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PAPER

Genetic parameters for milk yield and persistency in Carora dairy cattle breed using random regression model

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Abstract

In tropical environments, lactation curves with lower peaks and higher persistency (PS) might be desirable from both an economical and a physiological point of view. The objective of this study was to obtain genetic parameters for test day (TD) yields, and PS for the tropical breed Carora and to compare these with results from a standard 305-d-milk yield animal model. Four random regression models (RRM) were used on a dataset composed of 95,606 TD records collected in Venezuela and tested to find the best fitting the data. Estimated daily heritabilities for milk yields ranged from 0.21 to 0.30, with the lowest values around the peak of lactation. Lactation repeatabilities ranged from 0.50 to 0.56. Correlations between the breeding values obtained with the RRM and the lactation model currently used in Venezuela [single trait Animal Model (stAM)] are quite high and positive (Pearson correlation=0.71 and Spearman correlation=0.72). Correlations between PS and 305-d-milk yield estimated breeding values (EBV) ranged from -0.18 (PS as the deviation of daily productions in the interval 50-279 days in milk from a point at the end of lactation) to 0.52 (PS as EBV difference between the second and the first stage of lactation). The use of PS indexes accounting for milk yield may allow the selection of individuals

able to express their potential genetic values in tropical environment, without incurring in excessive heat stress losses.

Introduction

Random regression models (RRM) were introduced by Henderson (1982) and Laird and Ware (1982), but only later Schaeffer and Dekkers (1994) suggested their use in cattle breeding for the analysis of test day (TD) records. Information relative to single TD can be directly used for the genetic evaluation of dairy cows, as a replacement for the whole lactation record, and RRM allow the analysis of repeated measurements over time or age, thus accounting for the mean and covariance structure that changes with time or age, unlike the lactation models.

Areas of animal breeding that have already utilised RRM include conformation traits, body condition scores, feed intake and heart girth measures in dairy cattle (Schaeffer, 2004). An additional benefit of the RRM in dairy cattle is that it provides the possibility of genetic evaluation for persistency (PS) of the lactation (Mrode and Thompson, 2005). Lactation PS can be defined as the ability of a cow to produce constantly throughout her lactation (Strabel *et al.*, 2001), or its ability to produce milk at a high level after reaching the peak of lactation (Jamrozik *et al.*, 1998). Persistency gives an indication of the flatness of the production curve and for ease of interpretation, it should be independent of level of production (Jensen, 2001).

The reasons for being interested in a flatter lactation curve at a given level of production include the possibility of using cheaper feed (*i.e.*, roughage) around peak yields (Sölkner and Fuchs, 1987), and a reduction in stress due to high peak production (Zimmerman and Sommer, 1973). Jakobsen *et al.* (2002) investigated the genetic relationship between PS and disease resistance in dairy cattle, showing a favourable relationship between flat lactation curves and a higher disease resistance. Yamazaki *et al.* (2011) found that in order to promote an increase in lactation PS, modification of the lactation curve could help to maintain the health of dairy cows in late lactation without decreasing total milk yield. It is also often claimed that cows with a high PS are less susceptible to nutritional disorders and, perhaps as a result of this, more fertile. This could be the result of low energy needs at the onset of lactation, causing these cows to have lower negative energy balances (Mostert *et al.*,

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2008). Strabel *et al.* (2001) concluded that more persistent lactations are advantageous since they are associated with fewer health problems, reduced feeding and reproductive costs, and also result in a higher yield for longer lactation. These aspects are very important when dealing with tropical conditions, characterised by high temperature and inadequate quantity and quality of available feed.

The breed object of this study, Carora Cattle breed, is a short-horned *Bos taurus* cattle breed raised in Venezuela and other tropical Southern American countries, mainly for milk production. It is a synthetic breed developed in west-central Venezuela by using Brown Swiss semen on the local Creole population (Ganado Creole de Quebrada Arriba). Its origins can be traced back to the 1930s and it was declared to be a breed by the Venezuelan Government in 1975 (Morales *et al.*, 1989). Carora cattle are bred in a tropical environment with a large range of average temperatures, with relative humidity up to 90% and under different production systems, from extensive systems, characterised by grazing and manual milking in the presence of the calf, to intensive systems with high yields, machine milking, and feed supplementation. The primary selection objective of the breeders' association is the improvement of milk production in terms of

quantity and quality. The actual milk yield per lactation is estimated through the summation of monthly TD. Since 1992, the genetic evaluation of the Carora dairy breed was carried on with the single trait AM, using only part of available information.

