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Modeling lactation curve and comparison of model's fitness to different lactation data of indigenous and crossbred cows

Gebregziabher Gebreyohannes[1], Azage Tegegne[2], M.L. Diedhiou[2] and B.P. Hegde[3]*

[1]Bako Agricultural Research Centre, P. O. Box 3, Bako
[2]International Livestock Research Institute, P. O. Box 5689, Addis Ababa
[3]Alemaya University, P.O. Box 138, Dire Dawa

Abstract

Five lactation curve models were compared for their fitness to milk data of indigenous and crossbred cows using data from Bako Agricultural Research Center and Debre Zeit Research Station. The fit of the models was compared using the model R^2 value. The overall mean R^2 value was 81.5 ± 0.12% and was significantly ($p < 0.001$) affected by model type, data type, sire breed, parity, calving season and year, location and the interactions of model type with these fixed effects. The mean R^2 values for the Incomplete Gamma with two parameters (IG ($b = 1$)), Inverse polynomial (IP), Exponential, Incomplete Gamma (IG ($b \neq 1$)) and Parabolic exponential models were 90.1 ± 0.26, 90.2 ± 0.26, 67.2 ± 0.28, 74.7 ±
0.26 and 77.8 ± 0.26 percent, respectively. Higher values of R^2 were obtained for the Debre Zeit (80.5 %) herd than Bako. The sire breeds Friesian (81.6%) crosses had significantly the highest R^2 value compared to the other sire breeds. Cows that calved during Arfasa (83.4%) had a higher fit than those in other calving seasons. Among the data types considered, highest R^2 was observed for monthly mean (85.6%) and monthly total (85.6 %) milk data types. Besides, cows in the sixth parity (81.3 %) and those that calved in 1993 (84.5 %) had the highest R^2 value. The highest R^2 was obtained for IP fitted to monthly mean (95.4 %) and monthly total (95.4 %) milk data followed by the IG ($b = 1$) fitted to monthly mean (93.2 %) and monthly total (93.2 %) milk data types. The IP followed by IG ($b = 1$) fitted to milk data of the crossbreds had the highest R^2. The reverse is true for the indigenous breeds. Among the model type x parity, model type x season and model type x location interaction groups, the IP followed by IG ($b = 1$) had the highest R^2 for all parities, calving seasons and locations. From this study it can be concluded

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* Corresponding author

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that both the IP and IG (b=1) had the best fit and could be used to describe the lactation curves of both zebu and crossbred cows under study.

Key words: lactation curve, model, fitness, crossbred

Introduction

Lactation curve, the graphical representation of milk yields over time (Papajcsik and Bodero, 1988; Sherchand *et al.*, 1995), is determined by the biological efficiency of the cow and is used for selection and feeding management. When a functional form is used to describe a lactation curve, the predicted milk yield at any given stage of lactation can be used as a basis for decisions to cull or retain for breeding (Wood, 1969; Madalena *et al.*, 1979; Papajcsik and Bodero, 1988; Sherchand *et al.*, 1995). Mathematical models of lactation curve are required to abstract the true situation of milk secretion during the entire lactation (Singh and Bhat, 1978). Several models have been developed and tested to describe such a lactation pattern of milk production (Papajcsik and Bodero, 1988; Sherchand *et al.*, 1995; Olori *et al.*, 1999). Models vary with respect to the number of parameters in the equation, the method of estimating model parameters, method of fitting the equations to the lactation data, simplicity to fit to lactation data and interpret and relate these parameters to the actual situations. Based on these facts five lactation curve models (Incomplete Gamma with three and two parameters, Inverse Polynomial, Exponential and Parabolic exponential) have been selected for this purpose.

