Revista Brasileira de Zootecnia
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ISSN 1806-9290
www.sbz.org.br

R. Bras. Zootec., 44(5):174-179, 2015

Inbreeding on productive and reproductive traits of dairy Gyr cattle

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ABSTRACT - The objective of this study was to estimate genetic parameters and to evaluate the effects of inbreeding on productive and reproductive traits of dairy Gyr cattle. Single-trait animal models were used to estimate genetic parameters and solutions for inbreeding coefficients for milk (milk 305-d), fat (fat 305-d), protein (protein 305-d), lactose (lactose 305-d), and total solids (TS 305-d) yield up to 305 days of lactation, days in milk (DIM), age at first calving (AFC) and calving intervals (CI). The mean inbreeding coefficient was 2.82%. The models with linear and quadratic effects of inbreeding coefficients fitted the data better than the models without or with only linear effect of inbreeding coefficient for all traits. The increase in inbreeding coefficient caused several losses in productive and reproductive traits of dairy Gyr cattle. Estimates of heritability for milk 305-d, fat 305-d, protein 305-d, lactose 305-d, TS 305-d, DIM, AFC, and CI were 0.28, 0.27, 0.22, 0.21, 0.22, 0.17, 0.20, and 0.10, respectively. It is possible to achieve genetic progress in productive traits (especially in milk 305-d and fat 305-d) and age at first calving in dairy Gyr cattle through selection.

Key Words: dairy cattle, genetic parameter, heritability, inbreeding depression

Introduction

The Gyr (*Bos indicus*) breed, originating from India and introduced in Brazil between 1906 and 1962, has broad support from farmers in tropical and subtropical regions due to the adaptability to various production systems, especially those based on pastures. The dairy Gyr is a sub-population of Gyr, selected for milk production (Faria et al., 2009) and holds a genetic improvement program started in 1985, which, among other activities, carries the progeny test.

The reduced genetic basis of animals imported from India, the intensive use of a small number of proven bulls and the development and large-scale application of reproductive biotechnologies (artificial insemination, embryo transfer, and *in vitro* fertilization) increase the probability of co-selection of individuals belonging to the same family. The sum of these factors caused the increment of inbreeding in dairy Gyr cattle (Reis Filho et al., 2010).

Effects of inbreeding on economic traits attract considerable interest of research, taking into account that the increment of inbreeding resulting from the selection process seems inevitable. Several studies relate the increase of inbreeding in European breeds to the reduction of phenotypic means in traits of economic interest (Croquet et al., 2007; Gulisija et al., 2007), a phenomenon called inbreeding depression (Falconer and Mackay, 1996). Similar results were also observed in *Bos indicus* breeds, like Gyr (Queiroz et al., 1993) and Guzerat (Panetto et al., 2010). There are two possible causes of the decline of phenotypic means of quantitative traits by inbreeding. The first is that the favorable genes have a tendency to be dominant or partially dominant, and the second is the fact that heterozygous animals have a greater phenotypic value than the homozygous (Crow and Kimura, 1970). Because of the recent development of genetic improvement programs of the Gyr breed, new studies need to be conducted to determine the effects of inbreeding on economically important traits, and to support selection decisions and mating in Brazilian herds. The objectives of this study were estimate genetic parameters and evaluate the effects of inbreeding on productive and reproductive traits of dairy Gyr cattle.

Material and Methods

The data used in this study originated from the progeny test of dairy Gyr breed, coordinated by Embrapa Dairy Cattle and the Brazilian Association of Dairy Gyr Breeders (ABCGIL). The pedigree file used for this study included

Received December 17, 2014 and accepted March 5, 2015.
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http://dx.doi.org/10.1590/S1806-92902015000500002

data of 27,610 animals, 3,709 of which had one or both parents unknown. The data file consisted of lactations started from 1960 to 2004, from 8,879 purebred Gyr cows, daughters of 916 bulls and 5,375 cows, distributed into 26 Brazilian herds.

