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Germplasm Utilization in Beef Cattle

Keith E. Gregory, Larry V. Cundiff, Robert M. Koch, and Donald D. Lunstra[1]

Introduction

Heterosis achieved through continuous crossbreeding can be used to increase weight of calf weaned per cow exposed to breeding by 20%. Comprehensive programs of breed characterization have revealed large differences among breeds for most bioeconomic traits. About 55% of the U.S. beef breeding population involving 93% of the farmers and ranchers who produce beef cattle are in production units of 100 or fewer cows. Optimum crossbreeding systems are difficult to adapt in herds that use fewer than four bulls. Further, fluctuation in breed composition between generations in rotational crossbreeding systems can result in considerable variation among both cows and calves in level of performance for major bioeconomic traits unless breeds used in the rotation are similar in performance characteristics. Use of breeds with similar performance characteristics restricts the use that can be made of breed differences in average genetic merit to meet requirements for specific production - marketing situations. The potential of composite breeds as an alternative to continuous crossbreeding for using heterosis and for using genetic differences among breeds to achieve and maintain a more optimum additive genetic (breed) composition needed to be investigated in a comprehensive experiment. The primary objective of this experiment was to estimate the retention of combined individual and maternal heterosis in advanced generations of *inter sè* mated composite populations established with contributions from either four or five breeds. Retention of initial (F_1) heterozygosity after crossing and subsequent random (*inter sè*) mating within crosses is proportional to (n-1)/n when *n* breeds contribute equally to the foundation. When breeds used in the foundation of a composite breed do not contribute equally, percentage of mean F_1 heterozygosity retained is proportional to $1 - \sum_{i}^{n} P_i^2$, where P_i is the fraction of each of *n* contributing breeds to the foundation of a composite breed. This loss of heterozygosity occurs between the F_1 and F_2 generations, and if inbreeding is avoided, further loss of heterozygosity in *inter sè* mated populations does not occur. A primary question in this experiment was the extent to which retention of heterosis in composite populations is proportional to retention of heterozygosity.

Procedure

Populations. Matings were made to establish three composite populations (MARC I, MARC II, and MARC III) as indicated by Table 1. In this experiment the F1 is defined as the first generation that reflects the final breed composition of a composite population. As indicated by Table 1, F_1, F_2, and F_3 generations were mated *inter sè* to produce, respectively, F_2, F_3, and F_4 generation progeny. Composite populations were originally formed from the same sires and dams that were represented in the nine contributing parental breeds reflected by Table 1. The numbers of sires used and individuals born in each year for each contributing purebreed and for each generation of each composite population are provided by Table 2. Retained heterozygosity relative to F1 generation for different mating types and estimated increase in cow productivity assuming retained heterosis to be proportional to retained heterozygosity is shown in Table 3.

Contributing purebred contemporaries have been maintained for Pinzgauer since 1982 and for all other breeds produced in 1980, 7/8 Pinzgauer (purebred for female animals in breed registry) were produced in 1982, and 15/16 Pinzgauer (purebred for registry of male animals) have been produced since 1984. Pinzgauer females (7/8) producing (15/16) Pinzgauer progeny were included in the analyses.

