

Heritability of persistency traits and their genetic correlations with milk yield and udder morphology in dairy sheep.

A. Carta, S. Casu, M.G. Usai, S. Salaris

Research Unit: Genetics and Biotechnology, DIRPA-AGRIS Sardegna. 07100, Sassari, Italy.

Abstract

In Mediterranean dairy sheep farming systems, the ability of a ewe to recover a significant milk yield level in spring, when pasture availability is favourable for milk production and lactations are in an advanced stage, is of great interest for its technical and economic implications. The aim of this study was to derive a measure of persistency of lactation to appraise the ability of an ewe to show high milk yields in spring by applying a principal component analysis to test date milk yields. In particular, genetic parameters of a measure expressed as a ratio of spring and winter yields and principal components as well as their correlations with production and udder morphology traits were estimated. The results showed that principal component analysis of TD milk yields was able to detect a PC with twice the heritability and a high genetic correlation with the ratio of milk quantity produced in spring and that produced in winter. Moreover it showed a negligible genetic correlation with milk yield. On this basis, this variable seems an efficient selection criterion to select dairy sheep for the ability to exploit favourable environmental condition in late lactation in the classical Mediterranean farming system. Results also showed that udder morphology is not correlated with the main traits defining persistency.

Keywords: principal components, genetic parameters, persistency

Introduction

Lactation persistency is an economically important trait in dairy production. In dairy cattle, persistency is usually defined as the ability of a cow to continue producing milk at high level after the peak yield (Gengler, 1996; Grossman et al., 1999; Cole and VanRaden, 2006; Togashi et al., 2009). Economic reasons for improving persistency are related to reduction of feed, health and reproductive costs (Solkner and Fuchs, 1987; Dekkers et al., 1998; Muir et al., 2004; Harder et al., 2006). Swalve and Gengler (1999) classified the proposed measures of persistency in four groups: measures expressed as a ratio of yields, measures derived from variation between test day yields, measures based on parameters of lactation curves estimates from mathematical models and measures based on the application of random regression test day models (Grossman et al., 1999). The influence of environmental and genetic factors on these different measures was widely demonstrated. Estimates of heritability range from under 0.05 to over 0.30 according to criteria of persistency used (Swalve and Gengler, 1999).

In dairy sheep, persistency has been studied with the same approach of cattle (Elvira et al., 2013; Gutierrez et al., 2007; Jonas et al., 2011; Kominakis et al., 2001). However, dairy sheep production is mainly located in Mediterranean countries and the production system, often based on grazing, is strongly affected by environmental conditions (De Rancourt et al., 2006). The typical dairy sheep productive cycle is characterized by one yearly out-of-season lambing which makes for optimal exploitation of the herbage growth cycle. Lambings mainly occur in autumn when the grass starts to grow after the summer drought. Yearlings (on

average 25–30% of the total flock) usually lamb between January and March. Generally, lambs are slaughtered or weaned after around 30 days of suckling. After weaning, ewes are usually milked twice a day until late spring-early summer when they are simultaneously dried off, whatever the production level, because of summer drought. With this management, lactations from late winter lambings, in particular of yearlings, are forced to dry off when they still show high production levels. In spring, when rainfall and temperature are favourable to herbage growth, the ability of an adult ewe to recover a significant milk yield level, when its lactation is in an advanced stage, is of great interest for technical and economic reasons.

Macciotta et al. (2006) proposed a principal component analysis of TD milk yields in dairy cattle to derive a measure of persistency. The aim of this study was to apply the same approach to identify a measure of persistency of lactation to appraise the ability of a ewe to show high milk yields in spring in Mediterranean conditions. In particular, genetic parameters of a measure expressed as a ratio of yields and principal components as well as their correlations with production and udder morphology traits were estimated.

Material and methods

Data were recorded from 2000 to 2012 in an experimental population settled in a farm located in the southern part of Sardinia. Originally, the experimental population comprised ten families originated from F1 Lacaune x Sarda sires aimed at detecting QTLs for production and functional traits. Subsequently, the ewes were mated with Sarda rams for several generations. Carta et al. (2012) reported a detailed description of this population.

