Direct and correlated responses to selection for yearling weight on reproductive performance of Nelore cows


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ABSTRACT: Data from a selection experiment for growth carried out in Brazil were analyzed in order to evaluate the direct responses on yearling weight (YW) and the correlated responses on the size and reproduction traits of cows. The experiment was started in 1976, and in 1980 three lines of Nelore cattle were established: selection (NeS), traditional (NeT), both selected for higher YW, and control (NeC), selected for mean YW. The NeT was an open line that eventually received bulls from other herds. Yearling weight records for animals born from 1978 to 1998 and yearling hip height (H550) of females born from 1985 to 1998 were analyzed by fitting an animal model in order to obtain the genetic trends. The means for weight, height, and body condition score at the start of the breeding season, days to calving, and calving success of cows born from 1993 to 1996 (pertaining to the third to fourth generations of selection) were compared between the selected (NeS and NeT) and control lines. The genetic trends obtained after 16 yr for YW were 1.7 ± 0.2, 2.3 ± 0.2, and −0.1 ± 0.1 kg/yr for males and 1.9 ± 0.2, 2.4 ± 0.2, and −0.1 ± 0.1 kg/yr for females, for the NeS, NeT, and NeC lines, respectively. Corresponding values for H550 were 0.25 ± 0.03, 0.24 ± 0.04 and −0.04 ± 0.03 cm/yr for females. Heifers and cows from NeS and NeT were 19% and 15% heavier and 4% taller at the start of the breeding season than those from NeC. No significant differences between selected (NeS and NeT) and control females were detected for body condition scores and for reproductive performance. The results indicate that selection for body weight promoted high and consistent weight and height responses both at the yearling and later ages, without compromising the reproductive performance of the cows with respect to days to calving and calving success.

Key Words: Beef Cattle, Correlated Response, Growth, Reproduction, Selection, Zebu Breed

Introduction

Several papers and reviews have described negatively correlated responses on reproduction of cows selected for growth rate (Barlow, 1978; Scholtz and Roux, 1984; Luesakul-Reodecha et al., 1986). However, recent studies involving both experimental selection data (Mrode et al., 1990; Morris et al., 1992; Archer et al., 1998a) and field data (Meyer et al., 1991; Mercadante et al., 2000) have refuted this antagonism, indicating that selection of young animals based on body weights did not significantly affect the reproductive performance of cows. However, most of the recent studies have been carried out in less restrictive environments than tropical ones.

Correlation between growth and reproduction traits and experimental results in terms of the effects of selection for higher weight on the reproductive performance of cows have not been well documented in populations of Bos indicus (Mrode, 1988; Koots et al., 1994b; Lôbo et al., 2000). In 1976, a selection experiment for increased yearling weight (YW) in the Nelore Zebu breed, with the maintenance of a control population, was established at the Instituto de Zootecnia Experimental Station of Sertãozinho, state of São Paulo, Brazil. The experiment aimed to determine the response to selection for higher weights in a breed of interest in the tropics, since the few selection experiments available in the literature have been conducted on British breeds. Direct re-
sponses on the YW and correlated responses on birth and weaning weights were described through the years by Packer et al. (1986) and Razook et al. (1998). In these studies, the responses to selection were obtained separately for males and females by least squares analyses. The objective of the present study was to estimate the direct response of YW by mixed model methodology, and to evaluate the effects of this selection on traits related to the size and reproductive performance of cows.

Materials and Methods

Formation of Lines and Selection Procedure. The selection experiment was carried out at the Experimental Station of Sertâoçinho, a research unit of the Instituto de Zootecnia de Sertãozinho, located in the north of the State of São Paulo (latitude 21°10′ south and longitude 48°5′ west), Brazil. This region has a wet tropical climate, with average annual temperature and rainfall of 24°C and 1,312 mm, respectively. The pastures consisted mainly of Panicum maximum and Brachiaria brizantha, which are common tropical grasses in Brazil. The animals used were from the Nelore herd registered at Estacao Experimental de Zootecnia de Sertaozinho (EEZS) since 1933. Reorganization of the herd for later establishment of separate lines was started at the breeding season in 1976 with the use of some bulls from private breeders, as well as some from the existing herd, in order to expand the genetic base of the experimental herd. In 1980 separate lines were established using bulls born in 1977 and 1978, six of which had a high selection differential for YW, and four no differential.

