Estimates of genetic parameters for direct and maternal genetic effects on weaning weights in Dairymeade sheep

N Lopez-Villalobos[a*], M King[b], J King[b] and RS Morris[a]

[a]Institute of Veterinary, Animal and Biomedical Sciences, Massey University, Palmerston North, New Zealand.
[b]Kingsmeade Farm, Olivers Rd, RD6, Masterton, New Zealand.

[*]Corresponding author. Email: N.Lopez-Villalobos@massey.ac.nz

Abstract

Dairymeade is a newly registered breed of dairy sheep in the emerging New Zealand dairy sheep industry. The objective of this study was to estimate heritabilities and genetic correlations for direct and maternal genetic effects on weaning weight, as this trait reflects the genetic ability of the lamb to grow (direct genetic effect), and the genetic ability of the ewe to feed her lambs (maternal genetic effect) and protect them (maternal permanent environment). Records of weaning weight were used from 717 lambs born between 2013 and 2016, with a pedigree of 5091 animals over 11 generations. Average and standard deviation of weaning weight, age at weaning and litter size were 18.1±4.0 kg, 51.5±13.0 days and 2.16±0.7 lambs, respectively. At weaning, ewe lambs were 1.1 kg (SE=0.2 kg, P<0.05) lighter than ram lambs and singleton lambs were 4.1 kg (SE=2.9 kg, P<0.05) heavier than triplet lambs. Estimates of heritability (±SE) were 0.55 (±0.24), 0.24 (±0.17) and 0.28 (±0.13) for direct, maternal and total genetic effects, respectively. The proportion of total variance explained by maternal permanent environmental influences was 0.14 (±0.07). The estimated genetic correlation between direct and maternal genetic effects was –0.72 (±0.20). Maternal breeding values can be used to select ewe lambs specifically for milk production.

Keywords: dairy sheep; weaning weight; heritability; genetic correlation; maternal effect

Introduction

Dairymeade is a newly registered breed of dairy sheep in the emerging New Zealand dairy sheep industry. The breed was established in 1996, initially using Coopworth and Border Leicester dams and European East Friesian sires, with subsequent infusion since then only of East Friesian bloodlines. Selective breeding for milk yield, dairy conformation and prolificacy has been undertaken continuously for 20 years, with maintenance of complete pedigrees throughout.

Early growth is important for the profitability of meat, dairy and dual-purpose (milk and meat) sheep-production systems. The growth rate of a lamb until weaning reflects the genetic ability of the lamb to grow (direct genetic effect), and the genetic ability of the ewe to feed her lambs (maternal genetic effect) and protect them (maternal permanent environment) (Willham 1972). There are many studies in most of the farmed mammals on how the variation in direct and maternal effect influences growth of beef calves (Meyer et al. 1994; MacNeil & Mott 2006), pigs (Mondal et al. 2014), goat for meat (Shaat & Mäki-Tanila 2009) and sheep for meat or wool (Tosh &Kemp 1994; Näsholm & Danell 1996; Mondal et al. 2006). The estimates of genetic correlation between direct and maternal effects for weaning weight are often negative indicating that selection for weaning weight would negatively affect milk production when the animal becomes a mother. The cause of the relatively high negative correlation between direct maternal effects is not clear and explanations have been reviewed by Lee (2001) and David et al. (2015). Estimates of the direct-maternal genetic correlation in dairy sheep has been reported low and negative for milk yield (Kominakis et al. 1998), but no estimates for growth traits were found in the literature.

Lamb growth and ewe milk production are correlated during early lactation in non-dairy sheep (Snowder & Glimp 1991; Danso et al. 2016) and therefore weaning weight of lambs can be used as indicators of milk production by the ewe. This relationship may not exist in specialised breeds of dairy sheep, for example, Morrissey et al. (2007) reported that in East Friesian crossbred ewes, the growth rate of the lamb explained almost none of the variability in 120 d milk yield of the ewe, which suggests that lamb growth cannot be used to identify high yielding ewes. McKusick et al. (2001) and Morrissey et al. (2007) suggested that this low relationship is due to the fact that dairy ewes produce quantities of milk in excess of the requirements of the lamb.

Another way to identify high yielding ewes is using the genetic relationship between maternal genetic effects for lamb weaning weight and ewe milk production. This genetic correlation has been estimated to be greater than 0.76 in beef cattle (Meyer et al. 1994; Miller & Wilton 1999) and fine-wool sheep (Snyman et al. 2016), which provides strong evidence to consider breeding value for maternal weaning weight as an accurate indicator of breeding value for milk production (MacNeil & Mott 2006). The objective of this study was to estimate heritabilities and genetic correlations for direct and maternal genetic effects on weaning weight of Dairymeade lambs that can be used for future milk production.

