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Estimates of genetic parameters for lactation curves for milk, fat, protein and somatic cell score in New Zealand dairy goats

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Abstract

The aim of this study was to estimate genetic parameters of daily yields of milk (MY), fat (FY), protein (PY) and somatic cell score (SCS) of New Zealand dairy goats. The analysis used 113,895 herd-test records from 14,187 does, kidding between 2010 and 2016, distributed in 11 herds and representing 377 sires. Estimates of genetic and residual (co)variances, heritabilities (h^2) and repeatabilities were obtained using a random regression test-day animal model. The model included the fixed effects of contemporary group (herd-test-day), age of the doe (in years) and as covariates, deviation from median kidding date for a given herd and year, proportion of genes from Alpine, Nubian, Toggenburg and "unknown and other" breeds (Saanen was used as a base breed), heterosis, and days in milk (DIM) modelled as a third-order orthogonal polynomial. Random effects included additive animal genetic and doe-lactation permanent environment effects modelled using third-order orthogonal polynomials. Estimates of h^2 and repeatabilities at different stages of lactation ranged from 0.13 to 0.35 and 0.39 to 0.81, respectively. These results provide an opportunity to estimate breeding values at any and every day of lactation, and to change the shape of the lactation curve by selection.

Keywords: dairy goat; genetic parameters; test-day model; heritability; lactation curve; New Zealand

Introduction

The production efficiency of the dairy goat industry needs to improve to continue expanding and remain competitive with other dairy industries. Production efficiency can be improved by increasing milk production or maintaining persistent yields across the lactation period. Genetic improvement is the most attractive approach to promote permanent gains in livestock species. Milk solids (fat + protein + lactose yields) is among traits with highest economic relevance for the industry and maximising milk solid production is a key goal of dairy farmers. Characterising variation in milk-production traits at specific days during lactation is important for understanding the genetic associations between traits at different stages of lactation and would provide parameters required for estimating breeding values for milk traits at different stages of lactation.

Milk production during the lactation is an example of a longitudinal trait, characterised by repeated measures in the same individual over time. Random regression models (RRM) have become commonly adopted for the genetic analysis of longitudinal data and are currently used for the national genetic evaluation of production traits of dairy cattle in Australia, Belgium, Canada, Czech Republic, Denmark, Finland, Germany, Ireland, The Netherlands, New Zealand and Sweden (Interbull 2017). Under RRM, records on the sample day are considered directly in the analysis, therefore, RRM can account more precisely for environmental factors that could affect animals differently during lactation (Schaeffer & Dekkers 1994). In one class of RRM, a fixed curve for the population is calculated and individual curves are fitted as deviations from the population curve. Any RRM provides the opportunity to use a function to model any or all of the fixed and random curves.

The average shape of a lactation curve can inform the farmer of the predicted level of production over the lactation period, whereas the shape of lactation curves for individual animals can provide insight into the health status of the animal during the lactation process (i.e., health of the mammary gland, energy supply/deficit) and the environmental effects affecting its milk production (Hossein-Zadeh 2016). Information about milk production levels and the characteristics of the lactation curves allow evaluation of the production performance and subsequent implementation of improvement strategies, i.e., feeding, breeding and economic management. Knowledge of heritabilities (h^2) at each test-day and covariances among test days across the lactation period would provide the opportunity to estimate breeding values at any and every point in time during lactation.

The objective of this study was to estimate genetic parameters for daily yields of milk (MY), fat (FY), protein (PY) and somatic cell score (SCS) across the lactation period of New Zealand dairy goats using a random regression test-day model.

Materials and methods

The original data set was provided by Livestock Improvement Corporation (LIC) and included 304,648 herd-test records across seven lactations from 48,113 does kidding up to parity 14 between 2010 and 2016 and from 55 herds across the North Island of New Zealand. The pedigree of these lactating does included 422 sires and 11,803 dams. Breed composition of each doe was calculated from pedigree proportions of Alpine, Nubian, Saanen,

Toggenburg and "unknown and other" breeds. There was a total of 797 herd-test-day (HTD) contemporary groups. Somatic cell score (SCS) was calculated as $SCS = \log_2$ (somatic cell count) at each herd-test.

