# GENETICS AND BREEDING

## Dairy Production and Reproduction in Holstein-Friesian and Guzera Crosses

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### ABSTRACT

Data on 660 first and second lactations and on 506 calving intervals were used to characterize six red and white Holstein-Friesian × Guzera crossbred groups (1/4 to ≥31/32 European grade) on 65 farms stratified into high and low management classes. Milk, fat, and protein yield per lactation and per day of calving interval were analyzed with models including effects of management, farm, and year-season of freshening. Within-class regressions were fitted for direct gene effects and heterosis, or, alternatively, crossbred classification effect and its interaction with management class. The interaction between crossbred group and management class was important for most traits. In the high management class, component yield per day of calving interval declined slightly with increased European grade above the F1 for 3/4, 7/8, and ≥31/32 crosses in the first lactation, but the four groups had similar second lactation performance. Grades 1/4 and 5/8 (inter se) had very poor performance due to short lactations. In the low management class, performance declined substantially as the European gene fraction departed from 1/2. The additive breed differences (Holstein-Friesian minus Guzera) were large and positive for yield traits, and so were heterosis effects. The additive-dominance model adequately fitted F1 and backcross data but not inter se data.

(Key words: Zebu crosses, heterosis, tropical dairy production)

### INTRODUCTION

Information on performance of breeds and crosses, including estimates of interpopulation genetic parameters, is needed to design breeding systems aimed at the economic utilization of genetic resources (6). Heterosis for milk yield has considerable importance in *Bos indicus* × *Bos taurus* crosses. Mean heterosis from several studies was 28% of midparent value (4), which was much higher than the 3 to 8% reported for crosses between European breeds (24, 29). Yet, estimates from tropical regions may be biased downward because of data editing to eliminate short ("abnormal") lactations, as this procedure selectively reduces genetic variation between crossbred groups (16).

Barlow (1) concluded that for most traits heterosis appears to be more important in suboptimal environments. Cunningham (3) proposed a model for milk yield based on a double interaction of both additive and nonadditive breed differences by environment in which heterosis is more important than additive differences in good environments but vice versa in poor environments.

Retention of heterosis upon inter se matings of crossbreds is an important criterion for new breed development (6, 7). Apparent nonretention of heterosis has been reported for milk yield in several *Bos taurus* × *Bos indicus* experiments. Recombination loss of parental epistatic combinations could be a cause of heterosis breakdown, but other explanations could not be ruled out due to confounding with selection or environmental trends (4, 21).

To define breeding strategies appropriate to production systems of the southeast region of Brazil, a trial was set up to measure performance of six Holstein-Friesian × Zebu cross-

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TABLE 1. Description of crossbred groups, expected individual Holstein-Friesian (HF) gene fraction (q), and expected fraction of loci with one gene from HF and one gene from Guzera (Gu) (z).

| q | Sire | Dam | Description | z |
|---|---|---|---|---|
| 1/4 | Gu | F1[1] | First backcross to Gu | 1/2 |
| 1/2 | HF | Gu | F1 | 1 |
| 5/8 | 5/8 | 5/8 | Inter se | 30/64 |
| 3/4 | HF | F1 | First backcross to HF | 1/2 |
| 7/8 | HF | 3/4 | Second backcross to HF | 1/4 |
| HF[2] | HF | ≥15/16 HF | Registered grades | 0 |

[1]F1 dams of reciprocal backcrosses interchanged.

[2]q = 1 assumed for genetic models (actual value ≥31/32).

bred groups on farms of varying management. The rationale was given by Madalena (14). Results for single lactation traits are presented herein to characterize the crossbred groups and genetic background. Accumulated and economic performance are presented in a companion paper (19).

## MATERIALS AND METHODS

### Animals and Farms

Performance of contemporary females of six red and white Holstein-Friesian (HF) × Guzera (Gu) crossbred groups was compared. These groups are described in Table 1. Crossbred dams (1/2, 3/4, and 5/8 HF) were available from a previous project in which HF sires were initially crossed to Gu type females, the halfbred progeny were backcrossed to HF sires and 1/2 × 3/4 reciprocal crosses generated the 5/8. In addition, HF registered grade dams were bought from 11 farms and Gu dams were obtained from 4 farms. Females for present study were by artificial insemination. The Gu sires (21) were from local commercial studs. Crossbred 5/8 sires (8) had the same origin as 5/8 dams. Average inbreeding coefficient of their progeny was .036. Thirty HF sires were used, 14 of which sired 86% of the 1/2, 3/4, 7/8, and HF animals and were represented in all four groups. Most progeny in these groups (97%) were sired by 22 red and white HF bulls (14 Brazilian and 8 imported from Canada or the US) from local studs, but a few animals (3%) by imported semen of 8 black and white HF bulls were included to complete contemporary groups. Further details of the genetic history of the herd are given by Lemos et al. (13).

Experimental calves were born between March 1977 and December 1981 at Santa Monica Experimental Station, Municipality of Valença, State of Rio de Janeiro. Calf raising practices were described elsewhere (13, 28). Heifers were distributed for further evaluation to 65 commercial cooperator farms, where they were managed without direction from research staff. Mean age at distribution was 22 mo and mean weight was 263 kg. With a few exceptions, each farm received a batch of six contemporary heifers, one of each crossbred group. Mean within-farm absolute age difference was 36 d (mean range = 83 d). In addition, 97 heifers were retained at Santa Monica and 29 at another experimental station (UEPAE São Carlos).

Cooperator farms were located in the main milk producing areas of the States of Minas Gerais, São Paulo, Rio de Janeiro, and Espirito Santo, between 17°41' and 23°7' S and 40°46' and 49°28' W. Farms were chosen to cover a wide technological range of farms milking twice a day. However, because it proved difficult to find cooperators at the higher technology level, a large group of heifers was kept at Santa Monica, where better management could be provided than in most commercial circumstances. Farms were grouped for analyses into two classes: high and low management (HM and LM), according to milk yield, age at first calving, and subjective evaluation of husbandry practices. The HM farms fed more concentrates, used more family labor and had a better health program (Table 2). Climate corresponds to Cw of Koeppen's classification (mild, dry winter, hot summer). Temperature and rainfall data, for which differences between HM and LM were negligible, are given by Madalena (16).

