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Research Article

Effects of Embryo-Transfer, Recipient-Donor Mother and Environment on Lamb Weaning Weight and Variance Components

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Abstract: Factors affecting lamb weaning weight (WW) and the (co)variance components due to direct and maternal effects on weight were investigated using a small data set based on ewes involved in an embryo transfer trial. Records of 253 Welsh Mountain lambs for adjusted 50 day weaning weight were obtained from the nucleus flock of the CAMDA co-operative breeding scheme. DFREML was used for variance component analyses. Significant fixed effects included in the model were rearing dam age, sex, rearing type and year. Six different models were used to analyse variance components. Obtained h^2 walues from the models were 0.104, 0.034, 0.057, 0.044, 0.035 and 0.485 respectively. The main value of these data sets based on embryo transfer data is their emphasis on a large number of progeny from genetic dams. However, there are potential disadvantages associated with the small size of the data set and limited information on rearing dams. The results highlight the importance of rearing dams and suggest that the use of high quality dams as donors and low quality dams as recipients may not yield a practical system if good growth into weaning is desired.

Key Words: Lamb, embryo transfer, maternal effect, variance components, weaning weight

Embriyo Transferinin, Donor-Taşıyıcı Anaların ve Çevresel Faktörlerin Kuzularda Sütten Kesim Ağırlığına Etkileri ve Variyans Unsurları

Özet: Welsh Mountain kuzularının sütten kesim ağırlığına etki eden faktörler, (çevresel ve genetik) ve variyans unsurları araştırılmıştır. Bu amaçla doğal ve embriyo transferiyle elde edilen kuzular kullanılmıştır. Bunun yanında taşıyıcı anaların da doğan kuzular üzerine bir etkisi olup olmadığı doğal aşımla elde edilen kuzularla karşılaştırılarak incelenmiştir. Bu araştırmada 253 kuzunun düzeltilmiş 50. gün ağırlıkları kullanılmıştır. Kuzular CAMDA adındaki çiftçi derneğinden sağlanmış, variyans unsurlarının analizi için DFREML bilgisayar programından faydalanılmıştır. Taşıyıcı ananın yaşı, cinsiyet, doğum tipi ve yıl faktör olarak modellere dahil edilmişlerdir. Eldeki veriler, damızlık anaların normal yollarla elde edilemeyecek kadar çok sayıdaki yavrusunun embriyo transferi yoluyla bir defada değerlendirilmesi açısından önemlidir. Varyans analizleri için 6 değişik model kullanılmıştır. Modellerden elde edilen h^2 değeri sırasıyla 0.104, 0.034, 0.057, 0.044, 0.035, ve 0.485 olarak bulunmuştur. Analizlerin sonucuna göre, doğal olarak ve embriyo transferi yoluyla elde edilen kuzuların 50. gün ağırlıklarında istatistiksel bir fark bulunmamıştır (P>0.05). Diğer bir sonuç ise; genetik yönden kaliteli bir donordan alınan embriyo kalitesiz bir taşıyıcıya nakledilirse doğan kuzu, genetik yapısının gereği olan gelişmeyi sütten kesim süresine kadar gösteremeyebilir. Başka bir deyişle taşıyıcı ana bu gelişmeyi yavaşlatabilir.

Anahtar Sözcükler: Kuzu, embriyo transferi, analık etkisi, variyans unsurları, sütten kesim ağırlığı

Introduction

Estimates of genetic and environmental components of variance and their ratios form an essential part of animal breeding. The problem of maternal effects has been associated with animal breeding since domestication (1). The term “maternal effect” indicates an influence of the dam on its offspring other than through the genes transmitted to it. The genotype of the dam therefore affects the phenotype of the young through a sample of her direct, additive genes for growth as well as through her genotype for maternal effects on growth (2,3). Variation between females in maternal performance may arise from either genetic or environmental causes. Maternal effects are important in sheep because of the dependence of lambs on their mother`s milk until the time of marketing or weaning (4). It also was noted that maternal effects in animals have been studied extensively both because of their economic importance and because of their theoretical interest (5).