The Braunvieh population averages between 3/4 and 7/8 Braunvieh and was established by using semen from nine Braunvieh sires originating in Switzerland and the Federal Republic of Germany (Bavaria) on a foundation of purebred (registered and unregistered) Brown Swiss cows. The cows were obtained from dairy herds in Wisconsin and Minnesota as calves in 1967 and 1968. The breed substitution from Brown Swiss to Braunvieh started in 1969. The Simmental, Limousin, Gelbvieh, and Pinzgauer populations were established by mating 20 or more sires of each breed to purebred dams from the same Hereford and Angus populations used in the experiment (except as noted) followed by repeated backcrossing to the four breeds of sire. Grade-up programs to these breeds started at the U.S. Meat Animal Research Center in 1969 for Simmental, in 1970 for Limousin, in 1975 for Gelbvieh, and in 1977 for Pinzgauer. A sample of 3/4 Gelbvieh dams bred to produce 7/8 Gelbvieh progeny was purchased to augment the Gelbvieh population in 1977. The females had been graded up from a female population of Charolais x Angus with the same sample of Gelbvieh sires used in the Gelbvieh grade-up program at the Research Center. The Charolais population was established primarily with the purchase of registered purebred Charolais dams in 1977 and was augmented by Charolais graded-up from an Angus x Hereford base at the Research Center starting in 1967. Charolais sires were sampled from a broad genetic base. The Red Poll population was established from registered dams purchased from several sources in 1966, 1967, and 1968 with sires sampled from a broad genetic base. The Hereford and Angus breeds have been maintained as closed populations (except as noted) since about 1960. A sample of Hereford sires and dams was added in 1966, but this sample did not produce any male progeny that were used to maintain the population. A sample of Angus sires was introduced in 1967 and 1968, but no male progeny produced from these matings were used to maintain the population. Sires used to maintain the purebred populations were descended from males and females used in the foundation of the composite population to which a purebreed contributed. The purebreds have been maintained as registered populations recorded in the appropriate Herd Book of a breed record society. The data included in this study represent the progeny of from 37 to 78 sires of each parental breed and 14 or more sires in each generation of each composite population (Table 2).

Mating Procedure. All yearling heifers were exposed by natural service to yearling bulls (except as noted) for a mating season of 42 days. Since 1987 in Limousin and 1988 in Herefords, bulls 2 or more yr old have been used on yearling

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heifers because of late puberty in both sexes of these breeds. Dams 2 or more yr old were mated by AI for 28 days followed by natural-service exposure for 28 days for a mating season of 56 days. More than 80% of sires have been used in 2 or more yr. From 1978 until 1984, the mating season for yearling heifers was from mid-May until late June and for dams 2 or more yr old was from the first of June until late July. Since 1985, the mating season for yearling heifers has been from late May until near mid-July and for dams 2 or more yr old has been from mid-June until near mid-August. This adjustment of about 2 wk in mating and calving season was made to allow greater synchrony of breeding and calving with nutritive and climatic environment. Nonpregnant animals were retained in all breed groups, unless they were nonpregnant in two successive years, until 1985. Since 1985, all nonpregnant animals have been removed each year from all breed groups. Nonperformance criteria, such as age, color, and extremes in skeletal size, have been used to remove excess cows to maintain population size for each breed group. No females have been removed from the project before exposure to breeding. An attempt has been made to maintain a similar age distribution of dams in each breed group. The F_4 generation of each composite population was removed from the experiment at an age of 1 yr because further loss of heterosis is not expected beyond F_3 generation progeny (Table 1). Genetic expectations for individual and maternal heterosis ($H^I + H^m$) for each generation of each composite population are presented in Table 1.

Dams in each breed group were assigned to sires on a stratified random basis within ages. Half-sib or closer matings were avoided.

The same basic criteria have been used to identify bulls for breeding use in all populations. The intent has been to avoid extremes in regard to weight, condition, and muscular and skeletal anatomy. Avoiding dystocia has been considered in identifying bulls for use in all breed groups. Larger scrotal circumference also has been favored, particularly in breeds that are late to reach puberty (i.e., Hereford and Limousin). Polledness and color patterns of red or red with white markings have been preferred for bulls used in all generations of each composite population. An effort was made to maintain a broad pedigree base in all breed groups. Genetic defects in some breed groups (i.e., "double muscling" in Gelbvieh, MARC I, and MARC II; "parrot mouth" in Gelbvieh and Braunvieh; malocclusion in Hereford, Angus, and Simmental; hydrocephalus in Red Poll and MARC III; and ataxia in Simmental) resulted in some compromise of pedigree breadth by avoiding carriers or close relatives of carriers.

