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Genetic Characterization of Criollo Cattle in Bolivia: I. Genetic Parameters for Pre and Postweaning Growth Traits

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ABSTRACT: Heritabilities and additive genetic correlations for direct and maternal genetic effects among preweaning and postweaning growth traits were calculated for the dual-purpose cattle population of Criollo Saavedreño from the eastern lowlands of Bolivia. The traits considered were birth weight (BWT), gain from birth to weaning (GBW), gain from weaning to 365 d (GWY), and gain from 365 d to 550 d (GYH). Covariances were estimated using REML methodology, and computed using the DFREML package. Standard errors were obtained using the average information matrix. Fifty-five percent of the 56 estimated covariance components were larger than their estimated standard errors, which averaged 43 % of the value of the covariance components. Heritability estimates of direct (D) genetic effects were $.23 \pm .07$ for BWTD, $.19 \pm .06$ for GBWD, $.03 \pm .04$ for GWYD, and $.15 \pm .07$ for GYHD. Heritability values for maternal (M) effects were $.13 \pm .04$ for BWTM, $.10 \pm .04$ for GBWM, $.02 \pm .03$ for GWYM, and $.12 \pm .06$ for GYHM. Thus, traits that will be useful for selection in this Criollo population are BWT, GBW, and GYH. An additional selection trait could be direct gain from weaning to 550d (heritability = $.16 \pm .07$). Most genetic correlations (23 of 28) were small (less than $\pm .50$). The genetic correlation between GWYD and GYHD (-.44 \pm .55), and the environmental correlation between GWY and GYH (-.20 \pm .04) suggested that there was compensatory gain between 365 and 550 d of age. Environmental conditions may have prevented the full expression of the growth potential of animals in this population. Thus, dietary supplementation should be considered as an alternative to uncover more genetic variability, and perhaps to help increase genetic progress.

Key words: Criollo Cattle, Covariance Estimates, Growth Traits, Genetic Parameters

Introduction

The Criollo Cattle Project of the Research Center of Tropical Agriculture (CIAT) was founded with the purpose of contributing to the conservation, improvement, and dissemination of Criollo cattle. A herd of dual-purpose (milk-beef) Criollo cattle was established in the eastern lowlands of Bolivia in 1978 (Wilkins et al., 1983) with the objective of evaluating bulls for future use as sires in purebreeding and crossbreeding programs for milk and beef production. This herd may be considered as the base for a new population of Criollo cattle, the Criollo Saavedreño. Criollo cattle from Bolivia and four other Latin-American countries contributed to the formation of this population.

Although the Criollo Cattle Project has had an important impact on the livestock industry of the Bolivian eastern lowlands, a genetic evaluation of the Criollo Saavedreño population has yet to be performed. Such an evaluation would be the first step towards a broader program to further evaluate animals in all Criollo herds in Bolivia. Only through careful and complete genetic evaluation programs will the unique characteristics of the Criollo Saavedreño have a country-wide economic impact in Bolivia. However, before a genetic evaluation can be conducted, appropriate genetic parameters to this Criollo population must be estimated. Thus, the objectives of this study were to estimate heritabilities and additive genetic correlations for direct and maternal genetic effects among preweaning and postweaning growth traits of the dualpurpose Criollo Saavedreño.

Materials and Methods

Establishment of the Criollo Saavedreño herd

The herd was founded in 1978 by purchasing Criollo cows from producers located throughout the State of Santa Cruz (370,000 km²), eastern Bolivia. To avoid inbreeding, no more than two cows were purchased from any single producer. Approximately 100 cows were screened for each cow that was purchased (Wilkins et al., 1983). Criteria for purchasing cows were 1) absence of ticks, 2) at least one calving, 3) all calves born to a cow survived to weaning, and 4) good body condition of both cow and calf (Wilkins et al., 1983). A total of 85 cows were purchased from 1978 to 1985. Semen of 35 Latin-American Criollo sires (9 Bolivian, 7 Brazilian, 12 Costa Rican, 4 Cuban, and 3 Nicaraguan) was used in the Saavedreño herd between 1978 and 1997. Thus, the base population of the Criollo Saavedreño was formed by 85 Bolivian cows and 35 sires from five Criollo populations.

The Criollo Saavedreño herd was kept in the Saavedra Experiment Station located at 17°14' S and 63°10' W (65 km north of the city of Santa Cruz, Bolivia), at 320 m above sea level. Saavedra has a mean annual temperature of 23.4 °C, an annual precipitation of 1347 mm, and a mean annual relative humidity of 67.9 %. Two distinct seasons were defined: rainy and dry. The rainy season (October to March), which corresponded to the spring and summer months, received approximately two thirds of the annual rainfall. Pastures were abundant during the rainy season. The dry season (April to September), however, usually brought restrictions on pasture availability for cattle in the autumn and winter months.