Since the aim of this work was to study the ability of an ewe to recover high milk yields in spring when the pasture availability is high and lactations are in an advanced stage, adult lactations from lambings after January were excluded from the analysis. Lactations from yearlings were also discarded either for this reason and because several authors reported phenotypic and genetic differences with adult lactations both in dairy sheep (Kominakis et al., 2002) and cattle (Solkner and Fucks, 1987). In particular, first lactations show flatter curves with a less pronounced peak. The most widely accepted explanation is that the mammary gland has not completed its development at the beginning of the first lactation. Only lactations longer than 150 DIM were selected. The final dataset consisted of 37,814 milk test day yields (TD) recorded fortnightly at the two daily milkings on 2,513 ewes between 2 and 4 years old and with lambing from November to January. Milk yield in the milking period only was calculated using Fleishmann method and afterward projected as mature ewe equivalent (MY) following Carta et al. (1998). The winter (WMY) and spring milk yields (SMY) were calculated using TD in the interval between the lambing date and March 31th and between April 1th and May 31th, respectively. The ratio (SWR) between SMY and WMY was then calculated.

TD milk yields at fixed DIM (from 60 to 150) with fortnightly intervals (M060, M075, M090, M105, M120, M135, M150) were calculated with a linear interpolation of the two closest TD yields. Principal components (PC) to be used for genetic analysis, extracted from the correlation matrix of these 7 yields, were selected according to the explained portion of original variance.

Four udder morphology traits were appraised once a year with 9-point linear scales (Casu et al., 2006): teat placement (TP), udder depth (UD), degree of separation of the 2 halves (DS), and degree of suspension of the udder (SU). In order to appraise the udder volume, an indicator trait (VOL) was derived by multiplying the score of SU by the square of UD.

Genetic parameters of persistency measures and genetic and phenotypic (co)variances with milk and udder morphology traits were estimated with multiple-trait models. The repeatability animal model for lactation traits was:

$$Y_{ijklm} = \mu + YM_i + YA_j + a_k + pe_1 + e_{ijklm}$$

where Y_{ijklm} was equal to MY, WMY, SMY, SWR and retained PCs; μ was the overall mean; YM_i was the fixed effect of the interaction of year and month of lambing; YA_j was the fixed effect of the interaction of year of lambing, age, and litter size; a_k was the random additive genetic effect of animal; pe_1 was the random effect of permanent environment; e_{ijklm} was the random residual. The repeatability animal model for udder variables was:

$$Y_{ijklm} = \mu + LS_i + YC_j + a_k + pe_1 + e_{ijklm}$$

where Y_{ijklm} was equal to TP, UD, DS, SU and VOL; μ was the overall mean; LS_i was the fixed effect of lactation stage; YC_j was the fixed effect of year-classifier, a_k was the random additive genetic effect of animal; pe_1 was the random effect of permanent environment; e_{ijklm} was the random residual. The pedigree file comprised 4,262 individuals of which 322 sires and 1,427 dams without records. Mixed models were run using the statistical package ASReml (Gilmour et al., 2009).

Results

Table 1 depicts the descriptive statistics of lactations, selected PC and udder traits. The mean of MY was in the range of values reported for dairy sheep in Mediterranean area (Carta et al., 2009). WMY and SMY were on average 58% and 28% of MY respectively. On average, SMY was calculated between 118 and 179 DIM.

Table 1 – Descriptive statistics of milk yield in the milking period expressed as mature ewe equivalent (MY), winter milk yield (WMY), spring milk yield (SMY), SMY and WMY ratio (SWR), teat placement (TP), udder depth (UD), degree of separation of the 2 halves (DS), degree of suspension of the udder (SU), udder volume (VOL), first principal component (PC1) and second principal component (PC2).

Variable	n	Mean	Std Dev	Min	Max
MY (L)	5402	241	49	84	414
WMY (L)	5402	164	43	29	364
SMY (L)	5402	78	22	8	190
SWR	5402	0.512	0.212	0.032	2.310
TP	5379	7.7	0.9	3.0	9.0
UD	5306	5.8	1.0	2.0	9.0
DS	5121	6.4	1.1	1.0	9.0
SU	5402	4.6	1.4	1.0	8.0
VOL	5306	167	88	4	567
PC1	5402	0.026	2.313	-7.740	8.600
PC2	5402	-0.003	0.950	-4.655	3.214

Table 2 – Eigenvectors and associated eigenvalues of the first (PC1) and second (PC2) principal component issued from the correlation matrix between milk yields at fixed DIM .

