

(Co)variance components, genetic parameters and annual trends for calf weights in a Brahman herd kept on floodable savanna

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ABSTRACT. (Co)variance components and genetic parameters were estimated for body weights of an elite Brahman herd under a designed, supervised management and genetic program, including strategic artificial insemination (AI). Restricted maximum likelihood methods were used with a univariate animal model for birth weight (BW) and a bivariate model for weaning weight (205-day weight, 205W) and 18-month weight (548-day weight, 548W). Models included random animal direct and maternal genetic effects, maternal permanent environmental effect (c^2), and sex-year-month of birth-age of dam and genetic group (identified and unidentified paternity), as fixed effects. Analysis A_1 included all calves and analysis A_2 included only those with identified sires. Of the 8,066 calves born, 36% were progeny of AI, 11% from single sire and 53% from multi-sire herds. They were born from 1985 to 1998, from 2559 dams and 146 sires (78 identified). Estimates of direct, maternal and total heritabilities from A_1 for BW, 205W and 548W were: 0.23, 0.07 and 0.30; 0.08, 0.14 and 0.16; 0.16, 0.04 and 0.28, respectively. Corresponding estimates of direct maternal genetic correlations were 0.22, 0.07 and 0.86, and c^2 estimates were 0.04, 0.14 and 0.04, respectively. Estimates of direct and maternal genetic, and permanent

environmental correlations between 205W and 548W were: 0.66, 0.70 and 1.00. Variances and genetic parameters from A_1 and A_2 were, in general, very similar. Estimates of phenotypic, and direct and maternal genetic trends per year from A_1 were: 0.393, 0.004 and 0.003 kg (BW), 3.367, 0.142 and 0.115 kg (205W), 1.813, 0.263 and 0.095 kg (548W). Estimates of direct and maternal genetic trends from A_2 were: 0.033 and -0.002 kg (BW); 0.186 and 0.276 kg (205W); 0.471 and 0.136 kg (548W). The modern selection methods that have been used recently should be continued, with emphasis on the improvement of cow efficiency for sustainable beef production on floodable savanna combined with improved pasture.

Key words: Beef cattle, Heritability, Selection, Tropics, Weights

INTRODUCTION

Large numbers of observations are required to genetically characterize beef cattle populations in different environments. Thus, in countries where breeders' associations or governments have not yet implemented supervised on-farm production testing and official record keeping and processing, researchers depend on the collaboration of private breeders, who in turn need to be guided by scientists and technicians in the execution of their improvement programs. This combination of research and technical assistance makes scientific work more realistic and economical and shortens the time gap between the availability of research results and their practical application (Plasse, 1981).

Thirty percent of Venezuelan territory is covered by savannas, which are to an important extent seasonally flooded. In these regions extensive beef production based on zebu cattle is characterized by low production levels (Plasse, 1992). However, technology is available to increase yields (Plasse et al., 1989) particularly by selection and crossbreeding (Renand et al., 1992).

Since the successful implementation of crossbreeding programs in such ecosystems seems to be limited (Plasse, 2000), genetic improvement of these herds will rely principally on selection. For large commercial herds, a reasonable alternative is to generate an elite herd for the production of bulls to be used in the whole herd by selecting the highest grade zebu cows available. Strategic insemination of about 50% of the cows suitable for mating by artificial insemination has been shown to work in bull-producing herds under such extensive conditions (Plasse et al., 1988). If selected sons produced by artificial insemination with semen from proven bulls are used in natural service in the elite herd and in the commercial herd, genetic progress should be possible in the elite herd and could then be transferred to the commercial part of the population. Analysis of data from these herds involves the problem of how to use records of calves whose sires are not identified because the calves were produced in multi-sire herds, as a consequence of the large number of fenced pastures that would be required to assign all cows not included in the artificial insemination program to single-sire herds. Consequently, the objectives of the present study were: 1) to describe such a stratified herd in terms of (co)variances and genetic parameters, and to measure genetic and phenotypic trends for body weights over a 14-year period and 2) to compare results from an analysis including all calves with results from another analysis using only progeny with known sires.

MATERIAL AND METHODS

The study was done on the privately owned ranch “Santa Luisa”, located in the Venezuelan savanna in Apure state between 7 and 8° N and between 67 and 68° W, in a tropical climate. The mean annual rainfall for the last 38 years has been 1438 mm with 90% of this being received from May through October (rainy season). The floods caused by the river system comprising the Orinoco and its tributaries affect about 40% of the total ranch area and reach depths of 1.5 to 2.5 m, making this flooded part useable only during the dry season. The ranch has a two-way water regulation system to mitigate some of the negative effects of floods and droughts. There are 20,000 ha of savanna with native grasses, mainly *Leersia hexandra*, *Hymenachne amplexicaulis* and *Paspalum fasciculatum* and 4000 ha of cultivated pasture, seeded mainly with *Echinochloa polystachya*, *Brachiaria arrecta*, *humidicola* and *decumbens* and *Cynodon nlemfluensis*. During the years of this study, the number of breeding cows in the whole herd varied between 4250 and 5830.

