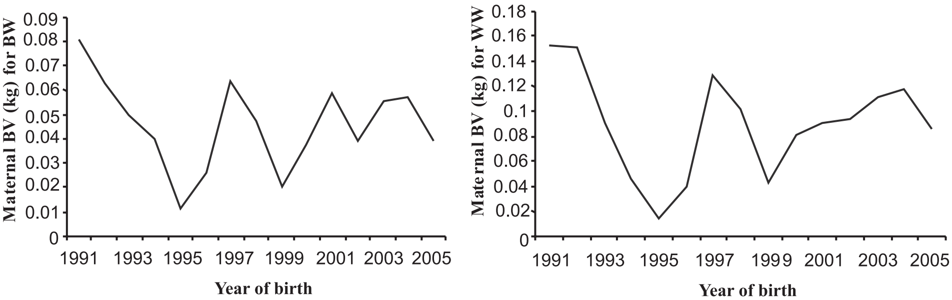

Figure 1. Maternal genetic trends for birth weight (BW) and weaning weight (WW)

to the negative r_{am}. For WW, because maternal genetic variance is low, the strong positive correlation (+0.99) between direct and maternal genetic effects must be an overestimate, makes interpretation difficult.

When the genetic correlation between growth and maternal performance is strongly negative, other breeding methods might be more desirable for overcoming the genetic antagonism between the two traits. With a large negative covariance, selection for maternal performance in one line and for growth in a second with eventual crossing has been suggested in such situations, although its applicability depends upon the nature of the action of the genes influencing the traits and the reproductive pattern of the species (Young and Legates, 1965). On the other hand, a negative correlation between direct and maternal genetic effects indicates that individuals will be ranked differently when the maternal contribution is omitted in the selection procedure (Szwaczkowski et al., 2006). Therefore, knowledge of the relationship between growth and postnatal maternal performance is most important for an accurate interpretation of selection response and in devising breeding programs for traits affected by maternal influences.

Maternal permanent environmental component was more important for BW than other weights. The permanent environmental effect of the dam on birth weight is mainly determined by uterine capacity, feeding level at late gestation and the maternal behaviour of the dam. Estimation of c^2 is necessary to obtain accurate estimates of m^2. Snyman et al. (1995) and Ekiz (2004) indicated that the exclusion of the maternal permanent environmental effects could cause maternal heritability to be overestimated.

CONCLUSIONS

Maternal effects play an important role in the early growth of Zandi lambs. Those effects diminish after weaning, when the influence of genes of the lamb increases, but due to carry-over effects, some maternal variation might persist in the post-weaning growth period. Due to the fact that significant variation in body weight, particularly before weaning, arise from maternal effects and possibly a negative correlation between direct and maternal genetic effects, genetic evaluation should be based on a model including maternal effects. It would seem that an index using estimated breeding values of all traits weighed by their net economic values is needed. For example, increased lambing difficulty associated with greater BW might lead to negative economic values for both direct and maternal genetic values. Birth weight by itself has no direct economic value. Its value comes indirectly from lambing difficulty and/or survival. Finally, the difference in estimates of genetic parameters determined in different models shows that model choice is an important aspect for obtaining accurate estimates of breeding values that are going to be used when deciding on a breeding program.

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REFERENCES

Akaike K., 1977. On entropy maximization principle. In: P.R. Krishnaiah (Editor). Applications of Statistics. North-Holand Publishing Co., Amsterdam (The Netherlands), p. 27

Atkins K.D., 1986. A genetic analysis of the components of lifetime productivity in Scottish Blackface sheep. Anim. Prod. 43, 405-419

Bahreini-Behzadi M.R., Shahroudi F.E., Van Vleck L.D., 2007. Estimates of genetic parameters for growth traits in Kermani sheep. J. Anim. Breed. Genet. 124, 297-306

Bosso N.A., Cisse M.F., Van der Waaje E.H., Fall A., Van Arendonk J.A.M., 2007. Genetic and phenotypic parameters of body weight in West African Dwarf goat and Djallonke sheep. Small Ruminant Res. 67, 271-278

Bradford G.E., 1972. The role of maternal effects in animal breeding: VII. Maternal effects in sheep. J. Anim. Sci. 35, 1324-1334

Dobek A., Wojtowski J., Szwaczkowski T., Molinski K., Gut A., 2004. Genetic variability for birth and fourth week weights in sheep. Arch. Tierzucht 47, 64-72

Ekiz B., 2004. Estimates of genetic parameters for direct and maternal effects with six different models on birth and weaning weight of Turkish Merino lambs. Turk. J. Vet. Anim. Sci. 28, 383-389

Legates J.E., 1972. The role of maternal effects in animal breeding: IV. Maternal effects in laboratory species. J. Anim. Sci. 35, 1294-1302

Maniatis N., Pollott G.E., 2003. The impact of data structure on genetic (co)variance components of early growth in sheep, estimated using an animal model with maternal effects. J. Anim. Sci. 81, 101-108

Meyer K., 1997. Estimates of genetic parameters for weaning weight of beef cattle accounting for direct-maternal environmental covariances. Livest. Prod. Sci. 52, 187-199

Meyer K., 2001. Programs to Estimate Variance Components for Individual Animal Models by Restricted Maximum Likelihood (REML). Ver .3.1. Users Notes. Institute of Animal Science, Armidale (Australia)

Miraei-Ashtiani S.R., Seyedalian S.A.R., Moradi Shahrbabak M., 2007. Variance components and heritabilities for body weight traits in Sangsari sheep, using univariate and multivariate animal models. Small Ruminant Res. 67, 271-278

SAS, 2004. Version 9.0. SAS Institute Inc. Cary, NC

Snyman M.A., Erasmus G.J., Van Wyk J.B., Olivier J.J., 1995. Direct and maternal (co)variance components and heritability estimates for body weight at different ages and fleece traits in Afrino sheep. Livest. Prod. Sci. 44, 229-235

Szwaczkowski T., Wojtowski J., Stanislawska E., Gut A., 2006. Estimates of maternal genetic and permanent environmental effects in sheep. Arch. Tierzucht 49, 186-192

Van Vleck L.D., Snowder G.D., Hanford K.J., 2003. Models with cytoplasmic effects for birth, weaning, and fleece weights, and litter size at birth for a population of Targhee sheep. J. Anim. Sci. 81, 61-67

Vesely J.A., Robison O.W., 1971. Conventional selection indexes for birth and weaning traits in beef cattle. J. Anim. Sci. 33, 537-540

Willham R.L., 1972. The role of maternal effects in animal breeding: III. Biometrical aspects of maternal effects in animals. J. Anim. Sci. 72, 1184-1190

Willham R.L., 1980. Problems in estimating maternal effects. Livest. Prod. Sci. 7, 405-418

Wilson A.J., Coltman D.W., Pemberton J.M., Overall A.D.J., Byrne K.A., Kruuk L.E.B., 2005. Maternal genetic effects set the potential for evolution in a free-living vertebrate population. J. Evolution. Biol. 18, 405-414

Wolf J.B., Brodie E.D., Cheverud J.M., Moore A.J., Wade M.J., 1998. Evolutionary consequences of indirect genetic effects. Trends Ecol. Evolut. 13, 64-69

Young C.W., Legates J.E., 1965. Genetic, phenotypic and maternal interrelationships of growth in mice. Genetics 52, 563-576