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Estimates of direct and maternal genetic effects for weights from birth to 600 days of age in Nelore cattle

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Summary

Estimates of direct and maternal variance and heritability for weights at each week (up to 280 days of age) and month of age (up to 600 days of age) in Zebu cattle are presented. More than one million records on 200 000 animals, weighed every 90 days from birth to 2 years of age, were available. Data were split according to week (data sets 1) or month (data sets 2) of age at recording, creating 54 and 21 data sets, respectively. The model of analysis included contemporary groups as fixed effects, and age of dam (linear and quadratic) and age of calf (linear) effects as covariables. Random effects fitted were additive direct and maternal genetic effects, and maternal permanent environmental effect. Direct heritability estimates decreased from 0.28 at birth, to 0.12–0.13 at about 150 days of age, stayed more or less constant at 0.14–0.16 until 270 days of age and increased with age after that, up to 0.25–0.26. Maternal heritability estimates increased from birth (0.01) to a peak of 0.14 for data sets 1 and 0.07–0.08 for data sets 2 at about 180–210 days of age, before decreasing slowly to 0.07 and 0.05, respectively, at 300 days, and then rapidly diminished after 300 days of age. Permanent environmental effects were 1.5 to four times higher than genetic maternal effects and showed a similar trend.

Zusammenfassung

Schätzung von direkten und maternal genetischen Effekten für Gewichte von der Geburt bis zum 600. Lebenstag beim Nelore-Rind

Es werden Schätzwerte für die direkte und maternale Varianz sowie für Heritabilitäten der Gewichte in jeder Woche (bis zum 280. Lebenstag) und für jeden Monat (bis zum 600. Lebenstag) beim Zebu Rind gezeigt. Mehr als eine Million Datensätze von 200.000 Tieren standen zur Verfügung, die alle 90 Tage bis zum zweiten Lebensjahr gewogen wurden. Die Daten wurden entsprechend dem Alter in Wochen (Datenset 1) oder Monaten (Datenset 2) aufgeteilt, woraus 54 bzw. 21 Datensets entstanden. Die Modelle beinhalteten Tiergruppen, die zur gleichen Zeit gelebt haben, als fixen Effekt, das Alter der Mutter (linear und quadratisch) und das Alter des Kalbes (linear) als Kovariablen. Als zufällige Effekte wurden der additive direkte, maternal genetische Effekt und maternal permanente Umwelteffekt berücksichtigt. Direkte Heritabilitätsschätzungen nahmen von 0,28 von Geburt auf 0,12–0,13 bei ca. 150 Lebenstagen ab, blieben mehr oder weniger konstant bei 0,14–0,16 bis zum 270. Lebenstag und nahmen ab dem 270. Lebenstag auf 0,25–0,26 zu.

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Maternale Heritabilitätsschätzungen nahmen von Geburt (0,01) zu einem Peak von 0,14 beim Datenset 1 und 0,07–0,8 beim Datenset 2 bis ca. 180–210 Lebenstagen zu, bevor sie langsam wieder auf 0,07 bzw. 0,05 bei einem Alter von 300 Tagen sanken. Nach 300 Lebenstagen sanken sie rapide ab. Permanente Umwelteffekte waren 1,5 bis vierfach höher als genetisch maternale Effekte und zeigten einen ähnlichen Trend.

Introduction

Variance and covariance estimates for growth traits in beef cattle, mainly *Bos taurus* in temperate regions, are abundant in the literature (see MOHIUDDIN 1993 and KOOTS et al. 1994 for reviews). MERCADANTE et al. (1995) and LÔBO et al. (2000) present reviews of parameter estimates for beef and dairy cattle in the tropics. There are comparatively few estimates of genetic parameters for Zebu breeds in the tropics and, most of them are based on small data sets. Very few estimates of direct and maternal effects on growth traits of Zebu cattle have been reported. MERCADANTE et al. (1995) and LÔBO et al. (2000) give average heritability estimates for weights at various ages in the tropics, for Zebu cattle and all breeds, respectively, similar to those reported by KOOTS et al. (1994), mainly for temperate regions.