Variable	Eigenvectors	
	PC1	PC2
M060	0.363	-0.435
M075	0.380	-0.414
M090	0.393	-0.283
M105	0.398	-0.053
M120	0.394	0.236
M135	0.373	0.453
M150	0.341	0.544
Eigenvalues (%)	5.43 (77.5)	0.90 (12.9)

TD milk yields at fixed DIM showed a progressive decline from 60 to 150 DIM. The average of M060 was 1,964 mL whereas the average of M150 was 1,335 mL. Eigenvectors and eigenvalues of the 2 principal components, explaining 90.4% of the whole original variation, are reported in Table 2. The first PC (PC1), which takes into account most variation, showed similar correlations with TD yields independently from DIM. The second PC (PC2) showed a high negative correlation with M060 and M075, close to zero with M105 and a high positive correlation with M135 and M150. These results are consistent with Macciotta et al. (2006) that attributed to PC1 and PC2 scores the meaning of phenotypic indicators of level of production for the whole lactation and lactation persistency, respectively.

Heritability and repeatability estimates for all traits are reported in Table 3.

Table 3- Additive genetic (σ_a^2), permanent environmental (σ_{pe}^2), residual (σ_e^2) and total variance (σ_{tot}^2), heritability (h^2) and repeatability (r) of traits.

Trait ¹	σ_a^2	σ_{pe}^2	σ_e^2	σ_{tot}^2	h^2	r
MY (L ²)	889	413	616	1919	0.46	0.68
WMY (L ²)	379	184	458	1020	0.37	0.55
SMY (L ²)	115	64	158	337	0.34	0.53
SWR	0.0016	0.0003	0.0118	0.0138	0.12	0.14
TP	0.412	0.120	0.277	0.810	0.51	0.66
UD	0.457	0.124	0.296	0.877	0.52	0.66
DS	0.449	0.272	0.520	1.241	0.36	0.58
SU	0.914	0.204	0.518	1.637	0.56	0.68
VOL	4377	1058	1828	7263	0.60	0.75
PC1	1.967	0.86	1.478	4.305	0.46	0.66
PC2	0.113	0.056	0.387	0.557	0.20	0.30

Standard errors in the magnitude of 0.013 - 0.041 for h^2 and of 0.012 - 0.018 for r for lactation traits and in the magnitude of 0.039 - 0.042 for h^2 and of 0.010 - 0.015 for r for udder traits.

¹Trait: MY = milk yield as mature ewe equivalent; WMY = winter milk yield; SMY = spring milk yield; SWR = SMY and WMY ratio; TP = teat placement; UD = udder depth; DS = degree of separation of the 2 halves; SU = degree of suspension of the udder; VOL = udder volume; PC1 = first principal component; PC2 = second principal component.

The heritability of MY was high if compared to estimates reported in other studies on dairy sheep (Carta et al., 2009). The large family size of the population and the high accuracy

of milk recording may explain this result. MY showed h^2 higher than WMY and SMY probably because the latter represent just portions of the total milk.

PC1 and MY showed similar h^2 and repeatabilities. As far as udder traits are concerned, h^2 ranged from 0.36 to 0.56 for the four original traits and were higher than those estimated by Casu et al. (2006). VOL showed the highest h^2 (0.60).

SWR showed a much lower h^2 respect to PC2. Estimates of h^2 of measures of persistency reported in literature concerned mainly dairy cattle and ranged from 0.01 to over 0.30 (Gengler et al., 1996). This variability was attributed to the different persistency measures adopted. In dairy sheep only Kominakis et al. (2002) reported h^2 of 0.15 for the slope of the regression of test day milk yields on days in milk, 0.13 for the coefficient of variation of test-day milk yields and 0.10 for the maximum to average daily milk yield ratio. These values are similar to h^2 of SWR and lower than PC2.

PC1 showed a positive and very high genetic correlation with MY, WMY and SMY (0.95 to 0.99) and moderate with SWR (0.33). Also the phenotypic correlations of PC1 with MY and, even if at less extent, with WMY and SMY, were high (0.82 to 0.97). These results confirm that PC1 is strongly related to milk yields independently from the lactation season.