The elite Brahman herd was founded in the 1950's with the importation of 20 Brahman cows from USA and the acquisition of several other groups of this breed in Venezuela, followed by a later introduction of 100 Brahman x Nelore cows, registered as Cebú Venezolano. Only registered Brahman and unregistered Brahman-sired bulls from the herd have been used since its foundation. Since 1983 this ranch has been included in our research-technical assistance program. The registered Brahman cows were artificially bred to registered bulls of the same breed or by natural service in single-sire herds. The unregistered cows were artificially inseminated or bred in multi-sire herds to Brahman bulls. The percentage of cows assigned to artificial insemination was limited by the restriction imposed of not sacrificing reproductive efficiency. Thus, only heifers weighing more than 300 kg, and in recent years 320 kg, nonlactating and early-calving (> than 30 days before the breeding season) cows were inseminated. On average, during the years of this study, 43% of the cows were assigned to the artificial insemination program. From 1984 to 1997, the herd increased from 700 to 820 cows.

The management program was based on a limited breeding season, which has gradually been shortened, and in recent years was 3.5 months for cows and 3 months for heifers, from February through April. The artificial insemination program lasted 2 months, followed by clean-up service for the rest of the season.

Cows were kept on native grass. For about 4 months of the year, they also had access to improved pasture. Parturition took place in calving pastures, where calves were identified and weighed within 24 h after birth. Calves stayed full time with their dams until weaning (8.5 months at the beginning of the experiment and 7 months in recent years). Calves and their dams had free access to a complete mineral mixture. Calves were weighed at weaning and then again at 18 months. Weights were adjusted to 205 and 548 days, respectively. These weights will be called 205-day weight and 548-day weight throughout this paper. After weaning, calves were separated according to sex and managed, together with all contemporaries from the ranch, on improved pasture or good quality savanna.

The health program of the calves included disease prevention for the newborn, vaccination of females against brucellosis and leptospirosis, vaccination of all calves against foot and mouth disease, vesicular stomatitis, rabies, clostridial diseases and *Campylobacter*, and frequent control of external and internal parasites.

Two-year-old heifers were selected for breeding if they weighed 280 kg (during the

first years) and 300 kg (the last years) before the breeding season. Those selected included on average 78% of those available at 2 years of age. During the 14 years of this study, an average of 21% of the cows were culled. The two main reasons were low reproductive efficiency (45%) and deficient maternal ability (20%).

Each year, 8 to 10 two-year-old bulls were selected to replace one third of the herd sires in natural service. Until 1989 this selection was for 548-day weight; from 1990 to 1994 selection was based on genetic value for 548-day weight estimated with the solutions from a least squares analysis. A superior 205-day weight and a satisfactory semen test were also required. Selection of half sibs was avoided. Since 1989, this herd has participated in a cooperative genetics program (Anonymous, 2002) including another six Brahman herds with a total of 6000 cows. EPDs (expected progeny differences) are being calculated for all bulls using the MTDFREML program (Boldman et al., 1995) with an animal model. EPDs for 548-day weights are used as the principal selection criterion. Young (2 years old) bulls are preselected from the whole population based on their EPDs for 548-day weight estimated from their own record and records of ancestors and collateral relatives. Estimates are associated with accuracies of 0.4 to 0.5. Young bulls were used for one year in at least three herds. Bulls were finally selected for the central semen bank after the EPDs for 548-day weight of progeny were available with an accuracy of 0.90 or greater, which in the program is usually the case with 70 to 80 offspring evaluated in three herds. Bulls for natural service were selected based on EPDs for 548-day weights calculated from the whole population but chosen within each herd or, in a few cases, in other collaborating herds.

Sires were bred to random groups of cows within the reproduction system. Mating of relatives was avoided to keep percentage of inbreeding at low levels. Until 1989 semen was bought from commercial semen banks or from progeny tested bulls of another cooperative program supervised by our group. After 1989, the semen came from the central sperm bank of the cooperative in which the herd participated. Sires chosen for artificial insemination were usually not utilized for more than 2 years. Herd sires in natural service were culled based on their EPDs for 548-day weight calculated annually (single sire herds), or after three years of service (multi-sire herds). Culling of progeny was not practiced until after 18 months of age. All data were included in the data bank. Sire solutions were used to estimate breeding values in order to eliminate inferior bulls. Since 1990 this evaluation has been part of the cooperative genetic program and has included all herds.

Of the 78 sires used by artificial insemination or in single sire herds during the investigation, 29 were homebred, 42 were from the central semen bank of the cooperative or from other herds technically assisted by our group, and seven were imported from the USA. Except for the imported bulls, some sort of estimate of their breeding value for birth, 205- and 548-day weights was available. Bulls were used for an average of 1.6 years. The 68 bulls used in multi-sire herds were selected from their herd of origin.