In this study, factors affecting lamb weaning weight (WW) and the (co) variance components due to direct and maternal effects on weight were investigated using a small data set based on ewes involved in an embryo transfer trial. Potentially, analysing embryo transfer data provides an opportunity to look at more data on genetic progeny than would be possible with natural mating and provides greater numbers of progeny to evaluate maternal genetic effects.

Material and Methods

Source of animals and data

Lambs were obtained from the nucleus flock of a Welsh mountain breeder (CAMDA). Weaning weights (WW) of lambs at approximately 50 days of age were recorded and weights adjusted for the effects of age. CAMDA used embryo-transfer for some of its animals in 1994. Records for all progeny of ewes used either as embryo donors or recipients in 1994 were abstracted from available records for these ewes in the period 1989-1994. All available records were included to provide as much information as possible on these ewes, and particularly to obtain more than one record per recording dam.

Records for 235 lambs are shown in Table 1.

Table 1. The numbers of animals (n) by rearing type, year, rearing dam age, genetic dam age, natural born-embryo transfer and sex groups.

Distribution of Animals in the Data set		
Rearing Type		
Single	1	118
Twin	2	117
Year		
	1989	14
	1990	38
	1991	37
	1992	40
	1993	35
	1994	71
Rearing Dam Age		
	2	48
	3	37
	4	39
	5	111
Genetic Dam Age		
	2	48
	3	51
	4	87
	5	49
Natural or Embryo-Transfer		
Embryo-Transfer	1	60
Natural	2	175
Sex		
Male	1	83
Female	2	152
Total		235

Thirty-eight sires, 61 genetic dams and 60 rearing dams were represented in the dataset. Genetic dams were the same as the rearing dams in years other than 1994. Information available for each lamb was as follows: sire number, genetic and rearing dam number, genetic and rearing dam age (2-5+), rearing type (single, twin), year of birth (1989-94), whether the lamb was produced by embryo-transfer, sex and adjusted weaning weight (to 50 days of age). The number of animals by year, dam ages, rearing type, years, sex and natural or embryo-transfer are given in Table 1. Dam ages greater than 5 were converted to 5 before analysis.

Statistical analyses

Preliminary analysis of lamb weight was conducted using a general linear model in the SAS statistical package (6). Initially a fixed effect indicating the type of lambs (embryo transfer or natural) was included in the analysis but this was not significant (P= 0.639). It was therefore excluded from subsequent analyses. The following model was used:

$$Y_{ijklm} = m+a_i+b_j+c_k+d_l+e_{ijklm} \qquad [i]$$

where Y_{ijkl} is the observation of lamb adjusted weaning weight,

μ is the overall mean,

a_i is the effect of rearing dam age (i=2-5),

b_j is the effect of lamb sex (j=1 (male); 2 (female)),

c_k is the effect of rearing type (k=1(single); 2 (twin)),

d_l is the effect of year (l=89-94),

e_{ijklm} is random error.

Variance components

Variance components were estimated by DFREML (7) for adjusted WW. Maternal genetic or permanent environmental effects were taken into account by including appropriate random effects in the model (8). Allowing for, and ignoring, genetic covariances between direct and maternal effects yielded up to six different analyses for the trait (2). Fixed effects included in the model were rearing dam age, sex, rearing type and year. These had been identified as significant factors in the preliminary analysis.

Model 1 was an animal model with animals` additive genetic effects as the only random factor.

$Y_{ijklmn}=F_{ijkl}+a_m+e_{ijklmn}$ [I]

Model 2 included the permanent environmental effect due to the dam, fitting this as an additional random effect, uncorrelated with all other effects in the model.

$Y_{ijklmon}=F_{ijkl}+a_m+P_o+e_{ijklmon}$ [II]

Model 3 included maternal effects but assigned to the genotype of dam, fitting the maternal genetic effect as a second random effect for each animal with the same covariance structure as the direct additive genetic effects.

$Y_{ijklmon}=F_{ijkl}+a_m+m_o+e_{ijklmon}$ [III]

with $\sigma_{AM}A=0$

Model 4 was as same as Model 3 but it allowed for a covariance between direct and maternal effects.