Traits were divided into two groups: Productive – total milk yield up to 305 days (milk 305-d), total fat yield up to 305 days (fat 305-d), total protein yield up to 305 days (protein 305-d), total lactose yield up to 305 days (lactose 305-d), total solids yield up to 305 days (TS 305-d), and days in milk (DIM); and Reproductive – age at first calving (AFC) and calving interval (CI). Lactations with abnormal termination causes or with duration shorter than 90 days were deleted from the database. The age at first calving was the beginning of the first controlled lactation that occurred between 18 and 66 months of age. Calving intervals between 300 and 730 days were considered valid.

To grant consistency to the analyses, herd × year of calving and herd × year of birth classes were created. Records of milk 305-d, fat 305-d, DIM, and CI from herd × year of calving classes with less than five records were deleted. Records of protein 305-d, lactose 305-d, and TS 305-d from herd × year of calving with less than three records were also deleted. Records of AFC from herd × year of birth with less than three records were deleted (Table 1).

The inbreeding coefficient (Figure 1) of each animal in the pedigree, defined as the proportion of loci which have identical alleles by descent (Wright, 1923), was calculated by using the MTDFNRM (Multiple Trait Derivative Free Numerator Relationship Matrix) package, a component of the MTDFREML system (Boldman et al., 1995). The effect of individual inbreeding coefficient was assessed in single-trait animal models with variance components obtained by Restricted Maximum Likelihood (REML). For each trait, three different animal models were fit. In the first one, inbreeding coefficient was not included; in the second model, linear effect of inbreeding coefficient was fit; and in the last model, linear and quadratic effect of inbreeding coefficient were fit.

In matrix notation, the single-trait animal models could be represented as follows:

$$y = X\beta + Z_1a + Z_2p + e,$$

in which y represents the vector of observations for each trait; X is the incidence matrix of fixed effects; β is the vector of solutions of fixed effects; Z_1 is the incidence matrix of random direct additive genetic effects; a is the vector of solutions for direct additive genetic effects (breeding values); Z_2 is the incidence matrix of random direct permanent environmental effects; p is the vector of solutions for direct permanent environmental effects;

Table 1 - Descriptive statistics of productive and reproductive traits of dairy Gyr cows

Trait	N of animals	N of observations	Mean	Standard error
Productive				
Total milk yield up to 305-d, kg	8,860	24,045	2,590.9	5.34
Total fat yield up to 305-d, kg	6,136	15,211	125.1	0.32
Total protein yield up to 305-d, kg	2,449	5,034	97.2	0.47
Total lactose yield up to 305-d, kg	2,425	4,960	107.1	0.60
Total solids yield up to 305-d, kg	2,423	4,956	368.7	1.82
Days in milk, days	8,860	24,045	299.5	0.37
Reproductive				
Age at first calving, months	6,236	6,236	44.3	0.06
Calving interval, days	5,613	14,205	492.5	0.81

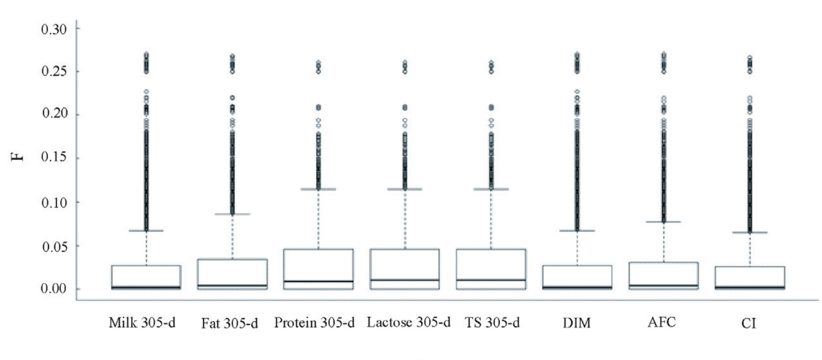

Figure 1 - Distributions of inbreeding coefficients (F) for dairy Gyr cows with records for total milk (Milk 305-d), fat (Fat 305-d), protein (Protein 305-d), lactose (Lactose 305-d), solid (TS 305-d) yield up to 305 days, days in milk (DIM), age at first calving (AFC) and calving interval (CI).

and e is the vector of random residuals. The fixed effects for productive and CI analysis were: herd, year × calving season, linear and quadratic effects of age at calving, and linear and quadratic individual coefficients of inbreeding (according to the model). The fixed effects for AFC analysis were: herd × birth year, birth season, and linear and quadratic individual coefficients of inbreeding (according to the model). Calvings occurring between April and September formed calving season 1, and calving season 2 comprehended the remaining months, except for three herds located in the Northeast of Brazil, where the opposite was considered. The birth seasons were obtained according to the same criteria used for the definition of calving seasons. Direct additive genetic and residual effects were included for all traits and direct permanent environmental effect was not considered for AFC.