Of the 350 heifers apt for reproduction, the youngest 180 were randomly assigned to the Control Nelore (NeC) (60 animals) and Selected Nelore (NeS) (120 animals) lines. The remaining 170 oldest females composed the Traditional Nelore (NeT) line.

For natural mating, four, six, and up to eight bulls were used annually in the NeC, NeS, and NeT lines, 50% being 2-yr-old (first mating) and 50% 3-yr-old (second and last mating). The bulls were selected, within line x year, for YW corrected to 378 d, obtained at the end of a 168-d long feedlot performance test. Replacement females were selected for weight corrected to 550 d on pasture. In general, 50% were retained, resulting in an annual culling rate of 20% of the cows. At the moment of selection, YW was not corrected for age of dam. From the selected NeS and NeT lines, males and females with a higher adjusted YW were selected, whereas males and females with a selection differential around zero were retained from the NeC line. The NeT line, with its more flexible cow and bull replacement scheme, initially used bulls from outside the station herds (AI), and eventually those culled from NeC and NeS.

Formation of Mating Groups and Female Management. After selection at 550 d of age, which occurred in April, the heifers were maintained on pasture until the start of their first breeding season in November, at about 2 yr of age (25.5 ± 1 mo). The mating groups were formed so as to avoid consanguineous mating. The females were allowed to mate naturally on pasture for 90 d, with either 15 (2-yr-old bulls) or 25 cows per bull for NeS and NeT and 15 for NeC. During the 15 yr considered in this study of reproduction traits, the beginning and the end of the breeding season were November 15th and February 15th, with slight variations across the year. The calves were weaned in April and May, at about 210 d of age. Cows have been culled primarily for unsoundness, for failing to calve in two consecutive years, for low maternal ability, or for advanced age of about 11 yr.

Definition of Traits. Corrected YW was calculated by adding weaning weight corrected to 210 d and either postweaning weight gain during the feedlot performance test for males or postweaning weight gain on pasture up to 550 d for females. The yearling hip height (H550) of females was corrected for 550 d by a regression coefficient for age obtained within line. The YW for animals born between 1978 and 1980 before the separation of lines were also incorporated into the analysis, being identified as the original line. Weight (WBS), height (HBS) and body condition score (CBS) at the beginning of the breeding season were collected annually for all females, with the exception of those which calved shortly after the beginning of the breeding season (about 5%). For such cows, the weight at calving was considered as WBS. Body condition score was evaluated by the same two technicians throughout the experiment, using scores from 1 to 9 for extremely thin cows up to extremely fat cows. However, since there were practically no animals at the extremes (1, 2, and 9), those referring to classes 1 and 2 were assigned to class 3 and those in class 9 were assigned to class 8, thus forming a scale from 3 to 8.

Days to calving (DC) were obtained for all the females that calved from the difference between the calving date and the date of the beginning of the breeding season. Values for DC between 268 and 407 d were considered valid. The date of the beginning of the breeding season for cows which calved shortly after the beginning of the breeding season (about 5%), was adjusted by adding 4 d to the calving date. This 4-d period is normally enough in order to allow the newborn calf to follow its dam. The calves were weaned in April and May, at about 210 d of age. Cows have been culled primarily for unsoundness, for failing to calve (Johnston and Bunter, 1996) in this study of reproduction traits, the beginning and the end of the breeding season were November 15th and February 15th, with slight variations across the year. The calves were weaned in April and May, at about 210 d of age. Cows have been culled primarily for unsoundness, for failing to calve in two consecutive years, for low maternal ability, or for advanced age of about 11 yr.

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traits (WBS1, HBS1, CBS1, DC1, CS1) and the CS of the second mating, considering that the heifer calved from the first mating (CS2/1) were analyzed. A summary of data structure is presented in Table 1.