$Y_{ijklmon}=Fijkl+a_m+mo_o+e_{ijklmon}$ [IV]

with $\sigma_{AM}A\neq0$

Model 5 and 6 included both a permanent environmental and genetic maternal effect, but did not allow a for genetic correlation between the direct and maternal genetic effects.

$Y_{ijklmon}=F_{ijkl}+a_m+m_o+p_o+e_{ijklmon}$ [V]

with $\sigma_{AM}A=0$

Model 6 included both a permanent environmental and genetic maternal effect and a genetic correlation between direct and maternal genetic effects.

$Y_{ijklmon}=F_{ijkl}+a_m+m_o+p_o+e_{ijklmon}$ [VI]

with $\sigma_{AM}A\neq0$

where,

$Y_{ijklmon}$: The adjusted weight with dam and fix effect combination.

a_n: The direct additive genetic effect,

m_o: The maternal additive genetic effect,

p_o: The permanent environmental effect due to the dam,

$e_{ijklmon}$: Random error.

F_{ijkl};

da_i is the dam age effect,

s_j is the sex effect,

rt_k is the rearing type effect,

y_l is the year effect.

Phenotypic variance (σ^2_P), direct additive genetic variance (σ^2_A), maternal additive genetic variance (σ^2_M), maternal environmental variance (σ^2_C), direct-maternal genetic covariance (σ_{AM}) and direct-maternal genetic correlation (r_{AM}) were estimated. The direct heritability (h^2), the maternal heritability (m^2), the permanent environmental variance due to the dam as a proportion of phenotypic variance (c^2), the genetic covariance between direct and maternal effects as a proportion of the total variance (c_{AM}) and the error variance (σ^2_E) were calculated. Total heritability (h^2_T) was calculated as $\sigma^2_T=(\sigma^2_A+0.5\sigma^2_M+1.5\sigma_{AM})/\sigma^2_P$ (5). Log likelihood (log L) was calculated for every model (2).

Results

Description of available data and results

Mean weight was 23.0 kg with a standard deviation of 3.87 kg. The lowest and highest records for the trait were 12.8 and 32.7 kg. The coefficient of variation was 17.2%. Sex, rearing type and year significantly affected 50 day weaning weight ($P< 0.05$). Rearing dam age did not significantly affect weight ($P=0.07$). Mean weight in 1989 was significantly ($P< 0.05$) higher than in 1990 and 1994 but not other years. Mean weight in 1992 was lower than in 1989, 1991 and 1993. Male lambs were heavier than female lambs and singles were heavier than twins by 3.5 kg.

Estimation of variance components

Results of (co)variance components and genetic parameters for weight together are presented in Table 2.

Table 2. Estimates of (co)variance components and genetic parameters for adjusted WW of Welsh mountain lambs (calculated standard errors are in parentheses).

	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
σ^2_A	0.922	0.289	0.489	0.366	0.295	4.062
σ^2_M			0.231	0.087	0.432	2.716
σ_{AM}				0.177		-3.322
σ^2_C		1.009			0.575	0.001
σ^2_E	7.365	7.470	8.091	8.186	7.509	4.914
σ^2_P	9.764	8.769	8.811	8.819	8.811	8.371
h^2	0.104	0.034	0.057	0.044	0.035	0.485
	(0.043)	(0.048)	(0.053)	(0.075)	(0.056)	(0.101)
m^2			0.025	0.010	0.048	0.324
			(0.027)	(0.055)	(0.031)	(0.049)
C_{AM}				0.021		-0.396
				(0.026)		(0.37)
r_{AM}				0.990		-1.000
C^2		0.115			0.065	0.001
		(0.025)			(0.034)	(0.036)
h^2_T	0.104	0.033	0.068	0.076	0.058	0.052
logL	0	-2	-1302	-1302	-1300	-1297

σ^2_A = direct additive genetic variance; σ^2_M = maternal additive genetic variance; σ_{AM} = genetic covariance between direct and maternal effect; $\sigma^{2}{}_{C}$ = maternal environmental variance; σ^2_E = error variance; σ^2_P = phenotypic variance; h^2 = direct heritability; m^2 = maternal heritability; C_{AM} = genetic covariance between direct and maternal effects as a proportion; σ_{AM} / σ^2_P; r_{AM} = direct-maternal genetic correlation; C^2 = the permanent environmental variance due to the dam as a proportion of the phenotypic variance; σ^2_C / σ^2_P; h^2_T = total heritability; logL = log likelihood

The h^2 and m^2 estimates were higher in Model 6 than in the other models. Only Model 6 had a negative estimate for genetic covariance between direct-maternal effects (σ_{AM}), genetic covariance between direct and maternal effects as proportion of σ_{AM}/σ^2_P (c_{AM}) and the direct-maternal genetic correlation (r_{AM}).