The objective of this study was to obtain genetic parameters for TD yields and PS for the tropical breed Carora and to compare these with results from a standard 305-d-milk yield animal model.

Materials and methods

Edited data consisted of 95,606 TD records of 4582 cows in 9543 lactations. These data were used to evaluate the genetic variability and estimate the variance components of the Carora breed for the daily milk production.

Test day records of the first three lactations (4582 first, 2915 second and 2039 third lactations) were collected in 57 herds located in Venezuela from 1992 to 2010. Lactations with the first TD recorded after the 40th day and with the first calving earlier than 18 months and later than 40 months of age were eliminated. Test day records ranged from the 5th to the 400th day of lactation and on average for each cow 10 controls were available. The pedigree file contained 9521 subjects, 9509 existing animals plus 12 phantom groups. These groups were obtained clustering animals with missing parents and the same year of birth, and assigning them virtual parents on the basis of a five-year period criterion.

Four RRM were tested to find the one that fitted the data best. The general structure of the model was:

$$y_{hijklmpt} = HYM_h + AC_i + NL_j + YOC_k + MOC_l + \sum_{p=0}^4 \phi_{mp} b_p + \sum_{p=0}^q \phi_{mp} a_{mp} + \sum_{p=0}^q \phi_{mp} pe_{mp} + e_{hijklmpt}$$

where $y_{hijklmpt}$ is the TD record of m^{th} animal at standardised time t ; HYM is the h^{th} random effect of herd-year-month of record ($h=1, 6104$); AC_i is the i^{th} fixed effects of age at calving ($i=1, 10$); NL_j is the j^{th} fixed effects of order of parity ($j=1, 3$); YOC_k is the k^{th} year of calving ($k=1, 18$); MOC_l are the fixed effects of month of calving ($l=1, 12$ levels); b_p are the fixed regression coefficient; a_{mp} and pe_{mp} are the random regression coefficients for the additive and permanent environmental (PE) effect for the m^{th} animal at TD t respectively; f_{mtp} is the

p^{th} Legendre polynomial for the TD record of cow m made on day t and order q ($q=3, 4$); and $e_{hijklmpt}$ is the random residual.

The models applied in this study differed by the order of Legendre polynomials used as covariates for the additive and PE effects and they were compared in order to evaluate the best one fitting the data. The Akaike information criterion (AIC) and the minus twice log likelihood ($-2 \log L$) were used for model comparison. The models used are reported below:

- Model 1: L3L3= $L_{a(3)}+L_{p(3)}$
- Model 2: L3L4= $L_{a(3)}+L_{p(4)}$
- Model 3: L4L3= $L_{a(4)}+L_{p(3)}$
- Model 4: L4L4= $L_{a(4)}+L_{p(4)}$

where the number in parentheses gives the order of Legendre polynomial for the additive genetic (AG) effect (L_a) or PE effect (L_p). The fixed regression function, in this case too was represented by fourth order Legendre polynomials for all the models. Each p^{th} order polynomial was calculated according to the equation:

$$\phi_p(t) = \sqrt{\frac{2p+1}{2}} \frac{1}{2^p} \sum_{r=0}^p \frac{(-1)^r (2p-2r)!}{r!(p-r)!(p-2r)!} t^{p-2r}$$

where p represented the chosen order for the function (in this study 4) and t was the standardised time interval (from -1 to +1) obtained as follows:

$$t = -1 + 2 \left(\frac{DIM - d_{min}}{d_{max} - d_{min}} \right)$$

where DIM are the days in milk in which the TD was collected and d_{min} and d_{max} are the smallest and the biggest TD recorded ($d_{min}=5$ and $d_{max}=400$).

The first six Legendre polynomials for a standardised unit of time t are reported in Table 1. Furthermore the best model was compared to the single trait Animal Model (stAM) on the same 9543 lactations, and the model was the following:

$$y_{hijklmpt} = H_h + AC_i + NL_j + YOC_k + MOC_l + a_m + pe_m + e_{hijklmpt}$$

where $y_{hijklmpt}$ was the j^{th} lactation for the m^{th} animal in the h^{th} herd (57 levels), in the i^{th} class of age at calving (10 levels), in the k^{th} year of calving (18 levels, from 1992 to 2010), in the l^{th} month of calving. The AG effect and the permanent genetic effect were represented respectively by a_m and pe_m . From the fitted RRM, daily genetic variances were calculated

as:

$$\sigma_{a_d}^2 = t_d G t_d'$$

where $\sigma_{a_d}^2$ is the genetic variance for each day in milk (DIM) d , G is the genetic variance matrix, and where t_d is the d^{th} row vector of the matrix containing the Legendre polynomials for standardised day t , with order of fit p .

