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Breed, heterosis, and recombination effects for lactation curves in Brazilian cattle

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ABSTRACT - The objective of this study was to estimate the breed, heterosis, and recombination effects on different components of the lactation curve of Girolando cattle. The dataset used consisted of 12,121 purebred cows of Holstein (H) and Gyr (G) breeds, and six H×G crossbred cows (Girolando). The model used presents random effects of herd and cow, regression coefficient associated with linear effect of proportion of H breed, regression coefficient associated with the linear effect of heterosis between H and G breeds, regression coefficient associated with the linear effect of recombination between H and G breeds, and random effect of residual. Dijkstra's (DJ), Nelder's (ND), Wilmink's (WL), and Wood's (WD) models were tested to fit production records of these different genetic groups. These models were then tested according to evaluation criteria of quality of fit (AIC, BIC, and RMSE), and the two best models (WD and WL) were chosen for estimation of 305-day milk yield (MY_{305}), peak yield, time to peak, and persistency of milk yield. The breed effect was significant for all traits and components of the lactation curve. The heterosis effect was significant for all traits, and was more significant for MY_{305} (945.62±79.17 kg). Peak yield was the component of lactation curve that presented the most significant heterosis effect, partially explaining the heterosis effect (12 to 21%) found for MY_{305}. The recombination effect was positive only for lactation period and time to peak of lactation in Girolando cows.

Keywords: crossbreeding, dairy cattle, peak yield, persistency

1. Introduction

Girolando is a dairy cattle breed created in Brazil by crossing the Gyr and Holstein breeds for milk production systems in tropical pastures (Canaza-Cayo et al., 2017). This crossing aimed to obtain heterosis and complementarity between these breeds (Canaza-Cayo et al., 2014). In Brazil, approximately 80% of the milk yield produced is from crossbred animals; in addition, milk yield of Girolando cows increased 57% over 18 years (Silva et al., 2020).

The use of crossbred animals for milk production requires analysis of performance of individual cows, and the lactation curve is one of the main tools used to predict such performance (Pereira et al., 2016). The main components of the lactation curve are peak yield, time to peak, and persistency of milk yield (Wasike et al., 2014). However, persistency of milk yield is the most important component, since the ability to maintain a high level of milk yield after peak yield is associated with production costs (Güler and Yanar, 2009). Animals with a less pronounced peak of lactation are less prone to physiological stress because they have lower production at peak and thus do not have as high of an energy deficit, which contributes to a lower occurrence of metabolic disturbances and reproductive problems (Grossman and Koops, 1999; Tekerli et al., 2000).

Considering that the shape of the lactation curve differs among breeds, and even among animals, obtaining individual parameters of this curve is important for studies evaluating the heterosis effect not only on components of the lactation curve, but also on the total milk production during lactation. Information about the heterosis effect on components of the lactation curve may assist breeders in decision-making, for example in choosing the most suitable genetic groups for crossbreeding.

In Brazil, the heterosis effect is important to increase 305-day milk yield in Girolando cattle (Facó et al., 2002, 2008; Daltro et al., 2020). However, further studies are needed, mainly on other traits of economic importance, such as components of the lactation curve. They are important because the heterosis obtained from crossbreeding is an extra benefit beyond the genetic gain that can be created by pure breeding (Sorensen et al., 2008). In the case of Girolando, this benefit would be a better use of the selection already conducted for purebred Holstein and Gyr, which contribute to the formation of the different genetic groups that compose the Girolando breed.

Therefore, a more appropriate use of key reproducers from certain genetic groups for crossbreeding would expand the benefits obtained by heterosis, indirectly adding this extra benefit to the high genetic gain achieved after several years of selection in these two pure breeds, contributing to improvements in the productive and reproductive efficiency of herds and in the Brazilian dairy sector. Moreover, the production of semen doses of Girolando increased by 15% in 2019 when compared with 2018 (Silva et al., 2020).

In this context, the objective of this study was to estimate breed, heterosis, and recombination effects on test-day milk yield, 305-day milk yield, and other components of the lactation curve (peak yield, time to peak, and persistency of milk yield) of Girolando cows.

2. Material and Methods

2.1. Data and editing procedure

The data used consisted of 96,431 test-day milk yield records of first lactation of 12,121 cows from 1,221 herds from the state of Minas Gerais, Brazil, from 1998 to 2014. The breeds of these cows were Holstein (H), Gyr (G), and Girolando. The Girolando breed consisted of H×G crossbreds that are officially called Girolando in Brazil, which have the following proportions of Holstein and Gyr genes: 1/4H×3/4G (1/4H), 3/8H×5/8G (3/8H), 1/2H×1/2G (1/2H), 5/8H×3/8G (5/8H), 3/4H×1/4G (3/4H), and 7/8H×1/8G (7/8H).

A minimum of four and maximum of ten test-days from 5 to 305 days of milking were considered to estimate lactation (Padilha et al., 2017; Pereira et al., 2019). Cows with test-day milk yield (MY) and 305-day milk yield (MY_{305}), or lactation period different from the mean (standard deviation higher than ± 3.0) were not considered for the study. The records of MY and MY_{305} were not considered when milk yields were not within the ranges of 3 to 45 kg and 686.07 to 11026.40 kg, respectively. Similar magnitudes for these two traits were reported by Pereira et al. (2019), when defining restrictions for the database. The descriptive analysis of the edited data is presented in Table 1.

2.2. Lactation curve models

The nonlinear models used to fit MY over the lactation of Holstein, Gyr, and Girolando breeds were:

Incomplete gamma function (WD) (Wood, 1967):

$$Y_t = at^b e^{-ct} \tag{1}$$

Exponential Wilmink (WL) (Wilmink, 1987):

$$Y_t = a + be^{-kt} + ct \tag{2}$$

Inverse quadratic polynomial (ND) (Nelder, 1966):

$$Y_t = t\,(a + bt + ct^2)^{-1} \tag{3}$$

Dijkstra (DJ) (Dijkstra et al., 1997):

$$Y_t = ae\left[\frac{b\,(1 - e^{-ct})}{c} - dt\right], \tag{4}$$

in which Y_t is milk yield (kg/d); t is the lactation time (d); e is the basis of the natural logarithm; a is the y-intercept that controls the vertical position of the curves when plotting daily milk yield against days in lactation; b and c are control parameters of the height of maximum yield; and d and k are parameters of the shift of the curve up or down to the y-axis. Parameters a, b, c, d, and k and days in milk define the shape and position of each curve. A constant k of 0.05 was considered due to the good fit of the model in preliminary analysis.