Incomplete Gamma function (Wood, 1967) is the most commonly used functional form for the lactation curve of the dairy cow. The model predicts a peak yield of "$a(b/c)^b \exp(-b)$" which occurs "b/c" days after calving and persistency of "$C^{-(b+1)}$". Exponential Model (Brody *et al.*, 1923) fits to the declining phase of the lactation curve. The drawback reported for this model was that it did not generate a rise in the curve because of exclusion of an inclining function (Sherchand *et al.*, 1995). A parabolic exponential model (Sikka, 1950) is used to represent a lactation curve with the day of peak yield "$(b/2c)$" corresponding to the mean of the distribution. The model gave good fit to first lactation data (Singh and Bhat, 1978). But it did not fit at all before the peak was attained, because the function is symmetric around peak yield (Sherchand *et al.*, 1995). The inverse polynomial (Nelder, 1966) has been used to model lactation curves (Yadav *et al.*, 1977; Singh and Bhat, 1978; Kumar and Bhat, 1979; Batra, 1986) and reported the model to give a good fit for lactations, which start at a low level and peak earlier than average (Kumar and Bhat, 1979). In the Incomplete Gamma with two parameters (Papajcsik and Bodero, 1988), the values of the Wood's parameter (Wood, 1967) "b", was considered as one. The fit of these models is different due to several reasons. To this effect different authors have tested and recommended different models for different herds. The objective in this study is therefore, to compare the fit of these five models to the lactation data of indigenous and crossbred cows and select a model, which best describes the lactation curves of both crossbred and indigenous breeds.

Materials and Methods

The study was conducted based on existing data from Bako Agricultural Research Center of Oromia Agricultural Research Institute and Debre Zeit Research Station of the International Livestock Research Institute (ILRI). Details of the two centers climatic condition, livestock management, breeding and health care are reported in previous works (Gemechu, 1992; Gebregziabher and Mulugeta, 1996). Lactation data of pure Horro and Boran and their F_1 crosses with Jersey, Friesian and Simmental exotic sire breeds were used for the study. The five models fitted to milk yield data of indigenous and crossbred cows and their logarithmic transformed equivalents are listed blow.

Model name and reference	**Original Model**	**Transformed model**
1. Incomplete gamma function (Wood, 1967)	$Y_N = AN^b \exp(-cN)$	$Ln(Y_N) = Ln(A) + bLn(N) - cN \quad b \neq 1$
2. Incomplete gamma function with two parameters (Papajicsik and Bodero, 1988)	$Y_N = AN^b \exp(-cN) \quad b = 1$	$Ln(Y_N / N) = Ln(A) - cN$
3. Exponential model (Brody et al., 1923)	$Y_N = A\exp(-cN)$;	$Ln(Y_N) = Ln(A) - cN$
4. Parabolic exponential model (Sikka, 1950)	$Y_N = A\exp(bN - cN^2)$	$Ln(Y_N) = Ln(A) + bN - cN^2$
5. Inverse polynomial model (Nelder, 1966)	$Y_N = N(A_0 + A_1N + A_2N^2)^{-1}$	Not transformed

In the models, "Ln" represents the logarithm to base "e", "Y_N" represents milk yield (total or mean) recorded at N interval (daily, weekly, fortnightly or monthly) from calving depending on the type of data used for a particular interval of recording. "Ln (A)" or "a", "b", "c", "A_0", "A_1" and "A_2" are to be estimated from the regression analysis. In the models the parameter "a" is defined as "the scale of production" (Wood, 1972) or "initial milk production" (Madalena *et al.*, 1979) while "c" represents the rate of change in the declining phase of lactation curve (Yadav *et al.*, 1977). In the IP function the parameters measure the rate of increase to peak production ("A_0"), the average slope of the lactation curve ("A_1") and the rate of decline after the peak ("A_2"). All models, except the IP, were first transformed to their linear form using logarithmic transformation. The models were fitted to each lactation data of each cow using the Regression Procedure of the Statistical Analysis System (SAS, 1999). The model R^2 obtained as an output of the regression analysis was subjected to analysis of variance using a General Linear Model to see the effects of both genetic and non-genetic factors following the method of Olori *et al*. (1999). The general linear model used for the analysis of this data included fixed effects of sire breed, model type, data type, calving season, calving year, parity and location and the interactions of model type with these fixed effects only. Detailed descriptions of these fixed effects are presented in Gebregziabher *et al*. (2003). Besides, seven milk yield data types (daily, weekly mean and total, fortnightly mean and total, monthly mean and total) and five model types were considered as fixed effects.

Results

The overall mean R^2 value was 81.5 ± 0.21%. The effects of sire breed, dam breed, parity, calving season and year, data type, model type and the interaction of model type with these fixed effects were significant ($p < 0.001$; Table 1). Significantly ($p < 0.001$) highest value of R^2 was obtained for IG (b = 1) (90.1 ± 0.26) and IP (90.2 ± 0.26) models and the poorest fit was observed on the exponential model (Table 2). Similarly the highest R^2 values was observed for Debre Zeit (80.5 ± 0.26 %) than Bako (79.3 ± 0.14) herd; for Friesian (81.6 ± 0.13%) and Jersey (81.1 ± 0.22 %) crosses; for cows that calved during Arfasa (83.5 ± 0.17%); for monthly mean (85.6 ± 0.22%) and monthly total (85.6 ± 0.22%) milk data types; for cows in the sixth parity (81.3 ± 0.23%); and for cows that calved in 1993 (84.5 ± 0.37%) compared to their contemporaries (Table 2).