In mammals, growth is influenced by the genes of the individual for growth, by the environment provided by the dam, both pre- and postnatal, what are known as maternal effects, and other environmental effects. Therefore, these traits are affected by two genotypes, that of the animal for growth, and of its dam for maternal ability. In beef cattle, maternal effects are important for growth traits until weaning although significant effects remain thereafter that have been identified for later weights, and differences between breeds have also been found (MACKINNON et al. 1991; MEYER 1992a; ROBINSON and O'ROURKE 1992; MEYER et al. 1993; ELER et al. 1995). Maternal effects must be considered when carrying out genetic evaluations of early growth traits, in addition to direct genetic effects.

In general (co)variance components and genetic evaluations for growth traits have been obtained by considering weights at standard ages (e.g. birth, weaning, yearling, 18 months of age and final) or weight gains between two ages as different traits.

Estimates of genetic parameters, in particular of maternal effects, for weights at early ages and in a sequence at small age intervals, are not available in the literature.

Nelore is a Zebu breed (*Bos indicus*), originating mainly from the Ongole type from India, that was taken to Brazil at the end of last century. Originally, fewer Nelore-type animals were imported than other breeds, but due to their 'easy care' traits, adaptation and production under an extensive system they became predominant, and today represent about 80% of the Brazilian cattle population.

This article presents direct and maternal variance and heritability estimates for weights at each week or month of age, from birth to 600 days for Brazilian Nelore cattle.

Materials and methods

Data were supplied by Brazilian Zebu Breeders Association (ABCZ). Performance recording started in 1968 and since 1974 a genetic improvement programme has been operational. To date more than 5 million weights on over a million animals have been recorded, and about 75% of those are from Nelore animals. The breeding programme considers growth, fertility and maternal ability traits.

The original data set consisted of 4 430 104 records on 663 393 Nelore animals, which were weighed every 90 days from birth to about 2.5 years of age. Calves were born all year round with a natural concentration of calves in the second semester of the year, and were weaned at about 240 days of age.

Records were extracted for animals which: (1) were raised on pasture without supplemental feeding; (2) did not have a foster dam; (3) did not receive veterinary treatment; (4) were born after 1975; (5) had dams older than 2 and younger than 21 years of age; (6) had birth weights between 15 and 50 kg; (7) had average daily gains (ADG) within the range given by the mean of all animals with the same age \pm three standard deviations; (8) had at least three valid weights (i.e. records meeting the conditions above); and (9) belonged to a contemporary group (CG) with at least four animals. Even if only one record of an animal did not meet the conditions (1) to (7) all records of that animal were deleted. Records obtained after 730 days of age were discarded. The main reasons for discarding animals were (1), (2), (3) and (9). The definition of CG included: herd's code; sex; category (suckling or weaned); and year and month of record.

After edits, 1 356 576 records on 247 845 animals, sired by 7492 sires were available. This data set was split according to week of age, creating a subset with birth weights only and 87 subsets with ages between 1 and 14, 7–21, . . . , 602–616. Records collected at greater ages were not used. After 448 days, only one age every 4 weeks was chosen (e.g. 462–476, 490–504, . . . , 602–616). Only one record per animal was kept in each data set. The CGs with less than four animals were deleted. For birth weight a minimum of 15 animals per CG was required. A total of 54 data sets with an average of 21 374 animals were analysed, and these will be referenced as data sets 1.