The MY_{305} was evaluated as described by Vargas et al. (2000). For all models, time to peak (TP) was assumed to be the month with the highest test-day milk yield of the cow and peak yield (PY) of a cow was the highest test-day milk yield of the lactation, calculated according to Bahashwan (2018) and Hossein-Zadeh (2018). The MY_{305}, TP, PY, and persistency of milk yield were estimated in the two best models, according to evaluation criteria of quality of fit (RMSE, AIC, and BIC). Lactation period (LP) was the difference (days) between calving and dry period.

2.3. Breed proportions, coefficients of specific heterosis, and recombination loss

Three dairy breeds in the Brazilian population were described, and the proportion of genes was calculated for each cow, using simple identification (Dickerson, 1973; Penasa et al., 2010a, 2010b):

$$\alpha_i^p = \frac{(\alpha_i^s + \alpha_i^d)}{2}, \tag{5}$$

in which α_i^p is the proportion of genes from breed i in progeny, α_i^s is the proportion of breed i in sire, and α_i^d is the proportion of breed i in dam. Three dairy breeds (Holstein, Gyr, and Girolando) were described as having sufficient records to estimate breed effects for production traits (Table 1). Each proportion of the Holstein genes (1/4H, 3/8H, 1/2H, 5/8H, 3/4H, and 7/8H) plus the proportion of Gyr genes was equal to 1. The classes of gene proportion for breed were defined as: 1 = 0%, 2 = 25%, 3 = 37.5%, 4 = 50%, 5 = 62.5%, 6 = 75%, 7 = 87.5%, and 8 = 100%.

Coefficients of specific heterosis and recombination were calculated between pairs of dairy breeds, using the following equation (Dickerson, 1973):

$$\delta_{ij}^p = \alpha_i^s\alpha_j^d + \alpha_j^s\alpha_i^d \text{ and } Y_{ij}^p = (\alpha_i^s + \alpha_j^d)(\alpha_j^s + \alpha_i^d) - \delta_{ij}^p, \tag{6}$$

Table 1 - Number of cows, herds, and lactations by genetic group

Genetic group	Percentage of Holstein gene	Number of herds	Number of cows	Number of lactations
H	100	103	566	4,138
1/4H	25.00	102	265	1,973
1/2H	50.00	262	2,590	20,221
3/4H	75.00	260	3,756	31,091
3/8H	37.50	75	311	2,487
5/8H	62.50	252	3,345	26,070
7/8H	87.50	118	990	8,255
G	0	49	298	2,196

H - Holstein breed; G - Gyr breed; 1/4H, 1/2H, 3/8H, 3/4H, 5/8H, 7/8H - crossbred (Holstein × Gyr) cows which are officially called Girolando in Brazil.

in which δ_{ij}^{p} is the coefficient of expected heterosis between fractions of breeds i and j in progeny, α_j^s is the proportion of breed j in sire, α_j^d is the proportion of breed j in dam, and Υ_{ij}^{p} is a covariable for recombination loss for the same crossbred animal p. Heterosis and recombination coefficients summed across breed combinations.

These specific heterosis effects were used for the six genetic groups of Girolando, because the distribution of cows in classes of coefficients of expected heterosis was suitable for this purpose (Penasa et al., 2010a). The coefficient of general heterosis for each cow was obtained by summing the specific heterosis coefficients previously calculated. The classes of heterosis coefficients were defined as: 1 = 0, 2 = 0.250, 3 = 0.375, 4 = 0.500, 5 = 0.625, 6 = 0.750, 7 = 0.875, and 8 = 1.

2.4. Statistical analyses

The models were fitted to test-day records using the NLIN procedure in the SAS program (Statistical Analysis System, version 9.1). The nonlinear models were fitted to milk yield records using the Gauss-Newton iteration method.

The nonlinear models were tested for goodness of fit using root mean square error (RMSE), Akaike's information criterion (AIC), and Bayesian information criterion (BIC).

RMSE was calculated using the equation:

$$RMSE = \sqrt{\frac{RSS}{n - p - 1}}, \tag{7}$$

in which RSS is the residual sum of squares, n is the number of observations (data points), and p is the number of parameters in the equation.

AIC was calculated using the equation:

$$AIC = n \times \ln(RSS) + 2p \tag{8}$$

BIC was calculated using the equation:

$$BIC = n \ln\left(\frac{RSS}{n}\right) + p \ln(n) \tag{9}$$

Smaller numerical values of RMSE, AIC, and BIC indicate better fit when comparing different models.

The heterosis effect of components of the lactation curve in crossbred genetic groups of Girolando cattle was estimated by the MIXED procedure of the SAS. Breed and heterosis effects were obtained after fitting the following mixed linear model:

$$Y_{jkl} = \mu + H_j + C_k + \sum_{q=1}^{2} \varphi_q a^q + \beta f + \lambda h + \Upsilon r + \varepsilon_{jkl}, \tag{10}$$

in which Y_{jkl} is the observation l taken in cow k and herd j, μ is the overall mean, H_j is the random effect of herd j, C_k is the random effect of cow k, φ_q are regression coefficients associated with linear (q = 1) and quadratic (q = 2) effects of cow age, β is the regression coefficient associated with the linear effect of proportion of Holstein breed (f), λ is the regression coefficient associated with the linear heterosis effect (h) between Holstein and Gyr breeds, Υ is the regression coefficient associated with the linear effect of recombination (r) between Holstein and Gyr breeds, and ε_{jkl} is the random effect of residual error with expectation and variance equal to 0 and σ_e^2. The estimate of regression coefficient associated with the proportion of Holstein (β) provides an estimate of the breed difference between Holstein and Gyr. The estimate of the regression coefficient associated with the linear effect of heterosis (λ) provides an estimate of the absolute difference between the expected performance of a first-cross cow (H×G) related to the average of the two straight breeds (H and G). The recombination (r) is intended to characterize the distance of the heterosis achieved from its additive component.