Estimated genetic and phenotypic correlations between milk or udder traits with PC2 and SWR are reported in Table 4.

Table 4 – Genetic (r_g) and phenotypic (r_p) correlations of measures of persistency with lactation and udder traits.

Trait ¹	Parameter			
	r_g		r_p	
	PC2	SWR	PC2	SWR
MY	0.10 (0.097)	0.31 (0.106)	0.06 (0.018)	0.13 (0.017)
WMY	-0.25 (0.091)	-0.05 (0.118)	-0.11 (0.017)	-0.28 (0.016)
SMY	0.33 (0.090)	0.53 (0.091)	0.27 (0.016)	0.50 (0.013)
SWR	0.92 (0.042)		0.37 (0.013)	
TP	-0.04 (0.095)	0.07 (0.111)	-0.01 (0.019)	0.01 (0.018)
UD	0.11 (0.096)	0.02 (0.114)	0.07 (0.019)	0.02 (0.018)
DS	-0.16 (0.109)	0.04 (0.125)	-0.01 (0.018)	0.001 (0.017)
SU	0.09 (0.093)	-0.05 (0.108)	0.00 (0.019)	-0.01 (0.018)
VOL	0.12 (0.091)	0.003 (0.108)	0.05 (0.020)	0.01 (0.018)

¹Traits: MY = milk yield as mature ewe equivalent; WMY = winter milk yield; SMY = spring milk yield; SWR = SMY and WMY ratio; TP = teat placement; UD = udder depth; DS = degree of separation of the 2 halves; SU = degree of suspension of the udder; VOL = udder volume; PC2 = second principal component.

The genetic correlations between PC2 and WMY or SMY reflected the same pattern of the eigenvectors with the first part and the last part of lactation, respectively. On the other hand, PC2 showed a highly positive and favourable genetic correlation with SWR (0.92). The genetic correlation between SWR and MY was moderately positive whereas the genetic correlation of PC2 and MY was negligible. This result fits the suggestion of Gengler et al. (1996) that stated that a good persistency measure should be independent from yield or corrected for the influence of yields. On the whole, considering that PC2 is highly correlated with SWR, showed an almost double h^2 than SWR and a weak correlation with MY, selective breeding for PC2 will have a high favourable correlated response on the ability of a ewe to produce in late lactation when, such as in the Mediterranean area, favourable environmental conditions arise. The direct selection for SWR is limited by the low h^2 and the not negligible positive correlation with MY. As far as the relationships between persistency traits and udder

traits are concerned, both phenotypic and genetic correlations were low suggesting that external udder morphology does not affect the ability of a ewe to produce late in lactation.

CONCLUSION

In dairy sheep industry which is often characterised by a seasonal production with an out-of-season lambing and a simultaneous dry-off of the whole flock independently from the individual milk yield level, persistency of lactation may assume different meanings than in dairy cattle. In particular, the ability of a ewe to recover high milk yield levels late in lactation according to the high grass availability is of great economic importance. This study showed that principal component analysis of TD milk yields was able to detect a PC with twice the heritability and a high genetic correlation with the ratio of milk quantity produced in spring and that produced in winter. Moreover, it showed a negligible genetic correlation with milk yield. On this basis, this variable seems an efficient selection criterion to select dairy sheep for the ability to exploit favourable environmental conditions in late lactation in the classical Mediterranean farming system. It has also been shown that udder morphology is not correlated with the main traits defining persistency. This result suggests that the recent implementation of udder morphology as selection objective in the main European dairy sheep breeds will not have any correlated response on persistency traits.