Herds comprising does with <80% of dams known or with contemporary groups with <10 herd-tested does were removed (44 herds and 604 HTD groups). After cleaning, the data set contained 113,895 herd-test records across seven lactations, representing 14 parities and included 14,187 does distributed in 11 herds. The does were the offspring of 377 sires and 8,043 dams and the known pedigree spanned up to nine generations. Many of the does were crossbred and there were very few purebred animals of Alpine (1), Nubian (3) or Toggenburg (40) breeds and, therefore, the covariates reflecting the proportion of these breeds were summed in a single combined-breed group hereafter called ANT. The remaining does included 1,358 Saanen, 12,766 crossbred and 19 animals of unknown and other breeds. There was a total of 229 HTD contemporary groups, mostly consisting of more than one breed or cross. The structure of the dataset is provided in more detail in Table 1.

Estimates of variance and covariance components for test-day yields of MY, FY, PY and SCS were obtained using the restricted maximum likelihood procedure in ASReml version 3 (Gilmour et al. 2009) to fit a single-trait random regression test-day model. The model included the fixed effects of contemporary group (herd-test-day) and age of the doe (in years). Covariates in the model included deviation from median kidding date, proportion of genes from ANT and "unknown and other" breeds (Saanen was used as a base breed) and general heterosis. Days in milk (DIM) was modelled as a third-order orthogonal polynomial. Random effects included additive animal genetic and doe-lactation permanent environment, were both modelled using third-order orthogonal polynomials.

General heterosis was calculated as $1 - \sum_{j=1}^{f} p_j^2$ where p_j is the proportion of each of the f breeds (Gregory & Cundiff 1980; Lamberson et al. 1993). General heterosis assumes that first-cross heterosis is the same for all breed combinations. Residual variances were assumed to be heterogenous across six stages of lactation, with different residual variances for 0 to 50, 51 to 100, 101 to 150, 151

to 200, 201 to 250 and 251 to 270 DIM. The genetic (co) variances across all DIM were estimated as;

$$\delta = \varphi' K \varphi$$

In which δ is the variance or (co)variance matrix for the traits, φ is the matrix of orthogonal polynomials for each DIM, and K is the matrix of the additive genetic (co)variance matrix of random orthogonal polynomial coefficients.

Initially, six RRMs were tested in order to identify the one which best fitted the production records. Models ranged in the orders of the orthogonal polynomial used to describe the additive animal genetic and doe-lactation permanent environment effects. The model with best fit had polynomials of 3rd order for the fixed curve of the population and both the additive animal genetic and doe-lactation permanent environment effects.

Results

Descriptive statistics for MY, FY, PY and SCS are in Table 2. Primiparous does produced the lowest yields compared to does in later parities. Parity had a significant (P<0.001) effect on test-day yields of MY, FY, PY and SCS over that lactation period. The coefficients of variation on test-day yields were high, reflecting considerable phenotypic variation in the shape of the lactation curve.

Orthogonal polynomials of order 3 were used to estimate lactation curves for daily yields of MY, FY, PY and SCS for does of different parity (Figure 1). The shape of lactation curves were the same for each parity for each trait. Primiparous does had the lowest yields for all traits while third-parity does had the highest yields. Peak yields were around day 95 for MY, day 1 for FY, days 12 to 106 for PY and day 270 for SCS.

Figure 2 graphically illustrates the additive genetic (σ_a^2), permanent environment (σ_{pe}^2), residual (σ_e^2) and phenotypic (σ_p^2) variances estimated using a single-trait RRM for test-day yields of MY, FY, PY and SCS during the lactation period. The σ_{pe}^2, and σ_p^2 were greatest at the beginning of lactation for all traits while the trajectories of σ_a^2, and σ_e^2, varied among traits.

Estimated h^2 by day of lactation for MY, FY, PY and SCS are in Figure 3. The h^2 ranged from 0.20 to 0.35 for MY, 0.21 to 0.28 for FY, 0.16 to 0.31 for PY and 0.13 to 0.22 for SCS. Average repeatability estimates were 0.63, 0.57, 0.61 and 0.45 for MY, FY, PY and SCS, respectively.