Sires of HM animals also had progeny in the LM. Number of HF, 5/8, and Gu sires in HM and LM were 15 and 30, 2 and 8, and 8 and 15

TABLE 2. Characteristics of management classes.

| | High | Low |
|---|---|---|
| Number of farms | 7 | 60 |
| Daily milk yield/cow, kg | 9.7 | 6.7 |
| Herd numbers[1] | | |
| Lactating cows | 49.8 | 42.2 |
| Dry cows | 19.7 | 20.4 |
| Heifers | 33.0 | 36.1 |
| Weaned males | 4.1 | 11.7 |
| Unweaned females | 26.5 | 19.5 |
| Unweaned males | 8.4 | 15.5 |
| Bulls | 1.5 | 2.1 |
| Breeding type of cows, %[1,2] | | |
| European breed and grade[3] | 43.8 | 9.3 |
| Predominantly European | 38.3 | 45.9 |
| Intermediate European Zebu | 12.7 | 29.6 |
| Zebu type[4] | 5.2 | 15.2 |
| Pastures, ha[1,5] | 94 | 159 |
| Elephant grass and sugar cane stands, % farms | 100.0 | 96.1 |
| Number of workers in dairying[1] | 3.8 | 3.9 |
| Family labor, %[1] | 5.0 | 24.3 |
| Concentrates fed, kg/cow per d | 4.5 | 1.6 |
| Mean concentrate composition, % | | |
| Commercial ration | 91.0 | 22.7 |
| Ground corn ears | 4.5 | 18.4 |
| Ground corn grain | 0 | 8.4 |
| Cottonseed meal | 3.4 | 15.0 |
| Wheat bran | 1.1 | 29.2 |
| Other | 0 | 6.3 |
| Mean silage composition, % | | |
| Corn | 91.9 | 59.5 |
| Sorghum | 0 | 13.2 |
| Elephant grass | 8.1 | 26.8 |
| Other | 0 | .5 |
| Experimental cows managed as indicated, % | | |
| Fed according to yield[6] | 86.5 | 6.5 |
| Fed silage during dry season | 100.0 | 69.2 |
| Machine milked | 95.5 | 15.0 |
| Natural mating only | 0 | 54.5 |
| Hand mating/AI[7] | 100.0 | 45.5 |
| Foot and mouth vaccination[8] | 100.0 | 100.0 |
| Brucellosis vaccination | 100.0 | 59.8 |
| Brucellosis testing | 100.0 | 48.0 |
| Tuberculosis testing | 89.5 | 22.5 |
| Mastitis testing[9] | 92.1 | 16.9 |
| Causes terminating lactation records, % | | |
| Rest before calving | 34.3 | 5.8 |
| Low yield | 53.2 | 47.4 |
| Natural drying off | 5.8 | 34.1 |
| Loss of calf | 1.2 | 6.5 |
| Illness, injury, or death | 5.5 | 6.2 |

[1]Experimental farms excluded.

[2]Based on visual inspection.

[3]Mostly Holstein-Friesian.

[4]Mostly Gir.

[5]Predominant species: *Melinis minutiflora, Hyparrhenia rufa, Brachiaria mutica, Brachiaria decumbens, Brachiaria* sp., *Pennisetum purpureum, Panicum maximum, Paspalum notatum.*

[6]Based on NRC requirements at Santa Monica experimental farm, except that for first 90 d a minimum 9 kg of concentrates per cow were fed daily.

[7]Includes natural mating bull for dry cows and heifers and AI clean up bull.

[8]Compulsory by sanitary regulations.

[9]Usually strip cup test.

respectively. One bull sired all 5/8 cows but one in HM and one third of cows in the LM. Heavy use had to be made of one 5/8 bull to keep progeny contemporaneity consistent with other groups, because development of the other 5/8 bull calves was retarded for managerial reasons beyond our control.

Milking cows in HM were kept practically free from ticks (*Boophilus microplus*), warble flies (*Dermatobia hominis*), and gastrointestinal parasites through chemical control and pasture rotation. Parasite control practices varied widely between farms in LM groups.

All farms, even those machine milking, followed the usual local practice of allowing calves to suckle briefly before milking to stimulate milk let down. However, on recording days no milk was intentionally left for calves nor were calves allowed to suckle between milkings. Lactations in this study occurred between June 1980 and August 1985. Milk yield was recorded monthly (fortnightly at Santa Monica). Monthly samples were sent to this research center for fat and protein testing (on Foss Electric Milko Tester Minor and Pro Milk Mk II apparatus A/S N. Foss Electric, Hillerod, Denmark). Drying off was forced in the HM class, but natural drying off was common in the LM class (Table 2). At the Santa Monica farm, where 77% of HM lactations occurred, cows were dried off 2 mo before expected calving or when milk yield dropped below 3 kg/d. All culling of first and second lactation cows was for reasons other than yield (19).

#### Statistical Analysis

The following traits were analyzed separately for each of the first two lactations: lactation length (LL); lactation milk (MY), fat (FY) and protein (PY) yield; fat (%F) and protein (%P) content; calving interval (CI) and milk, fat, and protein yield per day of CI (MY/CI, FY/CI and PY/CI). No record was discarded because of lactation length, calving interval, or reason for drying off to avoid biasing comparisons by selective data deletion (16).

Records of HM farms were grouped into a single farm class, because preliminary analyses indicated small nonsignificant differences among them. The LM farms with only one observation (due to death, culling, or delayed calving) were grouped in another single farm class.

Data were analyzed by least squares techniques using procedure GLM of SAS (26). The following models were utilized for single lactation traits:

$$Y_{ijklm} = b_0 + M_i + g_i g_j + h_i z_j + F_{2k} + YS_{il} + e_{ijklm} \quad [1]$$

$$Y_{ijklm} = \mu + M_i + G_j + MG_{ij} + F_{2k} + YS_{il} + e_{ijklm} \quad [2]$$

where:

$Y_{ijklm}$ alternatively represents one of the traits of the cow ijklm,

$b_0$ = intercept,
$\mu$ = mean,
$M_i$ = effect of management i (i = 1,2),
$g_i$ = breed additive difference (HF-Gu) in management i,
$q_j$ = expected proportion of HF genes in individuals of the crossbred group j (j = 1,...,6),
$h_i$ = heterosis effect in management class i,
$z_j$ = expected proportion of loci with one gene of each breed, in individuals of crossbred group j, [$q_j$ and $z_j$ = values shown in Table 1],
$F_{2k}$ = effect of farm k within the LM,
$YS_{il}$ = effect of year-season of freshening l within management i. Two seasons were considered, dry (April to September) and rainy (October to March).
$e_{ijklm}$ = random residual, assumed normally and independently distributed with zero mean and variance $\sigma^2$,
$G_j$ = effect of the crossbred group j, and
$MG_{ij}$ = interaction of management i with crossbred group j.