The same process was used to calculate the daily PE variance. Daily phenotypic variance was calculated as the sum of genetic PE and residual variances, making it possible to compute daily heritability h_d^2 and daily repeatability (r_d).

$$h_d^2 = \frac{\sigma_{a_d}^2}{\sigma_{a_d}^2 + \sigma_{pe_d}^2 + \sigma_{e_d}^2} = \frac{\sigma_{a_d}^2}{\sigma_{y_d}^2}$$

$$r_d = \frac{\sigma_{a_d}^2 + \sigma_{pe_d}^2}{\sigma_{y_d}^2}$$

The genetic and the PE variance were obtained multiplying the G and P matrix by the vector of the orthogonal polynomial coefficients for the whole lactation, obtained summing the 305 daily coefficients. The heritability and repeatability were therefore estimated as follows:

$$h_{305}^2 = \frac{\sigma_{a_{305}}^2}{\sigma_{y_{305}}^2}$$

$$r_{305} = \frac{\sigma_{a_{305}}^2 + \sigma_{pe_{305}}^2}{\sigma_{y_{305}}^2}$$

The daily and the total yield were obtained multiplying the vector of the regression coefficient of each animal for the orthogonal polynomial coefficients for each day and for the sum of the 305 days, respectively. In this way it was possible to estimate the day of maximum production for each lactation. Five measures of PS of lactation were calculated using the results of the RRM, adapting the equations of Jamrozik *et al.* (1997), Jakobsen *et al.* (2002) and Cobuci *et al.* (2004) to the Carora dataset, setting the peak to 50 days of lactation instead of 60. The equations for PS are reported below:

$$\begin{aligned} PS_1 &= (EBV_{270} - EBV_{50}) \\ PS_2 &= \left(\sum_{d=106}^{205} EBV_d - \sum_{d=6}^{105} EBV_d \right) \\ PS_3 &= \left(\sum_{d=206}^{305} EBV_d - \sum_{d=6}^{105} EBV_d \right) \\ PS_4 &= \sum_{d=51}^{269} (EBV_d - EBV_{50}) \\ PS_5 &= \sum_{d=50}^{269} (EBV_d - EBV_{270}) \end{aligned}$$

PS₁ represents the difference in EBV between the peak of lactation and a point in the end of the lactation (270th day). PS₂ and PS₃ represent the differences in EBV between the first third of lactation (d=6, 105), and the second third (d=106, 205) and the last third (d=206, 305) of lactation, respectively. PS₄ is the deviation of daily EBVs in the interval 51-270 DIM from the peak EBV, while PS₅ is the deviation of daily EBVs in the interval 50-279 DIM from the EBV at the end of the lactation (270th day).

Heritability for each PS measure was obtained according to the equation of Jakobsen *et al.* (2002):

$$h^2_{(ps)} = \frac{\sigma^2_{a(ps)}}{\sigma^2_{a(ps)} + \sigma^2_{pe(ps)} + k_{(ps)} * \sigma^2_{e(ps)}}$$

where (ps=PS₁, PS₂, PS₃, PS₄, PS₅) and k_(ps) is a constant taking the values 2, 200, 200, 48620, and 48620, for PS₁, PS₂, PS₃, PS₄, and PS₅, respectively. The solutions for RR coefficients for each animals were obtained using the REMLF90 programme (Misztal *et al.*, 2000; REMLF90, 2002) with the convergence criterion set to 10⁻¹².

Results and discussion

In the Carora dataset, the average milk daily production turned out to be 12.68±5.18 kg. Akaike information criterion and -2 logL are reported in Table 2. Those criteria were used to compare the models and to choose the best one fitting the data. The goodness-of-fit of the RRM for the Carora breed is the first step towards the implementation of this kind of model in the official genetic evaluation. Indeed, breeding values (BV) must be accurately estimated and predictions should not fluctuate if information accumulates (Pool *et al.*, 2000).