3. Results

3.1. Comparison of the models

There were differences in quality of fit among the evaluated nonlinear models (DJ, ND, WD, and WL) based on RMSE, AIC, and BIC values (Table 2). The RMSE, AIC, and BIC values of DJ, ND, WD, and WL models were different for the different genetic groups. The WL model presented the lowest RMSE values

Table 2 - Goodness of fit for average standard curves of milk yield (kg/day) by different nonlinear models in Holstein (H), Gyr (G), and Girolando (1/4H, 1/2H, 3/4H, 3/8H, 5/8H and 7/8H) cows

Genetic group	Model	Statistics		
		RMSE	AIC	BIC
1/2H	DJ	6.62	398247.10	109191.80
	ND	6.63	398344.60	109289.30
	WL	4.44	33677.03	10610.68
	WD	5.89	39284.16	11015.49
1/4H	DJ	6.62	33431.66	10965.52
	ND	6.62	33435.94	10969.8
	WL	3.00	1730.95	573.65
	WD	6.04	2332.65	949.82
3/4H	DJ	6.07	547022.80	142317.70
	ND	6.08	547158.70	142453.60
	WL	5.36	38744.64	11672.26
	WD	5.79	40696.00	12555.42
3/8H	DJ	6.28	34478.70	11089.20
	ND	6.29	34481.31	11091.82
	WL	3.38	917.84	345.93
	WD	5.82	2622.66	1042.57
5/8H	DJ	5.95	416643.50	109581.80
	ND	5.95	416673.80	109612.20
	WL	4.90	16594.17	5198.85
	WD	5.69	27672.23	8754.99
7/8H	DJ	5.98	129813.10	37108.36
	ND	5.99	129842.00	37137.19
	WL	5.78	8955.89	3143.69
	WD	5.78	8955.89	3143.69
G	DJ	5.68	703254.4	175647.10
	ND	6.39	1551512	385150.30
	WL	5.77	707686.80	177731.60
	WD	5.25	341.06	170.42
H	DJ	6.81	1540181.00	391394.20
	ND	6.82	1540457.00	391670.00
	WL	5.77	6505.87	2480.74
	WD	6.83	707686.80	177731.60

DJ - Dijkstra's model; ND - Nelder's model; WL - Wilmink's model; WD - Wood's model; RMSE - root mean square error; AIC - Akaike's information criterion; BIC - Bayesian information criterion.

for genetic groups 1/4H (3.00), 3/8H (3.38), 1/2H (4.44), and 5/8H (4.90). However, when this model was evaluated by criteria AIC and BIC, the lowest values were found for groups 1/4H, 3/4H, 3/8H, and 5/8H. The WD model presented the lowest RMSE values for groups G (5.25), 5/8H (5.69), and 7/8H (5.78). However, criteria AIC and BIC in WD model indicated the lowest values for groups 1/4H, 3/8H, and G. The DJ model presented the lowest RMSE for genetic groups G (5.68), 5/8 (5.95), 7/8 (5.98), and 3/4 (6.07); and the ND model presented the lowest RMSE for groups 5/8H (5.95), 7/8H (5.99), and 3/4H (6.08). However, DJ and ND models presented the lowest AIC and BIC values for groups 1/4H and 3/8H. The lowest values found for the evaluation criteria of quality of fit were, in general, for WD and WL models, regardless of the genetic group.

3.2. Estimates of equation parameters

The results of the parameters estimated by the different models (DJ, ND, WD, and WL) showed different estimated mean values for the genetic groups (Table 3). However, DJ, ND, and WD models estimated positive values for parameters a, b, and c, presenting values for b and c close to zero in all genetic groups. The WL model showed positive values for parameter a and negative values for parameters b and c in all genetic groups.

The lowest values of the parameters were estimated by ND model, and the highest by WL. Despite the different values of the estimated parameters and values of the evaluation criteria of quality of fit (RMSE, AIC, and BIC), all models (DJ, ND, WD, and WL) satisfactorily described the lactation curve of all genetic groups, except for 1/4H and 3/8H (Figure 1).

The curves estimated by the different models showed that DJ, WD, and WL models followed, in general, the pattern of the lactation curve of each genetic group. However, ND model showed greater difficulty in following the pattern of the lactation curve of all genetic groups, mainly at the beginning of lactation.

3.3. Average estimates of different traits

The means for MY, LP, MY_{305}, PY, and TP presented significant differences among the crossbred genetic groups (Table 4). Similarly, significant differences ($P<0.05$) were found among the genetic groups and means for the traits estimated by the two best models (WD and WL), according to the evaluation criteria of quality of fit (Table 5). The means for MY and MY_{305} of the different genetic groups ranged from 12.52 to 17.76 kg and from 3085.18 to 4974.07 kg, respectively. Genetic groups H (17.76 kg), 3/4H (17.57 kg), and 7/8H (17.66 kg) presented similar MY; these groups presented the highest yields. Similarly, the estimated MY_{305WD} and MY_{305WL} were higher in groups 3/4H (5226.36 and 5256.04 kg) and 7/8H (5227.62 and 5261.50 kg), followed by H (5202.36 and 5182.97 kg) and 1/2H (5076.96, and 4997.39 kg). Group G presented the lowest MY (12.52 kg), MY_{305} (3085.18 kg), MY_{305WD} (3674.44 kg), and MY_{305WL} (3485.15 kg).

The LP mean ranged from 272.11 to 345.49 days in the different genetic groups, and was higher in groups 7/8H and 3/4H. The lowest LP mean was found in genetic group G. The PY mean of the different genetic groups ranged from 16.83 to 22.83 kg. Groups H (22.83 kg), 7/8H (22.63 kg), and 3/4H (22.43 kg) presented the highest PY, and the highest estimated PY_{WD} (21.12 kg) and PY_{WL} (21.21 kg) were found in group H. The TP ranged from 77.97 to 99.07 days, with the highest values found in group 3/4H, followed by 7/8H. Contrastingly, the highest TP_{WD} mean (86.55 days) was found in group 7/8H, and the highest TP_{WL} mean (99.08 days) in group H. The lowest TP means of groups 3/8H, 5/8H, and G were similar. The lowest TP_{WD} were found in groups 5/8H and groups G. The lowest TP_{WL} of groups 5/8H and 1/2H were similar. The P_{WD} mean ranged from 7.14 to 7.48 in the different genetic groups, with the highest P_{WD} found in group 3/4H, followed by G and 7/8. Groups 3/4H (5.40) and 7/8H (5.53) had similar P_{WL} and presented the highest persistency of milk yield.