All effects except e were considered fixed. The g parameter corresponds to Dickerson's (6) average direct individual gene effects for each breed, measured from the Gu breed. The h parameter measures the individual heterosis effects (6).

The genetic model 1 is based on the model presented by Gardner and Eberhart (9) and applied to crossbred dairy cattle by Vencovsky et al. (30). Robison et al. (25) used multiple regression procedures to estimate interpopulation genetic parameters, including maternal and paternal effects. Genetic models to predict crossbred performance were reviewed by Eisen (8). In the present data, expected additive maternal HF gene proportions equalled $1 - z_j$ for all crossbred groups except for the 5/8, and because of this partial confounding, heterosis estimates are valid only on the assumption of no maternal effects. The heterosis parameter h contains dominance and epistatic effects (6), which are confounded in data sets containing only F1 and backcross information (11, 12). A model containing additive × additive epistatic deviations (11, 12) was also tested. Additive × dominance and dominance × dominance deviations could not be explicitly included in models because their coefficients were highly correlated with those of other genetic effects. However, the presence of epistatic effects was assessed by examining model 1 goodness of fit separately for 1) the whole data set and 2) the subset containing only F1 and backcross data. Should breed additive and dominance be the only genetic effects present, model 1 would fit equally well to the whole data set as to the subset without the 5/8 inter se. Goodness of fit of model 1 was assessed by F-tests on the extra mean squares due to fitting model 2 after model 1 against model 2 residual mean squares (25). To estimate error of inter se performance prediction, based on model 1 from F1 and backcross data, deviations ($d = Y - \hat{Y}_1$) of observed values minus model 1 "genetic" prediction ($\hat{Y}_1 = \hat{b}_0 + \hat{M}_i + \hat{g}_i q_j + \hat{h}_i z_j$) were analyzed under model 2 using data from all groups. Sire effects were not included in models because they were partly confounded with the environmental effects. Preliminary analyses indicated higher residual variances for LL, FY, and CI within the LM than within the HM, and for this reason weighted least squares analyses were performed for these traits.

## RESULTS

The F-values for model 2 are in Table 3. Management class significantly influenced all traits but LL and %P (*P*<.05). Crossbred group significantly affected all traits except second CI. Management × crossbred group interaction was significant for all first lactation traits but CI and %P, as well as for second lactation milk and component yield, MY/CI, and PY/CI. Year-seasons and farms affected most traits, as would be expected. These factors, however, will not be considered further, as they were included in models only to remove their effects and increase accuracy of genetic comparisons.

### Crossbred Group × Management Interactions

In HM, HF had longer first LL than other groups (Table 4). Differences in MY between groups 1/2, 3/4, 7/8, and HF were small in the first lactation, but the F1 dropped below the other three groups in second lactation LL and MY. Groups 1/4 and 5/8 had very short LL and MY in both lactations. In LM, the F1 had the longest LL and the highest MY; the 5/8 had very poor means for these traits and means of the other groups tended to decline as q deviated from 1/2. Thus, crossbred groups varied in their response to improved management, measured by the differential performance in the high and low management classes. Groups 1/4, 1/2, and 5/8 showed small response to improved management in MY and their LL was greatly reduced; groups 3/4 and 7/8 had substantially increased MY with moderate changes of LL; and HF had large increments of both LL and MY (Table 4).

Means for fat and protein content are shown in Table 5. In both lactations, mean %F was on average .4 percentage units lower in HM (where milk yield was higher) than in LM. However, mean %P was similar for both classes of management. Zebu breeding was associated with higher %F and %P, and, consequently, relative differences between crossbred groups for FY and PY were altered in relation to differences in MY (Table 4).

Mean CI on the HM reflected very reasonable reproductive management, whereas means on the LM were very high, particularly for first lactation cows (Table 6). There were some important differences in CI between crossbred groups, although the difference were not significant for second lactations (*P*>.10). However, as may be seen in Table 6, the longer first LL and higher MY of HF in the HM were accompanied by longer CI, which offset advantages of this group for milk and component yield per

TABLE 3. The F-values for model 2 ANOVA and residual standard deviations.

| Source | df | LL[1] | MY | FY | PY | %F | %P | CI | MY/CI | FY/CI | PY/CI |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | First lactation | | | | | |
| Management (M) | 1 | 3.37† | 33.48*** | 19.13*** | 33.28*** | 14.21*** | .70 | 71.47*** | 105.95*** | 71.10*** | 105.19*** |
| Crossbred group (G) | 5 | 14.88*** | 32.83*** | 38.94*** | 31.38*** | 12.57*** | 23.01** | 2.84* | 39.34*** | 46.10*** | 40.30*** |
| M × G | 5 | 7.36*** | 9.88*** | 8.79*** | 7.66*** | 3.30** | 2.18† | 1.51 | 6.39*** | 5.82*** | 4.82*** |
| Year-season/M | 12 | 2.75** | 1.91* | 2.65** | 2.13* | 1.51 | 1.57† | 2.74** | 1.62 | 1.92* | 1.96* |
| Farm/M | 56[2] | 2.34*** | 1.99*** | 1.91*** | 2.04*** | 2.95*** | 1.21 | 2.84*** | 2.19*** | 2.44*** | 2.34*** |
| Residual SD | 323[3] | 72.59 | 772.69 | 29.05 | 24.59 | .544 | .238 | 74.75 | 1.57 | 65 | 49 |
| | | | | | | Second lactation | | | | | |
| Management | 1 | .48 | 16.29*** | 3.94* | 18.63*** | 12.41*** | 3.56 | 15.25*** | 30.65*** | 8.57** | 33.05*** |
| Crossbred group | 5 | 6.71*** | 13.88*** | 11.79*** | 11.14*** | 9.53*** | 11.63** | 1.02 | 11.90*** | 9.05*** | 8.77*** |
| M × G | 5 | 1.57 | 4.98*** | 2.51* | 3.54** | .81 | 1.44 | .43 | 3.35** | 1.42 | 2.39* |
| Year-season/M | 10[4] | .99 | 2.14* | 2.66** | 1.90* | 1.21 | .82 | 1.65 | 3.01** | 3.23** | 2.50* |
| Farm/M | 40[5] | 1.59* | 1.89** | 1.89** | 1.98** | 1.09 | 1.23 | 1.11 | 1.38 | 1.90** | 1.59* |
| Residual SD | 195[6] | 69.13 | 823.59 | 30.56 | 25.39 | .622 | .327 | 58.84 | 1.88 | 78 | 58 |