Herd management

The Criollo Saavedreño herd was kept under an all-grazing regime with free access to mineralized salts. Artificial pastures consisted of one Gramineae or a combination of one Gramineae and one legume (e.g. *Brachiaria mutica* and *Leucaena leucocephala*). The Gramineae

species most commonly used were *Brachiaria humidicola*, *Brachiaria decumbens*, *Brachiaria mutica*, *Hyparrhenia rufa*, *Panicum maximum* var. Dwarf, and *Cynodon plectostachyus*, some of them in association with one legume, (*Leucaena leucocephala*, *Glycine wightii*, *Desmodium intortum*, and *Arachis pintoi*). Pastures were not fertilized because chemical fertilization of pastures is regarded as a non-profitable activity in Bolivia (J. V. Wilkins, personal communication).

The Saavedreño herd was managed in six groups, as follows: 1) preweaning male and female calves, (3 d to 250 d of age), 2) weaned bulls and heifers, (250 d to 15 mo of age), 3) bulls (15 mo and older), 4) heifers (15 mo to 22 mo), 5) pregnant non-lactating cows (last two mo of pregnancy), and 6) lactating cows. Preweaning calves were maintained on immature pastures composed of Panicum and Cynodon. Weaned calves (bulls and heifers) were grazed on low quality Brachiaria pastures. Fifteen mo and older bulls and heifers, and pregnant non-lactating cows were rotated on pastures composed of Brachiaria, Hyparrhenia, and Cynodon. Lactating cows had access to pastures composed of one Gramineae and one legume.

Calves were separated from their dams 3 days postpartum, and maintained on pasture. Dams were milked twice each day. Following an incomplete hand-milking, calves were allowed to suckle for 30 to 60 minutes. Approximately 700 kg of milk per calf was consumed preweaning (Wilkins et al., 1983). Calves were weaned at approximately 250 d of age. At weaning, bulls were screened for defects such as skin depigmentation (believed to be susceptible to sunburn) and testicular abnormalities. No culling was practiced on heifers. Bulls and heifers were kept together under the same management (rotational grazing without supplementation) from 3 d of age until 15 mo of age, or until they weighed between 230 and 240 kg. Subsequently, male and

female calves were grouped by sex to avoid uncontrolled matings. Bulls were castrated at 18 months of age.

Mating strategy

Animals were inseminated twice, then placed with a natural service bull for two months. The average number of AI services per pregnant cow was 1.8. In addition to the semen of the thirty-five Latin-American Criollo sires, semen from 24 sires bom in the herd has been used since 1986. To create connectedness across years, sires were used for 2.5 consecutive years on the average. A minimum of 3 and a maximum of 11 sires (8 sires per year on the average) were used each year. Bolivian base sires, and sires born in the herd were used for both AI and natural service. Calving occurred year around with an even distribution of calvings between the rainy and dry seasons. Eighty five base dams and 451 dams born in the herd averaged three calvings each.

Records and Traits

The data set included records for 1649 calves born from 1979 to 1997. The number of records per trait, means, and ranges are shown in Tab1e 1. Differences in the number of records among birth weight and the other traits were due to calf death and culling.

Traits considered were birth weight (BWT), gain from birth to weaning (GBW), gain from weaning to 365 d (GWY), and gain from 365 d to 550 d (GYH). Weaning weights were adjusted to 250 d because calves were weaned at an average age of 250 d. Yearling weights were adjusted to 365 d, and weight of calves at year and a half to 550 d. All weight adjustments were calculated using the Beef Improvement Federation formula (BIF, 1996). Gains were calculated as the difference between adjusted weights.

Estimation of variance components

Variance and covariance components among traits were estimated using Restricted Maximum Likelihood (REML; Patterson and Thompson, 1971). Direct and maternal (co)variance estimates for BWT, GBW, GWY, and GYH were computed with the Derivative Free Restricted Maximum Likelihood package (DFREML; Meyer, 1997) employing the Simplex procedure for a Multiple Trait Animal Model. Standard errors of estimates of covariance components were derived by the DFREML set of programs from the average information matrix (Johnson and Thompson, 1995). Asymptotic standard errors of heritability, and correlation estimates were computed using linear functions of the elements of the average information matrix provided by the DFREML package (Mood et al., 1974; Sorensen, 1997). The computer used for the analysis was an IBM PC Aptiva with a Pentium processor, 200 MHZ speed, and 48Mb RAM.