3.4. Breed, heterosis, and recombination effects on the traits

Breed, heterosis and, recombination effects were significant ($P<0.05$) for all traits evaluated, except for P_{WD} and P_{WL} (breed effect), LP and P_{WL} (heterosis effect), and TP and T_{WD} (recombination effect) (Table 6). Breed effect showed that Holstein cows had daily milk yields 8.28±0.45 kg higher than Gyr cows, and lactation periods 56.19±7.27 longer than Gyr cows. The MY_{305} of Holstein cows obtained from the Brazilian database and Wood's (MY_{305WD}) and Wilmink's (MY_{305WL}) models were, respectively, 2651.84±131.77 kg, 2920.53±115.12, and 2800.41±102.96 higher than those of Gyr cows. Peak yields of Holstein cows were 9.65±0.49 kg (PY), 10.94±0.57 kg (PY_{WD}), and 10.12±0.62 kg (PY_{WL}) higher than those of Gyr cows. Time

Table 3 - Estimated parameters (mean±SE) of milk yield (kg day^{-1}) by different nonlinear models in Holstein (H), Gyr (G), and Girolando (1/4H, 1/2H, 3/4H, 3/8H, 5/8H, and 7/8H) cows

Genetic group	Model	Parameter			
		a	b	c	d
1/2H	DJ	16.2114±0.3033	0.0089±0.0011	0.025±0.003	0.0013±0.0008
	ND	0.1340±0.0844	0.0451±0.0003	0.005±0.000	-
	WL	21.0371±0.1026	−7.6036±0.4224	−0.017±0.005	-
	WD	12.9066±0.3023	0.1305±0.0068	0.001±0.007	-
1/4H	DJ	12.1689±0.1427	0.0242±0.0131	0.0541±0.0184	0.0010±0.0001
	ND	0.1740±0.0342	0.0505±0.0014	0.0064±0.0008	-
	WL	18.6106±0.3189	−7.6573±1.2799	−0.0151±0.0019	-
	WD	11.2821±0.9193	0.1321±0.0239	0.0018±0.0002	-
3/4H	DJ	15.3844±0.2400	0.0107±0.0009	0.0262±0.0022	0.0013±0.0006
	ND	0.1731±0.0074	0.0443±0.0003	0.0061±0.0001	-
	WL	21.0555±0.0816	−9.1222±0.3369	−0.018±0.0004	-
	WD	11.7012±0.2251	0.1562±0.0055	0.0021±0.0005	-
3/8H	DJ	13.6123±1.4558	0.0158±0.0117	0.0524±0.0250	0.0010±0.0001
	ND	0.1168±0.0307	0.0529±0.0014	0.0071±0.0008	-
	WL	18.0382±0.0322	−5.1545±1.2462	−0.0161±0.0017	-
	WD	12.7554±0.9977	0.0926±0.0230	0.0016±0.0002	-
5/8H	DJ	13.6231±0.3816	0.0144±0.0027	0.0061±0.0001	0.0011±0.0005
	ND	0.1365±0.0093	0.0519±0.0004	−0.018±0.0004	-
	WL	18.2546±0.0905	−5.9027±0.3693	−0.0166±0.0005	-
	WD	12.1592±0.2827	0.1085±0.0068	0.0018±0.0007	-
7/8H	DJ	15.3112±0.5398	0.0122±0.0027	0.0336±0.0058	0.0011±0.0009
	ND	0.1466±0.0136	0.0453±0.0005	0.0058±0.0003	-
	WL	20.8029±0.1575	−7.9901±0.6494	−0.0172±0.0008	-
	WD	12.6105±0.4614	0.1329±0.0106	0.0018±0.0001	-
G	DJ	9.9583±1.8235	0.0265±0.0138	0.0474±0.0099	0.0014±0.0004
	ND	0.0700±0.0058	0.0724±0.0003	0.0020±0.0001	-
	WL	16.8874±0.0811	−13.0033±1.1265	−0.0186±0.0004	-
	WD	10.2919±0.3979	0.1284±0.0106	0.0021±0.0009	-
H	DJ	20.4244±0.1888	0.0144±0.0007	0.0339±0.0012	0.0012±0.0002
	ND	0.1392±0.0027	0.0315±0.0001	0.0043±0.0005	-
	WL	29.3186±0.0562	−13.5816±0.2316	−0.0243±0.0003	-
	WD	16.0160±0.1486	0.1601±0.0027	0.0020±0.0002	-

a, b, c, d - parameters that define the scale and shape of the curve in the model.
DJ - Dijkstra's model; ND: Nelder's model; WL - Wilmink's model; WD - Wood's model.

to reach peak yield of Holstein cows was 16.57±5.12 (TP), 19.27±4.48 (TP_{WD}), and 9.38±4.28 days (TP_{WL}) longer than those of Gyr cows. Persistency of milk yield of Holstein cows was 0.13±0.11 kg (P_{WD}) and 0.59±1.66 kg (P_{WL}) lower than those of Gyr cows, although it was not significant (P>0.05).