Figure 1 shows the number of animals with records and number of animals in the relationship matrix, for these data sets. There was only a small number of dams with more than one progeny with records, i.e. the data did not allow permanent environmental and maternal genetic effects to be separated. In this case, maternal genetic effects can be estimated only through the relationship matrix. Pedigree records were extracted for each data set, using information for up to three previous generations. The number of animals in the relationship matrix was three to four times greater than the number of animals with records (Fig. 1). All dams were known and had known parents. It was expected that most differences due to permanent environmental effects would be included in the estimates of

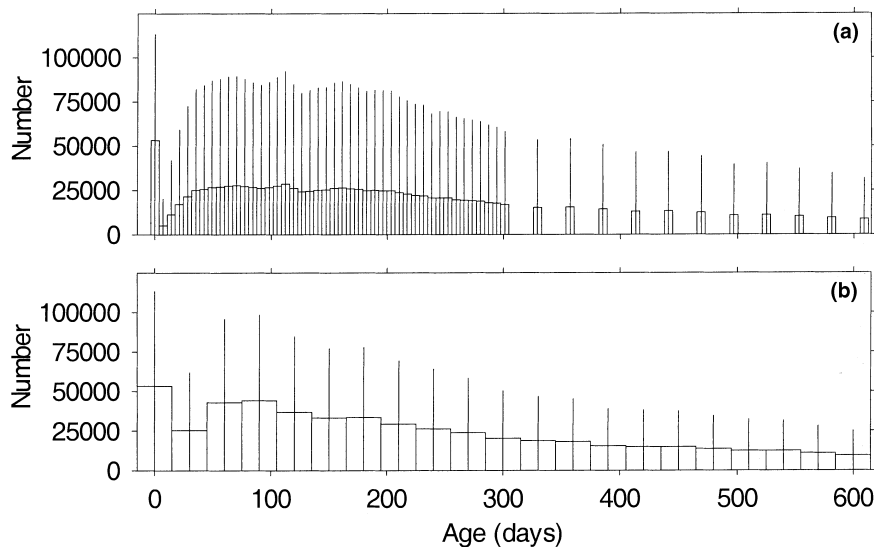


Fig. 1. Number of animals with records (boxes) and animals in the relationship matrix (bars), for individual ages. (a) data sets 1; (b) data sets 2

maternal genetic effects (MEYER 1992a). The numbers of sires varied from 1181 to 3469 and numbers of CG from 857 to 4114, with an average of 7.0 animals per CG.

To allow genetic and environmental maternal effects to be separated, the same data set (1 356 576 records) was split according to month of age, allowing ages between 1 and 60, 30–90, 570–630 days and keeping dams with at least two progeny. After this the same editing criteria, as described above, were applied reducing the average number of progeny per dam to 1.8. This yielded 21 data sets (data sets 2), with an average of 22 824 animals. Data from animals older than 630 days were disregarded. Numbers of animals with records and numbers of animals in the relationship matrix, for each age, are presented in Figure 1. The numbers of sires varied from 1195 to 3511, and the numbers of CG ranged from 2074 to 8665, with an average of 5.6 animals.

The model of analysis included CG as a fixed effect and, age of dam, linear and quadratic effects, and linear effect of animal age (within each data set and analysis, the maximum difference in age between the animals was 14 or 60 days) as covariables. Age of animal was not included in the model of analysis for birth weight. No special fixed effects to account for age of dam status (heifers versus cows) and birth type were included in the model as previous analyses have shown that they were not important for these data.

In order to assess the importance of different random effects, up to four models of analysis differing in the random effects fitted were applied.

$$\text{Model A: } \mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}_1\mathbf{a} + \boldsymbol{\varepsilon}$$

$$\text{Model B: } \mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}_1\mathbf{a} + \mathbf{Z}_2\mathbf{m} + \boldsymbol{\varepsilon}$$

$$\text{Model C: } \mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}_1\mathbf{a} + \mathbf{W}\mathbf{c} + \boldsymbol{\varepsilon}$$

$$\text{Model D: } \mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}_1\mathbf{a} + \mathbf{Z}_2\mathbf{m} + \mathbf{W}\mathbf{c} + \boldsymbol{\varepsilon},$$