Management of Heifers and Cows. Generally, female populations were fed and managed consistent with their requirements to maintain breed groups in similar condition. The general plan was to group females in three fully integrated management units under the day-to-day supervision of an operations coordinator who had operational responsibility for this project. When a composite population and its contributing parental breeds had similar feed and management requirements they were grouped and managed together: all generations of composite MARC I and Braunvieh, Charolais, and Limousin (Management Group 1); all generations of composite MARC II and Simmental, Gelbvieh, and Pinzgauer (Management Group 2); and all generations of composite MARC III and Hereford, Angus, and Red Poll (Management Group 3). The only deviation from this practice was during the 28-day natural service mating season when all dams were in single-sire mating pastures. The Pinzgauer females were managed with composite MARC II for two reasons: the three management groups had to contain similar numbers of animals and the feed and management requirements of Pinzgauer females are similar to those of Simmental and Gelbvieh. Even though the populations were grouped in the three management groups, efforts were made to apply uniform management protocols among the three units. Types of improved pastures (cool- and warm-season grasses), winter feeding programs, and all basic management practices were the same and were provided consistent with requirements. The sites were contiguous and were without boundaries (i.e., different management groups used the same pastures at different times). All groups received the same feed but the amounts were varied to be consistent with requirements.

Two-year-old dams were fed a mixture of corn silage and alfalfa haylage along with alfalfa and grass hay, starting from 2 to 3 mo before calving and continuing until pastures were adequate to meet their requirements, which was usually in mid- to late April. All older females were fed mixtures of alfalfa and grass hay to meet nutritive requirements, usually from November until mid- to late April. After 1986, economic considerations favored feeding these animals limited quantities of corn silage and alfalfa haylage during winter feeding.

Feeding Young Heifers and Young Bulls. Calves were weaned at an average age of 180 days. Mean birth date was April 7 and calves were weaned the first week of October in most years. After an adjustment feeding period (28 days), heifers were fed diets composed of corn silage, alfalfa haylage, and protein-mineral- vitamin supplement in varying proportions and lengths of time, depending on weather conditions and weight gains of heifers: 1) Period 1, 2.34 Mcal of ME/kg of DM, 11.62% CP; 2) Period 2, 2.24 Mcal of ME/kg of DM, 12.34% CP; and 3) Period 3, 2.18 Mcal of ME/kg of DM, 11.70% CP. Heifers were fed these diets until they were placed on improved cool-season grass pasture from mid- to late April, depending on adequacy to meet nutritive requirements. The three time periods were of approximately equal length. After an adjustment period of 28 days after weaning, intact males were fed a diet composed of corn silage, rolled corn, and protein-mineral-vitamin supplement (2.69 Mcal ME/kg of DM, 12.88% CP) for 140 days.

Data Collection. Calves were weighed at birth, at the middle of the breeding season (end of AI mating period), at weaning, and 28, 84, 140, and 168 days postweaning. Yearling heifers were weighed at the beginning and end of the mating season and when they were palpated for pregnancy. Thereafter, female animals were weighed, measured for height, and scored for condition three times each year (before calving, at the start of the breeding season, and when they were palpated for pregnancy in late October and early November). Observations of estrus were made in yearling heifers starting about March 1 and continuing until the start of the mating season. Yearling heifers were palpated for pregnancy determination per rectum about 2 mo after the end of the mating season and animals 2 or more yr old were palpated about 1 mo after calves were weaned.

Calving difficulty was subjectively evaluated using descriptive scores; i.e., 1 = no difficulty, 2 = little difficulty by hand, 3 = little difficulty with calf jack, 4 = slight difficulty with a calf jack, 5 = moderate difficulty with calf jack, 6 = major difficulty with calf jack, 7 = caesarean birth and 8 = abnormal presentation. Percentage calving difficulty was analyzed (scores 1 and 2 = 0; scores 3, 4, 5, 6 and 7 = 1; and scores of 8 were excluded from analyses). Scores of 8 also were excluded from analysis of calving difficulty score.

Analysis of Data. Data were analyzed by least squares mixed model procedures. The models included the fixed effects of breed group, year, age of dam, and other fixed effects as appropriate. Sire within breed group was included in all models for analysis of all traits as a random effect. Linear functions of means for parental breeds and for each generation of each composite population were computed to estimate retained heterosis. Retained heterosis was estimated from the mean of a composite population minus the mean of the contributing purebreeds weighted by their contribution (1/4 or 1/8) to the composite population. Sire within breed group mean square was used as the error term for linear contrasts to estimate retained heterosis effects.