Discussion

The mean and standard deviation of daily MY were greater than those reported in crossbred goats in Brazil (2.61±0.71 kg/day; Lobo et al. 2017) and Murciano-Granadina goats in Spain (1.93±1.01 and 2.18±1.01; Menendez-Buxadera et al. 2010) and for FY and PY in Murciano-Granadina goats (0.098 to 0.109±0.05 g/day for FY and 0.068 to 0.072±0.03 g/day for PY; Menendez-Buxadera et al. 2010). The lower MY could be due to climatic effects, especially for semi-arid climates in Brazil, which are known to negatively affect milk production
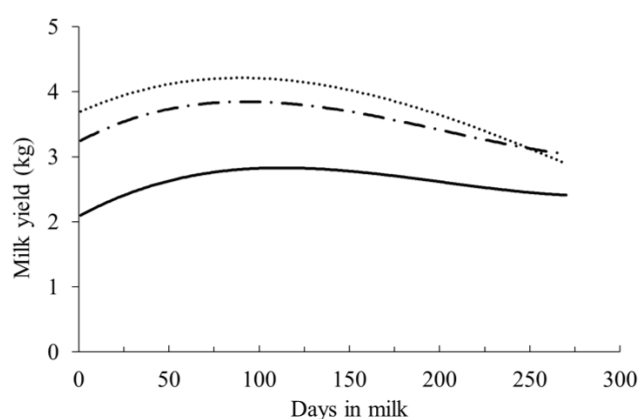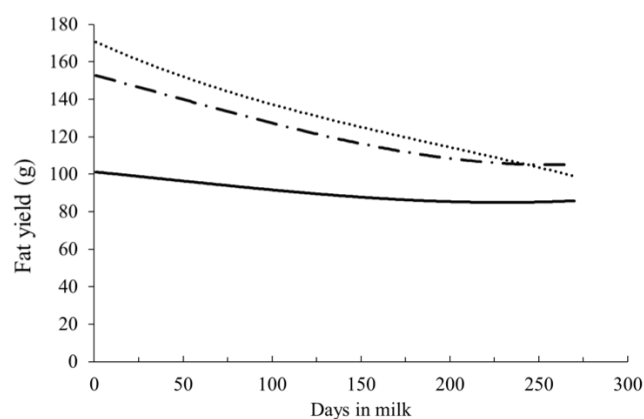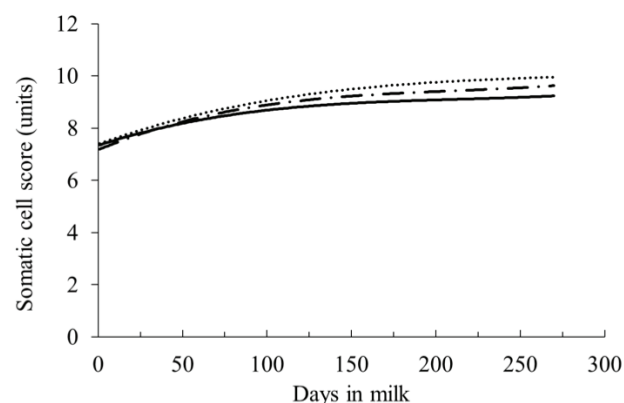
Table 1 Summary characteristics of dataset comprising test-day yields of dairy goats in New Zealand

Breed	Herds	Animals	Herd-test records	Animals with known sires
ANT[1]	3	44	184	1
Saanen	10	1,358	8,757	74
Crossbred	11	12,766	104,808	368
Unknown + other	6	19	136	3
Total	-	14,187	113,895	446

[1]ANT = Combined breed group including Alpine, Nubian and Toggenburg animals.

Table 2 Descriptive statistics of milking traits of New Zealand dairy goats kidding between 2010 and 2016.

	n	Milk yield (kg/day)			Fat yield (g/day)			Protein yield (g/day)			Somatic cell score (units/day)		
		Mean	SD[1]	CV[2]	Mean	SD[1]	CV[2]	Mean	SD[1]	CV[2]	Mean	SD[1]	CV[2]
Population	113,895	3.4	1.3	37	114.4	44.6	39	106.5	37.2	35	9.1	1.7	19
Parity													
1	31,728	2.6	0.9	35	90.1	32.8	36	84.1	27.8	33	8.7	1.8	21
2	29,305	3.6	1.1	32	122.3	42.5	35	112.8	34.1	30	8.9	1.7	19
3	19,329	3.9	1.3	33	130.5	46.4	36	121.4	37.6	31	9.2	1.7	18

[1]SD = standard deviation across herds.

[2]CV = coefficient of variation.