Table 1. The Legendre polynomial functions of standardised units of time *t*.

	Function
0	0.7071t ⁰
1	1.2247t ¹
2	-0.7906t ⁰ +2.3717t ²
3	-2.8062t ¹ +4.6771t ³
4	0.7955t ⁰ -7.9550t ² +9.2808t ⁴
5	4.3973t ¹ -20.5206t ³ +18.4685t ⁵

The model L3L4 showed the lowest values for AIC and -2 logL, suggesting that the fourth order for the PE effect and the third order for the AG effect are adequate to accurately describe the lactation curve in Carora breed.

Strabel *et al.* (2001) found that the typical shape of the lactation curve could be appropriately described by a third or fourth polynomial regression and the increase of the number of parameters for PE effect could lead to a reduction in the residuals variance. However, residual variances decreased <5% when substituting a fourth order with a fifth order regression (Pool *et al.*, 2000). Moreover, when only complete lactations are used for the estimation of parameters, which is the case of our study, a lower order regression could be fitted without significantly reducing the goodness-of-fit (Pool *et al.*, 2000; Misztal *et al.*, 2000).

In Figure 1 are shown the estimated trends

in daily heritability and repeatability (r_d) for test day model with the lowest values for AIC and -2 logL, (L3L4) that resulted the most adequate to describe the lactation curve in Carora breed.

Daily heritability ranged from 0.21 to 0.30 and it was lower at the beginning of the lactation. Repeatability ranged from 0.50 to 0.56, showing a slight decrease across lactation. The observed trends could be desirable in tropical conditions, because they are strongly influenced by non-genetic effects cumulated before calving and associated with the farmer's decision about drying off (Strabel *et al.*, 2001). On the other hand, Jamrozik *et al.* (1997) asserted that at the beginning of lactation, heritability should be high because the daily yields during the first 10 days might be critical to calf survival in terms of volume and content and could lead to a large genetic component.

Table 2. Akaike's information criterion, and minus twice log likelihood used for the model comparison.

Legendre polynomial coefficients for the additive genetic and permanent environmental effect ^o	Model short name	AIC	-2 logL
L _a (3)+L _p (3)	L3L3	513706.1	513678.1
L _a (3)+L _p (4)	L3L4	513274	513238
L _a (4)+L _p (3)	L4L3	518854.2	518818.2
L _a (4)+L _p (4)	L4L4	518825	518781

AIC, Akaike's information criterion; -2 logL, minus twice log likelihood. ^oThe number in parentheses gives the order of Legendre polynomial for the additive genetic effect (L_a) or permanent environmental effect (L_p).

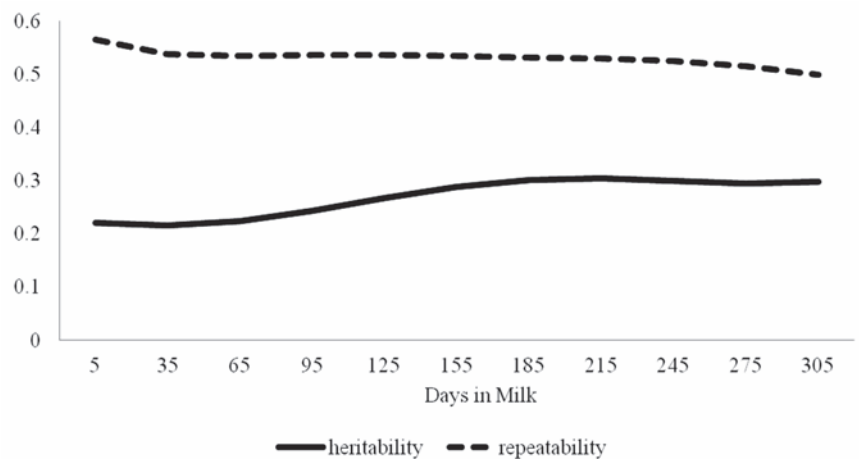


Figure 1. Estimated trends in daily heritability and repeatability for test day model with the lowest values for Akaike information criterion and the minus twice log likelihood (L3L4), which resulted the most adequate to describe the lactation curve in Carora breed.

Resulting values agreed with those found in the literature, particularly with those obtained by Santellano-Estrada *et al.* (2008) who worked on a Criollo breed in tropical conditions.