**Genetic and Statistical Analyses**

**Selection Differentials.** The weighted and unweighted selection differentials of the cows can provide insight into joint effects of natural and deliberate selection (Koch et al., 1994; Falconer and Mackay, 1996). The unweighted selection differentials for YW of males and females were obtained as the deviation of the individual yearling weight from the mean of contemporaries (line × yr). The effective selection differentials of the cows born before 1993 were obtained as the weighted mean of these deviations according to the number of progeny evaluated on selection up to 1998. Since NeT included animals from herds other than that of the EEZS in the early years and cows and bulls culled from NeC and NeS, these calculations were restricted to the NeC and NeS lines.

**Fixed Effects.** A series of analyses were performed to investigate fixed effects on traits using the MIXED procedures of SAS (SAS Inst. Inc., Cary, NC), other than the binomial traits. The repeated records of WBS, HBS, CBS, and DC were analyzed considering appropriate residual covariance structures chosen according to Akaike’s information criterion (Littel et al., 1996). The fixed effects and the interactions between main effects were included in the model when significant (P < 0.05). The YW of males and females, although obtained at different ages and with distinct postweaning management, were studied as a single trait. The model of analysis included the fixed effects of line, year of birth, month of birth (8, 9, 10, and 11), sex, age of dam (3, 4, ... , ≥ 10 yr of age) and the line × year, line × sex and year × sex interactions. The model for H550 included the fixed effects of line, year of birth and line × year interaction. For the WBS1, HBS1, CBS1, DC1 and CS2/1 traits, the model included the line and year of birth as fixed effects and the linear effect of age in days at the beginning of the breeding season, in addition the line × year interaction for WBS1, HBS1 and DC1.

The model for the WBS and CBS repeated traits included the line, year at the beginning of the breeding season, age class (2, 3, ... , ≥ 9 yr of age), previous reproductive status (calved or noncalved) as fixed effects, and the model for HBS included the effects of line, year of birth and age class. In addition, we included the line × year interaction for WBS and CBS, the line × year of birth interaction for HBS, the line × age class interaction for CBS, and the line × previous reproductive status interaction for WBS. The models for DC and CS included as fixed effects line, mating group (year + bull in service), age class and previous reproductive status, and line, year, age class (2, 3, ... , ≥ 6 yr of age) and previous reproductive status, respectively. The effect of service sire was included only in the model of repeated DC. For CS repeated records, the mating group effect and the main effects interactions were not included in the model to avoid the occurrence of subclasses with no variation.

**Means Comparison.** The performance of the selected animals was compared to the control using the information for the cows born from 1993 to 1996 (n = 274),
belonging to the third and fourth generations of selection, considering the animals born in 1981 as the first generation. The WBS1, WBS, HBS1, HBS, CBS1, CBS, DC1, and DC means were compared using the MIXED procedures of SAS, with previously described models. CS, CS1, and CS1/2 were analyzed as traits with a binomial distribution, with a probit link function in a generalized linear model, using the ASREML software developed by Gilmour et al. (1999). The probit model, also known as the threshold model, whose residual variance on the underlying scale is constrained to 1, assures that the estimates fall in the range from 0 to 1 (Littel et al., 1996). The estimates of the effect of line on the underlying scale were back-transformed to the probability scale. The means for the selected lines and the NeC were compared using the t-test. For CS the test was constructed with the values on the underlying scale, and the SE of the difference on the probability scale, obtained by the difference.

Variance Components, EBV, and Genetic Parameter. Estimates of variance were obtained from the Derivative Free Restricted Maximum Likelihood algorithm using the MTDFREML software developed by Boldman et al. (1993). Standard errors for heritability were obtained using the MTDFREML software modified by Do-denhoff and Van Vleck (personal communication). For all binary traits (CS1, CS2/1, and CS) the variance components were estimated using the ASREML software. The working algorithm of ASREML is based on generalized mixed models. The EBV for the animal additive genetic effect on the underlying scale was also back-transformed to the probability scale.

The variance components for YW, for the WBS, HBS, CBS, DC, and CS repeated records, and for CS1 and CS2/1 were obtained by single-trait analyses. For the remaining traits with a single record (WBS1, HBS1, CBS1, and DC1) the variance components were obtained by two-trait analyses with YW. An animal model was fitted for all traits, including a relationship matrix of 5,830 animals, of which 410 are base animals. Yearling weight was analyzed fitting a model including the additive genetic direct and permanent environmental effect of dam as random effects. Preliminary analyses, fitting different hierarchic models, indicated that this was a better model than also fitting additive genetic maternal effects. Models were compared using likelihood ratio tests with an error probability of 5%. In addition, in order to reduce the differences between YW obtained for males and females, analyses were also carried out with YW standardized by the standard deviation of each sex, as suggested by Koch et al. (1994).