From the data base of 8,075 calves born from 1985 through 1998, nine (0.1%) were eliminated because they were the only offspring of a bull (1), had no birth weight available (1), were born outside the normal calving season (5) or had an 18-month weight less than weaning weight (2). The data sets for analyses of birth, 205- and 548-day weights comprised 8,066 calves born alive, 7,634 weaned from their dam without any special treatment and 7,359 calves weighed under normal and comparable conditions at 18 months.

To determine the fixed effects to be included in the final animal model, 10 analyses

were performed for the three weights, using general linear model techniques with the SAS program (Freund and Littell, 1981). Based on these results, a contemporary group of sex-year of birth-month of birth-age of dam was defined. An additional fixed effect of genetic group (calves with identified versus non-identified paternity) was also included in the model. The three weights were analyzed with univariate (birth weight) and bivariate (205- and 548-day weights) animal models, which, in each case, included random direct and maternal genetic effects, the dam's permanent environmental uncorrelated effect and the error effect, in addition to the fixed effects.

The model was:

$$Y = Xb + Za + Mm + Wc + e$$

where for the univariate case, Y is the N x 1 vector of records, X, Z, M and W are the known incidence matrices that associate levels of b, a, m and c with Y, b denotes the unknown vector of fixed effects, a is the unknown vector of breeding values for direct genetic effects, m is the unknown vector of breeding values for maternal genetic effects, c is the unknown vector of permanent environmental effects contributed by dams to records of their progeny, and e is the vector of residual effects.

Estimation of (co)variance components was carried out by restricted maximum likelihood employing a simplex algorithm to search for variance components to minimize -2log likelihood (L) (Boldman et al., 1995). Convergence was assumed when the variance of the function values (-2log L) of the simplex was less than 10^{-9} . After first convergence, a restart was performed to verify that it was not a local minimum.

Breeding values were calculated utilizing all pedigree information available. Annual genetic trends were calculated for each trait by regressing the mean breeding values of calves on birth year. Phenotypic trends were calculated by regressing the adjusted weights on birth year. Adjusted weights were obtained from a least squares analysis (Harvey, 1987), which included sex, year and month of birth, age of dam and the year x month interaction.

The main effects had the following classifications: birth year, 1985-1998; month of birth, 11 to 4; age of cow at calving, 3-14 years; sex, males and females; genetic group, identified paternity, unidentified paternity. Analysis 1 included all calves and analysis 2 included only calves with identified sires. The dataset used for analysis 2 was reanalyzed including in the basic model the sire x year interaction as an additional random effect (analysis 3).

RESULTS AND DISCUSSION

The data structure is summarized in Table 1. Where applicable, the respective numbers are given for the two data sets utilized for analyses 1, 2 and 3. Differences in the numbers of calves with records of the three weights were due to death. Considering that only a single herd was involved, there was a satisfactory number of offspring per sire and dam for a tropical herd of beef cattle. Of the calves that were born, 36% were progeny of artificial insemination, 11% were from single sire herds and 53% from multi-sire herds. Although these percentages are not optimal for genetic progress, under such extensive conditions a limit is imposed on the percentage of cows assigned to artificial insemination by the need not to sacrifice reproductive efficiency.

Mean birth weight was greater than the values summarized for this breed in Latin America by Plasse (1978) and updated by Arango and Plasse (1994) and those published by

Table 1. Number of records analyzed, means and standard errors for birth, 205- and 548-day weights for two data sets.

Item	Analysis ^a	Birth weight	205-day weight	548-day weight
Animals (N) ^b	A ₁	9101		
	A ₂	5401		
Calves (N)	A ₁	8066	7634	7359
	A ₂	3791	3583	3441
Sires (N) ^{c, d}	A ₂	78	78	78
Dams (N)	A ₁	2559	2471	2449
	A ₂	1821	1753	1728
Progeny/sire (N) ^e	A ₂	48.6	45.9	44.1
Progeny/dam (N)	A ₁	3.2	3.1	3.0
	A ₂	2.1	2.0	2.0
Unadjusted means (kg)	A ₁	29.9 ± 0.05	162.4 ± 0.29	269.0 ± 0.38
	A ₂	30.8 ± 0.07	167.4 ± 0.43	274.2 ± 0.53

^aA₁ = Analysis 1 performed with all calves. A₂ = Analysis 2 performed on calves with known sires.

^bAnimals for which estimated breeding values were calculated.

^c78 sires used by artificial insemination and natural service in single-sire herds.

^dThere were 68 additional sires used in multi-sire herds.

^eApplies only to analysis 2.

Romero et al. (2001) and Plasse et al. (2002). Weaning weight was less than that reported by Romero et al. (2001) from a herd on cultivated pasture in a more favorable area, but similar to means from other reports. The mean for 548-day weight was similar to the averages given in Plasse (1979) and Arango and Plasse (1994) but less than means reported by Romero et al. (2001) and Plasse et al. (2002) from more favorable conditions.