Figure 1 Lactation curves of daily yields of milk, fat and protein and somatic cell score during the 270-day lactation for does in parity 1 (—), 2 (—•—) and 3 (•••) modelled with orthogonal polynomials of order 3.
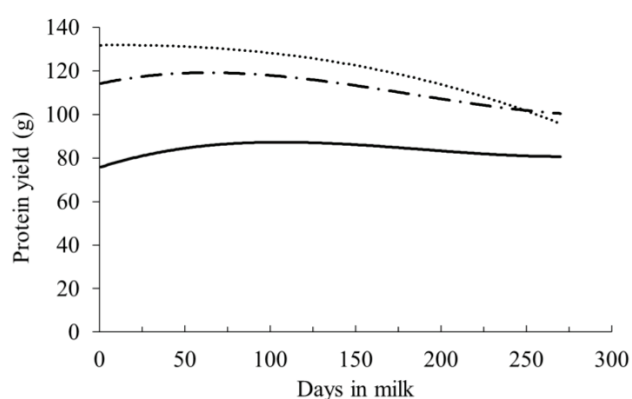

through reduced feed intake and increased maintenance requirements needed for homeothermy (sweating, panting) (Salama et al. 2014). In addition, the lower FY and PY in the Spanish study could be due to parity effect, as they only analysed does in first and second-parity, which are known to have lower milk production compared to older does (Amin et al. 2017; Lobo et al. 2017). The values obtained in this study for SCS were similar to those previously reported in goats in New Zealand of 9.35±1.69 units/day (Apodaca-Sarabia et al. 2009).

A typical lactation curve of MY for French dairy goats has been reported to comprise of a rapid increase at the start of lactation, peak around 50 DIM, then production stabilises for 50 days and then slowly decreases through to the end of lactation (Arnal et al. 2018). A similar pattern was also observed in the current study, but the peak was not until 90 to 100 DIM. For primiparous does, the peak yield is typically earlier and the lactation curve is generally flatter than multiparous does (Fernandez et al. 2002). The early peak was not observed for primiparous does in this study, however, the curve was flatter than for does in second and third parity. The lactation curves estimated for does of first, second and third parity followed a similar trend for each of the traits. Does in third parity produced the greatest MY, FY and PY throughout the lactation, until 250 DIM. Overall, second- and third-parity does produced

Figure 2 Estimates of additive genetic (—), permanent environment (---), residual (•••) and phenotypic variance (—•—) of test-day yields of milk, fat, protein and somatic cell score during the 270-day lactation in New Zealand dairy goats.
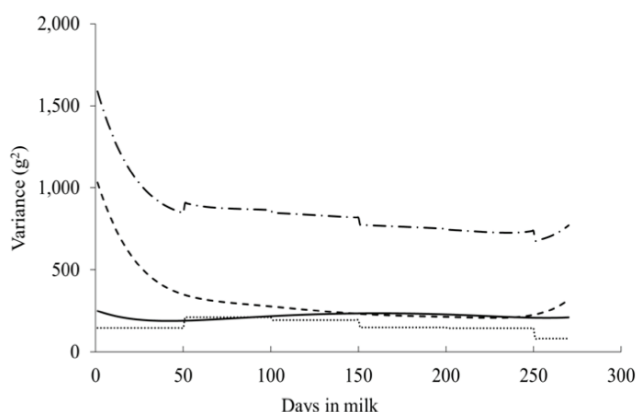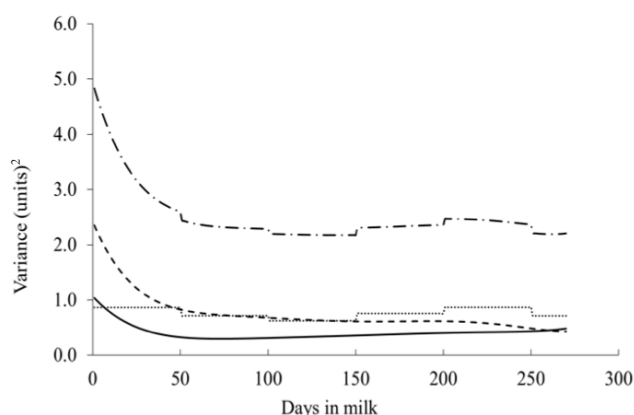
Milk
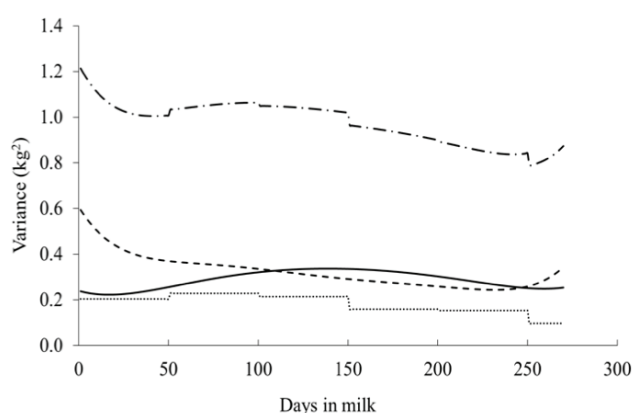
Fat
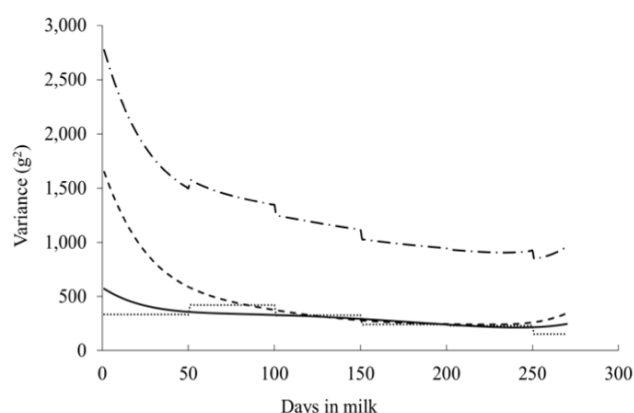
Protein