where \mathbf{y} is the vector of observations, $\boldsymbol{\beta}$ is the vector of fixed effects, \mathbf{a} and \mathbf{m} are the vectors of random direct and maternal additive genetic effects, \mathbf{c} is the vector of random maternal permanent environmental effects and $\boldsymbol{\varepsilon}$ is the vector of residuals. \mathbf{X} , \mathbf{Z}_1 , \mathbf{Z}_2 and \mathbf{W} are the incidence matrices for $\boldsymbol{\beta}$, \mathbf{a} , \mathbf{m} and \mathbf{c} , respectively. $E[\mathbf{y}]$ is $\mathbf{X}\boldsymbol{\beta}$, $V[\mathbf{a}]$, $V[\mathbf{m}]$, $V[\mathbf{c}]$ and $V[\boldsymbol{\varepsilon}]$ are $\mathbf{A}\sigma_a^2$, $\mathbf{A}\sigma_m^2$, $\mathbf{I}_{N_d}\sigma_c^2$ and $\mathbf{I}_N\sigma_\varepsilon^2$, respectively, where N_d is the number of dams, N is the number of records, \mathbf{A} is the numerator of the relationship matrix among animals, and \mathbf{I} is an identity matrix. The correlation between direct and maternal genetic effects was assumed to be zero. Heritability estimates were obtained as σ_a^2/σ_p^2 , σ_m^2/σ_p^2 , respectively, for direct and maternal genetic effects, where σ_p^2 is the sum of all variance components estimated by the model of analysis.

Data sets 1 were analysed using model B, with the exception of birth weight, which was analysed, with model D. In order to assess the importance of maternal genetic and permanent environmental effects on weights at different ages, models A, C and D were applied to data sets 2. All the estimates presented for data sets 2, were obtained with model D. Variance components were estimated by restricted maximum likelihood using ASREML software (GILMOUR et al. 1999). Models were compared using likelihood ratio tests (LRT), with an error probability of 5%.

Results and discussion

Mean weights and number of animals by week of age, for Data sets 1, are shown in Figure 2. Average weights varied from 29.9 kg (birth weight) to 298.8 kg (609 days age) and increased almost linearly with age of animal, with a reduction in rate of growth after weaning. Means for data sets 2 (not shown) were very similar to those for data sets 1. The same pattern was observed for standard deviations (Fig. 3), which varied from 3.11 to 50.14 kg, for birth and 609 days weights, respectively. The coefficient of variation (CV), for data sets 1, increased from birth (10.42%) until the animals were about 1 month of age (18.84%), decreased slightly until 90 days of age and then remained almost constant,

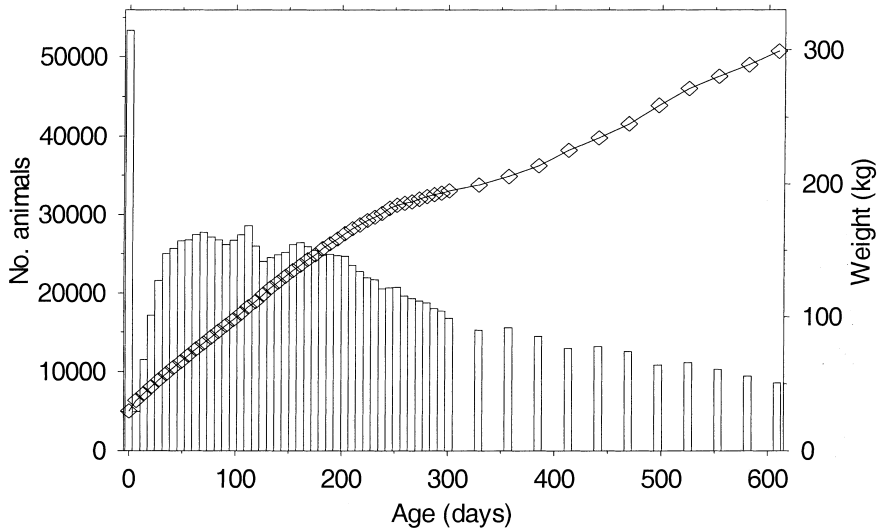


Fig. 2. Number of animals (bars) and mean weights (◇) for data sets 1

indicating strong association between means and SD (Fig. 3). The trend was similar for both sets of data, but for data sets 2 the CV showed a larger increase from birth to 1 month of age (25.15%).