The remaining single traits, H550, WBS1, HBS1, CBS1, DC1, CS1, and CS2/1, were analyzed fitting a model including the random additive genetic effect of the animal, and the models for the repeated traits (WBS, HBS, CBS, DC, and CS) also considered the permanent environmental effect. The EBV (µ) were used to obtain an estimate of the annual genetic trend by orthogonal contrasts, as utilized by Johnson et al. (1999). In a similar procedure, a vector of coefficients (k) was generated and entered into MTDFREML to produce linear contrasts of the µy on year of birth for each line-sex. The vector of orthogonal coefficients also was c' = −7.5, −6.5, −5.5, −4.5, −3.5, −2.5, −1.5, −0.5, 0.5, −1.5, 2.5, 3.5, 4.5, 5.5, 6.5, and 7.5 divided by the number of observations per line-year-sex. Regression coefficients were calculated as k'µ/c, and the variance of k'µ was calculated in MTDFREML as V(k'µ) = k'L22k, where L22 is the animal-by-animal part of the inverse of the coefficient matrix from the mixed-model equations at convergence for the variance components. The standard error of regression coefficients were also obtained as [V(k'µ)]0.5/c, and the significance of regressions was determined using a t-test with degrees of freedom yr-2, where year is the number of year in the contrast.

Results and Discussion

Selection of Females and Selection Differentials. In order to maximize the genetic gains, only animals with the highest deviations from the mean should have been used as parents of the next generation. However, for females, considering the low rates of reproduction in the tropics, potential selection intensity is less. From 1981 to 1996, 56% of the evaluated females from NeC and 50% from NeS were selected for cow replacement. This slight difference between the lines was due to the fact that the NeC heifers were not always registered by the Brazilian Zebu Breed Association due to their small size; thus, a proportionally larger number of them were kept until the registration decision. In some years all of them were registered and mated. Ratios of weighted to unweighted dam selection differentials were 1.24 and 0.93 for NeC and NeS, respectively, indicating a possible effect of natural selection on fertility of cows. These ratios showed a tendency for dams with higher selection differentials to have more progeny in the NeC line, and for those with smaller selection differentials to have more progeny in NeS line. Koch et al. (1994) observed higher than unit ratios of weighted to unweighted dam selection differentials (1.3 and 1.5) in the three selection lines, indicating a tendency for dams with higher selection differentials to have more progeny in 20 yr of experiments with Hereford. In contrast, Mac-Neil et al. (1992) showed that since the mid-1960s, Her-eford heifers from Line 1, that became dams, seemed to have weights slightly lower than average yearling weights. An explanation given by the authors was that the range environment in which these cattle produce calves places an upper limit on the growth potential that also permits reproduction.

Direct Response in Yearling Height of Females. The differences in EBV of YW over time generally reflected the trends in realized differences between the lines (Parnell et al., 1997). Figure 1 shows the change in EBV mean for YW in each line, only for females, through the year.
Means of EBV for YW of females by selection line (control ■, selection ○, and traditional ▲) and year of birth.

EBV mean for YW at the start of the experiment (1978 to 1980) was 0.9 kg for males and 0.3 kg for females. After 16 yr (1996) of selection, the EBV mean of YW were 0.8 kg and −1.3 kg for NeC, 36.5 kg and 36.4 kg for NeS, and 39.7 kg and 39.7 kg for NeT, for males and females, respectively. Although the first progeny of separate lines were born in 1981, in 1978, sires with positive selection differential for YW were used; thus, the progeny born in 1981 in NeS already had an EBV mean of YW different from the others lines. In 1983, the two selected lines already showed very similar EBV, which they maintained in subsequent years. In 1988, two sires born and used for 2 yr in NeC were used in the NeT line, a fact which resulted in a decrease in the EBV mean of YW of the progeny born in 1989.