Model. The model used for BWT, GBW, GWY, and GYH was a Multiple Trait Animal Model. Each trait was considered to have both direct (D), and maternal (M) effects.

Two fixed effects were considered in the model: contemporary group, and dam effects. Contemporary groups were defined as groups of calves that were born in the same year (1979 to 1997), in the same season (1 = dry, 2 = rainy), and were of the same sex (1 = bull, 2 = heifer). Dam effects were defined as age of dam at calving × sex of calf subclasses, where age of dam was classified as 2, 3, 4, 5, and 6 or more years.

Random effects in the model were direct additive genetic, maternal additive genetic, and residual. Additive relationships among animals in the population were accounted for. Thus, the covariance matrix among random genetic effects had the usual A^*V_g form, where A = additive

relationship matrix, * = direct product, and V_g is a multiple-trait additive genetic covariance matrix among direct and maternal genetic effects. Residual effects among animals were assumed to be uncorrelated. Thus, the residual covariance matrix was equal to I*V_e, where I = identity matrix, and V_e = multiple trait residual covariance matrix (Henderson and Quaas, 1976; Quaas and Pollak, 1980).

Computing strategy. Estimates of direct and maternal covariances from single trait analysis were used as priors for the multiple-trait analysis. Due to the small size of the data set, and the inclusion of direct and maternal effects for each trait in the model, it was not possible to analyze all traits together. Thus, four separate analyses were conducted in the following sequence: 1) BWT-GBW, 2) BWT-GWY, 3) BWT-GYH, and 4) GBW-GWY-GYH. Repeated estimates in this sequence were fixed. For example, the variance estimates obtained for BWT in the first analysis were fixed in the following two analyses (BWT-GWY, and BWT-GYH), meaning that those values were not computed again to avoid repeated estimates of the same parameters.

Convergence was assumed to have been achieved when the variance of function values (-2log L) in the Simplex was less than or equal to 1×10^{-9} . A global maximum was assumed when the -2log L values of two consecutive cold-starts had a difference of 1×10^{-2} or less. Two to four cold-starts were needed to achieve this criterion.

Results and Discussion

Accuracy of covariance components

A total of 56 covariance components were estimated, of which 36 were additive genetic, 10 were residual, and 10 were phenotypic covariances (Tables 2, 3, and 4). Because of the small

size of the data set, standard errors of covariance estimates were expected to be large. However, more than half (55.4 %) of the 56 values were larger than their estimated standard errors, with those standard errors averaging 42.9 % of the value of the variance components.

Estimates of 36 direct and maternal additive genetic covariance components for BWT, GBW, GWY, and GYH are shown in Table 2. There was substantial genetic variability for direct and maternal effects of BWT, GBW, and GYH in the Saavedreño population. The accuracy of estimation of genetic variances for these traits was reasonable. Standard errors of the six direct and maternal variance estimates averaged 38.7 % of the value of the estimates. On the other hand, the variance estimates for GWYD, and GWYM were small, and had standard errors that were larger than the variance estimates. The 13 covariance estimates of GWYD and GWYM with other traits' direct (BWTD, GBWD, and GYHD) and maternal (BWTM, GBWM, and GYHM) genetic effects were the only covariance estimates which consistently had standard errors that were larger than their estimates of covariance. This may be explained by the small gains or weight loss that occurred from weaning to yearling. Animals could not express their genetic potential for growth under the existing feeding conditions during this growth period. Thus, estimates of genetic variances and covariances involving GWYD and GWYM were more inaccurate than for the other traits.

Residual (Table 3) and phenotypic (Table 4) covariances among traits were small. Residual variance of preweaning traits represented a smaller percentage of phenotypic variance than residual variance of postweaning traits. Thus, if it is assumed that nonadditive genetic effects are small, environmental effects had a larger in fluence on postweaning traits than on preweaning. This is reflected in the values of the residual variances of GWY (300.15 \pm 15.66), and GYH (408.34 \pm 28.50), and the residual covariance among both (-70.21 \pm 15.54), which are the largest residual variance and covariance estimates.

Heritabilities

Eight estimates of heritability (h^2) for direct and maternal genetic effects were computed (Table 5). Estimates ranged from small (less than .20) to medium (.20 to .40). Six out of eight h^2 estimates were larger than their estimated standard errors. Standard errors of those six h^2 averaged 34.9 % of the value of the h^2 estimates. The only traits with standard errors larger than their h^2 estimates were GWYD ($.03 \pm .04$), and GWYM ($.02 \pm .03$). Small gains or weight loss from weaning to yearling (Table 1) most likely affected the expression of these traits.