Results

Heterosis for Growth Traits in Both Sexes. Heterosis effects for birth weight, 200-day weight, 368-day weight, 368-day height, 368-day condition score and 368-day muscling score (males only) were evaluated separately for each sex in F_1, F_2 and combined F_3 and F_4 generations in the three composite populations (Tables 4 and 5). Combined individual and maternal heterosis was significant in the F_1, F_2 and combined F_3 and F_4 generations for each composite population and for the mean of the three composite populations in both sexes for most of the traits evaluated. There was little reduction in heterosis between the F_1 and F_2 generations or between the F_2 generation and the combined F_3 and F_4 generations. In both sexes, mean heterosis retained in combined F_3 and F_4 generations was significantly greater than genetic expectation based on retained heterozygosity for birth weight and for 368-day weight, but did not differ ($P > .05$) from genetic expectation for other traits. These results support the hypothesis that heterosis in cattle for traits related to growth and size is due to dominance effects of genes (Tables 4 and 5).

Heterosis for Puberty Traits in Females and Scrotal Traits of Males. Heterosis effects were evaluated in F_1, F_2, and F_3 generations of females and in the F_1, F_2 and combined F_3 and F_4 generations of males in the three composite populations. Traits included percentage of females reaching puberty at 368, 410, and 452 days, adjusted age, and adjusted weight at puberty and scrotal circumference of males (Table 6). Heterosis was significant for most measures of puberty in each generation of each composite population and for the mean of the three composite populations. Although results are not presented, heterosis for age at puberty was largely independent of heterosis effects on 368-day weight.

Heterosis was significant for scrotal circumference in each generation of each composite population and for the mean of the three composite populations. Heterosis effects on scrotal circumference are mediated both through heterosis effects on growth rate and through factors that are independent of growth rate. There was close agreement in heterosis observed for puberty traits in females and for scrotal circumference in males and genetic expectation based on retained heterozygosity. These results support the hypothesis that puberty traits in females and scrotal circumference in males is due to dominance effects of genes (Table 6).

Heterosis for Birth Weight, Birth Date, Dystocia and Survival as Traits of Dam. Heterosis effects were evaluated as traits of the dam in F_2 progeny of F_1 dams and combined F_3 and F_4 progeny of combined F_2 and F_3 dams in the three composite populations. Traits included birth weight, birth date (Julian), percentage calving difficulty, and percentage survival at birth, 72 hr, and at weaning (Table 7). Effects of heterosis were significant for birth weight for each generation of each composite population and for the mean of the three composite populations. Generally, heterosis effects for percentage calving difficulty were not significant. Effects of heterosis were significant for date of birth (earlier) for each generation of each composite population and for the mean of the three composite populations. Heterosis effects on percentage survival to weaning were positive but generally were not significant. Heterosis retained for birth weight, birth date, and percentage survival in combined F_3 and F_4 generation progeny of combined F_2 and F_3 generation dams did not differ ($P > .05$) from expectation based on retained heterozygosity. These results support the hypothesis that heterosis in cattle for these traits is the result of dominance effects of genes (Table 7).

Heterosis for Reproduction and Maternal Traits. Heterosis effects in F_1 generation dams producing F_2 generation progeny and retained heterosis in combined F_2 and F_3 generation dams producing F_3 and F_4 generation progeny were evaluated. Traits included percentage pregnant, percentage calf crop born, percentage calf crop weaned, 200-day calf weight per female exposed, and 200-day calf weight (Table 8). Also, breed group means and estimates of heterosis of calf crop born based on females palpated pregnant are presented in Tables 9 and 10. Heterosis effects were significant for all traits in F_1 generation females producing F_2 generation progeny for each composite population and for the mean of the three composite populations (Table 8). For 200-day calf weight, heterosis effects were significant for all generations of each composite population and for the mean of the three composite populations. For 200-day calf weight, heterosis retained for the composite MARC II population and for the mean of the three composite populations was greater ($P < .01$) than genetic expectation based on retained heterozygosity.

Heterosis effects for reproductive traits in F_1 generation dams producing F_2 generation progeny were less in composite populations MARC II and MARC III than in composite population MARC I. In composite populations MARC I and MARC II, heterosis retained for reproductive traits in combined F_2 and F_3 generation dams producing F_3 and F4 progeny did not differ from genetic expectation based on retained heterozygosity. In composite population MARC III, loss of heterosis for reproductive traits, other than percentage pregnant, between F_1 generation dams producing F_2 generation progeny and combined F_2 and F_3 generation dams producing F_3 and F_4 generation progeny, was greater than genetic expectation based on retained heterozygosity (Table 8). This greater heterosis loss than genetic expectation for reproductive traits based on retained heterozygosity in composite population MARC III was the result of increased fetal death loss between pregnancy diagnosis and parturition (Tables 9 and 10).