Since the YW of males and females were obtained at distinct ages and with different postweaning management, their two-trait analysis indicated a below unit genetic correlation (0.88). Therefore, the analyses were carried out in two ways, using records with no standardization, and standardizing them by the respective standard deviation for each sex (35.78 kg for males and 39.20 kg for females). The EBV obtained were closely similar since the phenotypic standard deviations did not differ substantially. Annual trends in EBV mean of YW for each line obtained by the two types of analysis are shown in Table 2. The highest values were obtained for NeT, probably because this was an open line and used some progeny tested bulls from NeS. Another reason is the fact that in 1981 NeS already presented a different mean compared to NeC, whilst NeT did not (Figure 1). Razook et al. (1998) estimated the annual genetic trend in NeS as a deviation of NeC separately for males and females using the least squares procedure and reported a higher response than those reported in the present study (2.7 kg/yr or 0.11 standard deviation unit/yr). The methods used by Razook et al. (1998) have been extensively applied to the analysis of selection experiments when a control population is maintained (Baker et al., 1991; Koch et al., 1994; Parnell et al., 1997).

However, mixed model methods, in particular restricted maximum likelihood techniques using an animal model with a complete relationship matrix, appear to provide tools to allow for a better understanding of results from selection experiments (Baker et al., 1991; Meyer and Hill, 1991). Sorensen and Kennedy (1984) discussed the efficiency of the mixed model methods in order to partition adequately the phenotypic trend into its genetic and environmental components taking into account the variance due to genetic drift, if some conditions are satisfied. First, the genetic and phenotypic variances of the trait before selection started operating should be known; second, the selection should be a linear function of the records; and third, the complete relationship matrix, with all the animals involved in the selection decisions, should be used in the analysis. Of these conditions, probably the last two were met, since with rare exceptions (only in the cases of sickness and defects) the selection was always a linear function of the records, and the complete relationship matrix, starting from the foundation animals, was incorporated into the analysis. In addition, if a control line is used and is genetically related to the selected line, the use of all the data in a single analysis can yield estimates of fixed and random effects with smaller sampling variance, probably resulting from the greater contrast between lines.

The estimates of annual genetic trend obtained in the present study by mixed model were slightly lower than the estimate pooled from 10 experiments with Bos taurus reported in the literature, of 2.65 kg/yr or 0.08 standard deviation unit/yr (Mrode, 1988). More recent

<table>
<thead>
<tr>
<th>Trend</th>
<th>NeC</th>
<th>NeS</th>
<th>NeT</th>
</tr>
</thead>
<tbody>
<tr>
<td>YW (males) kg/yr</td>
<td>−0.05 ± 0.31</td>
<td>1.70 ± 0.22**</td>
<td>2.33 ± 0.22**</td>
</tr>
<tr>
<td>YW (females) kg/yr</td>
<td>−0.07 ± 0.29</td>
<td>1.78 ± 0.20**</td>
<td>2.39 ± 0.20**</td>
</tr>
<tr>
<td>YW (males) kg/yr b</td>
<td>−0.09 ± 0.30</td>
<td>1.65 ± 0.21**</td>
<td>2.24 ± 0.21**</td>
</tr>
<tr>
<td>YW (females) kg/yr b</td>
<td>−0.05 ± 0.31</td>
<td>1.85 ± 0.21**</td>
<td>2.39 ± 0.21**</td>
</tr>
</tbody>
</table>

*NeC = control Nelore; NeS = selection Nelore; NeT = traditional Nelore.

bStandardized by the SD of each sex and back-transformed to kilograms.

**P < 0.01.
results, obtained for lines selected for YW or yearling growth rate, were 2.49 ± 0.24 kg/yr, 2.16 ± 0.31 kg/yr, and 1.20 ± 0.12 kg/yr for three different lines of Angus and Hereford cattle (Baker et al., 1991), 2.64 kg/yr for Hereford cattle (Koch et al., 1994), and 2.19 kg/yr for Angus cattle (Parnell et al., 1997). The different estimates of annual genetic trends may be explained mainly by the generation intervals achieved in these lines. Whereas in the present experiment the average generation interval was 5.1 yr (Razook et al., 1998), Baker et al. (1991) reported averages of 3.2, 3.3 and 4.4 yr, Koch et al. (1994) reported averages of 4.2 yr, and Parnell et al. (1997) averages of 3.2 yr. Lower generation intervals are attributed to yearling matings in both sexes and also to a shorter retention of cows in the herd.