[1]LL = Lactation length (d), MY = milk yield (kg), FY = fat yield (kg), PY = protein yield (kg), %F = percentage of fat, %P = percentage of protein, CI = calving interval (d).

[2]df = 51 for CI and traits per CI.

[3]df = 307 for %F and %P; df = 233 for CI and traits per CI.

[4]df = 9 for CI and traits per CI.

[5]df = 29 for CI and traits per CI.

[6]df = 189 for %F and %P; df = 148 for CI and traits per CI.

†$P<.10$.

*$P<.05$.

**$P<.01$.

***$P<.005$.

TABLE 4. Number of observations, least squares means (LSM), and standard errors for lactation traits.

| Cross-bred group | High management | | | | | | | | | Low management | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | LL[1] | | MY | | FY | | PY | | | LL | | MY | | FY | | PY | |
| | n | LSM | SE | LSM | SE | LSM | SE | LSM | SE | n | LSM | SE | LSM | SE | LSM | SE | LSM | SE |
| | | (d) | | (kg) | | | | | | | (d) | | (kg) | | | | | |
| First lactation | | | | | | | | | | | | | | | | | | |
| 1/4 | 25 | 211 | 16 | 1396 | 175 | 55.0 | 6.6 | 47.9 | 5.6 | 49 | 268 | 20 | 1180 | 134 | 54.3 | 6.3 | 40.0 | 4.3 |
| 1/2 | 21 | 305 | 18 | 2953 | 193 | 132.4 | 7.2 | 99.8 | 6.1 | 57 | 375 | 16 | 2636 | 107 | 113.6 | 5.1 | 83.0 | 3.4 |
| 5/8 | 16 | 191 | 19 | 1401 | 205 | 46.3 | 7.7 | 42.9 | 6.5 | 44 | 283 | 20 | 1423 | 137 | 59.2 | 6.5 | 44.7 | 4.4 |
| 3/4 | 15 | 329 | 20 | 2981 | 212 | 121.3 | 8.0 | 94.3 | 6.8 | 51 | 367 | 18 | 2251 | 123 | 93.5 | 5.8 | 69.6 | 3.9 |
| 7/8 | 24 | 295 | 16 | 2821 | 174 | 104.1 | 6.5 | 83.8 | 5.5 | 45 | 304 | 21 | 1672 | 140 | 66.1 | 6.6 | 50.5 | 4.5 |
| HF | 14 | 365 | 20 | 3147 | 215 | 112.6 | 8.1 | 93.3 | 6.8 | 42 | 258 | 20 | 1226 | 137 | 49.0 | 6.5 | 37.6 | 4.3 |
| Mean | 115 | 283 | 10 | 2450 | 101 | 95.3 | 3.8 | 77.0 | 3.2 | 288 | 309 | 11 | 1731 | 72 | 72.9 | 3.4 | 54.2 | 2.3 |
| Second lactation | | | | | | | | | | | | | | | | | | |
| 1/4 | 23 | 185 | 16 | 1299 | 192 | 50.6 | 7.1 | 44.7 | 5.9 | 30 | 232 | 24 | 1247 | 177 | 55.9 | 8.3 | 40.1 | 5.5 |
| 1/2 | 20 | 252 | 18 | 2384 | 209 | 98.5 | 7.8 | 77.4 | 6.4 | 38 | 308 | 22 | 2370 | 166 | 104.2 | 7.7 | 72.1 | 5.1 |
| 5/8 | 13 | 218 | 21 | 1648 | 249 | 56.5 | 9.3 | 51.3 | 7.7 | 17 | 252 | 33 | 1333 | 249 | 50.6 | 11.6 | 38.1 | 7.7 |
| 3/4 | 14 | 283 | 19 | 2807 | 229 | 100.0 | 8.5 | 85.7 | 7.1 | 26 | 272 | 28 | 1873 | 210 | 72.1 | 9.8 | 53.1 | 6.5 |
| 7/8 | 23 | 318 | 16 | 2919 | 193 | 99.9 | 7.2 | 87.3 | 6.0 | 23 | 305 | 30 | 1879 | 222 | 78.1 | 10.3 | 55.8 | 6.8 |
| HF | 14 | 315 | 19 | 3147 | 223 | 96.4 | 8.3 | 87.9 | 6.9 | 16 | 278 | 34 | 1566 | 252 | 58.3 | 11.7 | 45.4 | 7.8 |
| Mean | 107 | 261 | 9 | 2367 | 107 | 83.7 | 4.0 | 72.4 | 3.3 | 150 | 275 | 16 | 1711 | 123 | 69.8 | 5.7 | 50.8 | 3.8 |

[1]LL = Lactation length, MY = milk yield, FY = fat yield, PY = protein yield.