Direct effects

Estimates of animal genetic standard deviations (σ_a), are presented in Figure 4. They increased with age, with the smallest σ_a at birth, 1.26 kg. From birth to around 400 days of age, σ_a increased less than the phenotypic SD, but increased at similar rates thereafter.

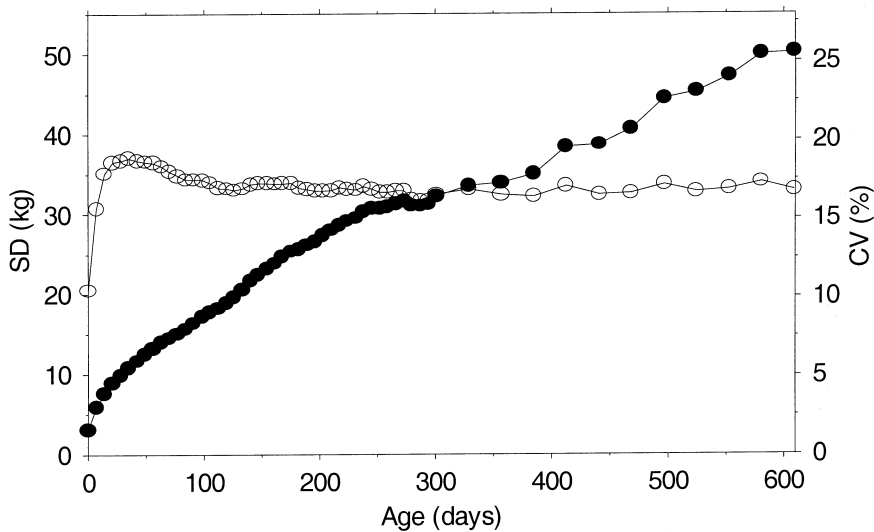


Fig. 3. Standard deviations (SD, ●) and coefficient of variation (CV, ○) for data sets 1

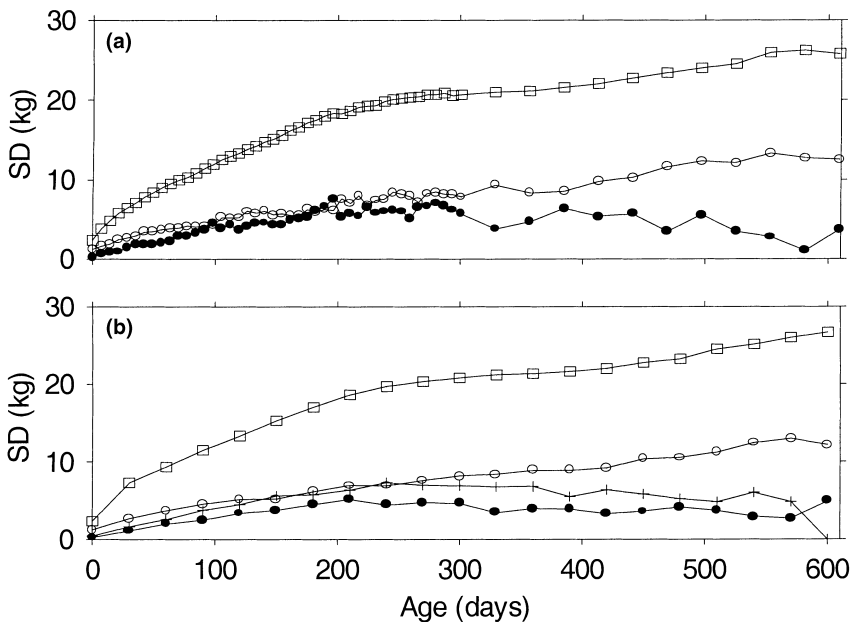


Fig. 4. Estimates of animal (\circ), maternal (\bullet), permanent environmental (+) and phenotypic (\square) standard deviations. (a) data sets 1; (b) data sets 2