Birth weight

Estimates of (co)variance components and genetic parameters for birth weight are given for analysis 1 (A₁) in Table 2. In general, results from A₁ were quite similar to those reported for a Brahman herd kept under more favorable conditions, which also received technical assistance from our group and which followed a similar genetic and management program (Plasse et al., 2002). However, direct heritability for A₁ (0.23) was lower than reported in Plasse et al. (2002) and also less than the averages given for *Bos indicus* cattle in the reviews by Mercadante et al. (1995) and for *Bos taurus* and *Bos indicus* cattle by Koots et al. (1994a), which were 0.33, 0.29 and 0.31, respectively. Maternal heritability was 0.07, close to the value of 0.08 found by Plasse et al. (2002), but lower than estimates given by Mercadante et al. (1995) and by Koots et al. (1994a) who reported averages of 0.12 and 0.14, respectively. Total heritability (Willham, 1972) was 0.30, similar to the estimates given for a Brahman herd by Plasse et al. (2002) and the average of the review by Mercadante et al. (1995). The correlation between direct genetic and maternal genetic effects was 0.22. Many publications report a negative direct-maternal

Table 2. Estimates of (co)variance components and genetic parameters for birth weight (BW), 205-day weight (205W) and 548-day weight (548W) (kg).

Trait	Analysis	Variance components					
		σ_d^2	σ_m^2	σ_{dm}	σ_c^2	σ_e^2	σ_p^2
BW	A ₁	3.47	1.05	0.42	0.58	9.81	15.33
	A ₂	5.94	1.12	-0.04	1.41	9.57	17.99
205W	A ₁	29.53	47.09	2.58	48.54	220.85	348.59
	A ₂	31.16	48.50	4.17	50.76	241.55	376.13
548W	A ₁	88.21	21.43	37.52	20.93	388.86	556.95
	A ₂	91.44	22.13	23.20	21.31	413.62	571.71
		Parameters					
		h_d^2	h_m^2	h_t^2	r_{dm}	c^2	e^2
BW	A ₁	0.23	0.07	0.30	0.22	0.04	0.64
	A ₂	0.33	0.06	0.36	-0.02	0.08	0.53
205W	A ₁	0.08	0.14	0.16	0.07	0.14	0.63
	A ₂	0.08	0.13	0.16	0.11	0.13	0.64
548W	A ₁	0.16	0.04	0.28	0.86	0.04	0.70
	A ₂	0.16	0.04	0.24	0.52	0.04	0.72

A₁ = Analysis with all calves. A₂ = Analysis performed on calves with known sires.

σ_d^2 , direct additive genetic variance; σ_m^2 , maternal additive genetic variance; σ_{dm} , covariance between direct additive and maternal additive genetic effects; σ_c^2 , maternal permanent environmental variance; σ_e^2 , temporary environmental variance; σ_p^2 , phenotypic variance.

h_d^2 , direct heritability; h_m^2 , maternal heritability; h_t^2 , total heritability [$(\sigma_d^2 + 0.5\sigma_m^2 + 1.5\sigma_{dm})/\sigma_p^2$]; r_{dm} , genetic correlation between direct additive and maternal additive effects; c^2 , fraction of phenotypic variance due to maternal permanent environmental effects; e^2 , fraction of phenotypic variance due to temporary environmental effects.

genetic correlation for birth weight. Mercadante et al. (1995) reported a weighted mean of -0.37. The same value was found by Plasse et al. (2002), while Koots et al. (1994a) obtained a weighted mean of -0.35. The permanent environmental maternal effect contributed 4% to the phenotypic variance, similar to the 3% reported by Plasse et al. (2002). Residual variance accounted for 64% of the phenotypic variance, similar to the respective values given by Plasse et al. (2002) in another Brahman herd.

205-Day weight

Estimates of (co)variances and genetic parameters for weaning weight are given in Table 2. In general, estimates of variances and genetic parameters were very similar to the estimates found in another Brahman herd under our technical supervision (Plasse et al., 2002). Direct, maternal and total heritabilities were 0.08, 0.14 and 0.16, respectively, in agreement with estimates published by Plasse et al. (2002) except that total heritability was higher than in that report, mainly because our direct-maternal correlation was slightly positive while in the other herd it was slightly negative. Maternal heritability was 75% higher than direct heritability, while in Plasse et al. (2002) it was twice as high. Eler et al. (1995) also found higher maternal than direct heritability, while Kriese et al. (1991) postulated that the maternal portion

of the total variation is more important in Brahman than in *Bos taurus* cattle. Our heritabilities were lower and the direct-maternal correlation higher than reported in the literature. Mercadante and Lobo (1997) calculated means of 0.26, 0.16 and 0.22 for direct, maternal and total heritability, respectively, and direct-maternal correlation of -0.31 from reports on *Bos indicus* populations, while for their own data on 3,237 Nelore females in Brazil the estimates were 0.29, 0.13, 0.35 and 0.00, respectively. The weighted means for direct and maternal heritabilities in the review by Koots et al. (1994a) were 0.24 and 0.13 with a direct-maternal correlation mean of -0.16. Our heritability values for maternal genetic effects, which are generally assumed to principally express the variation in milk production potential, and the small positive, direct-maternal genetic correlations show that genetic potentials for growth and milk production in Brahman cattle in the tropics are not antagonistic.