Estimates of variance components and fixed effects solutions according to REML were obtained with the REMLF90 program (Misztal et al., 2002). Convergence criteria were absolute squared differences between subsequent estimates $<10^{-10}$. Fits of different models were compared by examining the Akaike information criteria (AIC). Effects of inbreeding were estimated from the solutions of regression coefficients.

Results and Discussion

Models with linear and quadratic effect of inbreeding coefficient (F) fitted better the data than the models without or with only linear effect of inbreeding for all traits, according to AIC (Table 2). The productive and reproductive losses per 1% (0.01 in F) in inbreeding coefficient depended on the level of inbreeding (Figures 2 to 9). Inbreeding depression reduced milk 305-d (Figure 2), lactose 305-d (Figure 5), TS 305-d (Figure 6), and DIM (Figure 7) throughout the interval of F (0 to 0.27). Fat 305-d reduced in the interval of 0<F<0.241 and increased thereafter (Figure 3). Protein 305-d had a small increase from F = 0 to F = 0.051 and decreases with F>0.051 (Figure 4).

Results similar of those presented in this study, in which there was a linear effect of inbreeding coefficient on milk, fat, and protein production, have been reported with several dairy breeds such as Brown Swiss, Holstein, and Jersey (Casanova et al., 1992; Thompson et al., 2000a,b). In the Gyr breed, Queiroz et al. (1993) also observed a linear decrease in milk yield and DIM due to the increase

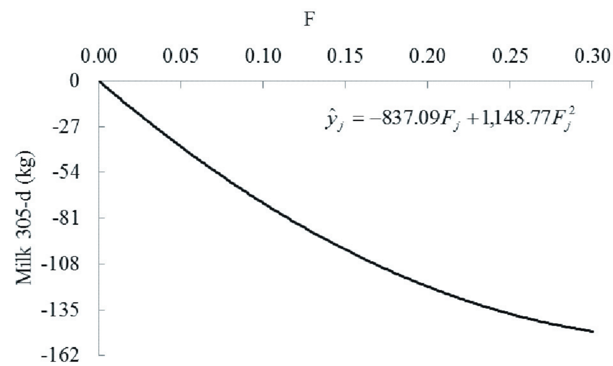

Figure 2 - Effect of inbreeding coefficients (F) on total milk yield up to 305 days (Milk 305-d) in dairy Gyr cattle.

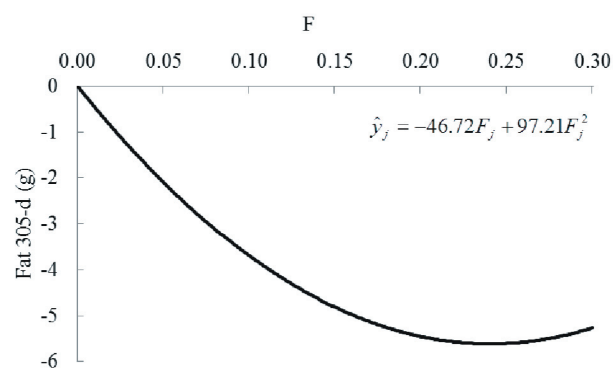

Figure 3 - Effect of inbreeding coefficients (F) on total fat yield up to 305 days (Fat 305-d) in dairy Gyr cattle.

Table 2 - Akaike information criteria (AIC) for analysis of productive and reproductive traits of dairy Gyr cattle with different models

Trait	Without effect of inbreeding coefficient	Linear effect of inbreeding coefficient	Linear and quadratic effect of inbreeding coefficient
Productive			
Total milk yield up to 305-d, kg	386,338	386,317	386,294
Total fat yield up to 305-d, kg	152,365	152,352	152,339
Total protein yield up to 305-d, kg	48,865	48,857	48,843
Total lactose yield up to 305-d, kg	50,621	50,612	50,599
Total solids yield up to 305-d, kg	61,450	61,333	61,318
Days in milk, days	261,647	261,640	261,628
Reproductive			
Age at first calving, months	36,202	36,181	36,162
Calving interval, days	169,003	168,993	168,978

in the inbreeding coefficient. It is important to highlight that only the linear effect of inbreeding was evaluated in these cited papers.