Among the model x data type interaction groups, except when fitted to daily data, the IP followed by the IG (b = 1) was found to have the best fit to the data. The highest R^2 was obtained for IP followed by the IG (b = 1) fitted to monthly mean and monthly total milk yield (Table 2). Among the model type by sire breed interaction groups the IP followed by IG (b = 1) fitted to milk data of the crossbred cows had the highest R^2; while the reverse is true for the indigenous breeds (Table 2). Among the model type x parity, model type x calving season and model type x location interaction groups, the IP followed by IG (b = 1) had the highest R^2 for all parities, seasons and locations (Table 2). Besides, all models had a better fit to lactation data of cows that calved during Arfasa (short rainy season) compared to the other calving season x model interaction groups. Both IP and IG (b = 1) were superior to the other models and had the best fit for lactation data of cows in the later (5 - 6) than earlier (1 - 4) parities (Table 2).

Table 1. Mean square, coefficient of variation (CV%) and R^2 from least square analysis of variance of R^2

Sources	**Df**	**Mean square**
Model	4	36.4 ***
Sire breed	4	1.5 ***
Calving season	3	10.2 ***
Calving year	18	2.8 ***
Data type	6	14.6 ***
Parity	5	1.2 ***
Location	1	0.3 ***
Data type x model	24	0.31 ***
Sire x model	16	0.33 ***
Parity x model	20	0.38 ***
Season x model	12	1.14 ***
Location x model	4	0.39 ***
Error	43927	0.025
CV (%)		19.4
R^2 (%)		31.9

Significance level *** $p < 0.001$

Discussion

The fitness of the models to the lactation data of indigenous and crossbred cows as measured by the overall mean R^2 value was 81.5 % (Table 2) which is lower than the highest value of 99% reported by Singh and Bhat (1978) but comparable to the 82% reported by Wood (1968). Variations in R^2 values are expected because of differences in locations, genotypes, parities, calving seasons and calving years, which directly or indirectly affect the fitness of the models (Cobby and Le Du, 1978; Keown *et al.*, 1986).

Several models have been tested for fitness to different data (Brody *et al.*, 1923; Sikka, 1950; Wood, 1967; Cobby and Le Du, 1978; Keown *et al.*, 1986) and vary in ease of application, parameters involved, method of application and estimation of model parameters (Cobby and Le Du, 1978). Thus, the variance explained by these models is different. The significantly higher variation in R^2 value among models (Table 2) obtained in this study could be attributed to these reasons.

The superiority of the IG (b = 1) over the exponential and IP (Papajicsik and Bodero, 1988) and the IP over the IG (b ≠ 1), the parabolic exponential and exponential functions (Singh and Bhat, 1978; Bhat *et al.*, 1981; Batra, 1986; Gahlot *et al.*, 1989) were already reported elsewhere. However, Singh *et al.* (1997) reported the superiority of IG (b ≠ 1) followed by parabolic exponential, IP and exponential function when fitted to the monthly milk records of first lactation cows. The reason for this difference could be due to differences in the type of data used. Gahlot *et al.* (1989), however, reported lower estimate of R^2 value for exponential function and higher estimates of R^2 value for IG (b ≠ 1) as compared to parabolic exponential and exponential functions. Similar results have been obtained in this study for all data types (Table 2). Besides, they reported that the IG (b ≠ 1) explained maximum variation for each genetic group, indicating better fit of the curve over parabolic and exponential function, while the exponential function had poor fit to the data. In a study by Sikka (1950) the addition of parabolic term to exponential function increased the proportion of variation explained by the parabolic exponential model, while Yadav and Sharma (1985) reported that the percentage variation accounted for by the exponential parabolic function was not greater than and in most cases they were lesser than that accounted for by an exponential function, which indicated that the addition of the parabolic term to exponential function did not improve the fit of the curve to Hariana crossbred cows. In this study addition of the parabolic term improved the fitness of the exponential function for all data types, which is in agreement to Sikka (1950). Comparison of the IG (b = 1) and IG (b ≠ 1) indicated that the IG(b = 1) was found to fit better than IG(b ≠ 1). The parameter “b” which represents the rate of increase to peak milk yield, when it equals one indicates that there is a steep slop to peak or shorter ascending phase of the lactation. Therefore, lactation data of the studied herds behaved that it started at higher level and then declines thereafter. This could be associated with the level of feeding during early periods of lactation.