Figure 2 shows the EBV annual means for H550, representing the correlated response on this trait estimated from two-trait analysis with YW. In 1985, when the H550 records started, there was already a difference between the EBV mean for H550 of the control line and of the selected lines (−0.17 cm, 1.00 cm, and 0.90 cm for NeC, NeS, and NeT, respectively). In 1996, the corresponding values were −0.85 cm, 3.5 cm and 3.6 cm. The rate of annual genetic trend was −0.04 ± 0.03 cm for NeC, 0.25 ± 0.03 cm for NeS, and 0.24 ± 0.04 cm for NeT.

Correlated Response for Size and Reproduction Traits of Cows. Table 3 presents the comparison of the means for females born after 1992 in the NeS and NeT selected lines as deviation from NeC. As expected, there was a significant difference for the traits related to the size of the animal. Results for body condition score varied between NeS and NeT. As a percentage, the heifers from the NeS and NeT lines were, on average, 19% heavier than those of the NeC line and 4% taller at the beginning of the first breeding season. These differences decreased for WBS (including heifers) to 15% and were maintained for height at 4%. The WBS1 was very close to the YW, since it was obtained, on average, 7.5 mo later, and the genetic correlation equal to 1.0 obtained by the two-trait animal model of YW with WBS1 confirmed this fact.

Although evidence exists that selection for YW leads to changes in the adult weight of the cows due to the relatively high positive correlation between selected weights and adult weight, and high heritability for adult weight (Koots et al., 1994a,b; Lóbo et al., 2000), few papers have reported the response on adult weight due to weight selection or gain at early ages. After 11 yr of yearling weight selection, Morris et al. (1992) observed 5.5% differences in weight at the start of the breeding season for selected cows, and 8.5% at the end, as compared to cows in the control herd. Archer et al. (1998b) reported that 2- and 5-yr-old cows, belonging to the third to fourth generations of selection for weight gain up to 1 yr, were respectively 10.5% and 12% heavier and 3% and 2.5% taller than those of the control line.

For the reproduction traits, no significant difference was detected between the selected and control lines. Despite the low heritability estimated for these traits, the means by year of birth for the EBV of DC1 and CS1 were plotted in Figures 3 and 4. The EBV mean for DC1 for the heifers born in 1981 were 3, 0, and 1 d for NeS, NeT, and NeC, respectively, and for those born in 1996, correspondent values were 3, 4, and −3, reflecting nonsignificant annual trends of −0.33 ± 0.42 d/yr, 0.03 ± 0.16 d/yr, and 0.19 ± 0.17 d/yr. Although there were differences in the results obtained by each procedure (comparison of the means for the last 4 yr and EBV means, obtained with the whole sample), they show that after 16 yr of selection for growth, there was no correlated change in heifers reproduction. The same was observed for CS1, which in this study was estimated to have no genetic variability.

The differences between means of selected and control lines for the trait CS2/1 (Table 3) were not significant, despite being negative. A similar result was shown for the repeated traits of DC and CS, whose differences were not significant. These results agree with the few reports showing no significant effects on the reproduction of females in the selection experiments for growth (Mrode, 1988).

Up to the mid-1980s, papers on the effects of growth selection indicated negatively correlated responses on the reproduction of cows (Barlow, 1978; Scholtz and Roux, 1984; Luesakul-Reodecha et al., 1986). In his review, Barlow (1978) concluded that the detrimental effect could be about a 1.1% decrease in the weaning percentage for each standard deviation of change in weaning weight, even though he suggested that the total impact was not clear and that interactions could occur depending on nutritional level. Baker and Morris (1984), in a critical review of responses correlated to growth selection, pointed out the lack of evidence for negative effects on reproduction.

