Maternal inheritance on reproductive traits in Brangus-Ibagé cattle

Herança materna em caracteres reprodutivos em bovinos brangus-ibagé

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ABSTRACT

Cytoplasmic inheritance influence on reproductive traits was investigated in the Brangus-Ibagé cattle (3/8 Nelore x 5/8 Aberdeen Angus). Additive genetic effects were responsible for 12% ± 11% of phenotypic variation observed in first calving interval, but their contribution dropped to zero when all calving intervals (CI) were considered. The heritability estimate for age at first calving (AFC, in days) was 0.19 ± 0.09. Mitochondrial lineage (MIT) had negligible effects on phenotypic variances of calving interval (0.0 ± 0.02), calf birth weight (0.0 ± 0.01), and cow weight at calving (0.0 ± 0.01). However, for the age at first calving, MIT accounted for 0.15 ± 0.07 of total variation. Cow weight at calving had a significant linear effect on CI and AFC. Three D-loop mtDNA mutations significantly affected either calving interval (T➜ C at sites 16,113 and 16,119) or calf birth weight (T ➜C at site 16,113). The C variants had decreased CI (29 and 32 days, respectively) and increased calf weight (0.6kg). Although the effects were small, direct selection for these mutation-carrier cows might improve the reproductive and developmental performance in this herd.

Key words: mtDNA, maternal inheritance, calving interval.

RESUMO

A influência da herança citoplasmática sobre características reprodutivas foi investigada em bovinos Brangus-Ibagé (3/8 Nelore x 5/8 Aberdeen Angus). Os efeitos genéticos aditivos foram responsáveis por 12% ± 11% da variação fenotípica observada no primeiro intervalo entre partos, mas esta contribuição decresceu para zero quando todos os intervalos entre partos (IEP) foram considerados. A herdabilidade da idade para o primeiro parto (IPP, em dias) foi estimada em 0,19 ± 0,09. A linhagem mitocondrial teve um efeito negligenciável na variância fenotípica do intervalo entre partos (0,0 ± 0,02), peso do terneiro ao nascer (0,0 ± 0,01) e peso da vaca ao parto (0,0 ± 0,01). No entanto, para a idade ao primeiro parto, a linhagem mitocondrial contribuiu com 0,15 ± 0,07 da variação total. O peso da vaca ao parto teve efeito linear significativo em IEP e IPP. Três mutações na região D-loop do mtDNA afetaram significantemente o IEP (T➜C nos sítios 16.113 e 16.119) ou o peso do terneiro ao nascer (T➜C no sítio 16.113). As variantes C diminuíram o intervalo entre partos (29 e 32 dias, respectivamente) e aumentaram o peso do terneiro (0,6kg). Embora os efeitos sejam pequenos, a seleção de fêmeas portadoras dessas mutações poderia melhorar o desempenho reprodutivo e o desenvolvimento deste rebanho.

Palavras-chave: mtDNA, herança materna, intervalo de partos.

INTRODUCTION

Dams can influence their progeny phenotypes through nuclear maternal genetic effects, permanent environmental maternal effects, and cytoplasmic inheritance (BELL et al., 1985). Many

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studies have focused on cytoplasmic effects on economic traits in dairy cattle (BELL et al., 1985; BOETTCHER et al., 1996). The first studies highlighted the influence of cytoplasmic lineages on production traits. Later, analyses including polymorphisms on mitochondrial DNA (mtDNA) suggested their effects on physiological functions (SMITH & ALCIVAR, 1993) and on economic traits in dairy and beef cattle (SCHUTZ et al., 1994; MANNEN et al., 1998).

Mitochondria are the only source of DNA in the cytoplasm and the site of aerobic respiration, playing a central role in energy provision to eukaryotic cells. Almost 90% of the ATP of mammals is produced in mitochondria. The structure and gene organisation are highly conserved in mammalian mtDNA (WOLSTENHOLME, 1992). Nonetheless, the control region or displacement loop (D-loop) is extremely variable and, despite its functional importance, has a rate of nucleotide substitution 5 - 10 times higher than that of nuclear DNA. This feature has been widely used to trace mammalian phylogenies (TROY et al., 2001, MAGEE et al., 2002).

The aim of this study was to verify the influence of cytoplasmic and mitochondrial lineages on reproductive traits in a beef cattle herd. A further objective was to determine the association of specific polymorphisms in mtDNA with reproductive performance.