Somatic cell score

significantly greater daily yields than primiparous does. This is in agreement with findings of Amin (2017) and Lobo et al. (2017) who reported that yields increased as the age of doe increased until about fourth parity, and then decreased. This parity effect is common for milk-production animals and is suggested to be due to younger does having lower body weight, body condition score and body reserves than older does, and consequently, the body and mammary gland of young animals are still developing during the first lactation. It is also common that the level of SCS is lowest at the beginning of lactation and increases during the lactation period (Lobo et al. 2017) and that SCS is lowest in primiparous animals and increases as the number of lactations increases (Amin 2017; Lobo et al. 2017).

Orthogonal polynomials of third order were applied for modelling the average production curve of the population (fixed effect) and for modelling production curves of the random effects (additive animal genetic and doe-lactation permanent environment). Although models with more parameters are more accurate (Brito et al. 2017), this generates greater computational demand and can lead to

problems of convergence and estimation, especially when using a RRM for genetic evaluations on large datasets. Therefore, it is important to use less-parameterised models without losing quality of fit. Considering heterogeneity of residual variances rather than homogenous residual variance can improve the modelling of the random effects (Brito et al. 2017). Therefore, if performing genetic evaluation on a large data set, we recommend using a RRM with orthogonal polynomials of order 3 for fixed and random effects and assume heterogenous residual variances.

For MY the highest value for σ_a^2 was observed just after peak production (124 DIM). This trajectory was similar to that seen in dairy goats in Brazil using a multiple-trait analysis, but their peak lactation was around 60-90 days (Irano et al. 2015) and 40 days (Brito et al. 2017). In contrast, Silva et al. (2013) found higher values of σ_a^2 at the end of the lactation curve using a single-trait animal model for random regression.

The σ_a^2 declined from the beginning of the lactation for FY, PY and SCS until days 40-50, then for SCS the variance increased for the rest of the lactation, for PY this increased for 100 days before slightly decreasing and for FY the

Figure 3 Estimates of heritability for test-day yields of milk (—), fat (---), protein (•••) and somatic cell score (—•—) during the 270-day lactation in New Zealand dairy goats.
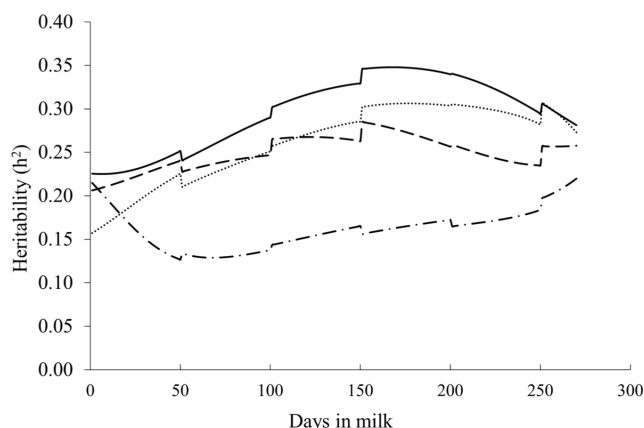
variance plateaued for 100 days before slightly decreasing along the remaining days in milk. Despite there being no literature on dairy goats, this decrease in genetic variability during the lactation period is commonly observed in dairy cattle (Biassus et al. 2011).