Baker et al. (1991) and Morris et al. (1992) did not observe significant differences between lines selected for YW and control in the percentages of pregnant cows,
Table 3. Comparison of the means of lines for size and reproductive traits of cows and heritability estimates

<table>
<thead>
<tr>
<th>Trait</th>
<th>NeC</th>
<th>NeS</th>
<th>NeT</th>
<th>P-value</th>
<th>P-value</th>
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<tbody>
<tr>
<td>WBS1, kg</td>
<td>275 ± 2</td>
<td>54 ± 3</td>
<td>50 ± 3</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>WBS, kg</td>
<td>339 ± 4</td>
<td>49 ± 5</td>
<td>54 ± 4</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>HBS1, cm</td>
<td>132.0 ± 0.4</td>
<td>6.4 ± 0.4</td>
<td>5.0 ± 0.5</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>HBS, cm</td>
<td>136.9 ± 0.5</td>
<td>6.0 ± 0.6</td>
<td>6.0 ± 0.6</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>CBS1, score</td>
<td>6.54 ± 0.37</td>
<td>−0.01 ± 0.08</td>
<td>0.08 ± 0.08</td>
<td>0.31</td>
<td>0.09 ± 0.07</td>
</tr>
<tr>
<td>CBS, score</td>
<td>6.24 ± 0.14</td>
<td>−0.42 ± 0.14</td>
<td>0.22 ± 0.14</td>
<td>0.25</td>
<td>0.20 ± 0.03</td>
</tr>
<tr>
<td>DC1, d</td>
<td>354 ± 5</td>
<td>−4 ± 6</td>
<td>−12 ± 6</td>
<td>0.03</td>
<td>0.08 ± 0.06</td>
</tr>
<tr>
<td>DC, d</td>
<td>353 ± 4</td>
<td>3 ± 5</td>
<td>−8 ± 4</td>
<td>0.08</td>
<td>0.10 ± 0.03</td>
</tr>
<tr>
<td>CS1</td>
<td>0.64 ± 0.07</td>
<td>0.07 ± 0.08</td>
<td>0.11 ± 0.08</td>
<td>0.65</td>
<td>0.04 ± 0.06</td>
</tr>
<tr>
<td>CS2/1</td>
<td>0.62 ± 0.09</td>
<td>−0.11 ± 0.12</td>
<td>−0.02 ± 0.12</td>
<td>0.95</td>
<td>0.10 ± 0.07</td>
</tr>
<tr>
<td>CS</td>
<td>0.82 ± 0.07</td>
<td>−0.02 ± 0.04</td>
<td>0.62</td>
<td>0.01 ± 0.04</td>
<td>0.80</td>
</tr>
</tbody>
</table>

aWBS1 = weight at the beginning of the first breeding season; WBS = weight at the beginning of the breeding season; HBS1 = height at the beginning of the first breeding season; HBS = height at the beginning of the breeding season; CBS1 = body condition score at the beginning of the first breeding season; CBS = body condition score at the beginning of the breeding season; DC1 = days to calving of the first mating; DC = days to calving; CS1 = calving success of the first mating; CS2/1 = calving success of the second mating considering that the heifer calved from first mating; CS = calving success.

bNeC = control Nelore; NeS = selection Nelore; NeT = traditional Nelore.

cLeast squares means ± SEM.

dProbability of observing a greater t-value.

eTwo-trait analysis with YW, SEM from single-trait analysis.

Rates, significant differences were observed for reproductive traits such as days to calving and pregnancy rate, but little change in cow weights was observed as a correlated response (Davis et al., 1993; Morris et al., 2000). All these reports, together with the results of the present study, confirm earlier results (reviewed by Baker and Morris, 1984) and point out that there is substantial evidence for no negative effects of selection for growth on reproduction.

**Heritability Estimates.** The estimated heritabilities were 0.37 ± 0.04 and 0.45 ± 0.06 for YW and H550, respectively, and the permanent maternal environment effect was responsible for 11% of the YW total variance. Razook et al. (1998) reported realized heritabilities for perinatal and postnatal calf mortality, weaning rate or reproductive rate. The correlated effects on reproductive performance in females for selected lines of Angus cattle in Australia were described by Archer et al. (1998a). After 10 yr of the experiment, no difference was detected in the rates of pregnancy, days to calving or gestation length in cows from the selected and control lines.