Materials and methods

Records of weaning weight were used from 717 lambs born between 2013 and 2016, with a pedigree of 5091 animals over 11 generations, representing 1077 sires, 36 maternal grandsires and 462 paternal grandsires. Most sires were home bred but some outside sires were introduced. Information available was animal, sire and

dam identification, birth date, weaning date, sex of lamb and size of the litter in which the lamb was born and reared.

Lambing occurred each year largely during August and September, and for the first four weeks or to at least 13.5 kg body weight, lambs suckled on ewes for 12 hours, and were fed separately for 12 hours prior to milking of ewes. Lambs were then weaned, and ewes used entirely for milk production for the remainder of the lactation. Ewes were grazed continuously on irrigated pastures. Milk is used for the production of specialty sheep cheeses.

Statistical analysis

Variance components were obtained using ASReml version 3 (Gilmour et al. 2009) with a linear mixed model that included fixed effects of year of birth, dam age, lamb sex, litter size at birth and lamb age at weaning as covariable with linear effect and the random effects for direct genetic, maternal genetic, covariance direct-maternal genetic and maternal environmental influences.

Variance components for direct genetic (σ_d^2), maternal genetic (σ_m^2), maternal permanent environment (σ_c^2), covariance direct-maternal genetic (σ_{dm}) and residual (σ_e^2) effects for lamb weaning weight were used to estimate the direct ($h_d^2 = \sigma_d^2 / \sigma_p^2$), maternal ($h_m^2 = \sigma_m^2 / \sigma_p^2$) and total heritability ($h^2 = (\sigma_d^2 + 0.5\sigma_m^2 + 1.5\sigma_{dm}) / \sigma_p^2$) and the genetic correlation between direct and maternal genetic effect for lamb weaning weight ($r_{dm} = \sigma_{dm} / (\sigma_d\sigma_m)$), where σ_p^2 is the phenotypic variance ($\sigma_p^2 = \sigma_d^2 + \sigma_m^2 + \sigma_{dm} + \sigma_c^2 + \sigma_e^2$).

Results

Average and standard deviation of birth date, weaning weight, age at weaning and litter size are presented in Table 1 and least squares means for fixed effects influencing weaning weight are presented in Table 2. Average weaning weight was 18.1 kg at an average age at weaning of 51.5 days. Average litter size at birth was 2.16 lambs. At weaning, ewe lambs were 1.1 kg (P<0.05) lighter than ram lambs and singleton lambs were 2.1 kg heavier (P<0.05) than twin lambs. Age of dam had a significant effect (P<0.01) on weaning weight of lambs with a quadratic effect, lamb weaning weight increased linearly as dam age increased from 2 to 4 years and remained stable after this dam age.

Estimates of variance components and genetic parameters for weaning weight are presented in Table 3. Estimates of heritability were 0.55, 0.24 and 0.28 for direct, maternal and total genetic effects, respectively. The proportion of total variance explained by maternal permanent environmental influences was 0.14. The estimated genetic correlation between direct and maternal genetic effects was –0.72.

Table 1 Descriptive statistics for variables related to weaning in Dairymeade sheep

Trait	N	Mean	SD	Min	Max
Birth weight (kg)	710	4.53	1.03	1.75	8.03
Weaning weight (kg)	717	18.09	4.04	7.50	39.60
Age at weaning (kg)	717	51.52	12.96	23.00	129.00
Litter size	717	2.16	0.67	1.00	4.00

Table 2 Effect of sex, litter size and age at weaning on weaning weight in Dairymeade sheep

Effect	N	Mean (kg)	SEM
Sex			
Male	358	18.0[a]	0.31
Female	357	16.9[b]	0.30
Litter size			
1	99	20.6[a]	0.60
2	411	18.5[b]	0.51
3	196	16.7[c]	0.55
4	11	14.7[c]	1.13
Dam age			
2	30	15.2[a]	0.75
3	51	16.9[b]	0.74
4	126	17.9[bc]	0.62
5	148	18.7[c]	0.62
6	359	18.6[c]	0.59
Age at weaning†	717	0.16**	0.009

[a,b,c]Means with different superscript, within effect, are significantly different (P<0.05).

† Measured as the regresssion coefficient of weaning weight on age at weaning.

**P<0.05.

Table 3 Estimates of variance components and genetic parameters for weaning weight in Dairymeade sheep

Effect		
Direct genetic effect (kg²)	σ_d^2	6.74
Maternal genetic effect (kg²)	σ_m^2	2.92
Covariance between direct and maternal (kg)	σ_{dm}	–3.21
Maternal permanent environment (kg²)	σ_c^2	1.70
Residual variance (kg²)	σ_e^2	4.07
Total variance (kg²)	σ_p^2	12.23
Heritability for direct genetic effect	h_d^2	0.55±0.24
Heritability for maternal genetic effect	h_m^2	0.24±0.17
Total heritability	h^2	0.28± 0.13
Genetic correlation between direct and maternal genetic effects	r_{dm}	-0.72±0.20

Discussion

This study evaluated the effects of environmental factors and provided estimates of genetic parameters for weaning weight in a new breed of dairy sheep. The weaning weight of 18.07 kg found in this study at an average weaning age of 51.5 days was similar to the average weaning at day 49 of Suffolk×Romney crossbred lambs reported by van der Linden et al. (2009).