The type of data to which the models were fitted also affected the R^2 values. Several works reported on the fit of the models to daily (Madalena *et al.*, 1979; Abubakar and Buvanendran, 1981), weekly (Rao and Sundaresan, 1982; Yadav and Sharma, 1985; Batra, 1986) and monthly (Singh *et al.*, 1997) milk data based on the mean or the total milk yield. Similarly, this study confirmed the variation in the fit of the models to different data types. Highest fit of the models was observed for monthly followed by fortnightly and weekly data and the lowest for daily milk yield data. This could be associated with the high individual variability (high standard deviation) in the daily data compared to the monthly, fortnightly and weekly mean milk data, which has relatively lower individual variability or standard error.

The variation among calving seasons in fitness is related to variation in the availability of feed both in quantity and quality. The flush of pasture growth during the wet season (Gana) gives a stimulus to milk production since cows that calved during Arfasa (short rainy season) had their peak milk yield that coincided with the wet season. Those animals have only one hump in their lactation curve that is due to one peak yield. The model, therefore, gave a better fit to those lactations than those commencing during the other periods where the wet season may stimulate increase in milk yield resulting in a second hump in addition to the peak in the lactation curve which is in agreement to the report of Abubakar and Buvanendran (1981).

The fact that the lactation curves of crossbred cows had better fit compared to those of indigenous breeds could be related to the fact that the indigenous breeds are not selected for milk production. These lactation curve models are developed for specialized dairy breeds. Besides, the sire breed difference could be related to the lactation yield and lactation length of the cows where the crossbreds yielded higher and milked longer than the indigenous breeds (Sendros *et al.*, 1987). Similar breed differences were also reported from Indian studies (Singh and Bhat, 1978; Yadav and Sharma, 1985).

The fitness of the five models was different among the data types (Table 2). Similarly, Wood (1969) reported that the exponential function had better fit accounting for 95.4% of the variation in monthly milk yield as against 84.4% for the IP function. Olori *et al.* (1999) also reported the dependence of the goodness of fit on whether the objective is to predict the cumulative yield or individual daily yields, and on whether the observation units are groups of animals or individual animals. Rowlands *et al.* (1982), in their work to determine the goodness of fit of models to weekly records, found a wide range in variation which they attributed to the effects of several environmental and genetic factors. Collins-Lusweti (1989, 1991) also reported lower goodness of fit (R^2) values for the monthly than weekly total milk yields, with the R^2 values being 74.8 and 79.2 percent, respectively. This is contrary to the higher R^2 values obtained for data based on monthly than weekly total milk data in the present study (Table 2).

Lactation curve models and estimation of their parameters is geared to wards practical use in dairy farm management and for milk yield estimation. Different data types have been compared in this study. The fitness of the models to monthly data is better than fortnightly and weekly data. However, for practical intervention of any management practice the interval of measurement has to be short so that any thing that might happen within that interval could be addressed immediately. The formulation of feeding ration is based on the milk output in specific stages of lactation thus, information on the milk output of the cows in a weekly or biweekly interval is required.

Conclusion

From this study the following conclusions could be drawn

- Five models were fitted to lactation data of zebu and crossbred cows. The fitness of the models was different for different data types, breeds, locations, parities and calving seasons, calving year, model type and the interaction of model type with the other fixed effects.
- Among the models compared, the IP and IG (b = 1) were the best models to describe the lactation curve of both indigenous and crossbred cows. However, the fitness was better for crossbred than indigenous cows.
- The fitness of the models was best for monthly milk data types. However, using monthly records do not ease practical application of the models to any management interventions. Thus, it is recommended to use the selected models on weekly total milk data.