In addition to the selection experiments, many studies obtaining mixed model solutions for reproductive traits in populations selected for greater growth have shown very low genetic trends (Mrode et al., 1990; MacNeil and Newman, 1994), as observed for the annual EBV means of DC1 (Figure 3) and CS1 (Figure 4). In lines directly selected for higher or lower reproductive rates, significant differences were observed for reproductive traits such as days to calving and pregnancy rate, but little change in cow weights was observed as a correlated response (Davis et al., 1993; Morris et al., 2000). All these reports, together with the results of the present study, confirm earlier results (reviewed by Baker and Morris, 1984) and point out that there is substantial evidence for no negative effects of selection for growth on reproduction.

Figure 3. Means of EBV for DC1, by selection line (control ■, selection ●, and traditional ▲) and year of birth. Figure 4. Means of EBV for CS1, by selection line (control ■, selection ●, and traditional ▲) and year of birth.
YW higher than those obtained using the animal model, equal to 0.45 for males and 0.42 to 0.55 for females. A possible explanation for this is that the method used by those authors ignored the maternal effects, which could inflate the additive genetic variance and not always the residual variance (Meyer, 1992), increasing the estimate of heritability. However, while in theory additional random effects, such as maternal genetic effects could be accommodated in the mixed model analyses, often the data structure in selection experiments does not provide sufficient contrasts to distinguish the different effects (Baker et al., 1991; Meyer and Hill, 1991). Although the analysis of field data has shown the importance of the maternal genetic effect for YW in Nelore cattle (Eler et al., 1995; Mercadante and Lôbo, 1997), the maternal genetic effect for the YW was not significant, but showed substantial variance due to the maternal environment.

The heritability estimates (Table 3) are in agreement with those reported in the literature, both for growth and reproduction traits obtained in selection experiments and from field data. Weights and heights showed medium to high heritabilities (Meyer, 1992; Johnston et al., 1996; Rosa et al., 2000); body condition score and pregnancy rate showed lower heritabilities ranging from 0.11 to 0.21 (Johnston et al., 1996; Johnston and Bunter, 1996; Doyle et al., 2000) and days to calving showed low to almost zero values of 0.07 to 0.12 (Meyer et al., 1991; Johnston and Bunter, 1996; Pereira et al., 2000). With the exception of the selection experiments to increase the reproduction rate (Davis et al., 1993; Morris et al., 2000), most of the beef cattle herds will continue to be selected for higher growth and the slow improvement in fertility of Bos indicus will probably come as a result of selection involving precocious matings of heifers around 1 yr of age.

The results of the present study, comparing the reproductive performance of females selected for YW for 3.5 generations of selection (Razook et al., 1998) with females selected for medium YW, together with the results of papers published in the last decade, with both experimental data (Mrode et al., 1990; Wolfe et al., 1990; Morris et al., 1992; Archer et al., 1998a) and field data (Meyer et al., 1991; Johnston and Bunter, 1996; Mercadante et al., 2000) indicate that selection for body weight does not compromise female reproductive performance for herds reared in temperate climates and in the tropics. Herd (1995), analyzing two divergent lines (high weight and low weight) in an experiment with Angus cattle in Australia, observed that the high weight line cows had a daily maintenance energy requirement similar to that of the low weight line cows. Despite the difference in body weight of the cows from the two selected lines (24%), the high weight cows required about 79% of the metabolizable energy per day of that required by the low weight cows to maintain each kilogram of body weight. The high weight cows had more fat and less protein per unit of live weight as compared to the low weight cows, and the cost of maintaining 1 kg of protein is higher than the cost of maintaining 1 kg of fat. This fact could explain the similar reproductive performance between selected lines despite differences in their growth traits. It should be noted that none of these experiments were evaluated for more than five generations of selection, which might not be sufficient for the manifestation of reproductive problems.

**Implications**

The experiment showed the efficiency of selection for body weight within a herd to promote high and consistent genetic change in the selection weight and correlated responses for height in both young and older Nelore animals under tropical environmental conditions. Positive genetic trends for growth occurred without compromising the reproductive performance of the cows, specifically days to calving and calving success. These findings are comparable to those achieved in previous selection experiments with Bos taurus breeds, highlighting the great potential of zebu for growth in the tropics and contributing to clarifying the controversial issue of selection for growth negatively affecting reproduction in zebu cattle.

**Literature Cited**