The effect of litter size at birth and rearing on lamb growth is well documented in the literature about sheep production (Kenyon, 2008). In meat (Snowder & Glimp

1991) and wool (Yazdi et al. 1998; Safari et al. 2007) sheep, singleton lambs are heavier at birth and weaning than twin lambs because twin lambs are competing for the same maternal environment (nutrients during foetal development, and milk and maternal care from birth to weaning). The magnitude of differences in live weight generally declines after weaning (Snowder & Glimp 1991; Yazdi et al. 1998) and twin lambs can grow faster than single lambs after weaning if they are well enough fed. In specialized dairy sheep the competition for maternal milk in twin lambs can be less from birth to weaning because the ewes will be producing more milk but still the growth rate for single lambs has been reported to be greater than for twin lamb progeny of East Friesian crossbred ewes (Morrissey et al. 2007). These results agree well with the results found in this study, in which singleton lambs were heavier at weaning than twin, triplet and quadruplet lambs.

Effect of lamb sex on weaning weight has been widely reported in non-dairy sheep (Ghafouri-Kesbi & Notter 2016). Ram lambs are heavier at birth, have higher growth rates, and consequently are heavier at weaning compared to ewe lambs. The same trend has been reported in dairy sheep (Morrissey et al. 2007), Effect of dam age on lamb weaning weight has been reported to be significant with a quadratic effect in Merino (Safari et al. 2007) and dual-purpose (meat and wool) New Zealand (Pickering et al. 2012) sheep. The same trend was observed in this study.

The estimates of heritability for direct (0.55) and maternal (0.24) genetic effect for weaning weight were within the range of estimates reported by Mondal et al. (2006) in meat sheep breeds (0.07 to 0.54 for h_d^2 ; and 0.07 to 0.49 for h_m^2). The estimate of r_{dm} of -0.72 agree with the often negative values reported for growth traits of various sheep breeds (Mondal et al. 2014). These estimates suggest that selection for greater weaning weight would need to consider maternal genetic and maternal permanent environmental effects as well as the negative genetic correlation between direct and maternal effects. This topic is not new and has been reviewed in beef cattle (Lee 2001). Christian et al. (1965) indicated that selection for weaning weight in heifers could possibly result in decreased milk production and Mangus and Brinks (1971) suggested that there is a negative environmental correlation between dams and their offspring for effect on weaning weight. They postulated that it results from excess fat deposition in the mammary tissue of heifers raised by superior milking dams, which lowers their milking production potential and affects the weaning weight of their progeny (Willham 1972). This seems an unlikely explanation, and in milking sheep the negative correlation is more likely to be due to feeding patterns of individual progeny, which have to share the milk supply with commercial use of the milk but have *ad libitum* access to other feed as well.

The partitioning of additive direct, additive maternal and permanent environmental maternal effects requires data on the performance of individual ewe lambs across several generations. This means that the data set should contain the weaning weight of ewe lambs and the weaning weight of their progeny. The data set used in this study contained 11 generations of pedigree recording but with only four years of weaning weight records. This can introduce large standard errors of the estimates of the genetic parameters, as observed in this study, and estimates should be interpreted with caution.

This study found a moderate estimate of heritability for the maternal genetic effect on weaning weight and, therefore, maternal breeding values can be estimated with moderate reliability. If the correlation between maternal genetic effect of weaning weight and the direct genetic effect of milk production is high, then maternal breeding values can be used as proxy of milk breeding values, as suggested by Meyer et al. (1994) and Miller & Wilton (1999) in beef cattle. Snyman et al. (2016) reported a genetic correlation of 0.37 to 0.99 between the direct effect of total milk production and the maternal effect of weaning weight in four South African woollen sheep flocks. This high correlation indicates that selection based on the breeding value for maternal weaning weight may be an effective way to identify ewes of high genetic merit for milk production. A further study is underway to estimate this correlation as soon as breeding values for lactation yields will be produced in this new dairy sheep breed.

Acknowledgements

References

Christian LL, Hauser ER, Chapman AB 1965. Association of preweaning and postweaning traits with weaning weight in cattle. Journal of Animal Science 24: 652-659.

Danso AS, Morel PCH, Kenyon PR, Blair HT 2016 Relationships between prenatal ewe traits, milk production, and preweaning performance of twin lambs. Journal of Animal Science 94: 3527-3539.