The h^2 estimates for BWTD (.23 ± .07), and BWTM (.13 ± .04) were similar to those estimated for a Colombian Criollo breed, Romosinuano (.16 for BWTD and .18 for BWTM; Elzo et al., 1998). In addition, similar values of h^2 for BWTD were also reported for non-Criollo beef breeds, such as Angus (.26, Bennet and Gregory, 1996; .22, Elzo and Wakeman, 1998), Hereford (.18, DeNise et al., 1988), and Nigerian Red Poll (.26, Iloeje, 1986). Similar values of h^2 for BWTM were found by Trus and Wilton (1988) for Angus (.13), Hereford (.13), and Shorthorn (.20), and by Elzo and Wakeman (1998) for Angus (.17).

The h^2 estimates for GBWD (.19 ± .06), and GBWM (.10 ± .04) were approximately 50 % of the values reported by Trus and Wilton (1988), Brown et al. (1990), and Meyer et al. (1994) for Angus, Hereford and Shorthorn cattle. The small h^2 estimates of weaning weight direct (.09), and maternal (.09) of the Criollo Romosinuano (Elzo et al., 1998) had more similarity with the values reported here for the Criollo Saavedreño. Environmental conditions (such as amount of milk received per calf, and quality and composition of pastures) may have caused small gains

preweaning. It seems probable that the amount of milk that calves were allowed to suckle was insufficient to completely express their genetic potential. Furthermore, because calves were allowed to suckle for only a short period of time (30 to 60 min) twice a day, maternal effects are unlikely to have been fully expressed. Quality and composition of pastures may also have been a restrictive environmental condition. Preweaning calves were kept in pastures composed exclusively of Gramineae without protein supplementation during a growth period that has high protein requirements.

The h² estimates for GWYD (.03 \pm .04) and GYHD (.15 \pm .07) were approximately 20 % of the values of estimates reported in the literature for direct postweaning gains of Angus, Braunvieh, Hereford, Pinzgauer, and Red Poll (Iloeje, 1986; DeNise et al., 1988; Bennet and Gregory, 1996). The small h² estimates of GWYD and GWYM (.02 \pm .03) can be explained by the animals' small gains or loss of weight between weaning and 365 d (Table 1). These small gains may have been caused by the stress of weaning, and the management practice of providing pastures of low quality to weaned bulls and heifers. The higher h² estimate (.15 \pm .07) for GYHD was the result of a calf's own ability to grow, and the compensatory growth that occurred between 365 d and 550 d. The h² value for GYHM (.12 \pm .06) was similar to that estimated for preweaning traits. A lower estimate for the h² of GYHM was expected because it represents the h² of the remnants of preweaning maternal effects. It suggests that preweaning maternal influences were long-lasting in the Saavedreño herd.

Bulls were usually sold at 18 months of age in the Criollo Saavedreño herd. Thus, an additional analysis that considered gain from weaning to 550 days (GWH) was performed. Heritability of GWHD ($.16 \pm .07$) was higher than the h² estimate for GWYD, but similar to that

of GYHD (.15 \pm .07). Heritability of GWHM was almost zero (.05 \pm .05), and it was similar to the estimate for GWYM (.02 \pm .03). The h² estimate of GWHD was similar to the one estimated for the Criollo Romosinuano (.14), but the estimate of GWHM was smaller than the estimate (.23) reported for that breed (Elzo et al., 1998). The h² estimates obtained for direct and maternal effects of GWH indicated that small gains or weight loss between weaning and 365 d disappeared due to compensatory gain between 365 d and 550 d. This would not have been noticed if the postweaning period had been considered as one trait only.

The majority of growth studies involving non-Criollo cattle estimated maternal h² for postweaning weights (yearling weights, 18-mo weight) instead of postweaning gains. The heritabilities of GWYM and GWHM for Saavedreño cattle were smaller than most of the values estimated for maternal yearling weight and maternal 18-mo weight in non-Criollo *Bos taurus* breeds (Meyer et al., 1993; Nuñez-Dominguez et al., 1993; Meyer, 1994). However, Meyer (1992) reported estimates of maternal yearling weight (.06) and maternal 18-mo weight (.00) for Angus cattle, and maternal 18-mo weight (.07) for Hereford cattle that were similar to the values reported here for GWYM and GWHM in the Criollo Saavedreño.