Estimates of direct heritabilities for data sets 1, using model B, and for data sets 2, using model D, are presented in Figure 5. Standard errors of heritability estimates varied from 0.018 to 0.052 for data sets 1 and from 0.016 to 0.035 for data sets 2. Heritability estimates were slightly larger for data sets 1 than for data sets 2. This difference could be associated with the model of analysis or sampling (co)variances (MEYER 1992b). Although

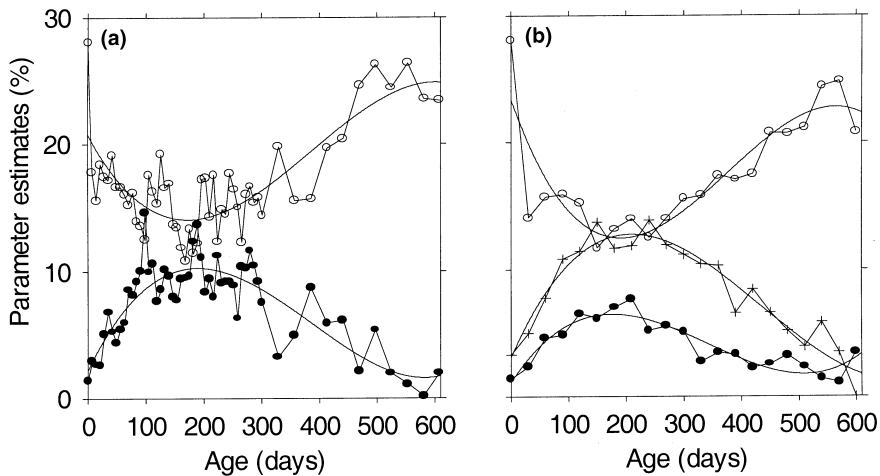


Fig. 5. Estimates of direct (\circ) and maternal (\bullet) heritabilities and permanent environmental (+) variance components as proportion of phenotypic variances. (a) data sets 1; (b) data sets 2

estimates oscillated from week to week for data sets 1, overall trends were similar for both data sets. Direct heritability estimates were largest for birth weight (0.28). Estimates then decreased from birth until about 150 days of age (0.12–0.13), remained almost constant until about 270 days of age, with estimates around 0.13–0.16 for both sets and thereafter, increased with age, being around 0.24–0.26 for data sets 1 and 0.21–0.25 for data sets 2 at 570–600 days of age. A similar trend was described by MEYER (2000b) for heritability estimates until 280 days of age, for two breeds of Australian cattle.

Direct heritability estimates obtained are within the range described in the literature for Nelore cattle in Brazil (MERCADANTE *et al.* 1995). LÔBO *et al.* (2000) give average direct heritability estimates for local and Zebu cattle in tropical countries for weights at birth, 6 and 12 months of age, of 0.29, 0.12 and 0.22, respectively. MERCADANTE *et al.* (1995) found a weighted mean for direct heritability estimates for weights of Zebu cattle at 550 days of age of 0.38, which is higher than the value found in the present study.

Maternal effects

For data sets 2, maternal effects were split into their genetic and permanent environmental components. Estimates of genetic and permanent maternal SD are shown in Figure 4. For both data sets, maternal genetic SD increased with age from birth to 200–210 days of age and started to decrease slowly after that. For data sets 1 maternal genetic SD decreased faster after 300 days of age. Direct additive genetic SD increased at higher rate after this age. A similar pattern as described for additive maternal SD was observed for permanent environmental maternal SD, in data sets 2.

Estimates of maternal heritabilities and of permanent environmental variance component as a proportion of phenotypic variance are presented in Figure 5. Standard errors of maternal heritability estimates varied from 0.012 to 0.038 for data sets 1 and from 0.005 to 0.018 for data sets 2. For permanent environmental effects the standard errors varied from 0.007 to 0.020.