TABLE 5. Number of observations, least squares means (LSM), and standard errors for milk components.

| Crossbred group | n | High management %F LSM | %F SE | %P LSM | %P SE | n | Low management %F LSM | %F SE | %P LSM | %P SE |
|---|---|---|---|---|---|---|---|---|---|---|
| | | (%) | | | | | (%) | | | |
| | | | | | First lactation | | | | | |
| 1/4 | 25 | 3.90 | .12 | 3.40 | .05 | 44 | 4.58 | .10 | 3.39 | .04 |
| 1/2 | 21 | 4.40 | .14 | 3.36 | .06 | 57 | 4.30 | .08 | 3.16 | .03 |
| 5/8 | 15 | 3.44 | .15 | 3.12 | .06 | 41 | 3.97 | .10 | 3.07 | .04 |
| 3/4 | 15 | 4.00 | .15 | 3.16 | .07 | 51 | 4.16 | .09 | 3.10 | .04 |
| 7/8 | 24 | 3.61 | .12 | 2.97 | .05 | 42 | 3.97 | .10 | 3.06 | .05 |
| HF | 14 | 3.58 | .15 | 2.97 | .07 | 38 | 3.95 | .10 | 3.01 | .04 |
| Mean | 114 | 3.82 | .07 | 3.16 | .03 | 273 | 4.15 | .05 | 3.13 | .02 |
| | | | | | Second lactation | | | | | |
| 1/4 | 23 | 3.74 | .15 | 3.46 | .08 | 29 | 4.11 | .14 | 3.20 | .07 |
| 1/2 | 20 | 4.11 | .16 | 3.23 | .08 | 38 | 4.31 | .13 | 3.08 | .07 |
| 5/8 | 12 | 3.10 | .20 | 3.00 | .10 | 17 | 3.52 | .19 | 2.79 | .10 |
| 3/4 | 14 | 3.54 | .17 | 3.05 | .09 | 25 | 3.82 | .16 | 2.84 | .08 |
| 7/8 | 23 | 3.39 | .15 | 2.96 | .08 | 21 | 4.01 | .17 | 2.95 | .09 |
| HF | 14 | 3.06 | .17 | 2.81 | .09 | 15 | 3.78 | .20 | 2.92 | .10 |
| Mean | 106 | 3.49 | .08 | 3.09 | .04 | 145 | 3.92 | .09 | 2.96 | .05 |

%F = Percentage of fat, %P = percentage of protein.

day CI. Conversely, the 5/8 had excellent reproductive performance in the HM, which was not compensated by their poor MY, so the mean MY/CI for this group was very low. In the HM class, FY/CI and PY/CI were reduced with increased HF grade above 1/2 for the 3/4, 7/8, and HF in the first lactation, but in the second lactation, the four groups had similar performance. The HF-sired groups had smaller differences in MY/CI, FY/CI, and PY/CI among themselves than with 1/4 and 5/8 groups, which had lower means. In LM, the group means for those traits declined as q departed from 1/2, but 5/8 performance was as poor as for HF and only slightly better than for 1/4.

#### Genetic Models and Parameters

The F-values for extra variation due to fitting crossbred group classification effects, after regressions g and h, were significant for all first lactation traits but %P when observations from all groups were considered. However, when the 5/8 group observations were excluded, the extra variation became nonsignificant for all traits but LL and CI (Table 7). Thus, excepting those traits, model 1 fitted F1 and backcross data – but not inter se data – as well as model 2. The lack of fit of model 1 to inter se data indicates that other genetic effects in addition to average direct gene effects and dominance were present, that could not be detected in the restricted data subset, and must, therefore, have been confounded with gene and heterosis effects.

Estimates of gene and heterosis effects from F1 and backcross data are in Table 8. Estimates for MY, FY, and PY, and for these traits per day CI were significant, positive, and large. Thus, HF direct gene effects conferred a favorable performance ability for these traits, which was enhanced by heterosis from Zebu crossing. Estimates of gene effects for LL were also positive, large, and significant, but heterosis effect estimates for this trait were lower in second lactation. In spite of the good fit of model 1, estimates of MY and related traits for purebred Gu were very low or even negative, suggesting that the model could probably not be extrapolated below the 1/4 HF gene fraction.

Heterosis for %F was positive and significant in HM but not in LM, whereas estimates of gene effects for this trait tended to be negative and not significant (Table 8). All four estimates of gene effects for %P were negative,

TABLE 6. Number of observations, least squares means (LSM), and standard errors for calving interval (CI) and lactation traits per day CI.

| Crossbred group | High management | | | | | | | | | Low management | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | CI | | MY/CI[1] | | FY/CI | | PY/CI | | | CI | | MY/CI | | FY/CI | | PY/CI | |
| | n | LSM | SE | LSM | SE | LSM | SE | LSM | SE | n | LSM | SE | LSM | SE | LSM | SE | LSM | SE |
| | | (d) | | (kg/d) | | (g/d) | | | | | (d) | | (kg/d) | | (g/d) | | | |
| First lactation | | | | | | | | | | | | | | | | | | |
| 1/4 | 23 | 390 | 19 | 3.77 | .40 | 145 | 16 | 127 | 12 | 37 | 546 | 27 | 1.70 | .32 | 84 | 12 | 59 | 10 |
| 1/2 | 21 | 394 | 19 | 7.89 | .41 | 348 | 17 | 264 | 13 | 50 | 514 | 21 | 5.06 | .25 | 218 | 13 | 158 | 8 |
| 5/8 | 13 | 353 | 24 | 3.87 | .50 | 123 | 20 | 115 | 15 | 25 | 583 | 31 | 2.47 | .37 | 101 | 15 | 74 | 11 |
| 3/4 | 14 | 434 | 23 | 7.46 | .48 | 296 | 20 | 233 | 15 | 38 | 576 | 25 | 3.88 | .30 | 160 | 15 | 119 | 9 |
| 7/8 | 23 | 375 | 19 | 7.94 | .40 | 289 | 16 | 235 | 13 | 28 | 564 | 30 | 3.48 | .36 | 147 | 12 | 110 | 11 |
| HF | 14 | 464 | 21 | 7.01 | .45 | 246 | 18 | 206 | 14 | 22 | 584 | 33 | 2.33 | .39 | 93 | 14 | 72 | 12 |
| Mean | 108 | 402 | 12 | 6.32 | .26 | 241 | 11 | 197 | 8 | 200 | 561 | 15 | 3.15 | .17 | 134 | 7 | 99 | 5 |
| Second lactation | | | | | | | | | | | | | | | | | | |
| 1/4 | 20 | 389 | 15 | 3.57 | .47 | 137 | 20 | 120 | 15 | 18 | 440 | 29 | 2.99 | .52 | 135 | 22 | 97 | 16 |
| 1/2 | 19 | 404 | 15 | 6.43 | .49 | 267 | 20 | 210 | 15 | 28 | 435 | 23 | 5.87 | .42 | 243 | 17 | 175 | 13 |
| 5/8 | 11 | 364 | 20 | 5.40 | .63 | 180 | 26 | 167 | 20 | 12 | 459 | 36 | 3.69 | .65 | 152 | 27 | 113 | 20 |
| 3/4 | 13 | 370 | 17 | 7.89 | .54 | 282 | 23 | 239 | 17 | 17 | 427 | 31 | 4.67 | .55 | 181 | 23 | 128 | 17 |
| 7/8 | 21 | 408 | 15 | 7.46 | .47 | 249 | 20 | 223 | 15 | 14 | 475 | 34 | 5.11 | .62 | 207 | 26 | 148 | 19 |
| HF | 14 | 406 | 16 | 7.95 | .51 | 243 | 21 | 222 | 16 | 11 | 490 | 37 | 4.26 | .66 | 174 | 28 | 131 | 21 |
| Mean | 98 | 390 | 8 | 6.45 | .26 | 227 | 11 | 197 | 8 | 100 | 454 | 14 | 4.43 | .26 | 182 | 11 | 132 | 8 |