Genetic correlations

Genetic correlation estimates (Table 5) ranged from small (less than \pm .50) to large (greater than \pm .70). Most of them (23 out of 28) were small. Nine out of 28 correlations (32.1 %) were larger than their estimated standard errors, which averaged 65.8 % of the value of the correlation estimates. Two traits, GWYD and GWYM, consistently had correlation estimates with the largest standard errors. It seems that the inability of animals to express their genetic potential from weaning to yearling greatly decreased the accuracy of correlation estimates when any of

these two traits were involved.

Genetic correlations among direct effects across traits. Genetic correlations among direct effects (r_{DD}) were small, and ranged from -.44 to .42 (Table 5). The largest positive r_{DD} (.42 ± .22) was between the preweaning traits, BWTD and GBWD, which is larger than the value reported in the Criollo Romosinuano (.15; Elzo et al., 1998). The largest negative r_{DD} (-.44 ± .55) was between the postweaning traits, GWYD and GYHD. The r_{DD} estimate between GBWD and GWYD (-.26 \pm .52) suggests that weaning stressed the calves. The lower quality of pastures provided to heifers and bulls postweaning may also have contributed. The influence of these environmental factors was reflected on limited weight gains, and(or) loss of weight between weaning and 365 d, and would explain the negative correlation between GBWD and GWYD. Heifers and bulls manifested compensatory gain between 365 d and 550 d of age, which was reflected on the positive r_{DD} (.25 ± .33) between GBWD and GYHD. This may also explain not only the negative r_{DD} between the two postweaning traits mentioned earlier, but also the almost zero h² estimate for GWYD, and the somewhat larger h² estimate for GYHD. This explanation also seems to be supported by the positive r_{DD} value between GBWD and GWHD (.43 ± .29), which suggests that the effect of small gains or weight loss between weaning and 365 d disappeared due to compensatory gain between 365 d and 550 d. For the Criollo Romosinuano, Elzo et al. (1998) reported an r_{DD} value of -.24 between weaning weight direct and GWHD (vs .43 in the Saavedreño). The difference in the sign of these genetic correlations suggests that Romosinuano calves were more severely stressed postweaning than Saavedreño calves. Romosinuano dams were not milked like Saavedreño dams, and consequently Romosinuano calves stayed with their dams throughout the preweaning period. Thus, Romosinuano calves are

likely to have received more milk, were less prepared to utilize grasses, and either lost more weight or gained less weight than Saavedreño calves during this growth period.

The r_{DD} among pre- and postweaning growth traits estimated here were within the range of values reported in the literature for *Bos taurus* non-Criollo breeds (DeNise et al., 1989; Bennet and Gregory, 1996), and were also similar to the r_{DD} averages reported by Koots et al. (1994).

Genetic correlations among maternal effects across traits. Estimates of genetic correlations among maternal effects (r_{MM}) were small, and ranged from -.38 to .21 (Table 5). The largest negative r_{MM} was between GWYM and GYHM (-.38 ± .63). A negative r_{MM} was also detected between GBWM and GYHM (-.34 ± .33). These two negative estimates corroborate the existence of compensatory gain. Elzo et al. (1998) reported a negative r_{MM} (-.23) between weaning weight maternal and GWHM for the Romosinuano, which is similar to the value estimated here between GBWM and GWHM (-.33 ± .46). Most published estimates of r_{MM} among pre- and postweaning growth traits in non-Criollo *Bos taurus* breeds referred to weights rather than gains. Estimates of r_{MM} among pre- and postweaning weights found in the literature (Meyer et al., 1993; Bennet and Gregory, 1996) were about 50 % larger than those found among pre- and postweaning gains in the Saavedreño herd. This discrepancy is likely to be due to the part-whole correlation that exist among weight traits.

Genetic correlations between direct and maternal effects within traits. The four correlation estimates between direct and maternal genetic effects (r_{DM}) within traits, (Table 5), ranged from small (.25) to large (-.87). The r_{DM} estimates were positive for BWT (.54 ± .26), and GBW (.25 ± .31). The Criollo Romosinuano also had a positive r_{DM} estimate (.23) for weaning weight, but a small negative r_{DM} (-.19) for BWT (Elzo et al., 1998). Most r_{DM} values on growth

traits reported in the literature for non-Criollo breeds are negative (Trus and Wilton, 1988; Brown et al., 1990; Meyer, 1992). Positive r_{DM} values for BWT have been reported on Angus (.27) by Meyer (1992), and on Shorthorn (.55) by Trus and Wilton (1988). The positive r_{DM} estimates between BWTD and BWTM, and between GBWD and GBWM in the Criollo Saavedreño indicate that selection for direct birth weight would result in changes of both direct and maternal effects. A similar result might be expected for selection of GBWD.