MATERIAL AND METHODS

Records from a Brangus-Ibagé herd (3/8 Nelore x 5/8 Aberdeen Angus composite breed) from the Southern Brazilian Livestock Research Centre (EMBRAPA-Pecuária Sul, Bagé, RS, Brazil, 54°23'W and 30°47'S) were used in this study. This herd resulted from the crossing of Aberdeen Angus cows and Nelore bulls and has been selected only for adult male body weight and large frame structure, since its formation in 1945. Selection for reproductive performance has not been attempted so far. All animals have been managed exclusively on native pasture under extensive conditions (OLIVEIRA et al., 1998).

Mitochondrial lineages were established by tracing the ancestry of cows to the founder females in the herd. Production records of 1577 females born between 1953 and 1996 were analysed. Parity ranged from 1 to 13 with an average of 3.1 calvings per female. There were 151 different mitochondrial lineages. Sequence information from a 277 nucleotide fragment from the D-loop mtDNA was available for 49 of these

mitochondrial lineages (Henkes, unpublished data). Of the 18 haplotypes found in that study, 16 were used in this analysis.

Five reproductive traits were analysed: first calving interval (CI1) in days, calving interval (CI) in days (average of all CI information), age at first calving (AFC) in days, calf birth weight (CBW) in kg and cow weight at calving (CWC) in kg. All females were first mated at around 3 years of age. The number of observations varied according to the analyses performed due to missing observations.

Data were analysed using the General Linear Models (GLM) of SAS V6 (SAS/STAT, 1990) to determine significant fixed effects. Cow weight at calving (CWC) was fitted in the model as a covariate for CI1, CI and AFC. Sire (s) and mitochondrial lineage (mit) were included as random effects as suggested by TESS & MACNEIL (1994) and RORATO et al. (1999), according to equations:

$$y_{ijklm} = \mu + yob_i + po_j + yob*po_{ij} + \beta CWC_{ijklm} + s_k + mit_l + e_{ijklm} \qquad (1a)$$

$$y_{ijklm} = \mu + yob_i + po_j + yob*po_{ij} + s_k + mit_l + e_{ijklm} \qquad (1b)$$

where, y_{ijklm} is the CI1, CI or AFC phenotype (model 1a) or CWC and CBW phenotype (model 1b) of the mth individual; m is the effect of a population mean; yob_i is the effect of the ith year of birth; po_j is the effect of the jth parity order; $yob*po_{ij}$ is the effect of the year of birth x parity interaction; β is the regression coefficient for cow weight at calving; CWC_{ijklm} is the effect cow weight at calving; s_k is the additive effect of the kth sire; mit_l is the effect of the lth mitochondrial lineage; and e_{ijklm} is the residual effect associated with y_{ijklm} observation.

Only significant fixed effects (p < 0.05, at least) found in (1) were included in the models for estimating variance components (year of birth, parity order, and yob x po interaction).

For the genetic estimates and variance component analyses the contributions of the additive genetic, maternal genetic and direct permanent environmental, and residual effects to total phenotypic variance for CI1, CI, AFC, CWC, and CBW were calculated using Restricted Maximum Likelihood (REML) with an average information algorithm and fitting various animal models to the data. The Average Information Restricted Maximum Likelihood (AIREML) statistical package (JOHNSON & THOMPSON, 1995) was used for analyses.

(a) The equation including the maternal (nuclear, cytoplasmic and in-uterus environmental) effects was:

$$y = X\beta + Z_d u + Z_m m + Z_p p + e \qquad (2)$$

where, y is the vector of CI, CI1, AFC,CWC or CBW observations; β is the vector for fixed effects (yob, po, and yob*po interation); u is the vector of random additive genetic effects; m is the vector of maternal (genetic and in-uterus environmental effects); p is the vector of direct permanent environment effect, and **e** is the vector of random residual effects, and X, Z_d, Z_m, and Z_p are incidence matrices relating records to fixed, additive genetic, maternal and direct permanent environmental effects, respectively.

In model 2 dam was fitted as a second animal effect with covariance matrix uncorrelated with direct additive effect.

(b) The equation for the mitochondrial lineage effects was:

$$y = X\beta + Z_d u + Z_m m + Z_t mit + Z_p p + e \qquad (3)$$

where, y is the vector of CI1,CI,AFC,CBW or CWC observations; β is the vector of fixed effects (yob, po, and yob*po interation); u is the vector of random additive genetic effects; m is the vector of maternal (nuclear and in-uterus environmental effects); mit is the vector of mitochondrial lineage effect (which groups females with the same mitochondrial haplotypes), p is the vector of direct permanent environmental effects, and e is the vector of random residual effects, and X, Z_d Z_m $Z_{t,}$ and Z_p are incidence matrices relating records to fixed, additive genetic, maternal, mitochondrial lineage, and direct permanent environmental effects, respectively.