The estimated heritability value for a 305 day lactation (h^2_{305}) achieved with the RRM was 0.33, *i.e.* higher than the value estimated with the official stAM (0.18). The same situation was found for the repeatability; in fact using RRM (r_{305}) the resulting value was 0.53, while using the stAM this value was 0.39. This difference could be related to the gap between the amount of information available for each cow in the two models, since the in the RRM, around 10 TD for each lactation for each cow were considered, while instAM only the cumulative yield was included.

Correlation values between the BVs obtained with the RRM and the stAM are high and positive (Pearson correlation=0.71 and Spearman correlation=0.72), indicating a good association between the models. This result was confirmed also by the outcomes found in the literature (Jakobsen *et al.*, 2002). The BV obtained with the RRM were first compared to stAM-BVs to evaluate the correlation, and sub-

sequently were used to calculate the PS values.

In Table 3 the mean (\pm standard deviation), maximum and minimum values of six measures of estimated breeding values (EBV) of PS are reported. The coefficient of variability was similar with the exception of PS₅ which was very high. Since PS₅ and PS₄ are the deviations between EBV from the 50th to 269th day respect to a point at the end of lactation (270th day) and the peak (50th day) respectively, it can be argued that EBV at the end of lactation are more variable than that of the peak itself and this variability can be due to less observation at the end of lactation.

Heritabilities and correlations among EBV for PS and 305 days milk yield obtained from RRM and stAM are reported in Table 4.

Different values of PS were reported by Jakobsen *et al.* (2002) and Cobuci *et al.* (2007) in temperate breeds. It is difficult to compare our values with those found in literature, firstly, because day of peak occurs earlier in Carora breed than in temperate breeds, and, secondly, because the definition of PS was not consistent across the studies (only three PS measures out of five were reported as EBV). High

values of PS₁, PS₂, PS₃ and PS₄ and low values of PS₅ indicated high value of PS of the lactation, since in this study we were dealing with EBV. Regarding the values of PS₁, this could be explained by the fact that this measure was the result of a difference of EBV between the peak of the lactation (50th day) and a point in the last part of the lactation (270th day). A larger positive value of this deviation indicated a higher production ability in the last part of the lactation, or in other words, a more constant level of production. The average positive correlation with the 305 days milk yield (0.41), confirmed the increase in production related to the increase of PS.

The same consideration could be done for PS₂ and PS₃, which were obtained dividing the lactation in three periods and subtracting the cumulative EBV of the yield of the first third of the lactation (reference period: 6-105 days) from cumulative EBV of the central (PS₂-reference period: 106-205 days) and of the last part of the lactation (PS₃ - reference period: 206-305 days). Also for these measures, larger positive values were associated to a more constant level of production in the central and final part of the lactation; furthermore the increase of production was confirmed by the correlation with the 305 milk yield EBVs that was 0.52 and 0.30 with PS₂, and PS₃, respectively.

Another positive correlation was obtained between the EBVs for total milk yield and the EBVs for PS₄ (0.50). This measure represented the summation of the daily deviations within the interval 51-279 days from the 50th day. High values of PS₄ indicated a slight slope of the lactation curve, since these values was obtained as a sum of negative values, the more the value is close to 0 the more the lactation is constant. Different results were found for PS₅ values, which were the sum of the daily deviations of the interval 50-269 day from the 270th day of lactation. In this case lower values indicated high PS since the deviations from the 270th day were smaller when lactation curves presented a less marked slope. For this measure of PS the correlation with the 305 days milk yield was -0.18. The Pearson correlations between PS₅ and the other measures (ranging from -0.66 to -0.98), confirmed the opposite tendency of this measure respect to the others.

Heritabilities for the five measures of PS were slightly higher than those reported by Jakobsen *et al.* (2002), but the moderate value of heritability of PS₂ (0.25) and PS₃, and the moderate value of correlation with the 305 milk yield (0.52 and 0.30, respectively) could be interesting when selecting for quantity of milk yield and PS.

Correlation values between the BVs

Table 3. Mean±standard deviation minimum and maximum values of estimated breeding values for persistency of lactation.