[1]MY = milk yield, FY = fat yield, PY = protein yield.

TABLE 7. Model 1 goodness of fit. F-values for extra variation due to fitting crossbred group classification after gene effect and heterosis effect regressions.

| Data set | df[1] | LL | MY | FY | PY | %F | %P | CI | MY/CI | FY/CI | PY/CI |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | First lactation | | | | | | | | | |
| F1, backcross and inter se | 6 | 6.55*** | 6.81*** | 9.60*** | 7.20*** | 3.06*** | 1.62 | 3.16*** | 6.70*** | 9.04*** | 7.76*** |
| (residual df) | | (323) | (323) | (323) | (323) | (307) | (307) | (233) | (233) | (233) | (233) |
| F1 and backcross only | 4 | 3.57*** | 1.90 | 1.82 | 1.95 | .76 | .67 | 3.42*** | 1.12 | .71 | .79 |
| (residual df) | | (266) | (266) | (266) | (266) | (254) | (254) | (198) | (198) | (198) | (198) |
| | | Second lactation | | | | | | | | | |
| F1, backcross and inter se | 6 | 1.23 | 2.16* | 2.68* | 2.28* | 2.92* | 1.90† | 1.29 | .98 | 1.39 | 1.06 |
| (residual df) | | (195) | (195) | (195) | (195) | (189) | (189) | (148) | (148) | (148) | (148) |
| F1 and backcross only | 4 | .77 | .27 | .65 | .50 | .64 | .59 | 1.24 | .61 | .67 | .80 |
| (residual df) | | (167) | (167) | (167) | (167) | (162) | (162) | (127) | (127) | (127) | (127) |

[1]Numerator df. LL = lactation length, MY = milk yield, FY = fat yield, PY = protein yield, %F = percentage fat, %P = percentage of protein, CI = calving interval.

†$P<.10$.

*$P<.05$.

**$P<.01$.

***$P<.005$.

while none of the heterosis effects estimates were significant. Thus, Zebu direct gene effects conferred better milk quality than HF genes, and heterosis was detected only for %F in HM.

Interactions of gene and heterosis effects × management were indicated by significant slope heterogeneity of those regressions in both management classes (Table 8). As might be expected, slope heterogeneity was significant ($P<.05$), or approached significance ($P<.10$), for traits displaying significant M × G interaction under model 2 (Table 8). Estimates of gene effects for MY, FY, and PY, and for these traits per day CI, were larger in HM than in LM (Table 8). Heterosis for LL, MY, FY, and PY, and for these traits per day of CI, tended to be higher in LM than in HM classes, but slope heterogeneity was generally not significant for these traits. Management × h interaction was also significant for first lactation %F and %P, for which heterosis effect estimates were positive in HM and negative in LM class. Although slopes could not be considered heterogeneous for several traits when measured in actual units, the absolute values for the ratios of heterosis effects to gene effects were consistently higher in the LM than in the HM class for all traits but %F and %P.

When deviations from model 1 predicted performance estimated from F1 and backcross data were analyzed under model 2, least squares means for several traits were significantly different from 0 for the 5/8 but not for other groups, except in the case of first LL (Table 9). Significant mean deviations for the 5/8 were negative and of large magnitude, indicating that inter se performance would be grossly overestimated by the additive-dominance model.

## DISCUSSION

Short lactations have long been recognized as a major problem for tropical milk production (23), although not always receiving adequate attention in the literature. The LL means in Table 4 indicate that the nature of this problem is different for European-type cattle (unable to sustain lactation under stressful husbandry conditions) than for high Zebu grades, which showed very short lactations at the better managed farms. Supporting evidence was found in two Brazilian HF × Gir herds milked without

TABLE 8. Regression estimates of breed additive difference (g, Holstein-Friesian minus Guzera), heterosis effects (h), and significance of heterogeneity of slopes within management class.