The r_{DM} estimate for GYH was large and negative (-.87 ± .38). A negative correlation was also obtained for GWH (-.34 ± .54). These estimates were quite different from the near zero r_{DM} estimate (.08) reported for postweaning gain in the Criollo Romosinuano (Elzo et al., 1998). The negative r_{DM} estimates indicate that there was a negative association between direct genetic effects for postweaning gain and the remnants of preweaning maternal effects. This negative correlation suggests that calves that received less preweaning maternal milk were in better condition to utilize postweaning grass pastures, thus they grew faster than calves that received more maternal milk preweaning. It also indicates that preweaning maternal influences under the restrictive nutritional conditions may have a more permanent or longer-lasting environmental effect on postweaning growth than under less constrained nutritional conditions.

Genetic correlations between direct and maternal effects across traits. Twelve correlations among direct and maternal effects(r_{DM}) were estimated (Table 5). Nine out of twelve r_{DM} were small (less than ± .50), two out of twelve were large (greater than ± .70), and one out of twelve was medium (± .50 to ± .70). Positive r_{DM} estimates ranged from close to zero (.03 ± .62 between GBWD and GWYM) to large (.72 ± .59 between GWYD and GYHM). Negative r_{DM} were small, and ranged from almost zero (among BWTD and both maternal postweaning traits) to $-.24 \pm .65$ between GWYD and GBWM.

Maternal effects of BWT had positive r_{DM} values with GBWD (.71 ± .23), GWYD (.35 ± .55), GYHD (.38 ± .31), and GWHD (.75 ± .27). These results differed from the values obtained for the Criollo Romosinuano, where correlations between BWTM and weaning weight direct (.05), and between BWTM and GWHD (-.06) were almost zero (Elzo et al., 1998). Correlation values obtained here suggest that selection for direct weight gain from birth to weaning, and from weaning to 550 d might increase not only adult weight, but also the maternal genetic potential to give birth to heavier calves. Thus, heifers selected for direct weight gain will be heavier than the previous generation and have heavier newborn calves. This would be due not only to the positive correlation between BWTM and BWTD (.54 ± .26). This effect would be undesirable if heavier newborn calves caused dystocia problems. However, heavier calves would be born to larger cows, thus, dystocia would be unlikely.

Saavedreño and Romosinuano calves also differed in the r_{DM} value between BWTD and GBWM, which was -.16 ± .28 in the Saavedreño herd and almost zero (.02) in the Romosinuano herd (Elzo et al., 1998). Both Criollo breeds had similar r_{DM} values (almost zero) between BWTD and postweaning gain maternal. The small (and inaccurate) negative r_{DM} between BWTD and GBWM might indicate that lighter newborn Saavedreño heifers have the ability to produce more milk than heavier ones.

The r_{DM} estimate between GBWM and GWYD (-.24 ± .65) suggests that those animals that received more milk from their dams from birth to weaning may have felt more stress from weaning than those that received less milk. However, these same animals tended to have larger

compensatory gains between 365 d and 550 d than those which received less maternal milk, as suggested by the positive r_{DM} between GBWM and GYHD (.57 ± .37). The positive r_{DM} value between GBWM and GWHD (.47 ± .37) also seems to suggest that compensatory gains between 365 d and 550 d offset the effects of small gains or weight loss from weaning to 365 d. Estimates of r_{DM} among pre- and postweaning growth traits in the Saavedreño herd were similar to the mean values computed for nine *Bos taurus* breeds (Bennet and Gregory, 1996).

Residual and phenotypic correlations

Residual and phenotypic correlation estimates were small (less than \pm .50), and ranged form -.20 to .15 (Table 6). Most estimates (8 out of 12) were close to zero. Eight out of 12 correlation estimates were larger than their estimated standard errors. The standard errors averaged 53.3 % of the value of the correlation estimates.

The values of the six residual correlations ranged from -.20 to .07. Most of them (four out of six) were close to zero. The largest residual correlations were found between the two preweaning traits ($-16 \pm .06$), and between the two postweaning traits ($-20 \pm .04$). Assuming that nonadditive genetic effects are small, residual correlations may be considered to be mostly relationships among environmental effects. Thus, the values estimated here suggest that environmental restrictions from birth to weaning resulted in a negative environmental correlation estimate between BWT and GBW. The negative environmental correlation estimate between GWY and GYH indicates that lower gains (or weight losses) due to environmental causes (e.g., poor quality Brachiaria pastures) between weaning and yearling were associated with higher weight gains between 365 d and 550 d of age.