Table 2. Least square mean (± SE) R^2 values (%)

Source of variation	**N**	**Mean ± S.E.**
Overall mean	44045	81.5 ± 0.21
Model type		***
Incomplete gamma (IG) (b = 1)	9005	90.1 ± 0.26 ^{a}
Incomplete gamma (IG (b ≠ 1))	8920	74.7 ± 0.26 ^{c}
Exp (EXP)	8215	67.2 ± 0.28 ^{d}
Pexp (PEXP)	8902	77.8 ± 0.26 ^{b}
IP (IP)	9003	90.2 ± 0.26 ^{a}
Sire breed		***
Friesian crossbreds	21215	81.6 ± 0.13 ^{a}
Jersey crossbreds	8084	81.1 ± 0.22 ^{b}
Simmental crossbreds	4059	80.8 ± 0.26 ^{bc}
Boran	2321	76.1 ± 0.34 ^{d}
Horro	7566	80.2 ± 0.28 ^{c}
Calving season		***
Gana (June - August)	9174	81.2 ± 0.20 ^{b}
Birra (September-November)	9860	76.5 ± 0.19 ^{d}
Bona (December – February)	10440	78.7 ± 0.18 ^{c}
Arfasa (March – May)	14571	83.5 ± 0.17 ^{a}
Data type		***
Daily	6242	72.1 ± 0.22 ^{d}
Weekly mean	6284	77.5 ± 0.22 ^{c}
Weekly total	6202	77.3 ± 0.22 ^{c}
Fortnight mean	6306	80.9 ± 0.22 ^{b}
Fortnight total	6304	80.7 ± 0.22 ^{b}
Monthly mean	6314	85.6 ± 0.22 ^{a}
Monthly total	6313	85.6 ± 0.22 ^{a}
Parity		***
1	7514	77.2 ± 0.21 ^{c}
2	7565	80.1 ± 0.22 ^{b}
3	8883	80.3 ± 0.20 ^{b}
4	7797	80.1 ± 0.21 ^{b}
5	5845	80.6 ± 0.23 ^{b}
6	6441	81.3 ± 0.23 ^{a}

Table 2. Continued.

Source of variation	**N**	**Mean ± S.E.**
Location		***
Bako	28230	79.3 ± 0.14^{a}
Debre Zeit	15815	80.5 ± 0.26^{b}
Calving year		***
1980	3183	83.1 ± 0.36^{c}
1981	3040	83.8 ± 0.35^{abc}
1982	2842	79.9 ± 0.36^{e}
1983	2263	78.1 ± 0.38^{f}
1984	1565	74.6 ± 0.44^{g}
1985	1709	84.2 ± 0.42^{ab}
1986	2200	80.1 ± 0.38^{e}
1987	1951	78.3 ± 0.39^{f}
1988	1697	80.2 ± 0.42^{e}
1989	616	83.7 ± 0.65^{abc}
1990	3157	79.8 ± 0.30^{e}
1991	1920	75.2 ± 0.38^{g}
1992	2073	81.4 ± 0.37^{d}
1993	2162	84.5 ± 0.37^{a}
1994	3131	78.8 ± 0.31^{f}
1995	3480	83.3 ± 0.29^{bc}
1996	3302	80.4 ± 0.36^{e}
1997	2609	80.2 ± 0.33^{e}
1998	2145	69.4 ± 0.37^{h}
Interactions		
Model * data type		***
IG ($b = 1$) x Daily	1287	85.7 ± 0.48^{e}
IG ($b = 1$) x Weekly mean	1287	88.6 ± 0.48^{d}
IG ($b = 1$) x Weekly total	1287	88.6 ± 0.48^{d}
IG ($b = 1$) x Fortnight mean	1287	90.6 ± 0.48^{c}
IG ($b = 1$) x Fortnight total	1287	90.7 ± 0.48^{c}
IG ($b = 1$) x Monthly mean	1285	93.2 ± 0.48^{b}
IG ($b = 1$) x Monthly total	1285	93.2 ± 0.48^{b}
IG ($b \neq 1$) x Daily	1264	65.6 ± 0.48^{o}
IG ($b \neq 1$) x Weekly mean	1274	71.0 ± 0.48^{l}
IG ($b \neq 1$) x Weekly total	1274	70.7 ± 0.48^{l}

Table 2. Continued.