In this study, σ^2_{pe} followed the same pattern for MY, FY and PY, decreasing as the number of lactation days increased until 250 DIM before slightly increasing for the last 20 DIM. These inflated variances at the start of the lactation period were also reported by Thepparat et al. (2015) using a single-trait RRM, and Oliveira et al. (2016) using a multiple-trait RRM with different functions to describe each trait. In contrast, Brito et al. (2017) reported that σ^2_{pe} and σ^2_p were lower in early lactation and increased at the end of lactation compared with the other lactation stages. They proposed that this was expected as there was a greater reduction in the number of records at the end of lactation, however, this reduction in records also occurred in this study. Moreover, more variability during the beginning and end of lactation would be expected, as non-genetic factors, such as management, tend to influence milk production more expressively during this period. The σ^2_p variance generally decreased as the number of lactation days increased, but also followed a similar trend to that of residual variance, which peaked during the 2nd and 3rd stage of lactation (days 51-100 and 101-150) for MY, FY and PY.

The h^2 estimates were greatest from the middle to late lactation. This is expected and is in agreement with reports by Sarmento et al. (2008) and Oliveira et al. (2016), but are in contrast to the report by Menendez-Buxadera et al. (2010) who reported h^2 values decreased throughout the lactation period and Silva et al. (2013) and Brito et al. (2017) who found that the h^2 values increased in the final third of the lactation. The lower estimates for MY, FY and PY during early lactation and late lactation could be due to the greater influence of environmental effects at these stages, while production in mid-lactation is more influenced by the genetic and permanent effects. For example, most does are

in an advanced stage of pregnancy during late lactation, which can explain the decreased h^2 at that latter stage.

Despite the differing patterns of h^2 in the literature, the h^2 estimates obtained in this study were similar, with the range of values published for daily MY of 0.12 to 0.66 (Andonov et al. 2007; Sarmento et al. 2008; Zumbach et al. 2008; Menendez-Buxadera et al. 2010; Irano et al. 2015; Thepparat et al. 2015; Oliveira et al. 2016; Brito et al. 2017), daily FY of 0.12 to 0.25 (Menendez-Buxadera et al. 2010), daily PY of 0.10 to 0.18 (Menendez-Buxadera et al. 2010) and daily SCS of 0.12 to 0.25 (Apodaca et al. 2009). Our results suggest that there is enough genetic variability to make genetic progress for test-day MY, FY, PY and SCS in dairy goats in New Zealand and it would be possible to modify the shape of the curve by selective breeding. In order to maximise milk production, the estimation of breeding values during early lactation would enable identification and selection of animals with low genetic merit for culling and of high genetic merit for breeding decisions. However, the lower σ^2_a and h^2 near the beginning and end of the lactation would result in lower genetic response when selecting for increased yield in just the first or last part of lactation. Instead, the point with the greatest heritability would be the most applicable stage for practicing selection. The estimate of the h^2 to select for increased persistency between 150 and 250 days in milk in this goat population, was between 0.23 and 0.35 for MY, FY and PY.

At farm level, the biological interpretation of the parameters estimated in this study can contribute to the improvement of goat milk production throughout the lactation period. The estimation and interpretation of test-day yields and h^2 suggest that selection can help to raise milk production and persistency in dairy goat herds in New Zealand. This will be of great relevance to the implementation of genetic evaluations in dairy goats.

Conclusion

Parity has a significant effect on milk production in New Zealand dairy goats. Most lactation curves of does in second and third parity had similar shapes, while does in first parity tended to have lower values throughout the lactation. The results showed that the amount of variation changes during the lactation and the lactation curves for production varies with parity. The use of a RRM for genetic evaluation of dairy goats may allow for selection to alter the shape of the lactation curve. Estimates of h^2 obtained throughout the lactation were moderate, indicating there is enough genetic variability to make genetic progress for test-day yields of MY, FY, PY and SCS in dairy goats.

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