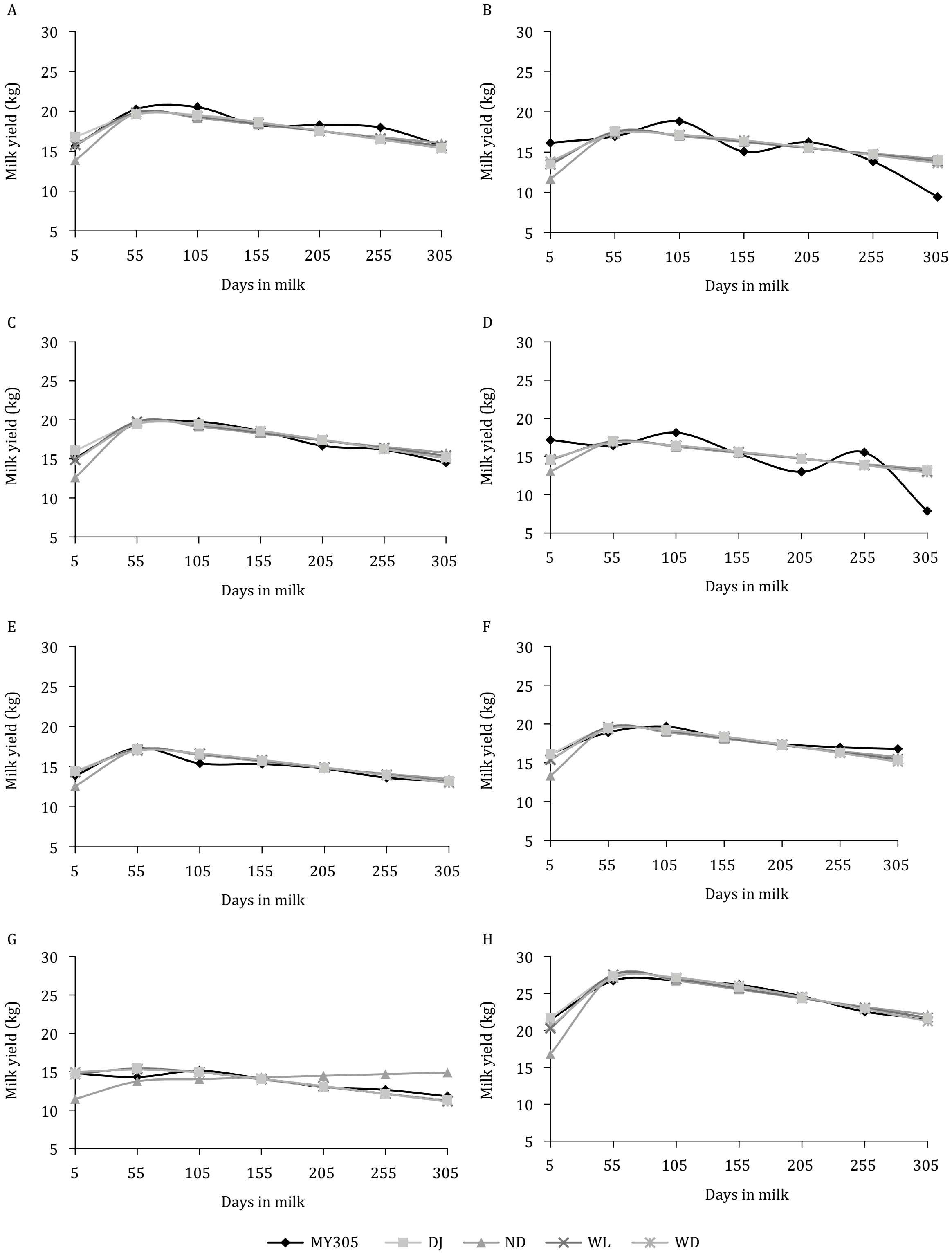

Figure 1 - Trajectory of lactation curves estimated by 305-day milk yield from database (MY_{305}), Dijkstra's (DJ), Nelder's (ND), Wilmink's (WL), and Wood's (WD) models for genetic groups 1/2H (A), 1/4H (B), 3/4H (C), 3/8H (D), 5/8H (E), 7/8H (F), G (G), and H (H).

Table 4 - Least square means and standard errors for daily milk yield (MY), lactation period (LP), 305-day milk yield (MY_{305}), peak yield (PY), and time to peak (TP) of Holstein (H), Gyr (G), and Girolando (1/4H, 1/2H, 3/4H, 3/8H 5/8H and 7/8H) cows

Genetic group	MY (kg)	LP (day)	MY_{305} (kg)	PY (kg)	TP (kg)
1/2H	17.06b±2.57	319.78b±9.68	4725.48b±42.25	21.87b±2.61	91.65bc±7.83
1/4H	15.25c±2.59	297.91de±9.57	4062.91c±45.34	19.52c±2.67	84.95cd±7.68
3/4H	17.57a±2.51	338.36a±10.16	4944.21a±41.72	22.43a±2.53	99.07a±7.82
3/8H	15.11c±2.59	298.56cd±9.42	4052.39c±43.28	19.62c±2.66	77.97d±7.44
5/8H	15.12c±2.47	312.37bc±9.79	4085.80c±41.66	19.24c±2.52	83.71d±7.67
7/8H	17.66a±2.53	345.49a±10.54	4974.07a±42.38	22.63a±2.52	94.06b±7.66
G	12.52d±2.40	272.11e±10.37	3085.18d±41.91	16.83d±2.55	81.20d±7.46
H	17.76a±2.80	300.17de±10.77	4673.81b±47.09	22.83a±2.85	89.69bc±7.43

a-e - Estimates of least square means followed by different letters in the same column are significantly different ($P<0.05$).

Table 5 - Least square means and standard errors for daily milk yield, 305-day milk yield, peak yield, time to peak, and persistency of milk yield, according to the best models (WD and WL) evaluated by criteria of quality of fit

Genetic group	MY_{WD} (kg)	MY_{WL} (kg)	MY_{305WD} (kg)	MY_{305WL} (kg)	PY_{WD} (kg)	PY_{WL} (kg)	TP_{WD} (day)	TP_{WL} (day)	P_{WD}	P_{WL}
1/2H	17.76b±6.72	17.84b±6.68	5076.96b±34.84	4997.39b±40.64	19.78b±2.66	19.80c±2.60	83.71bc±7.25	89.51c±5.89	7.33b±1.05	4.35b±3.84
1/4H	15.29d±6.74	15.41d±6.66	4397.84c±109.69	4304.88c±125.61	17.84c±2.70	17.43d±2.62	80.28bd±6.97	90.02bc±5.72	7.27bc±1.10	3.81abc±3.61
3/4H	17.48c±6.15	14.67bc±6.11	5226.36a±28.87	5256.04a±33.90	20.49ab±2.87	20.19ab±2.48	78.82cd±7.12	90.90bc±6.11	7.48a±1.07	5.40c±3.77
3/8H	14.76d±6.41	14.67d±6.38	4405.00c±100.44	4268.73c±118.51	17.54c±2.61	17.53d±2.54	78.82cd±7.12	93.07ac±5.78	7.14c±1.06	3.61ab±3.53
5/8H	14.89d±6.12	14.85d±6.09	4414.91c±30.58	4350.73c±35.20	17.37c±2.51	17.44d±2.45	79.29d±7.14	89.55c±5.83	7.15c±1.07	3.10a±3.61
7/8H	17.35c±6.07	17.37c±6.02	5227.62a±56.03	5261.50a±65.40	20.66ab±2.56	20.51ab±2.54	86.55ab±7.07	94.60ab±5.73	7.34b±1.34	5.53c±3.82
G	13.86e±5.98	13.39e±5.72	3674.44d±105.25	3485.15d±125.06	15.22d±2.50	14.86e±2.41	79.63d±7.25	94.45ab±5.72	7.35ab±1.20	3.03ab±3.64
H	23.66a±7.88	25.23a±6.67	5202.36ab±75.87	5182.97ab±89.21	21.12a±2.96	21.21a±2.83	83.56bd±7.50	99.08a±6.28	7.21bc±1.25	4.70bc±3.84

a-e - Estimates of least square means followed by different letters in the same column are significantly different ($P<0.05$).
MY_{WD} and MY_{WL} = daily milk yield by the Wood's and Wilmink's models, respectively; $305MY_{WD}$ and $305MY_{WL}$ = 305-day milk yield by Wood's and Wilmink's models, respectively; PY_{WD} and PY_{WL} = peak yield by Wood's and Wilmink's models, respectively; TP_{WD} and TP_{WL} = peak time by Wood's and Wilmink's models, respectively; P_{WD} and P_{WL} = persistency of milk yield by Wood's and Wilmink's models, respectively.