Source of variation	**N**	**Mean ± S.E.**
IG (b ≠ 1) x Fortnight mean	1277	75.6 ± 0.48 ^{l}
IG (b ≠ 1) x Fortnight total	1277	75.2 ± 0.48 ^{ij}
IG (b ≠ 1) x Monthly mean	1277	82.3 ± 0.48 ^{g}
IG (b ≠ 1) x Monthly total	1277	82.3 ± 0.48 ^{g}
Exp x Daily	1144	60.7 ± 0.48 ^{p}
Exp x Weekly mean	1166	64.5 ± 0.52 ^{o}
Exp x Weekly total	1164	64.4 ± 0.51 ^{o}
Exp x Fortnight mean	1184	67.8 ± 0.51 ^{mn}
Exp x Fortnight total	1182	67.6 ± 0.51 ^{n}
Exp x Monthly mean	1188	72.8 ± 0.51 ^{k}
Exp x Monthly total	1187	72.8 ± 0.51 ^{k}
Pexp x Daily	1262	69.1 ± 0.51 ^{m}
Pexp x Weekly mean	1270	74.3 ± 0.49 ^{ij}
Pexp x Weekly total	1270	74.2 ± 0.48 ^{jk}
Pexp x Fortnight mean	1272	78.6 ± 0.48 ^{h}
Pexp x Fortnight total	1272	78.6 ± 0.48 ^{h}
Pexp x Monthly mean	1278	84.2 ± 0.48 ^{f}
Pexp x Monthly total	1278	84.2 ± 0.48 ^{f}
IP x Daily	1285	79.3 ± 0.48 ^{h}
IP x Weekly mean	1207	89.3 ± 0.48 ^{d}
IP x Weekly total	1287	88.8 ± 0.48 ^{d}
IP x Fortnight mean	1286	91.7 ± 0.48 ^{c}
IP x Fortnight total	1286	91.1 ± 0.48 ^{c}
IP x Monthly mean	1286	95.5 ± 0.48 ^{a}
IP x Monthly total	1286	95.4 ± 0.48 ^{a}
Sire breed x model		***
Friesian crossbreds * IG (b = 1)	4320	90.4 ± 0.27 ^{de}
Friesian crossbreds * IG (b ≠ 1)	4286	76.4 ± 0.27 ^{j}
Friesian crossbred * Exp	4012	70.5 ± 0.28 ^{l}
Friesian crossbred * Pexp	4279	79.0 ± 0.27 ^{h}
Friesian crossbred * IP	4318	91.6 ± 0.27 ^{ab}
Jersey crossbred * IG (b = 1)	1665	90.4 ± 0.46 ^{cde}
Jersey crossbred * IG (b ≠ 1)	1635	75.9 ± 0.47 ^{j}
Jersey crossbred * Exp	1487	68.8 ± 0.49 ^{m}
Jersey crossbred * Pexp	1632	78.7 ± 0.47 ^{h}

Table 2. Continued.

Source of variation	**N**	**Mean ± S.E.**
Jersey crossbred * IP	1665	91.5 ± 0.46 ^{abc}
Simmental crossbred * IG (b = 1)	1001	89.3 ± 0.56 ^{ef}
Simmental crossbred * IG (b ≠ 1)	988	74.7 ± 0.56 ^{k}
Simmental crossbred * Exp	886	69.4 ± 0.59 ^{lm}
Simmental crossbred * Pexp	985	77.8 ± 0.56 ^{hi}
Simmental crossbred * IP	999	92.7 ± 0.56 ^{a}
Boran * IG (b = 1)	488	89.4 ± 0.72 ^{def}
Boran * IG (b ≠ 1)	484	69.5 ± 0.73 ^{lm}
Boran * Exp	379	58.9 ± 0.82 ^{n}
Boran * Pexp	782	74.5 ± 0.73 ^{k}
Boran * IP	488	87.9 ± 0.72 ^{fg}
Horro * IG (b = 1)	1531	90.9 ± 0.51 ^{bcd}
Horro * IG (b ≠ 1)	1527	76.8 ± 0.51 ^{ij}
Horro * Exp	1451	68.4 ± 0.52 ^{m}
Horro * Pexp	1524	78.0 ± 0.51 ^{hi}
Horro * IP	1533	86.9 ± 0.51 ^{g}
Parity *model		***
1 x IG (b = 1)	1562	89.1 ± 0.44 ^{cd}
1 x IG (b ≠ 1)	1540	71.2 ± 0.44 ^{l}
1 x Exp	1309	60.7 ± 0.49 ^{o}
1 x Pexp	1541	73.4 ± 0.44 ^{k}
1 x IP	1562	91.1 ± 0.44 ^{ab}
2 x IG (b = 1)	1546	88.6 ± 0.46 ^{d}
2 x IG (b ≠ 1)	1522	75.6 ± 0.48 ^{ij}
2 x Exp	1440	67.3 ± 0.46 ^{n}
2 x Pexp	1513	78.7 ± 0.46 ^{f}
2 x IP	1544	90.1 ± 0.43 ^{bc}
3 x IG (b = 1)	1799	89.2 ± 0.43 ^{cd}
3 x IG (b ≠ 1)	1794	75.7 ± 0.45 ^{ij}
3 x Exp	1704	69.2 ± 0.43 ^{m}
3 x Pexp	1787	78.3 ± 0.43 ^{fg}
3 x IP	1799	89.4 ± 0.45 ^{cd}
4 x IG (b = 1)	1592	90.2 ± 0.45 ^{bc}
4 x IG (b ≠ 1)	1579	74.5 ± 0.48 ^{k}
4 x Exp	1445	68.2 ± 0.45 ^{mn}