The calculated proportional permanent environmental (dam) effect ($c^2 = 0.14$) is similar to that reported by Plasse et al. (2002), but higher than the average of 0.11 calculated from the *Bos indicus* literature and the estimate for a Nelore herd, which was 0.10 (Mercadante and Lobo, 1997). Based on our results, it appears that permanent environmental effects due to the dam are of considerable importance in Brahman herds and could be just as important as genetic maternal effects. This agrees with the results of Haile-Mariam and Kassa-Mersha (1995) for Boran and of Robinson (1996a) for Australian Angus.

548-Day weight

Direct and total heritabilities were higher and maternal heritability and c^2 effects much lower than for weaning weight. The direct and total heritabilities were 0.16 and 0.28, somewhat higher than those found by Plasse et al. (2002), while maternal heritability (0.04) was only half the value found in that study. The direct-maternal correlation was 0.86, much higher than reported by Plasse et al. (2002), and c^2 was slightly larger.

Most work with postweaning weights has been carried out with yearling weight and is therefore not comparable with our data, because in the tropics the after-weaning stress period usually extends beyond one year of age. For this reason we consider 18-month weight more appropriate for studying genetic differences in postweaning weights and for use as a selection criterion. Estimates published in the literature are generally higher than ours for direct and maternal heritability, higher or lower for total heritability and close to zero or negative for the direct-maternal correlation (Eler et al., 1995; Mercadante and Lobo, 1997).

The permanent environmental effect of the cow contributed 4% to the phenotypic variance, the same as that found in a bivariate analysis of weaning weight published by Eler et al. (1995). It was within the range obtained by Mercadante and Lobo (1997) with uni- and bivariate analyses, and was slightly higher than the estimate reported by Plasse et al. (2002) with a univariate analysis.

Correlations between 205- and 548-day weights

Estimates of the correlations from the bivariate analysis of 205- and 548-day weights are given in Table 3. The additive genetic correlation between the two weights was 0.66, similar to the estimate found by Plasse et al. (2002) in another Brahman herd and lower than the average calculated from the *Bos indicus* literature by Mercadante et al. (1995). It was also lower

Table 3. Estimates of correlations between 205- and 548-day weights.

Analysis	Correlation				
	r_{d1d2}	r_{m1m2}	r_{c1c2}	r_{e1e2}	r_{p1p2}
A ₁	0.66	0.70	1.00	0.57	0.64
A ₂	0.59	0.70	0.78	0.58	0.64

A₁ = Analysis with all calves. A₂ = Analysis performed on calves with known sires.

r_{d1d2} , direct additive genetic correlation; r_{m1m2} , maternal additive genetic correlation; r_{c1c2} , permanent environmental correlation; r_{e1e2} , temporary environmental correlation; r_{p1p2} , phenotypic correlation.

than the mean genetic correlation between weaning and yearling weight (0.81), given in the review by Koots et al. (1994b). Our value was also somewhat less than the estimate of the genetic correlation between weaning and final (16-23 months) weights (0.69) reported for cross-bred Australian Zebu (Meyer, 1994). The maternal genetic correlation was 0.70, while Meyer (1994) and Plasse et al. (2002) reported estimates close to unity. The permanent environmental correlation was unity. Several within run estimates were out of the parameter space, but since REML estimates have to be within bounds, the program forced them to unity. Meyer (1994) published an estimate of 0.91 and Haile-Mariam and Kassa-Mersha (1995), as well as Plasse et al. (2002) estimated permanent environmental correlations to be unity. The high maternal genetic and permanent environmental correlations between weaning and 18-month weights suggest that important genetic and environmental effects due to the dam might still be present at 18 months in beef cattle and, supposedly, are a carry-over effect from the preweaning period produced through a part-whole relationship. Similar observations have been made by other authors (Meyer 1994; Tosh et al., 1999; Plasse et al., 2002). The estimate of the residual (temporary environmental) correlation was 0.57, lower than that found by most authors (Meyer, 1994; Eler et al., 1995; Plasse et al., 2002). The phenotypic correlation between weaning and 18-month weight was 0.64, which equals the average reported by Mercadante et al. (1995) from the world literature on zebu cattle, but is lower than the value found by Plasse et al. (2002) in another Brahman herd.

Estimates of heritabilities and genetic correlations indicate that milk production could be improved by selecting for maternal genetic effects at weaning, and that this would not be antagonistic to genetic improvement of growth rate, which should be improved by selection for 18-month weight rather than using weaning weight as a criterion.