According to Croquet et al. (2007), few studies have tested linear and curvilinear regressions in real situations with large databases. Nevertheless, these authors evaluated both models and concluded that the former would be the best options to describe the effect of inbreeding on production traits. The results obtained with dairy Gyr cattle (Table 2) corroborate those presented by Croquet et al. (2007). The positive and negative estimates of linear and quadratic effects of F, respectively, on milk 305-d, fat 305-d, and lactose 305-d in dairy Gyr cattle show that inbreeding depression tends to reduce with increase of F.

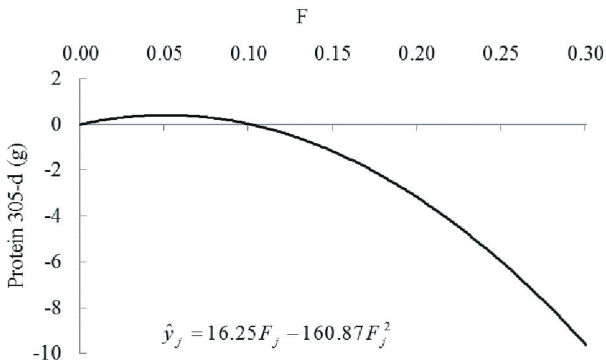

Figure 4 - Effect of inbreeding coefficients (F) on total protein yield up to 305 days (Protein 305-d) in dairy Gyr cattle.

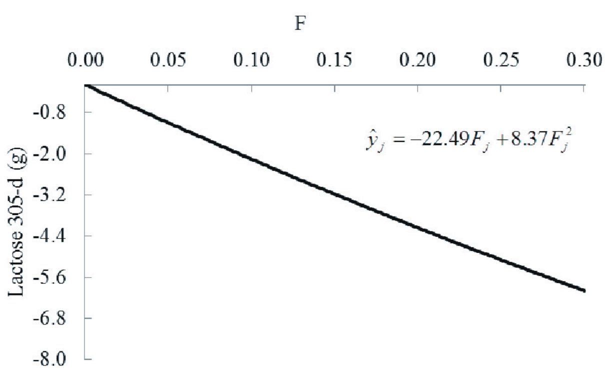

Figure 5 - Effect of inbreeding coefficients (F) on total lactose yield up to 305 days (Lactose 305-d) in dairy Gyr cattle.

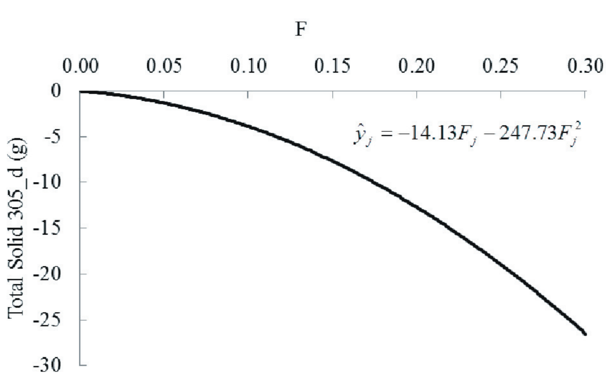

Figure 6 - Effect of inbreeding coefficients (F) on total solid yield up to 305 days in dairy Gyr cattle.

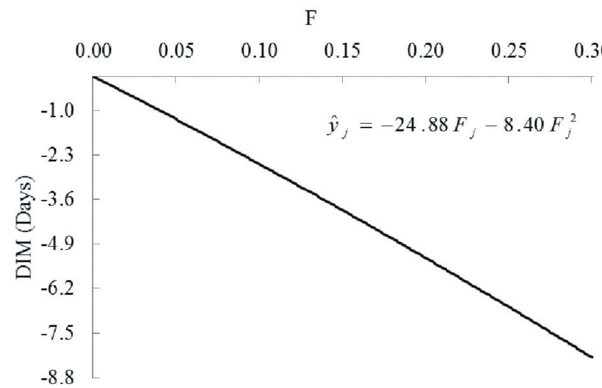

Figure 7 - Effect of inbreeding coefficients (F) on days in milk (DIM) in dairy Gyr cattle.