Table 2. Continued.

Source of variation	**N**	**Mean ± S.E.**
4 x Pexp	1588	77.5 ± 0.45 ^{gh}
4 x IP	1593	90.2 ± 0.50 ^{bc}
5 x IG (b = 1)	1190	91.6 ± 0.50 ^{a}
5 x IG (b ≠ 1)	1180	74.7 ± 0.52 ^{jk}
5 x Exp	1106	68.9 ± 0.50 ^{m}
5 x Pexp	1179	76.9 ± 0.50 ^{ghi}
5 x IP	1190	90.7 ± 0.49 ^{ab}
6 x IG (b = 1)	1316	91.6 ± 0.49 ^{a}
6 x IG (b ≠ 1)	1305	76.3 ± 0.51 ^{hj}
6 x Exp	1211	68.9 ± 0.49 ^{m}
6 x Pexp	1294	80.2 ± 0.49 ^{e}
6 x IP	1315	89.3 ± 0.49 ^{cd}
Calving season * model		***
Gana x IG (b = 1)	1869	89.5 ± 0.41 ^{b}
Gana x IG (b ≠ 1)	1855	76.1 ± 0.41 ^{g}
Gana x Exp	1735	70.7 ± 0.43 ^{l}
Gana x Pexp	1846	785 ± 0.42 ^{f}
Gana x IP	1869	90.9 ± 0.41 ^{a}
Birra x IG (b = 1)	2050	88.4 ± 0.41 ^{c}
Birra x IG (b ≠ 1)	2007	68.8 ± 0.41 ^{j}
Birra x Exp	1759	63.4 ± 0.44 ^{k}
Birra x Pexp	1995	73.0 ± 0.41 ^{h}
Birra x IP	2049	88.9 ± 0.41 ^{bc}
Bona x IG (b = 1)	2140	91.2 ± 0.39 ^{a}
Bona x IG (b ≠ 1)	2123	73.3 ± 0.39 ^{h}
Bona x Exp	1906	62.4 ± 0.42 ^{k}
Bona x Pexp	2131	77.0 ± 0.39 ^{g}
Bona x IP	2140	89.3 ± 0.39 ^{bc}
Arfasa x IG (b = 1)	2946	91.1 ± 0.35 ^{a}
Arfasa x IG (b ≠ 1)	2935	80.5 ± 0.35 ^{e}
Arfasa x Exp	2815	72.4 ± 0.37 ^{h}
Arfasa x Pexp	2930	81.8 ± 0.35 ^{d}
Arfasa x IP	2945	91.4 ± 0.35 ^{a}
Model * Location		***
IG (b = 1) x Bako	5777	89.8 ± 0.26 ^{b}

Table 2. Continued.

Source of variation	**N**	**Mean ± S.E.**
IG (b = 1) x Debre Zeit	3228	90.3 ± 0.46^{ab}
IG (b ≠ 1) x Bako	5711	74.9 ± 0.26^{e}
IG (b ≠ 1) x Debre Zeit	3209	74.5 ± 0.47^{e}
Exp x Bako	5258	65.1 ± 0.27^{g}
Exp x Debre Zeit	2957	69.3 ± 0.49^{f}
Pexp x Bako	5708	77.9 ± 0.26^{d}
Pexp x Debre Zeit	3194	77.2 ± 0.49^{d}
IP x Bako	5776	89.1 ± 0.26^{c}
IP x Debre Zeit	3227	91.2 ± 0.47^{a}

Means in a column within a group with different superscripts vary significantly ($p < 0.001$)

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