List of References

- Carta, A., S. Casu, and S. Salaris. 2009. Invited review: Current state of genetic improvement in dairy sheep. *J. Dairy Sci.* 92 :5814–5833
- Carta, A., M.G. Usai, S. Sechi, S. Salaris, S. Miari, T. Sechi, G.B. Congiu, G. Mulas, S. Murru and S. Casu. 2012. Fine mapping of QTLs and genomic selection for production traits in an experimental population of Sarda dairy sheep. Proc. 38th ICAR Annual Meeting. Cork, Ireland
- Casu, S., I. Pernazza, and A. Carta. 2006. Feasibility of a Linear Scoring Method of Udder Morphology for the Selection Scheme of Sardinian Sheep. *J. Dairy Sci.* 89:2200–2209
- Cole, J. B., and P. M. VanRaden. 2006. Genetic evaluation and best prediction of lactation persistency. *J. Dairy Sci.* 89:2722–2728.
- Dekkers, J. C. M., J. H. Ten Hag, and A. Weersink. 1998. Economic aspects of persistency of lactation in dairy cattle. *Livest. Prod. Sci.* 53:237–252.
- de Rancourt, M., N. Fois, M.P. Lavìn, E. Tchakérian, and F. Vallerand. 2006. Mediterranean sheep and goats production: An uncertain future. *Small Rum. Res.* 62: 167–179
- Elvira, L., F. Hernandez, P. Cuesta, S. Cano, J.-V. Gonzalez-Martin, and S. Astiz. 2013. Accurate mathematical models to describe the lactation curve of Lacaune dairy sheep under intensive management. *Animal*, 7:6, pp 1044–1052
- Gengler, N. 1996. Persistency of lactation yields: a review. in Proc. Int. Workshop of Genet. Improvement of Functional Traits in Cattle, Gembloux, Belgium. INTERBULL Bull. No. 12, Univ. Agric. Sci., Uppsala, Sweden. Pages 87–96
- Gilmour, A.R., B.J. Gogel, B.R. Cullis, and R. Thompson. 2009 ASReml User Guide Release 3.0 VSN International Ltd, Hemel Hempstead, HP1 1ES, UK www.vsnl.co.uk
- Grossman, M., S. M. Hartz, and W. J. Koops. 1999. Persistency of lactation yield: A novel approach. *J. Dairy Sci.* 82:2192–2197.
- Gutiérrez, J.P., E. Legaz, F. Goyache. 2007. Genetic parameters affecting 180-days standardised milk yield, test-day milk yield and lactation length in Spanish Assaf (Assaf.E) dairy sheep. *Small Rum. Res.* 70, 233–238.

- Harder, B., J. Bennewitz, D. Hinrichs, and E. Kalm. 2006. Genetic Parameters for Health Traits and Their Relationship to Different Persistency Traits in German Holstein Dairy Cattle. *J. Dairy Sci.* 89:3202–3212
- Jonas, E., P.C. Thomson, E.J.S. Hall, D. McGill, M.K. Lam, and H.W. Raadsma. 2011. Mapping quantitative trait loci (QTL) in sheep. IV. Analysis of lactation persistency and extended lactation traits in sheep. *Genet. Sel. Evol.* 43:22
- Kominakis, A., M. Volanis, E. Rogdakis. 2001. Genetic modelling of test day records in dairy sheep using orthogonal Legendre polynomials. *Small Rum. Res.* 39: 209-217.
- Kominakis, A. P., E. Bogdakis and K. Koutsotolis. 2002. Genetic aspects of persistency of milk yield in Boutsico dairy sheep. *Asian-Aust. J. Anim. Sci.* 15:315-320.
- Macciotta, N.P.P., D. Vicario, and A. Cappio-Borlino. 2006. Use of Multivariate Analysis to Extract Latent Variables Related to Level of Production and Lactation Persistency in Dairy Cattle. *J. Dairy Sci.* 89:3188–3194
- Muir, B.L., J. Fatehi, and R. L. Schaeffer. 2004. Genetic relationships between persistency and reproductive performance in first-lactation Canadian Holsteins. *J. Dairy Sci.* 87:3029–3037.
- Solkner, J., and W. Fuchs. 1987. A comparison of different measures of persistency with special respect to variation of test day yields. *Livest. Prod. Sci.* 16:305–319.
- Swalve, H.H., and N. Gengler, 1999. Genetics of lactation persistency. in *Metabolic Stress in Dairy Cows*. J. D. Oldham, G. Simm, A. F. Groen, B. L. Nielsen, J. E. Pryce, and T. L. J. Lawrence, ed. BSAS occasional publication 24. Br. Soc. Anim. Sci. Penicuik, UK. 75–82
- Togashi, K., and C.Y. Lin. 2009. Economic weights for genetic improvement of lactation persistency and milk yield. *J. Dairy Sci.* 92:2915–2921