Table 6 - Breed, heterosis, and recombination effects with standard errors for daily milk yield (MY), lactation period (LP), 305-day milk yield (MY_{305}), peak yield (PY), time to peak (TP), and persistence of milk yield according to Wood's and Wilmink's models

Trait	Breed effect	Heterosis effect	Recombination effect
MY (kg)	$8.28 \pm 0.45^{***}$	$3.33 \pm 0.27^{***}$	$-2.80 \pm 0.36^{***}$
MY_{WD} (kg)	$10.51 \pm 0.51^{***}$	$4.25 \pm 0.30^{***}$	$-2.47 \pm 0.38^{***}$
MY_{WL} (kg)	$9.78 \pm 0.51^{***}$	$3.86 \pm 0.30^{***}$	$-2.77 \pm 0.32^{***}$
LP (day)	$56.19 \pm 7.27^{***}$	3.30 ± 4.49	$19.79 \pm 6.61^{**}$
MY_{305} (kg)	$2651.84 \pm 131.77^{***}$	$945.62 \pm 79.17^{***}$	$-430.14 \pm 106.19^{***}$
MY_{305WD} (kg)	$2920.53 \pm 115.12^{***}$	$826.84 \pm 75.18^{***}$	$-755.02 \pm 15.90^{***}$
MY_{305WL} (kg)	$2800.41 \pm 102.96^{***}$	$907.29 \pm 66.01^{***}$	$-846.15 \pm 98.04^{***}$
PY (kg)	$9.65 \pm 0.49^{***}$	$3.64 \pm 0.29^{***}$	$-2.81 \pm 0.46^{***}$
PY_{WD} (kg)	$10.94 \pm 0.57^{***}$	$4.90 \pm 0.33^{***}$	$-3.62 \pm 0.41^{***}$
PY_{WL} (Kg)	$10.12 \pm 0.62^{***}$	$4.33 \pm 0.36^{***}$	$-3.22 \pm 0.44^{***}$
TP (day)	$16.57 \pm 5.12^{***}$	$7.07 \pm 2.52^{***}$	2.25 ± 4.71
TP_{WD} (day)	$19.27 \pm 4.48^{***}$	2.53 ± 2.62	2.84 ± 3.19
TP_{WL} (day)	$9.38 \pm 4.28^{*}$	$8.15 \pm 2.47^{***}$	$11.83 \pm 2.91^{***}$
P_{WD}	0.13 ± 0.11	$-0.18 \pm 0.07^{**}$	$-0.26 \pm 0.13^{*}$
P_{WL}	0.59 ± 1.66	-1.82 ± 1.28	$-3.93 \pm 2.05^{*}$

MY_{305WD} and MY_{305WL} = 305-day milk yield by Wood's and Wilmink's models, respectively; PY_{WD} and PY_{WL} = peak yield by Wood's and Wilmink's models, respectively; P_{WD} and P_{WL} = persistency of milk yield by Wood's and Wilmink's models, respectively.
* $P<0.05$; ** $P<0.01$; *** $P<0.001$.

The positive heterosis effect of MY was 3.33±0.27 kg in crossbred cows compared with the average daily milk yield of the pure breeds. The heterosis effect of LP was 3.30±4.49 days in milk, although it was not significant ($P>0.05$). The heterosis effect of 305-day milk yield was 945.62±79.17 kg (MY_{305}), 826.84±75.18 (MY_{305WD}), and 907.29±66.01 kg (MY_{305WL}) higher in crossbred animals when compared with those of their parental pure breeds. The PY obtained from the dataset and models presented heterosis of 3.64±0.29 (PY), 4.90±0.33 (PY_{WD}), and 4.33±0.36 kg (PY_{WL}). The heterosis of time to peak was significant for TP and TP_{WL}, showing 7.07±2.52 and 8.15±2.47 days, respectively. However, the heterosis was not significant for TP_{WD} (2.53±2.62 days). The heterosis effect of persistency of milk yield was significant ($P<0.01$) only for P_{WD} (−0.18±0.07 kg).

The estimated recombination losses were negative for all traits, except for LP, TP, TP_{WD}, and TP_{WL}. However, only LP (19.79±6.61 days) and TP_{WL} (11.83±2.91 days) showed significant effect ($P<0.01$) among all traits that presented positive recombination effect.

4. Discussion

4.1. Model dynamics and estimates of equation parameters

The nonlinear models (DJ, ND, WD, and WL) could, in general, describe the lactation curve of all genetic groups, except for groups 1/4H, 3/8H, and G (Figure 1B, 1D, and 1G). However, there is no single and simple method to assess similarities and differences among nonlinear models, and the selection of a model to explain a specific set of data should not be entirely based on the model dynamics (Fathi Nasri et al., 2008). Thus, the use of statistical tests to classify and evaluate models is important (Motulsky and Ransnas, 1987).

Regarding the classification of quality of fit of the different models evaluated, values of RMSE, AIC, and BIC criteria indicated that WL and WD models were the best in terms of quality of fit due to their lower values. The WL model presented the best quality of fit of productive data of most genetic groups (1/2H, 1/4H, 3/4H, 3/8H, 5/8H, and H).

Sitkowska et al. (2020) compared the fit of productive records of primiparous and multiparous Holsteins cows in Poland and found lower RMSE, AIC, and BIC values for Wilmink's model when compared with Wood's model, denoting its best fit. Other studies have successfully used only Wilmink's model to describe lactation of dairy cows of different breeds (Macciotta and Vicario, 2005; Otwinowska-Mindur and Ptak, 2016).

Contrastingly, Torshizi et al. (2011) used both Wood's and Wilmink's models to investigate the lactation curve of Holsteins cows and found lower RMSE values for Wood's model, indicating that it has a better quality of fit of daily milk production records of a population.

In the present study, WD model presented the lowest RMSE, AIC, and BIC values only for groups 7/8H and G, indicating a better fit for more specific groups when compared with WL model. Ferreira et al. (2015) compared different models (Brody, Dijkstra, and Wood) for fit of lactation data of Holsteins cows in Paraná, Brazil, and chose Wood's model due to its best fit to the data of local population, which was probably due to its simplicity and fewer parameters. Similarly, in the present study, DJ model did not stand out among the models regarding values of the evaluation criteria of quality of fit.