Phenotypic and genetic trends

Birth weight increased by 0.393 kg per year (Table 4) improving from an adjusted mean of 27 kg in the first year to 32 kg in the last 3 years of this study (Figure 1). The trend was quite linear and highly significant. As a consequence, birth weights under 20 kg, shown by Beltrán (1976) as a critical limit, below which early mortality is high, were recorded in only 67 (0.8%) of all calves born, with a minimum of 10 kg. Of these, only nine were born during the last 6 years. Of the 67 calves, 42% died before weaning; 46% among those died during the first 3 days after birth. On the other hand, the mean was not due to abnormally high birth weights (maximum 49 kg) and the frequency of dystocia was almost zero. The 205-day weight had a highly significant trend of

Table 4. Annual phenotypic and direct and maternal genetic trends for birth (BW), 205-day weight (205W), 548-day weight (548W) and milking ability (1985-1998).

Trait	Analysis ^b	Annual trend (kg) ^a		
		Phenotypic ^c	Direct genetic	Maternal genetic
BW ^d	A ₁	0.393 ⁺⁺	0.004	0.003
	A ₂		0.033	-0.002
205W ^c	A ₁	3.367 ⁺⁺	0.142 ⁺⁺	0.115 ⁺⁺
	A ₂		0.186 ⁺⁺	0.276 ⁺⁺
548W ^c	A ₁	1.813 ⁺⁺	0.263 ⁺⁺	0.095 ⁺⁺
	A ₂		0.471 ⁺⁺	0.136 ⁺⁺

⁺⁺⁺P<0.01.

^bA₁ = Analysis including all calves. A₂ = Analysis performed on calves with known sires.

^cUsing least square solutions for year of birth.

^dFrom univariate analysis.

^eFrom bivariate analysis.

3.367 kg per year, which was quite linear. From 146 kg in the first year, the mean increased to 184 kg in the last year, with a maximum reached at 186 kg in the penultimate year. Weight at 548 days was 254 kg during the first and 280 kg during the last year, with a maximum of 283 kg one year earlier. The mean annual phenotypic trend of 548-day weight compares well with the estimates reported for Brahman in Venezuela (Hoogesteijn and Verde, 1998; Plasse et al., 2002). The annual phenotypic trend (Figure 1) for 548-day weight was quite irregular, which may be explained by the deterioration of pasture between 1990 and 1995.

Estimates of annual direct and maternal genetic trends for the three weights during the 14-year period are given in Table 4 and in Figure 2. Direct genetic change for birth weight calculated from the yearly means of estimated breeding values was not significant and was close to zero. This shows that selection for 548-day weight did not produce a strong correlated genetic change in birth weight. Genetic trend was irregular over the years (Figure 2) and of no practical importance. The same pattern applies to maternal genetic trend, which was not significantly different from zero. The direct genetic trend for 205- and 548-day weights was 0.142 kg (P<0.01) and 0.263 kg (P<0.01), respectively, and the maternal genetic trend was 0.115 kg (P<0.01) and 0.095 kg (P<0.01), respectively, per year. Genetic trend in milk production is reflected by the maternal genetic trend in Table 4 and Figure 2 and shows that annual lactation milk yield increased enough to support an increase in weaning weight of 0.115 kg per year. Although direct and maternal genetic trends are expressed phenotypically in different generations, over a long time period it should be acceptable to add both means in order to estimate total genetic progress achieved for each weight by direct and correlated response through selection for growth rate until 18 months in males and maternal ability in females. For 205- and 548-day weights this would amount to 0.257 kg and 0.358 kg per year. This would mean that of the phenotypic change in 14 years of 47 kg for 205-day weight and 25 kg for 548-day weight, 3.6 and 5.0 kg, respectively, would have been due to genetic selection during the 14-year period.

When comparing these results with the literature, it is necessary to keep in mind that only 36% of the calves born were produced by artificial insemination and only half of these were from proven bulls with high breeding values for 548-day weight with accuracy over 0.90.