David I, Bouvier F, Banville M, Canario L, Flatres-Grall L, Balmisse E, Garreau H 2015. The direct-maternal genetic correlation has little impact on genetic evaluations. Journal of Animal Science 93: 5639-5647.

Ghafouri-Kesbi F, Notter DR 2016. Sex influence on genetic expressions of early growth in Afshari lambs. Archives Animal Breeding 59: 9-17.

Gilmour AR, Gogel B, Cullis B, Thompson R, Butler D 2009. ASReml User Guide Release 3.0. VSN International Ltd, Hemel Hempstead, UK.

Kenyon PR 2008. A review of in-utero environmental effects on sheep production. Proceedings of the New Zealand Society of Animal Production 68: 142-155.

Kominakis A, Rogdakis E, Koutsotolis K 1998. Genetic parameters for milk yield and litter size in Boutsico dairy sheep. Canadian Journal of Animal Science 78: 525-532.

Lee C 2001. On the negative estimates of direct and maternal genetic correlation - A review. Asian-Australasian Journal of Animal Sciences 15: 1222-1226.

Mangus WL, Brinks JS 1971. Relationships between direct and maternal effects on growth in Herefords: I. Environmental factors during preweaning growth. Journal of Animal Science 32: 17-25.

MacNeil MD, Mott TB 2006. Genetic analysis of gain from birth to weaning, milk production, and udder conformation in Line 1 Hereford cattle. Journal of Animal Science 84: 1639-1645.

McKusick BC, Thomas DL, Berger YM 2001. Effect of weaning system on commercial milk production and lamb growth of East Friesian dairy sheep. Journal of Dairy Science 84: 1660-1668.

Meyer K, Carrick MJ, Donnelly BJP 1994. Genetic parameters for milk production of Australian beef cows and weaning weight of their calves. Journal of Animal Science 72: 1155-1165.

Miller SP, Wilton JW 1999. Genetic relationships among direct and maternal components of milk yield and maternal weaning gain in a multibreed beef herd. Journal of Animal Science 77: 1155-1161.

Mondal SK, Kumar A, Dubey PP, Sivamani B, Dutt T 2014. Estimation of variance and genetic parameters for pre-weaning weights of individual Landrace X Desi synthetic piglets. Journal of Applied Animal Research 42: 338-344.

Morrissey AD, Cameron AWN, Caddy DJ, Tilbrook AJ 2007. Predicting milk yield in sheep used for dairying in Australia. Journal of Dairy Science 90: 5056-5061.

Näsholm A, Danell O 1996. Genetic relationships of lamb weight, maternal ability, and mature ewe weight in Swedish finewool sheep. Journal of Animal Science 74: 329-339.

Pickering NK, Dodds KG, Blair HT, Hickson RE, Johnson PL, McEwan JC 2012. Genetic parameters for production traits in New Zealand dual-purpose sheep, with an emphasis on dagginess. Journal of Animal Science 90: 1411-1420.

Safari E, Fogarty NM, Gilmour AR, Atkins KD, Mortimer SI, Swan AA, Brien FD, Greeff JC, van der Werf JHJ 2007. Across population genetic parameters for wool, growth, and reproduction traits in Australian Merino sheep. 1. Data structure and non-genetic effects. Australian Journal of Agricultural Research 58: 169-75.

Shaat I, Mäki-Tanila A 2009. Variation in direct and maternal genetic effects for meat production traits in Egyptian Zaraibi goats. Journal of Animal Breeding and Genetics 126: 198-208.

Snowder GD, Glimp HA 1991. Influence of breed, number of suckling lambs, and stage of lactation on ewe milk production and lamb growth under range conditions. Journal of Animal Science 69: 923-930.

Snyman MA, Cloete SWP, Olivier WJ 2016. Genetic parameters for milk production of ewes in four South African woolled sheep flocks under different grazing conditions. Grootfontein Vol 16 No. 1.

Tosh JJ, Kemp RA 1994. Estimation of variance components for lamb weights in three sheep populations. Journal of Animal Science 72: 1184-1190.

van der Linden DS, Kenyon PR, Blair HT, Lopez-Villalobos N, Jenkinson CMC, Peterson SW, Mackenzie DDS 2009. Effects of ewe size and nutrition on fetal mammary gland development and lactational performance of offspring at their first lactation. Journal of Animal Science 87: 3944-3954.

Willham RL 1972. The role of maternal effects in animal breeding: III. Biometrical aspects of maternal effects in animals. Journal of Animal Science 35: 1288-1293.

Yazdi MH, Eftekhari-Shahroudi F, Hejazi M, Liljedahl LE 1998. Environmental effects on growth traits and fleece weights in Baluchi sheep. Journal of Animal Breeding and Genetics 115: 455-465.