| Trait | High management | | | | | Low management | | | | | Slope heterogeneity | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | g | SE | h | SE | h/g | g | SE | h | SE | h/g | g | h |
| First lactation | | | | | | | | | | | | |
| LL,[1] d | 216*** | 35 | 78* | 30 | .36 | 134*** | 40 | 182*** | 33 | 1.36 | NS | * |
| MY, kg | 3140*** | 372 | 1532*** | 318 | .49 | 1719*** | 265 | 2262*** | 220 | 1.32 | *** | † |
| FY, kg | 127.1*** | 14.0 | 90.4*** | 12.0 | .71 | 58.0*** | 12.6 | 94.2*** | 10.4 | 1.63 | *** | NS |
| PY, kg | 90.4*** | 11.8 | 57.7*** | 10.1 | .64 | 46.3*** | 8.4 | 68.6*** | 7.0 | 1.48 | *** | NS |
| %F | .03 | .25 | .91*** | .22 | 29.48 | –.83*** | .19 | –.05 | .15 | .06 | *** | *** |
| %P | –.54*** | .11 | .16 | .10 | –.29 | –.58*** | .09 | –.13† | .07 | .23 | NS | * |
| CI, d | 33 | 38 | –21 | 32 | –.63 | 29 | 56 | –56 | 46 | –1.89 | NS | NS |
| MY/CI, kg/d | 7.79*** | .74 | 4.49*** | .62 | .58 | 4.33*** | .62 | 4.69*** | .50 | 1.08 | *** | NS |
| FY/CI, g/d | 312*** | 31 | 252*** | 25 | .81 | 160*** | 25 | 196*** | 21 | 1.23 | *** | † |
| PY/CI, g/d | 223*** | 23 | 164*** | 19 | .74 | 122*** | 19 | 141*** | 15 | 1.16 | *** | NS |
| Second lactation | | | | | | | | | | | | |
| LL, d | 211*** | 33 | 34 | 28 | .16 | 124* | 51 | 78† | 40 | .63 | NS | NS |
| MY, kg | 2940*** | 405 | 745* | 347 | .25 | 1473*** | 393 | 1450*** | 309 | .98 | * | NS |
| FY, kg | 96.6*** | 15.3 | 49.2*** | 13.1 | .51 | 52.2*** | 18.6 | 68.5*** | 14.6 | 1.31 | † | NS |
| PY, kg | 78.9*** | 12.5 | 28.4*** | 10.7 | .36 | 37.5*** | 12.1 | 43.2*** | 9.5 | 1.15 | * | NS |
| %F | –.29 | .32 | .86*** | .27 | –2.96 | –.15 | .32 | .49† | .25 | –3.20 | NS | NS |
| %P | –.85*** | .16 | –.03 | .14 | .03 | –.49*** | .16 | –.04 | .13 | .08 | NS | NS |
| CI, d | 22 | 32 | 5 | 27 | .25 | 17 | 70 | –44 | 50 | –2.57 | NS | NS |
| MY/CI, kg/d | 7.45*** | 1.00 | 2.31*** | .84 | .31 | 4.35*** | 1.23 | 3.70*** | .88 | .85 | † | NS |
| FY/CI, g/d | 244*** | 41 | 147*** | 35 | .60 | 158*** | 51 | 146*** | 36 | .92 | NS | NS |
| PY/CI, g/d | 204*** | 31 | 90*** | 26 | .44 | 112*** | 38 | 101*** | 27 | .90 | † | NS |

[1]LL = Lactation length, MY = milk yield, FY = fat yield, PY = protein yield, %F = fat percentage, %P = protein percentage, CI = calving interval.

†$P<.10$.

*$P<.05$.

**$P<.01$.

***$P<.005$.

TABLE 9. Mean differences between observed (Y) and predicted values ($\hat{Y}_1$) for the 5/8 inter se, in actual units ($\bar{d} = Y - \hat{Y}_1$) and relative to model 2 least squares means (LSM) for observed traits ($\bar{d}$/LSM).[1]

| | First lactation | | | | | | Second lactation | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | High[2] | | | Low | | | High | | | Low | | |
| Trait | $\bar{d}$ | SE | $\bar{d}$/LSM | $\bar{d}$ | SE | $\bar{d}$/LSM | $\bar{d}$ | SE | $\bar{d}$/LSM | $\bar{d}$ | SE | $\bar{d}$/LSM |
| LL,[3] d | −92*** | 19 | −.48 | −28 | 20 | −.10 | −49* | 21 | −.22 | −25 | 33 | −.10 |
| MY, kg | −1065*** | 205 | −.76 | −352** | 137 | −.25 | −784** | 249 | −.48 | −418† | 249 | −.31 |
| FY, kg | −50.3*** | 7.7 | −1.09 | −16.8** | 6.5 | −.28 | −30.9*** | 9.3 | −.55 | −22.2† | 11.6 | −.44 |
| PY, kg | −35.0*** | 6.5 | −.82 | −11.3** | 4.4 | −.25 | −23.5*** | 7.7 | −.46 | −14.6† | 7.7 | −.38 |
| %F | −.44*** | .15 | −.13 | −.28*** | .10 | −.07 | −.50* | .20 | −.16 | −.52** | .19 | −.15 |
| %P | −.06 | .06 | −.02 | −.09* | .04 | .02 | −.15 | .10 | −.05 | −.24* | .10 | −.09 |
| CI, d | −46† | 24 | −.13 | 24 | 31 | .04 | −27 | 20 | −.07 | 2 | 36 | .00 |
| MY/CI, kg/d | −2.65*** | .50 | −.68 | −.88* | .37 | −.36 | −1.05† | .63 | −.20 | −.72 | .65 | −.19 |
| FY/CI, g/d | −127*** | 20 | −1.03 | −45*** | 15 | −.45 | −49† | 26 | −.27 | −33 | 27 | −.22 |
| PY/CI, g/d | −88*** | 15 | −.77 | −33*** | 11 | −.45 | −30 | 20 | −.18 | −21 | 20 | −.17 |

[1] $\hat{Y}_1 = \hat{b}_0 + \hat{M}_i + (5/8)\,\hat{g}_i + (30/64)\,\hat{h}_i$, estimated under additive-dominance model 1, using only F1 and backcross data. $\bar{d}$ are 5/8 group means, estimated under model 2 using all data. LSM are in Tables 4 to 6.

[2] Management class.

[3] LL = Lactation length, MY = milk yield, FY = fat yield, PY = protein yield, %F = fat percentage, %P = protein percentage, CI = calving interval.

†$P<.10$.

*$P<.05$.

**$P<.01$.

***$P<.005$ for $t$ tests of $\bar{d} = 0$.

the presence of the calf (16). However, incidence of short lactations varies widely for populations reported in the literature (15). An examination of causes of termination of lactation records in HM indicated that 89.5% of lactations in the 1/4 group terminated either naturally or by forced drying off, because limiting low yield was attained before the 2 mo precalving resting period; in groups 1/2, 3/4, 7/8 and HF, the corresponding figure was between 36.6 and 44.8%, and in the 5/8 it was 72.4%. The depressing effect of pregnancy on milk yield is suspected to be more pronounced in Zebus than in European breeds (J. De Alba, personal communication), and, if so, pregnancy could be a cause for the relatively shorter lactations of Zebu cows on HM. This aspect will be examined in a further paper. Gestation could not interfere with lactation in LM, given the poor reproductive performance of cows in this class.