Phenotypic correlations were as small as residual correlations. Their estimates ranged from

-.20 to .15, and most of them (four out of six) were close to zero. The largest phenotypic correlation estimate was between GWY and GYH ($-.20 \pm .04$), which is similar to the value (-.24) reported by DeNise et al. (1989) for Hereford cattle. This negative value corroborates the influence of compensatory gain discussed previously. The values estimated here between BWT and GYH (.15 \pm .05), and between BWT and GWH (.18 \pm .05) were similar to the weighted mean phenotypic correlation between BWT and postweaning gain (.19) reported by Koots et al. (1994). The remaining phenotypic correlations in this study (Table 6) were smaller than the values reported for the Romosinuano cattle (Elzo et al., 1998) and for other breeds, such as Hereford (DeNise and Torabi, 1989; Meyer et al., 1993; Koots et al., 1994). The small values of residual and phenotypic correlations between pre- and postweaning growth traits estimated here may be due to the preweaning practice of letting calves suckle for only 30 to 60 min twice a day. This practice must have drastically reduced preweaning maternal influences in the Saavedreño herd. Because most of the preweaning environmental effects can be attributed to maternal milk influences, if maternal milk is controlled, then near zero residual and phenotypic correlations between pre- and postweaning growth traits will result.

Results of this study suggest that the traits of choice to be used in future selection programs of the Criollo Saavedreño herd would be BWT, GBW and GWH. However, GWY would not be a useful selection trait. The small heritability estimates for its direct and maternal effects, and the inaccuracy of its genetic correlation estimates made this trait inadequate as a selection criterion. This might change, however, if the restrictive environmental conditions that affected weight gain after weaning were improved.

The influence of environment on limiting postweaning growth seems to have been

important for the expression of genetic potential for growth in this herd. This influence may have gone unnoticed if the postweaning period had been considered as one trait only (GWH), instead of two (GWY and GYH). Availability of improved pastures composed of a mixture of Gramineae and legumes for young animals, specially after weaning, would help offset current nutritional restrictions, and uncover more genetic variability.

The availability of genetic parameters for this population will allow the Criollo Cattle Project to conduct a genetic evaluation of its herd. Prediction of EBV can be computed for all animals used in the herd and genetic trends can be evaluated. Moreover, future genetic evaluations of Saavedreño cattle should include data not only from the Saavedra Experiment Station, but also from all available herds that are using Saavedreño sires. Application of BLUP methodology in these genetic evaluations would help accelerate genetic changes and further promote the breed.

The availability of EBV for Saavedreño sires and cows is expected to have at least two positive consequences. First, it may stimulate the participation in genetic evaluations of other Criollo populations in Bolivia, such as the Criollo Chaqueño and Criollo Yacumeño populations. Participation can be made feasible through the Association of Criollo Cattle Breeders of Bolivia, which is already very active at providing technical assistance and keeping the Herd Books. Secondly, it should stimulate the interest of commercial beef cattle producers in Criollo breeds and increase the demand for Criollo sires to be used in crossbreeding programs. Increased use of Criollo sires of good quality would ensure the conservation of this population and its constant improvement.

Implications

Estimates of direct and maternal genetic parameters for BWT, GBW and GWH in the Criollo Saavedreño herd indicated that selection for these traits is feasible. However, the population size was small and environmental conditions were insufficient for animals to fully express their growth potential. Thus, selection progress for growth traits under these conditions will be slow. An improvement of environmental conditions (e.g., dietary supplementation, improvement of pastures) might uncover more genetic variance and result in faster selection progress. Furthermore, improvement of nutritional conditions will be important if Saavedreño cattle are to fairly compete against improved *Bos taurus* and(or) *Bos indicus* breeds (usually maintained under better environmental conditions) and(or) participate in crossbreeding programs.

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Trait ¹	No. records	LS Means	SD	Range (kg)	
		(kg)	(kg)	Min.	Max.
BWT	1649	30.22	4.82	15.00	52.00
GBW	1452	117.57	23.39	46.68	203.49
GWY	1354	47.86	20.05	-26.70	130.59
GYH	1218	72.46	27.38	-14.92	173.76

 Table 1.
 Number of records, least square means, standard deviations, and ranges per trait.

¹ BWT = birth weight; GBW = gain from birth to weaning; GWY = gain from weaning to 365 d; GYH = gain from 365 d to 550 d.

Table 2.Estimates \pm standard errors of additive genetic variance components (kg²) for
direct and maternal effects of growth traits.