(c) Analyses of nucleotide substitution effects: Repeated measurements analysis of variance, by using a sire model, was used to compare trait means for groups of animals with and without specific nucleotide substitution. Model equations 4 and 5 were used for the studied traits.

$$y_{ijklm} = \mu + yob_i + s_j + sub_k + b_{ijk} + r_l + yob_i{*}r_l + s_j{*}r_l + sub_k{*}r_l + e_{ijklm} \qquad (4)$$

$$y_{ijkl} = \mu + yob_i + s_j + sub_k + e_{ijkl} \qquad (5)$$

where, y_{ijklm} is the CI or CBW or CWC observation of the mth individual (Equation 4) and y_{ijkl} is the AFC observation of of the lth individual (Equation5); μ is the effect of population mean; yob_i is the effect of ith year of birth; s_j is the random effect of jth sire; sub_k is the random effect of kth nucleotide substitution, b_{ijk} is the between-subject error term, r_l is the effect of lth repeated measurements of each trait, $yob_i{*}r_l$ is the effect yob and r interaction, $s_j{*}r_l$ is the effect of the sire(s) and r interaction, $sub_j{*}r_l$ is the effect of the nucleotide substitution and r interaction, and e_{ijklm} and e_{ijkl} are the within-subject error term.

RESULTS

Table 1 summarises the descriptive statistics and genetic parameters for the traits. Analysis of variance showed that parity, year of birth, and the interaction between parity and year of birth were significant ($p < 0.001$) fixed effects.

The covariate cow weight at calving (CWC) was significant ($p < 0.001$) for both CI and AFC. Estimates of fractions of total phenotypic variance for additive genetic, maternal genetic and animal permanent environmental effects for CI1, CI, AFC, CBW, and CWC are also shown in Table 1. The heritability estimates for CI and CBW were negligible. However, when only the first calving interval record of each cow (CI1) was considered, the direct heritability estimate was 0.12 ± 0.11. The estimate dropped dramatically when all intervals were considered. The maternal heritability ($\hat{h}^2 m$) for the first CI was 0.04 ± 0.08 but soon decreasing to 0.00 ± 0.04 when all intervals were analysed.

Mitochondrial lineage effects contributed little to total variance for all traits except for AFC (0.15 (0.07).

Significant effects of polymorphisms were not detected for AFC and CWC. However, some mtDNA nucleotide substitutions have a significant influence on CI and CBW (Table 2). Mutation T$\rightarrow$C at position 16,113 reduced average CI by 29 days. Likewise, T$\rightarrow$C transition at position 16,119 reduced average CI by 32 days. A small but significant effect was observed for CBW where cows with a T$\rightarrow$C transition at position 16,113 gave birth to calves 0.6 kg heavier than non-carriers.

DISCUSSION

In general, reproductive traits are known to have low heritability, with calving interval being one of the best examples. The low heritability estimate found in this herd is similar to an estimate of 0.16 reported for animals reared in native grassland livestock systems (PEREIRA, 1999). Even lower estimates (0.004 and 0.10) were presented in reviews by KOOTS et al. (1994) and KIRKPATRICK (1999). As the permanent environment has an extreme effect on CI, the reduction of direct heritability estimate from 0.12 at the first CI to near zero when all CI were considered might have been due to the gradual increase of effects of non-genetic factors.

The heritability estimate for AFC (0.19 ± 0.09) was lower than the range (0.2 to 0.39) reported for **Bos taurus** and **Bos indicus** cattle and their crosses

Table 1 - Number of observations (n), means ± standard error (se), number of cytoplasmic lines used in the analyses of variances fractions of phenotypic variance (± se) for direct heritability ($\hat{h}^2d$), maternal genetic ($\hat{h}^2m$) and direct permanent envir ($\hat{c}^2$) effects, and mitochondrial effects (ME) for calving interval at first parity (CI1), calving interval at all parities (CI first calving (AFC), calf birth weight (CBW), and cow weight at calving (CWC) in a Brangus-Ibagé herd.