Model 1 had greater σ^2_A and h^2 vaulues than the other models (expect Model 6). Fitting a permanent environmental effect (Model 2) decreased the values of σ^2_A and h^2. σ^2_M was included in Model 3 and this model produced h^2 and σ^2_A values higher than Model 2. Allowing for σ_{AM}, c_{AM} and r_{AM} (Model 4) reduced the estimates of h^2 and m^2. Model 5 was similar with Model 2 as difference σ^2_M and m^2 values were estimated. While h^2 was lower, m^2 was higher than in model 4. Model 1 and 2 gave higher LogL values than others. The logL of the other four models were very similar (Table 2).

Discussion

Factors affecting WW

Sex, rearing type and year affected ($P<0.05$) weight but lamb type (natural or embryo transfer) did not affect weight significantly ($P=0.627$). Rearing dam age did not affect ($P>0.05$) weight but weight tended to increase with dam age. The effects of these factors on weight were also reported for Hyfer sheep by Fogarty et al. (9) and for Dorset Down by Nsoso et al. (10) and Nsoso et al. (11). An effect of rearing type and dam age on liveweight was noted by Atkins et al. (12) and by Gilmour et al. (13).

(Co)variance components

In estimating (Co)variance components, the choice of the appropriate model to examine traits, composed of both a direct and a maternal effect, is critical (5). Six models were used to analyse weaning weight in this study. The estimates of h^2, m^2 and c^2 from all models were generally low. These low results suggest that a considerable proportion of variance in weight is unaccounted for in these analyses. Unknown management factors may have caused this, for example different grazing areas. Although Model 6 produced a greater h^2 values than other models, the results of Models 3, 4, 5 and 6 were ignored because of low log-l values.

Oliver et al. (14) reported (co)variance components for the Grootfontein Merino stud. Their estimates were higher than those obtained in this study. Maria et al. (15) evaluated maternal and direct effects on birth weight, weaning weight and 90 day weight of Romanov sheep. All the reported values of genetic parameters and (co)variance components were greater than those estimated here.

Models 1 and 2 gave comparable log-L values, but Model 2 is more sensible, given the structure of the data set and the well known role of maternal permanent environmental effects. C^2 values were greater than h^2 values clearly highlighting the importance of dam permanent environmental effects and, in the context of embryo-transfer, the possible input of the recipient dam on lamb growth to 50 days. Model 1 had higher σ_A^2 and h^2 values than Model 2 but C^2 was not estimated in model 1, and this might have caused the higher estimated values for σ_A^2 and h^2.

The main value of these data sets based on embryo transfer data is their emphasis on a large number of progeny from genetic dams. It is expected that these data sets would give more accurate estimates of genetic maternal effects than other parameters.

The results suggest that care is needed in the choice of recipients, and selected ewes should be high quality dams. To use high quality dams as donors and low quality dams as recipients may not yield a practical system if early growth is desired. In this situation, the growth of high genetic merit animals could be restricted by the maternal permanent effects of low quality rearing dams.

This study was conducted with a very restricted data set, yielding low estimates for genetic parameters. However, the analysis has highlighted the considerable importance of maternal permanent environmental effects. Increasing use of embryo transfer in sheep flocks will allow comparable analyses with larger data sets.

However, the estimate of m^2 was negligible despite the well known effect of genetic maternal influences. Caution is therefore needed in the use of embryo transfer data since the benefits associated with increase in progeny per dam may be criticised due to low total numbers of data and low number of genetic dams and sires. The weakness in the estimates of genetic parameters would also result in poor estimates of breeding values.

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