Variation between crossbred groups in LL has implications on data editing decisions. A preliminary study indicated that after deleting short lactations (LL<120 d), LL and correlated MY means of some groups were raised more than those of other groups. As a result, genetic and heterosis estimates for MY, FY, and PY were reduced from 12 to 19%. A similar effect was reported by De Alba and Kennedy (5). Madalena (16) showed that a downward bias in gene (or heterosis) effects estimates for MY would result from reducing variation in LL, if gene (or heterosis) effects for the latter trait were positive. Likewise, "abnormal" lactations were not deleted either, to prevent reducing genetic variation, because the frequencies of lactations terminated by loss of calf and cow illness, injury, or death were affected by crossbred group (18).

Local unselected sires were used because the trial aimed at the evaluation of crossbreeding effects unconfounded with selection, which may be superimposed to any crossbreeding program with predictable results from existing theory. Furthermore, there were no local selection programs when the trial started and it would have been unrealistic to assume that farmers would use expensive imported semen for crossbreeding. Estimates of gene and heterosis effects in Table 8 assume equal mean breeding value of the various generations involved to obtain the contemporary crossbred groups. Breeding values of sires in the last generation might conceivably have been different from breeding values of founder animals. Sampling does not appear to be a likely source of discrepancy, given the reasonable number of sires used, except for the 5/8 animals (13). In the absence of local improvement programs, only foreign selection permeating into the local HF sires could have caused some breeding value difference with founder sires. However, type and relationships with famous bulls have more weight in bulls and semen imports than production traits (17), so it does not seem likely that selection was important in crossbred group performance.

Milk yield PD (PDM) have recently become available for 15 HF bulls, siring 53.3% of the 1/2, 3/4, 7/8, and HF females in the present trial, and for six 5/8 bulls, siring 93.9% of the 5/8 females. Average PDM, weighted by number of progeny in this trial, was –2.1 kg for the HF bulls and 6.9 kg for the 5/8, and average repeatability was 74 and 59% (16). Although PDM cannot be compared across programs, these values indicate that both sire sets were representative of average Brazilian HF and crossbred sires in AI studs. The heavily used 5/8 bull had –15 kg PDM with 61% repeatability.

Previous Brazilian reports agree with present results when crossbred groups compared were in the same environmental conditions. The F1 had generally higher MY and shorter CI, but their superiority over higher European grades declined as the production level increased (14). At the higher level (MY $\cong$ 4000 kg and MY/CI $\cong$ 10 kg/d), performance of 3/4 and 7/8 Holstein × Gir crosses was practically equal to that of purebred Holstein (16). McDowell (20) estimated that differences in milk yield between European × Zebu crossbreds and Holsteins would be small at such production levels, whereas the Holsteins would exceed if higher energy intake allowed higher performance. Because the national average is 2.0 kg/cow per d, husbandry practices in Brazil would have to be substantially improved before Zebu genes would become a hindrance to milk production. However, given the important genotype × environment interactions observed, results should not be extrapolated beyond the limits of the management levels represented in the trial.

Vencovsky et al. (30) also found a very good fit of the additive-dominance model to milk yield data of Holstein-Friesian × Guzera crosses by purebred sires. They reported estimates of g = 799 kg and h = 620 kg. Martinez et al. (22) reported very low h estimates, but they used records intended for within farm selection, with unequal distribution of breeds and crosses over farms, years, and seasons (16). Their estimates may also have been biased downwards due to exclusion of short lactations and to adjustment for age at calving, which is influenced by crossbred group effects (28), and by failure to identify inter se groups.

Recent reviews of dairy cattle crossbreeding results in tropical countries agreed on the general superiority of F1 over other grades for milk yield and calving interval (4, 21). McDowell (21) stated that unless 3/4 crosses were well cared for, their performance would be poorer than that of F1. Cunningham and Syrstad (4) averaged results from several studies, reporting linear improvement of milk yield and calving interval with increasing European gene fraction, up to 1/2, and from then on, slight increase in calving interval and no clear trend in milk yield. Their average gene and heterosis estimates for milk yield are lower than those in Table 8, but the ratio of heterosis effects:gene effects was near .4.

Fat content decreased with increased European grade for HF and Brown Swiss crosses with Zebu, but not for Jersey crosses (4, 15). We are not aware of previous gene and heterosis effects estimates for %F and %P in Zebu × European breeds. Heterosis for %F has been small in Jersey × Criollo (5) and in crosses of temperate breeds (24, 29).

Rotational crosses should theoretically be expected to exceed the best breed performance for milk and component yield per day CI, for the ratio of heterosis effects:gene effects values shown in Table 8, particularly in LM (2). The higher ratio of heterosis effects:gene effects found in that management class agree with previous suggestions that heterosis is more important under stressful conditions (1, 3).

Drift may not be ruled out as a cause of discrepancy between model 1 expected and observed performance of the 5/8 cross, particularly in the HM, where only one sire was represented. Effective numbers of sires in the previous three generations were 10.0, 4.7, and 6.4 (13). Nonetheless, Table 9 $\bar{d}$ values are within the range of 20 to 60% decrease reported for milk yield of F2 in relation to F1 (21), except for first lactation in HM. The additive-dominance model has failed to account for poor inter se milk yield in the experiments reviewed by Cunningham and Syrstad (4), who listed, as possible discrepancy causes, selection effects, changes in management with time, differences in calf rearing methods, and breakdown of epistatic combinations. Only the latter cause would apply to the present trial. Sheridan (27) proposed a model of parental epistasis to explain lack of heterosis retention in crossbred generations past the F1. Hill (11) and Willham and Pollak (31) showed that this effect could be described in terms of additive × additive and dominance × dominance two loci interactions. Koch et al. (12) presented several examples where epistatic losses were not important in animals, but emphasized differences between traits and species in this respect. They indicated that long-term selection may increase the frequency of favorable combinations of nonallelic genes, which is an appealing hypothesis for the presence of additive × additive interactions in the present situation (10), given the different selection history of the HF and Gu breeds. However, the inclusion of additive × additive interactions in model 1 eliminated the discrepancy with model 2 fit only for second lactation data, but still left significant variation between crossbred groups unaccounted for in first lactation traits. Irrespective of the nature of the interactions involved, the present results suggest that the additive-dominance model is not appropriate to describe dairy performance of Holstein-Friesian × Zebu crosses.

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