	n	Mean ± se	Lines	($\hat{h}^2d$)	$\hat{h}^2m$	ME	$\hat{c}^2$
CI1 (days)	1104	585.9 ± 6.0	151	0.12 ± 0.11	0.04 ± 0.08	0.00 ± 0.03	*
CI (days)	2399	524.5 ± 4.0	151	0.03 ± 0.06	0.00 ± 0.04	0.00 ± 0.02	0.22 ±
AFC (days)	662	1142.2 ± 2.9	151	0.19 ± 0.09	0.00 ± 0.07	0.15 ± 0.07	*
CBW (kg)	3592	379.4 ± 1.0	151	0.00 ± 0.03	0.10 ± 0.03	0.00 ± 0.01	0.03 ±
CWC (kg)	3472	30.5 ± 0.6	151	0.23 ± 0.04	0.00 ± 0.02	0.00 ± 0.01	0.04 ±

* Not applicable

(BARBOSA, 1991). MARTIN et al. (1992) reported an average heritability estimate of 0.40 for age at puberty, after reviewing studies of a wide variety of beef cattle breeds. In that review the Brangus breed (resulting, in this case, from the crossing between Aberdeen Angus and Brahman breeds) was reported to have the second highest age at puberty, ranging between the estimates of Aberdeen Angus and Brahman breeds. The heritability estimate for AFC and the variation observed for this trait indicates that the average AFC (1142.2 ± 173.0 days) in the Brangus-Ibagé herd studied might be improved by selection. On the other hand, the heritability due to mitochondrial lineages for AFC was 0.15 ± 0.07 and therefore cytoplasmic lines might be considered when selection is applied.

Cow weight at calving had a significant linear effect on CI and AFC. Younger age at first calving and shorter calving intervals are expected for dams with greater body weights. A medium/high nutritional status is essential to increase weight at calving since body condition at calving is one of the most important components influencing reproductive performance (OSORO & WRIGHT 1992).

Two polymorphisms (at sites 16,113 and 16,119) were associated with a decrease in calving intervals in about 29 and 32 days, respectively. Despite the little magnitude of these findings a reduction of 30 days on CI could lead to a slight increase in lifetime production of the mutant dams, thus resulting in some economic gains for farmers.

At the time of this study, information for the effects of mtDNA mutations was available in literature only at positions 16,053, 16,057 and 16,147 (SCHUTZ et al., 1994). Mutations at positions 16,113 and 16,119 do not lie within any conserved position of the D-loop sequence (STEINBORN et al., 1998), being therefore difficult to explain their effect on reproductive performance. It cannot be excluded that these polymorphisms are in fact markers for differences in structural genes of mitochondria, which in turn have effects on reproductive traits. In further research more individuals need to be either sequenced or screened by single-strand conformation

Table 2 – mtDNA nucleotide (*nt*) mutation effects on mean calving interval (CI) and birth weight at calving (CBW) in a Brangus-Ibagé herd.

Position in D-loop	nt[1]	Trait					
		CI (days)			CBW (kg)		
		n[1]	Means ± s.e	p[1]	n[1]	Means ± s.e	p[1]
16,113	T *	202	545.7 ± 7.0	0.02	119	30.4 ± 0.2	0.04
	C	98	517.0 ± 10.1		76	31.0 ± 0.3	
16,119	T *	231	543.6 ± 6.6	0.02			
	C	69	512.0 ± 12.0				

The symbol * indicates reference sequence according to Anderson *et al.* (1982); [1]nt: nucleotide; n: observed number; p = significance level.

polymorphism in order to detect more lineages with these mutations. Selecting animals with these mutations and confirming that their reproductive performance is better than the non-carrier cows could allow the future use of these polymorphisms as a tool for marked assisted selection.

CONCLUSIONS

The results showed that progress could be made on reproduction by selection for first CI ($\hat{h}^2 = 0.12 \pm 0.11$) and AFC ($\hat{h}^2 = 0.19 \pm 0.09$). Conversely, since the h^2 estimate of all calving intervals was near zero, other ways of improvement such as pasture and feeding supplements could be introduced in order to increase reproductive performance. Mitochondrial lineages did not account for variation in CI and therefore this type of inheritance appears to have no importance for genetic selection. Age at first calving was the only trait that appeared to have been affected by mitochondrial lineages (0.15 ± 0.07). Selection for animals with T$\rightarrow$C transition at sites 16,113 and 16,119 on mtDNA could slightly improve the average CI of the herd. The effect of the 16,113 C$\rightarrow$T transition on calf birth weight is too small to be considered on breeding programmes.

ACKNOWLEDGMENTS

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