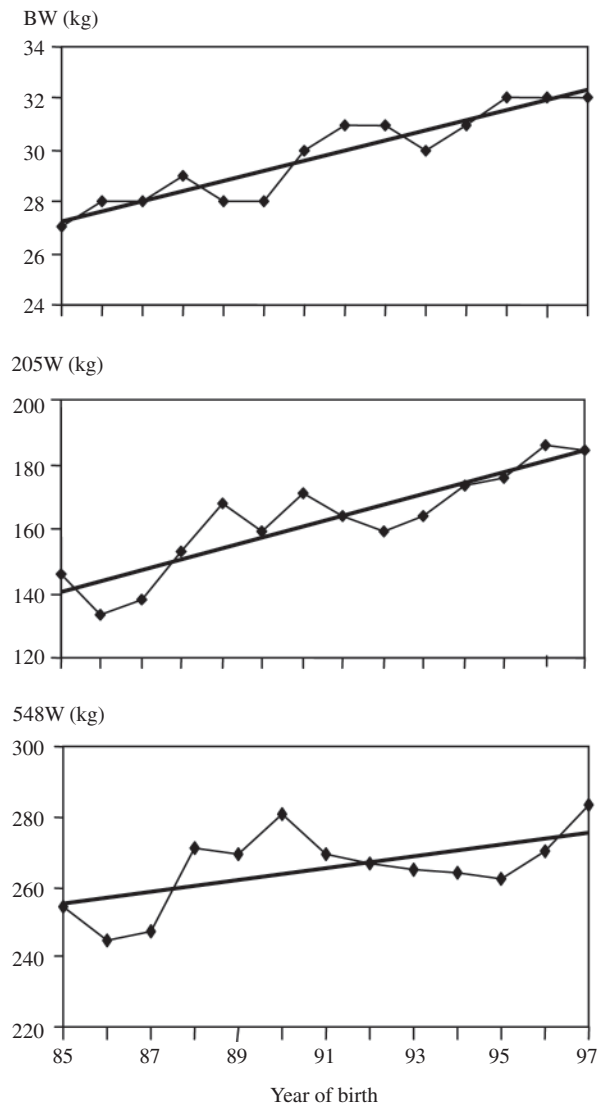


Figure 1. Annual phenotypic trends (kg) by year of birth for birth weight (BW), 205-day weight (205W) and 548-day weight (548W).

The other half of the calves produced by artificial insemination were sired by bulls preselected based on a breeding value estimated through the bulls' own weights and those of their relatives available in the pedigree information, but with no progeny records. The accuracies were between 0.40 and 0.50. This situation is similar to that found in the entire population of the genetic cooperative to which this herd belongs. Mean direct genetic trends per year in the whole population for the years 1990-2001 were 0.07, 0.64 and 1.13 kg for birth, 205-day and 548-day weights, respectively, while for maternal genetic trends the respective changes were -0.01, 0.20 and 0.06 kg (Anonymous, 2002). This comparison shows that the herd in our study was progressing at a much slower rate than the population average, mainly because it is managed under much more extensive conditions, and with a lower than average percentage of cows

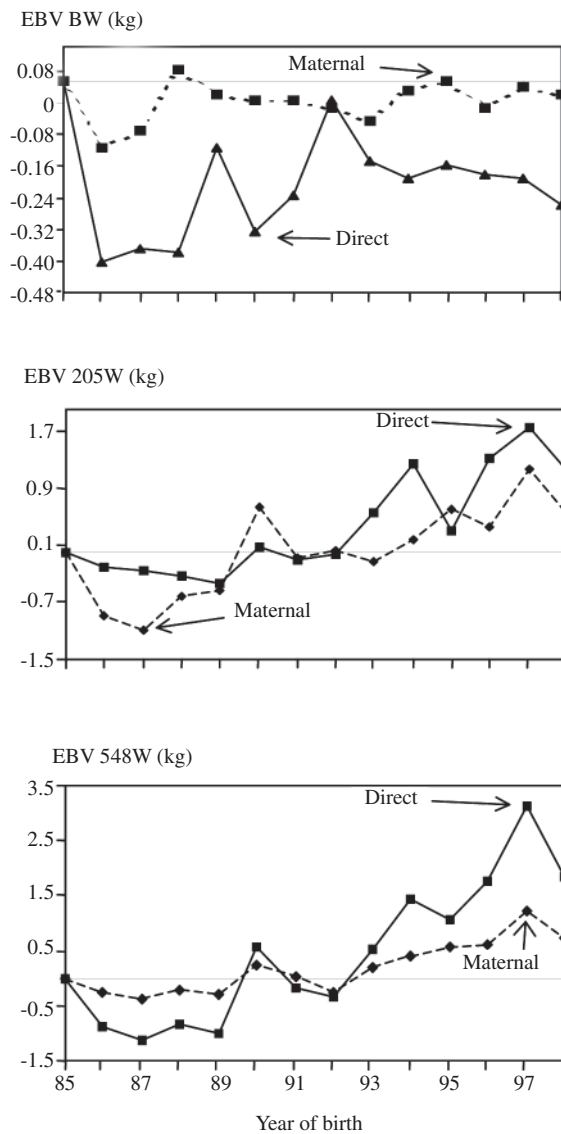


Figure 2. Annual direct and maternal genetic trends (kg) by year of birth for birth weight (BW), 205-day weight (205W) and 548-day weight (548W). EBV, estimated breeding value.

assigned to the artificial insemination program. However, the direct genetic trends during the last 6 years have been much higher than for the 14-year period. This improvement is probably due mainly to the benefits of the cooperative genetic program and the use of modern genetic analysis methods. The other published data that we cited are from progeny produced by artificial insemination or in single sire herds by natural service. This means that selection pressure was much less in this herd than in those discussed by Hoogesteijn and Verde (1998) and Plasse et al. (2002) who calculated higher genetic progress in calves with known paternity. Plasse et al. (2002) reported direct genetic trends per year over a 30-year period of 0.06, 0.13 and 0.49 kg

for birth, 205-day and 548-day weights, while the respective estimates for maternal genetic trend were 0.00, -0.04 and 0.25 kg per year. As a reference for what could be achieved in the future with large-scale genetic programs, the results of Crump et al. (1997) are summarized. They found the mean annual genetic trend for 400-day weight of the registered populations of Simmental, Limousin, Charolais, South Devon and Angus breeds in Great Britain to be 1.04 to 2.49 and 0.82 to 1.86 kg for the period 1980-1992 and for all years on record respectively.