Trait ¹	BWTD	GBWD	GWYD	GYHD	BWTM	GBWM	GWYM	GYHM
BWTD	5.25							
	(1.60)							
GBWD	8.47	78.79						
	(4.67)	(27.21)						
GWYD	2.56	-7.52	10.58					
	(3.64)	(15.15)	(13.88)					
GYHD	6.27	18.88	-12.46	74.66				
	(5.80)	(25.36)	(16.18)	(35.06)				
BWTM	2.14	10.85	1.84	5.31	2.97			
	(0.88)	(3.77)	(3.02)	(4.36)	(0.92)			
GBWM	-2.33	14.02	-5.05	31.20	2.04	40.22		
	(4.14)	(17.36)	(13.38)	(21.12)	(2.90)	(18.40)		
GWYM	28	.67	2.01	8.52	50	3.29	6.27	
	(3.17)	(13.82)	(10.48)	(15.33)	(2.33)	(10.30)	(10.98)	
GYHM	79	-14.83	17.75	-57.13	1.55	-16.30	-7.32	57.92
	(4.79)	(22.06)	(15.47)	(27.44)	(3.48)	(16.27)	(12.44)	(25.73)

¹ BWTD = birth weight direct; GBWD = gain from birth to weaning direct; GWYD = gain from weaning to 365 d direct; GYHD = gain from 365 to 550 d direct; BWTM = birth weight maternal; GBWM = gain from birth to weaning maternal; GWYM = gain from weaning to 365 d maternal; GYHM = gain from 365 to 550 d maternal.

Trait ¹	BWT	GBW	GWY	GYH
BWT	12.02			
	(1.01)			
GBW	-9.27	277.37		
	(3.20)	(19.58)		
GWY	.63	-14.11	300.15	
	(2.87)	(12.82)	(15.60)	
GYH	5.07	-9.96	-70.21	408.34
	(4.10)	(18.69)	(15.54)	(28.50)

Table 3. Estimates \pm standard errors of residual covariances (kg²) among growth traits.

¹ BWT = birth weight; GBW = gain from birth to weaning; GWY = gain from weaning to 365 d; GYH = gain from 365 to 550 d.

Trait¹ BWT GBW GWY GYH BWT 22.37 (1.08)GBW 410.40 5.50 (4.71)(18.63) GWY 3.46 -20.53 319.00 (3.59) (14.96) (12.67)GYH 15.16 483.79 .80 -76.85 (4.89)(20.93)(20.65)(15.81)

Table 4. Estimates \pm standard errors of phenotypic covariances (kg²) among growth traits.

¹ BWT = birth weight; GBW = gain from birth to weaning; GWY = gain from weaning to 365 d; GYH = gain from 365 to 550 d.

Table 5.Additive genetic parameters $^1 \pm$ standard errors for direct and maternal effects of
growth traits.

Trait ²	BWTD	GBWD	GWYD	GYHD	BWTM	GBWM	GWYM	GYHM
BWTD	.23							
	(.07)							
GBWD	.42	.19						
	(.22)	(.06)						
GWYD	.34	26	.03					
	(.47)	(.52)	(.04)					
GYHD	.31	.25	44	.15				
	(.28)	(.33)	(.55)	(.07)				
BWTM	.54	.71	.35	.38	.13			
	(.26)	(.23)	(.55)	(.31)	(.04)			
GBWM	16	.25	24	.57	.19	.10		
	(.28)	(.31)	(.65)	(.37)	(.26)	(.04)		
GWYM	05	.03	.25	.39	12	.21	.02	
	(.55)	(.62)	(1.37)	(.69)	(.57)	(.65)	(.03)	
GYHM	04	22	.72	87	.13	34	38	.12
	(.27)	(.33)	(.59)	(.38)	(.28)	(.33)	(.63)	(.06)

¹ diagonal = ratios of additive genetic variances to phenotypic variances; offdiagonal = additive genetic correlations.

² BWTD = birth weight direct; GBWD = gain from birth to weaning direct; GWYD = gain from weaning to 365 d direct; GYHD = gain from 365 to 550 d direct; BWTM = birth weight maternal; GBWM = gain from birth to weaning maternal; GWYM = gain from weaning to 365 d maternal; GYHM = gain from 365 to 550 d maternal.

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Table 6.

Residual and phenotypic correlations¹ \pm standard errors among growth traits.

Trait ²	BWT	GBW	GWY	GYH
BWT		16	.01	.07
		(.06)	(.05)	(.06)
GBW	.06		05	03
	(.05)		(.04)	(.06)
GWY	.04	06		20
	(.04)	(.04)		(.04)
GYH	.15	.00	20	
	(.05)	(.05)	(.04)	

¹ Above diagonal = residual correlations; below diagonal = phenotypic correlations.

² BWT = birth weight; GBW = gain from birth to weaning; GWY = gain from weaning to 365 d; GYH = gain from 365 to 550 d.