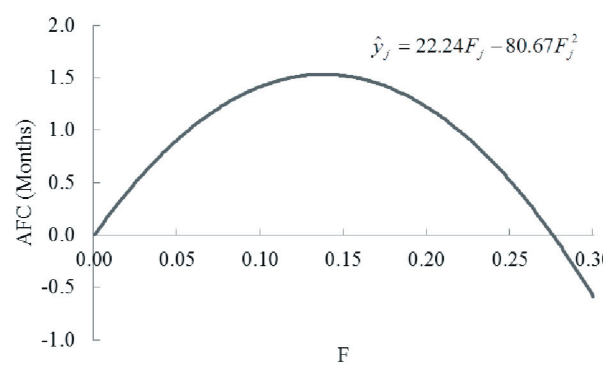

Figure 8 - Effect of inbreeding coefficients (F) on age at first calving (AFC) in dairy Gyr cattle.

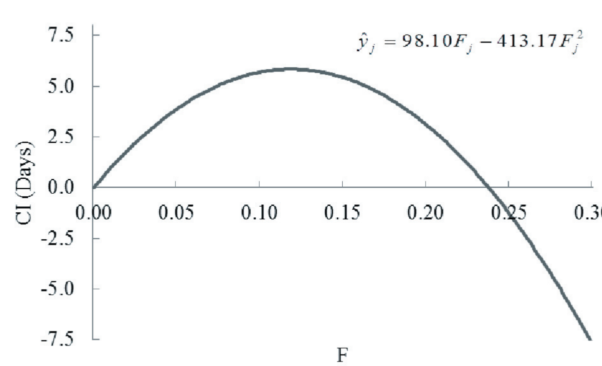

Figure 9 - Effect of inbreeding coefficients (F) on calving interval (CI) in dairy Gyr cattle.

Kristensen and Sorensen (2005) highlighted that the non-linearity of inbreeding depression would be difficult to interpret because there are different elements that are not directly related to inbreeding. The authors cited as the first example the possibility of confounding between inbreeding trends and variation in the environment, because the distribution of animals between different classes of inbreeding is influenced by time.

Another element that could interfere with the interpretation of curvilinearity of inbreeding depression would be the assumption of the independence and homoscedasticity of the inbreeding coefficients (Lynch, 1988). A third element would be the deviation in the expected ratio of loci identical by descent for the actual ratio (Weir et al., 1980). Croquet et al. (2007) add that losses in milk 305-d for each 1% increment in inbreeding can also be explained by the survival of genetically superior individuals with high inbreeding coefficients. In this case, the selection process acts by eliminating inbred animals that express deleterious recessive alleles of major effect. This may produce non-linearity in the relationship between a trait and the inbreeding level (Gulisija et al., 2007) and cause imbalance of the number of animals in different inbreeding levels. This imbalance can be explained by the choice of breeders to avoid mating with related individuals or even incomplete pedigree files (Croquet et al., 2007).

The estimates of AFC and CI increase up to F = 0.138 (Figure 8) and F = 0.119 (Figure 9), respectively, and reduce thereafter. These results did not agree with the generalization that inbreeding tends to reduce fitness (Falconer and Mackay, 1996). Smith et al. (1998) found a linear effect of F on AFC and first CI in the Holstein breed. However, non-significant inbreeding effects on these traits were found by Queiroz et al. (1993) in Gyr, Dias et al. (1994) in Caracu, and Falcão et al. (2001) for CI in Brown Swiss.