Persistency	Mean±SD	Minimum	Maximum
PS ₁	0.318±0.857	-2.859	4.617
PS ₂	28.462±58.461	-194.984	288.839
PS ₃	-38.618±69.925	-300.097	304.69
PS ₄	57.945±124.194	-421.817	638.818
PS ₅	-12.316±82.588	-404.847	353.918

SD, standard deviation; PS₁, difference in EBV between the peak of lactation and a point at the end of the lactation (270th day); PS₂, difference in EBV between first (d=6, 105) and second (d=6, 105) third of lactation; PS₃, difference in EBV between second (d=6, 105) and last (d=206, 305) third of lactation; PS₄, deviation of daily EBV in the interval 51-270 DIM from the peak EBV; PS₅, deviation of daily EBV in the interval 50-279 DIM from the EBV at the end of lactation (270th day); EBV, estimated breeding values; DIM, days in milk.

Table 4. Heritability, Pearson and Spearman correlations among persistency values, breeding values of 305 days obtained with the random regression models and the single trait Animal Model.

	PS ₁	PS ₂	PS ₃	PS ₄	PS ₅	BV _{ST}	BV _{RRM}
PS ₁	<i>0.26</i>	0.90	0.97	0.95	-0.87	0.45	0.41
PS ₂	0.88	<i>0.25</i>	0.77	0.99	-0.58	0.56	0.52
PS ₃	0.96	0.73	<i>0.26</i>	0.83	-0.97	0.35	0.30
PS ₄	0.93	0.99	0.80	<i>0.18</i>	-0.66	0.54	0.50
PS ₅	-0.85	-0.53	-0.96	-0.62	<i>0.18</i>	-0.22	-0.18
BV _{ST}	0.44	0.55	0.34	0.54	-0.21	<i>0.18</i>	0.71
BV _{RRM}	0.39	0.53	0.28	0.50	-0.15	0.72	<i>0.33</i>

PS₁, difference in EBV between the peak of lactation and a point at the end of the lactation (270th day); PS₂, difference in EBV between first (d=6, 105) and second (d=6, 105) third of lactation; PS₃, difference in EBV between second (d=6, 105) and last (d=206, 305) third of lactation; PS₄, deviation of daily EBV in the interval 51-270 DIM from the peak EBV; PS₅, deviation of daily EBV in the interval 50-279 DIM from the EBV at the end of lactation (270th day); EBV, estimated breeding values; DIM, days in milk; BV_{ST}, breeding values; BV_{RRM}, breeding values following random regression models. Heritability values are on the diagonal (in italics); Pearson values are above the diagonal; Spearman values are below the diagonal.

obtained with the RRM and the lactation model currently used in Venezuela (stAM), are quite high and positive (Pearson correlation=0.71 and Spearman correlation=0.72), when all the animals are considered.

Considering only males with more than 10 daughters, the correlations between BVs obtained with the two models rise up to 0.79 and 0.76 for Pearson's and Spearman's correlation, respectively. Further increases are observed when the number of daughters for each sire is higher than 20 (Pearson correlation=0.84 and Spearman correlation=0.79).

The similarity between values obtained with Spearman and Pearson correlation in the three different scenarios (whole population, sires with more than 10 daughters and sires with more than 20 daughters) indicate that there is no extreme re-ranking among animals, meaning that animals tend to maintain their position using the two different evaluation models.

Observing the PS of sires with re-ranking higher than 20 positions, it is possible to see how the values for the PS₁, PS₂, PS₃ and PS₄ and average for PS₅ are low. This aspect should be taken in account during the choice of sires to be used in the selection programmes, since the BV obtained with the RRM need to be associated with the ranking for the PS. In general, these values of heritability are low to moderate and selection for PS could be included in breeding programmes. The negative correlation of PS₅ appeared interesting, since lower values of this measures indicated higher milk yields.

Conclusions

The use of a RRM to analyse longitudinal traits makes it possible to study changes over time, and in a dairy cattle context favours a better comprehension of the genetics of lactation. The correlation between the stAM with the TD-RRM indicates the possibility to use this kind of model instead of the lactation model currently used by the Carora Breeders Association. The use of a RRM could be useful especially when dealing with records collected in tropical environment, because of the large impact of the environment on daily milk production. Furthermore, by RRM, genetic merit of animals can be predicted based on daily milk yield records from early lactations.

The five measures of PS calculated in this study could open new selection opportunities.

The importance of these traits should be better investigated, especially considering the moderate heritability and the positive relation with the total milk yield. The magnitude of heritability and the moderate to high strength of correlation coefficients indicate that in Carora breed parameter PS₂ or PS₃ can be an appropriate measure of PS. However, further studies are needed to evaluate the effectiveness of measures of PS as selection criteria for the simultaneous improvement of lactation yield and PS.

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