Contrastingly, Dijkstra et al. (1997) and Val-Arreola et al. (2004) found that Dijkstra's model fits better to milk production records than empirical equations, such as Wood's model. Both studies used a high number of cows and observations per lactation, which may have contributed to significant differences among the evaluated equations (Fathi Nasri et al., 2008). The results found in the present work are consistent with those of Pollott and Gootwine (2000), who concluded, based on many dairy recording schemes using a maximum of ten monthly test-day records per lactation, that equations with more parameters, such as Dijkstra's, are over-parameterized and will not yield better fits than Wood's model. In these cases, it is common to find no recordings, or at most one recording, made before the peak yield, which makes the estimation of the cell proliferation phase of lactation and peak yield less accurate (Fathi Nasri et al., 2008).

Sitkowska et al. (2020) found that Wood's and Wilmink's are among the best models for modeling lactation curves; however, a different model may present a better fit depending on the type and homogeneity of data.

Therefore, it is difficult to find a single model to fit lactation curves that is the best in all aspects (Naeemipour Younesi et al., 2019). This difference in quality of fit of the models may be due to difference in breed, cow age, calving season, and production level of animals (Gantner et al., 2010). Studies have shown that the fit of mathematical models to lactation curves of animals depends not only on mathematical functions but on calving order (Şeahin et al., 2015) and biological aspects of the lactation of cows, which varied randomly (Gantner et al., 2010).

Thus, there is no consensus on the best criterion to be used to choose mathematical models to fit test-day milk yield records (Cobuci et al., 2011). Finding the best model is difficult, and different criteria may not indicate the same model. Therefore, nonlinear models should be evaluated in each specific condition to be recommended (Fathi Nasri et al., 2008).

4.2. Estimation of equation parameters and productive traits

Wood's and Wilmink's models classify lactation curves as typical (standard) or atypical, based on parameters *b* and *c* (Sitkowska et al., 2020). The results in the present work indicate that the estimate of parameters of the best models (WD and WL) presented typical lactation curves for the different genetic groups, because *b* and *c* should be above zero in WD model, and the typical curve presented negative values for parameters *b* and *c* in WL model (Kocaman and Kurc, 2018).

The MY mean found for groups H, 3/4H, 1/2H, 3/8H, and 1/4H were higher than those reported by McManus et al. (2008) for the same groups. Similarly, MY_{305} means were higher than those found by Facó et al. (2002) for 1/4H, 1/2H, 3/4H, and 5/8H, and those reported by Balancin Júnior et al. (2014) for 1/2H, 3/4H, and 7/8H. These results indicated that the two models (WD and WL) followed the same trend for MY and MY_{305} when fitted to test-day records, except for the curve estimated for group H. Sitkowska et al. (2020) found that WD and WL models overestimated MY and MY305 of Holsteins cows, and WL model showed closer values to those observed in the database of the population.

Contrastingly, the present study showed that both models overestimated MY and MY_{305} of group H. However, WL model presented closer values to those observed in the database of the population, which is a similar result to that found by Sitkowska et al. (2020).

The means for the estimates of MY_{305} of group H were lower than those of groups 7/8H, 3/4H, and 1/2H. However, means for the estimates of MY_{305WD} and MY_{305WL} of group H were lower only than those of groups 7/8H and 3/4H. This indicates that crossbred animals present better adaptation to tropical environmental conditions of Brazil than purebred Holstein animals. It may also be dependent on management and technification level of the predominant production system. Similar results were found by Facó et al. (2002), who reported that, in the Center-West, Southeast, and Northeast regions of Brazil, the mean for test-day milk yield of Holstein cows is lower than that of groups 7/8H, 3/4H, and 1/2H. This can be an evidence of lower adaptation of pure breeds to local environmental conditions. The term adaptation, in a broad sense, means that the type of gene acting on crossbred animals improves the performance of these animals (McManus et al., 2008).

Higher MY and longer LP were more positively associated with groups 3/4H and 7/8H, followed by group 1/2H. Similarly, Guimarães et al. (2002) reported higher milk yield and longer lactation period for 7/8H and 3/4H animals, and explained this result by the genetic proportion of Holstein in crossbred groups, combined with their better adaptability to environmental conditions, when compared with pure breeds.

The shortest lactation periods were found for Gyr breed because zebu breeds have, in general, shorter lactation periods (Glória et al., 2006). Cows with higher peak yields may reach higher 305-day milk yields than cows with lower peak yields (Hossein-Zadeh et al., 2016). These results indicate that the selection focused only on 305-day milk yield may increase peak yield (Hossein-Zadeh, 2014). This is the current situation of many breeding programs in Brazil that are focused only on one trait, such as 305-day milk yield. High peak yields are associated with health problems in cows and low milk quality for the industry (Borges et al., 2015; Remppis et al., 2011).

The TP estimated for TP_{WD} and TP_{WL} were different among the genetic groups. According to the means found for TP, TP_{WD}, and TP_{WL}, groups 3/4H, 7/8H, and H had the longest time to reach peak, respectively; and the lowest TP of groups G, 5/8H, and 3/8H were similar. The shortest TP_{WD} was found in groups 5/8H and G, and the shortest TP_{WL} in groups 5/8H and 1/2H.

Similarly, Jacopini et al. (2016) evaluated Girolando primiparous cows and found the highest and lowest time to reach peak yield, respectively, in groups 7/8H (50.46 days) and 5/8H (38.54 days). Balancin Júnior et al. (2014) reported that crossbred cows (Holstein × Gyr) took 28 to 44.67 days to reach peak yield, and the longest time to peak was found in group 7/8H.

However, cows of the same breed may present a considerable variation in time to reach peak yield (Cobuci et al., 2004). Time to reach peak yield of crossbred animals (Holstein × Gyr) may have great variation compared with pure breeds and can be affected by different factors, such as group genetics, calving order, cow age, metabolic processes, and behavioral factors (Oliveira et al., 2007; Borges et al., 2015; Jacopini et al., 2016). This contributes to changes in the shape of the lactation curve of animals.

Persistency of milk yield is defined as the rate of milk yield after peak yield (Hickson et al., 2006). It is the most important component of the lactation curve because it is associated with economic, health, and welfare aspects on farms (Güler and Yanar, 2009). Hossein-Zadeh (2016) found a positive relationship between persistency of milk yield and 305-day milk yield in Holstein cows when using different nonlinear models. According to Gengler (1996), persistency of milk yield is affected by production level.