According to Queiroz et al. (1993), Dias et al. (1994), and Falcão et al. (2001), some heifers and cows with reproductive problems (caused by genetics or environment) do not have AFC and CI records because they have to calve at least once (for AFC recording) and twice (for CI recording). The numbers of cows with F>0.138 (AFC) and F>0.119 (CI) were 168 (out of 6,236) and 265 (out of 5,613), respectively, and indicate that estimates of inbreeding depression for F>0.138 and F>0.119 could be biased. Bias in the evaluation of AFC and CI can also be caused by management practices, e.g.: problems with perception of heat cycles in Gyr (silent heat); the common practice of delaying breeding of lactating cows for fear of drop in milk production; the non-identification, in the database studied, of donor cows subjected to embryo transfer and *in vitro* fertilization programs; and or the culling of inbred cows with low reproductive efficiency, since the analyzed herds have commercial purposes.

The results of this study suggest that the relationships between the quantitative traits and inbreeding may be more complex than expected, under the hypothesis of additive and dominant effects to be the only responsible for the genetic differences between the animals. If partial dominance and overdominance are the only non-additive genetic effects, the inbreeding depression in a trait is a linear function of the inbreeding coefficient. If epistatic interactions between genes are also responsible for a significant part of this type of gene action, the reduction in phenotypic means can be represented by a nonlinear function of the inbreeding coefficient (Lynch and Walsh, 1998). Thus, the results of this paper suggest that the epistatic effects can also control a significant part of the variation observed for productive and reproductive traits.

Estimates of heritability for productive traits and AFC were moderate (from 0.17 to 0.28; Table 3). Estimates of heritability for milk 305-d, fat 305-d, and DIM were higher than the previously values of 0.21 and 0.24 (Balieiro et al., 2000; Lagrota et al., 2010), 0.21 (Balieiro et al., 2000), and 0.11 (Balieiro et al., 2000), respectively, reported in

Table 3 - Genetic parameters[1] of productive and reproductive traits of dairy Gyr cattle

Trait	$\hat{\sigma}^2_a$	$\hat{\sigma}^2_p$	$\hat{\sigma}^2_e$	$\hat{h}^2$	$\hat{c}^2$
Productive					
Total milk yield up to 305-d	208,900.00	146,700.00	402,000.00	0.28	0.19
Total fat yield up to 305-d	458.10	309.20	931.80	0.27	0.18
Total protein yield up to 305-d	255.70	233.70	678.60	0.22	0.20
Total lactose yield up to 305-d	386.80	309.30	1,179.00	0.21	0.16
Total solids yield up to 305-d	3,728.00	3,308.00	10,140.00	0.22	0.19
Days in milk	600.40	429.90	2,540.00	0.17	0.12
Reproductive					
Age at first calving	5.19	-	20.49	0.20	-
Calving interval	975.20	693.20	7,840.00	0.10	0.07

[1] $\hat{\sigma}^2_a$ - genetic variance; $\hat{\sigma}^2_p$ - permanent environmental variance; $\hat{\sigma}^2_e$ - residual variance; $\hat{h}^2$ - heritability; $\hat{c}^2$ - direct permanent environmental variance as a proportion of the phenotypic variance.

Gyr cattle. The estimated heritability for AFC is in the interval between 0.17 (Balieiro et al., 1999) and 0.22 (Santana Júnior et al., 2010) in the same breed. These results support the possibility of genetic progress though selection. The heritability estimate for CI was low (0.10). Balieiro et al. (1999) also reported a low heritability estimate for CI (0.06), indicating that environmental factors, like pre and post-partum nutritional management, are very important to explain differences of CI between animals.

Permanent environmental effects were also important for productive traits. Estimates of repeatability ($\hat{h}^2 + \hat{c}^2$) for productive traits were moderate to high (from 0.29 to 0.47). Estimates of repeatability for milk 305-d, fat 305-d, and DIM were very close to the values of 0.51, 0.47, and 0.32 reported by Balieiro et al. (2000). Balieiro et al. (1999) estimated repeatability of 0.17 for CI, which is the same value presented in this paper. For CI, and for productive traits as well, accuracies of genetic evaluation could be increased by means of repeated records in the same animal. However, this strategy can increase the generation interval and an optimum number of records for each animal should be defined to achieve an optimum genetic response per year.

Conclusions

The increase in inbreeding coefficient causes losses in productive and reproductive traits, and mating should be carefully design to avoid inbreeding depression in dairy Gyr cattle. It is possible to achieve genetic progress in productive traits (especially in milk 305-d and fat 305-d) and age at first calving in dairy Gyr cattle through selection.

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