Maternal effects heritability estimates (Fig. 5), for data sets 2, increased from birth (0.01) to 180–210 days of age (0.07–0.08). Then, the estimates decreased slowly with age, decreasing faster after 300 days of age. A similar pattern was observed for data sets 1, although the estimates were slightly higher. Nelore animals are weaned at about 240 days of age and results showed that maternal genetic effects start to decrease in importance close to weaning. Additive maternal effects were, with few exceptions, statistically significant from birth to 390 days of age (model D versus model C). MEYER *et al.* (1993) and ELER *et al.* (1995) found that maternal effects on post-weaning weights were a 'carry over' of those on weaning. This happens because early weights are part of later weights. For animals kept on pasture, the compensatory gain from weaning to yearling is not enough to overcome maternal effects on weaning weight (ELER *et al.* 1995).

For Zebu breeds in the tropics, MERCADANTE *et al.* (1995), found weighted means of maternal heritability estimates for weights at birth, weaning, 365, and 550 days of age, of 0.12, 0.18, 0.16 and 0.05, respectively. These estimates are higher than those found in the present study, however, in addition to the fact that only a few estimates were available, almost all the papers reviewed by MERCADANTE *et al.* (1995) reported average to high negative correlations between direct and maternal genetic effects. MEYER (1997) found that large, negative estimates of direct and maternal genetic covariances are associated with overestimates of additive direct and maternal genetic variances. Considering the difficulties in obtaining reliable estimates of the correlation between direct and maternal genetic effects, in the present study, this correlation was assumed as zero.

Permanent environmental variances as proportion of phenotypic variance (c^2) were 1.5 to four times larger than maternal heritability estimates but showed a similar trend (Fig. 5). The inclusion of permanent environmental effects over and above additive direct effects (model C versus model A) significantly increased the log-likelihood from birth to 540 days

of age. Permanent environmental effects are related to factors that affect all progeny of a dam and their influence on post-weaning weights, probably are due to effects on pre-weaning weights.

Difficulties in separating additive genetic (both direct and maternal) and environmental maternal effects (WILLHAM 1980; MEYER 1992b) using field data continue to exist. There are indications that, when only one of these effects (maternal genetic or permanent environmental) is considered in the model of analyses, most of maternal variation is likely to be accounted for (MEYER 1992a). In many situations, the knowledge of the behaviour of total maternal effects (genetic plus permanent environmental) at early ages, obtained by univariate analyses can be of interest and may represent the best compromise.

Total maternal effects SD and as a proportion of phenotypic variances, according to animal age, are presented in Figure 6. The SD increased from birth to 210 days of age, remained constant until 300 days and then decreased with animal age. In the same manner, the total maternal variances as a proportion of phenotypic variances, increased from birth (0.05) until the animal was 150 days of age (0.20), stayed almost in a plateau until 240 days of age and then decreased with age.

The trend observed in this work for total maternal variance component estimates as a proportion of phenotypic variance, was similar to that described by MEYER (2000b) using random regression models (RRM); although the estimates started to decrease earlier than in the present data, after 150 days of age. Generally, *Bos taurus* are earlier maturing (in most or all physiological aspects) than *Bos indicus*. Presumably, the proportional contribution of maternal effects is reduced when the calf increases the ingestion of pasture and become a fully developed ruminant and this may happen at a younger age in *Bos taurus* than in *Bos indicus*. Management practices could also contribute for this difference, since the Nelore calves were kept entirely on pasture and did not receive any special management which could promote early rumen development.