The WL model showed better fit to milk production records, since the groups with higher MY_{305} were the same that had longer lactations (H, 3/4H, 7/8H, and 1/2H). Some studies in Brazil have pointed out the superiority of groups 3/4H and 7/8H in milk yield, indicating an adaptation of these animals to the Brazilian environment (Balancin Júnior et al., 2014; Facó et al., 2002; McManus et al., 2008).

4.3. Breed, heterosis, and recombination effects

Heterosis and additive effects from improved purebred animals are the most important reasons for crossbreeding (Wakchaure et al., 2015). Crossbreeding can improve the profit of most dairy producers when they use breeds with approximately the same genetic level for total merit. Crossbred animals are more robust and economically efficient when compared with their parental breeds (Mäki-Tanila, 2007).

The heterosis effects found for animals of the different genetic groups of Girolando breed presented positive results for most traits of lactation curve. These results were expected, since heterosis occurs due to increases in heterozygosity by crossbreeding and is attributed to genetic interactions within or between loci (Syrstad, 1985; Facó et al., 2008).

Thus, 305-day milk yield presented the greatest heterosis effects, regardless of the method used (MY_{305}, MY_{305WD}, and MY_{305WL}). Overall, animals of the different genetic groups of Girolando breed produced 12 to 21% more milk than the average of their purebred parents.

Variations in results among groups are expected, since the heterosis magnitude depends on the genetic dominance level of the trait and is related to the genetic distance between parental breeds; in general, the greater this genetic distance, the higher the heterosis effect (Mäki-Tanila, 2007).

Previous studies have found lower gains in MY_{305} for animals resulting from crossbreeding between the Holstein and Jersey breeds (López-Villalobos et al., 2010; Sneddon et al., 2016). Heins et al. (2008) evaluated first-lactation yields of purebred Holstein and crossbred cows from Jersey sires and Holstein dams and found that crossbred animals produced 558 kg less milk. Penasa et al. (2010b) estimated 477 kg more milk production for animals resulting from crossbreeding between Holstein and Jersey when compared with their purebred parents; they attributed this result to specific heterosis effects. Daltro et al. (2020) estimated 1,112.73 kg more milk production for genetic group 1/2H of Girolando cows in the first lactation when compared with their purebred parents, due to specific heterosis effects.

Heterosis effects observed for peak of lactation (PY, PY_{WD}, and PY_{WL}) and time to peak (TP and TP_{WL}) showed that Girolando cows had superiority over their purebred parents, regardless of the method used to obtain heterosis effects. These results are important for the breeder and dairy industries in general because, in terms of profitability, cows must quickly reach the peak and maintain it for a long time (Knight, 2005). However, obtaining peak of lactation in the second month after delivery is preferable for health reasons and total production per lactation (Guliński, 2017).

However, the persistency of milk yield (P_{WD} and P_{WL}) did not show positive heterosis effect. This indicates that persistency of milk yield in different genetic groups of Girolando has larger variation than that of their parental breeds. The heterosis level is difficult to predict; it differs depending on the type and number of breeds in the crossbreeding system (Sorensen et al., 2008).

Although no studies evaluating the heterosis level for components of the lactation curve were found, heterosis for these components in Girolando cattle was expected in the present study, since crosses between temperate and tropical breeds often show heterosis (Wakchaure et al., 2015).

In addition, the heterosis effect for peak yield and 305-day milk yield may be due to associations between these traits in the parental pure breeds. However, cows with high peak yields present metabolic problems caused by negative energy balances (Remppis et al., 2011). Atashi et al. (2013) found that greater persistency of milk yield and lower peak yield improve tolerance of cows to stress caused by lactation and metabolic disorders, lowering their energy imbalance, followed by a less mobilization of body reserves to meet the nutrient demand for milk production.

Although the heterosis effect for peak yield was higher in Girolando cows compared with that in their parental breeds, its magnitude was lower than that in Holstein cows. The results of heterosis effect for peak yield and 305-day milk yield in Girolando cows have contributed to increase the average national milk yield in Brazil. The next step for Brazilian breeding programs could be the selection of cows for persistency of milk yield, besides 305-day milk yield. Breeding programs tend to increase milk yield and decrease costs throughout lactations by maintaining a high milk production but lower than the highest peaks, thus improving the welfare and health of cows. An index including 305-day milk yield, peak yield, persistency of milk yield, and other economic traits of interest could be studied to introduce genes in Girolando cattle by crossbreeding.

Nemes et al. (2014) reported that a planned crossing leads to an optimal gene recombination, resulting in increases in production and maintenance of the variability necessary for a continuous positive success of selection of the observed properties. However, a negative recombination effect was found in the present study for all traits, except for LP and time to peak (TP, TP_{WD}, and TP_{WL}). This negative recombination effects indicate losses in the performance of such traits caused by the recombination of genes from parental breeds. This recombination can undo favorable interactions between alleles of different loci, which were created by selection within the breed over time (Fries et al., 2000). The incorporation of genes from different breeds in the same individual promotes gains by dominance, but causes losses due to gene recombination (Kippert et al., 2008).

Most studies report negative values for the recombination effect (Madalena et al., 1990; Nemes et al., 2014; Birhanu et al., 2015). Facó et al. (2008) reported significant and negative recombination effects for MY and MY_{305} traits in Holstein × Gyr crossbred cows, indicating that the gene recombination observed in some types of crosses produces depressant effects on milk production.

5. Conclusions

The benefits of the heterosis effect on tested genetic groups of Girolando breed were evident for test-day milk yield and 305-day milk yield, with expressive improvements of approximately 20%, which partially explains the interest of Brazilian breeders for the use of this type of crossing under tropical conditions. Among the components of the lactation curve, peak yield presents the highest correlation with 305-day milk yield, which was shown by the heterosis effect of these traits. However, the recombination effect is positive only for lactation period and time to peak of lactation in Girolando cows.

Conflict of Interest

The authors declare no conflict of interest.

Author Contributions

Conceptualization: D.S. Daltro and A.H. Padilha. Data curation: D.S. Daltro. Formal analysis: D.S. Daltro, A.H. Padilha, L.T. Gama and J.A. Cobuci. Investigation: D.S. Daltro. Methodology: L.T. Gama and J.A. Cobuci. Project administration: M.V.G.B. Silva and J.A. Cobuci. Supervision: L.T. Gama, M.V.G.B. Silva and J.A. Cobuci. Visualization: M.V.G.B. Silva and J.A. Cobuci. Writing-original draft: D.S. Daltro and J.A. Cobuci. Writing-review & editing: D.S. Daltro and J.A. Cobuci.

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