Analysis of calves with known paternity (analysis 2)

Results of A_1 and A_2 would be expected to be different, because A_1 was done with data from the whole population where pedigree relationships could be established only through the dam for 53% of the calves, whereas A_2 included calves from a subpopulation, where genetic relationships could be traced through the sire and the dam for all calves. In general, slightly higher variances were found for all weights in A_2 than in A_1 (Table 2). However, among the three weights considerable differences were found only in the direct-maternal genetic covariance and for birth weight, also in the permanent environmental variance of the dams. For birth weight, most genetic parameters were quite different between the two analyses. For 205- and 548-day weights estimates of the direct-maternal genetic correlations differed somewhat between A_1 and A_2 , but estimates of other parameters were similar. Genetic and phenotypic correlations between 205- and 548-day weights (Table 3) were essentially the same for both analyses. This was expected from a bivariate analysis, which uses extra information, increases accuracy of estimation and improves data structure, as reported by Ducrocq (1994).

The annual genetic trend for 205- and 548-day weights was considerably higher for offspring of artificial insemination and of single-sire herds (Table 4, A_2) than for the whole population (A_1). For direct genetic trend the superiorities for the two weights were 31 and 79%, and for maternal genetic trend they were 140 and 43%. The direct genetic trend for 548-day weight in calves with known sires was 0.471 kg per year, comparable to the report for another Brahman herd (Plasse et al., 2002) and slightly less than in the report for 450-day weight of 147 Nelore herds participating in a genetic cooperative in Brazil (Lobo et al., 2001).

Sire x year interaction

The small positive genetic-maternal correlation at weaning is contrary to most of the values reported in the above-cited literature and is partly explained by the results of the analysis, which included the sire x year interaction in the model. This analysis (A_3) was performed with 124 sire-years and a mean of 1.6 years per sire. The interaction term was close to zero, and the results of the models with and without the random interaction term were not significantly different when a likelihood ratio test was performed. Consequently, the genetic parameters were essentially the same. Robinson (1996a), when discussing direct-maternal genetic correlations at weaning, concluded that “negative estimates were more likely to be a consequence of additional variation between sires or sire x year variation, than evidence of a true negative genetic relationship” and was able to confirm this hypothesis with the results for a simulated data set (Robinson, 1996b). Meyer (1997) suggested that lower negative genetic-maternal correlations are obtained in experimental than in field data, and that “most of the direct-maternal covariance in Herefords is environmental rather than genetic.” Lee and Pollak (1997) con-

cluded, from the results of different analyses of simulated data sets, that a large part of the negative direct-maternal genetic covariance in weaning weight is produced by a sire x year interaction. We believe that the data used in our study, although they came from a private herd, can be considered to be “experimental data” because of the scientific design and the technical supervision of the genetic and management programs. Probably this fact and a proper definition of the contemporary groups in our model would have mitigated the reasons for the generation of an apparent negative covariance in other studies. However, the relatively low number of observations and the low mean number of years for each sire, might prevent such an interaction from becoming manifest. The effect of sire x year or herd interaction needs to be studied in the entire population of the genetic cooperative.

CONCLUSIONS

We found that artificial insemination used strategically in part of, rather than in the whole herd, is feasible even with extensive beef cattle production systems, if it is based on a designed management plan and accompanied by a genetic selection program. To be successful, however, artificial insemination must be restricted to the cows most likely to conceive.

While estimates of moderate genetic progress in weights and milk production were found over the whole period, genetic gains accelerated during the last years, when modern genetic-analytical methods were used for breeding value evaluation in the context of a cooperative genetic program. Reproductive efficiency apparently was not impaired by selection for 548-day weight, since pregnancy rate increased during the study from 71 to 85%. Direct heritabilities were low, and maternal heritability at weaning was higher than the direct heritability. This fact, the relatively high proportion of maternal permanent environmental variance at weaning and the high maternal permanent environmental correlation between 205- and 548-day weights confirm the importance of the preweaning maternal environment that the cows provide to their progeny for weights up to 18 months of age. Our results support the advantage of multiple over single trait genetic evaluation.

The data from this herd indicate that an adequate design of the genetic and management program might avoid sire x year interactions and the resulting negative estimates of direct-maternal genetic correlations. Comparing an analysis of the data of the whole population with that from a subpopulation in which sires of all calves were identified, generally showed considerable similarity in the estimates of variances and genetic parameters. So the choice of which type of analysis should be preferred for practical and theoretical purposes, would depend on the objective of the study.

Annual genetic trend was markedly higher in the subpopulation with identified sires and shows the definite genetic advantage of the strategic use of artificial insemination with genetically proven bulls in part of the herd.

The results suggest that the selection program used in this herd, which emphasizes reproductive efficiency in cows and in sires growth rate up to 18 months, estimated by 548-day weight, should be continued. Optimum cow efficiency should be the goal in order to continue to improve sustainable beef production on natural and improved pasture while preserving the unique ecological characteristics of floodable tropical savannas.

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