ALENCAR et al. (1988) using the weigh-suckle-weigh method compared the monthly milk production of Nelore \times Charolais (Canchim) and Nelore cows in Brazil. They found that Canchim cows produced significantly more milk than Nelore cows, until 180 days of

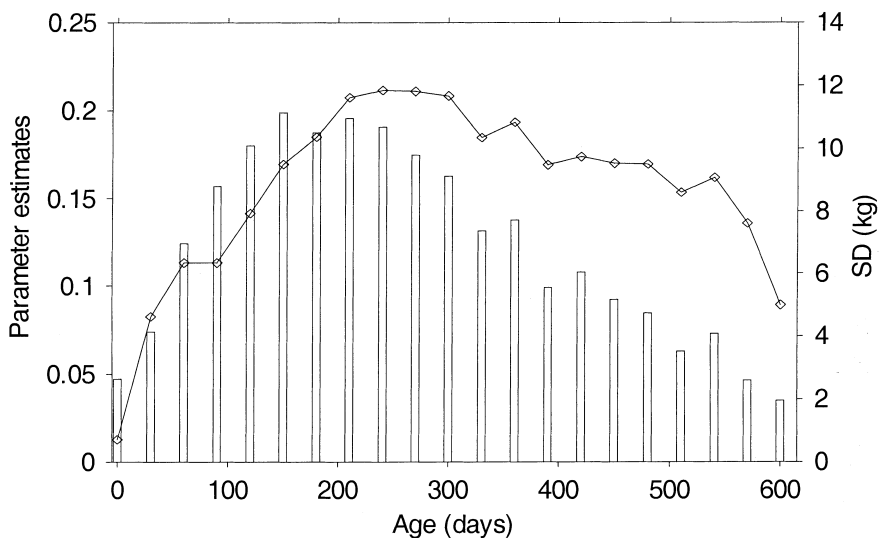


Fig. 6. Estimates of maternal standard deviations (SD, bars) and total maternal variance component ($m + c$) as proportion of phenotypic variances (\diamond), for data sets 2

lactation, but that the latter were more persistent. This could explain the extended plateau of total maternal effects observed in the present work. ALENCAR (1989) found that dam monthly milk production significantly affected weight gain per month of their offspring until the fifth month of age, which is consistent with the peak of total maternal effects in the present work.

Milk production has been considered the main cause of the maternal effects, and phenotypic correlation between the milk production of the dam and the performance of its offspring from birth to weaning in cattle, vary from 0.29 to 0.90 (NEVILLE 1962; CLUTTER and NIELSEN 1987; ALBUQUERQUE et al. 1993). MEYER et al. (1994) found a correlation between direct effects for milk yield and maternal effects for weaning weight of 0.80. Correlations from 0.89 to 1.0 were found between the cow permanent effect for milk yield and the dam permanent effect for weaning weight. The authors concluded that milk yield is the main factor causing maternal effects.

More recently, covariance functions (CF) and random regression models (RRM) have been proposed as an alternative to deal with traits that are recorded repeatedly during the life of animal, i.e. longitudinal data (KIRKPATRICK et al. 1990, 1994; SCHAEFFER and DEKKERS 1994). Until now RRM have been applied mostly for test-day records of dairy cattle (e.g. JAMROZIK and SCHAEFFER 1997; VAN DER WERF et al. 1998; OLORI et al. 1999). In beef cattle, a few papers using RRM have been published and most dealt with adult weights (MEYER 1999, 2000a, b). A next step will be to model these data using RRM.

Conclusions

Direct heritability estimates were low to moderate, varying from 0.11 to 0.28. The estimates decreased from birth to 150 days of age, levelled off between 150 and 300 days and increased with age thereafter. The lowest direct heritability estimates occurred for weights around 180–210 days when the largest maternal heritability estimates were found. The importance of maternal genetic effects on weights started to decrease close to weaning (180–210 days), although they were statistically significant from birth to 390 days of age. Permanent environmental maternal effects showed a similar trend, increasing from birth (0.03) to 240 days (0.14) and decreasing to zero at 600 days of age. These effects were statistically important for weights until 540 days of age. Therefore, maternal effects must be considered for genetic evaluations of Nelore cattle even for weights after weaning.

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