In another major experiment involving Angus, Hereford and Shorthorn, we did not find any evidence of individual heterosis (H^I) for either embryonic or fetal survival but did find that maternal heterosis (H^m) was important for early embryonic survival but not for fetal survival between pregnancy diagnosis and parturition. Results from this experiment do not indicate an effect of heterosis in either the F_1 generation or the combined F_2 and F_3 generations for fetal survival between pregnancy diagnosis and parturition in composite populations MARC I and MARC II (Table 10). Negative recombination effects are suggested for fetal survival between pregnancy diagnosis and parturition in F_1 generation dams 5 or more yr old and in combined F_2 and F_3 generation dams for the three age groups (Table 10).

For composite population MARC III, the F_1 generation as defined in this experiment was produced by reciprocally crossing two single crosses (Table 1). One-half of any losses from the negative effects of recombination of genes are expected in the F_1 generation as defined in this experiment. The negative effects of recombination of genes are generally considered in the context of assumed heterosis. However, negative effects of recombination of genes in descendants of crosses result from loss of favorable epistatic gene combinations that have accumulated and are maintained by either deliberate or natural selection in a parental purebreed. Thus, the presence of heterosis is not required to explain decreased performance in descendants of crosses of parental purebreeds when favorable epistatic gene combinations contribute to the performance of the parental breed(s). These results suggest that combinations of genes with favorable epistatic effects on fetal survival have evolved in either the Red Poll or Pinzgauer breed or possibly both. These combinations are distinctly different from those that have evolved in Hereford, Angus, or other breeds that contributed to composite MARC I or MARC II. The basis for this suggestion is that the Hereford and Angus breeds contribute to all three composite populations, whereas, the Red Poll and Pinzgauer breeds contribute only to composite MARC III.

For composite populations MARC I and MARC II, these results support the hypothesis that heterosis for reproductive and maternal traits in cattle is the result of dominance effects of genes. The same conclusion can be made for maternal traits in composite MARC III (e.g., 200-day calf weight). However, in composite population MARC III these results suggest that favorable epistatic gene combinations contribute to fetal survival between pregnancy diagnosis and parturition in either the Red Poll or Pinzgauer purebreeds, or possibly in both. Evidence suggests that these favorable epistatic gene combinations are recombined in a manner that does not result in a favorable effect on fetal survival in crosses and subsequent *inter sè* matings involving these breeds.

Heterosis on Actual Weight, Adjusted Weight, Hip Height, and Condition Score in Females. Heterosis effects were evaluated in the three composite populations in F_1, F_2 and F_3 generations separately and combined. Because heterosis did not differ ($P > .05$) between generations, only the results from the analysis of combined (F_1, F_2, and F_3) generations from two through seven or more yr old females are presented. Traits included actual weight, weight adjusted to a common condition score, hip height, and condition score (Table 11). The effects of heterosis were generally important ($P < .05$) for all traits in F_1, F_2, and F_3 generations separately and combined in the three composite populations. Although the estimates of heterosis on these traits in one-yr-old females are not presented, generally the magnitude of heterosis observed at one year did not differ from that observed in females from two through seven or more yr old. Thus, heterosis effects on weight did not change after an age of one yr. Adjusting weight to a common condition score resulted in an average reduction of heterosis effects on actual weight by about one-fourth. Thus, about one-fourth of the effects of heterosis on weight results from heterosis effects on condition score. Although estimates of heterosis are not presented separately for each of the three generations of either one-yr-old females or from two through seven or more yr old females of the three composite populations and from the mean of the three composite populations, retained heterosis in the F_3 generation did not differ ($P > .05$) from genetic expectation based on retained heterozygosity. These results support the hypothesis that heterosis for weight, hip height, and condition score of females is the result of dominance effects of genes.

Retained Heterosis for Milk Yield and 200-Day Weight. Retained heterosis in F2 generation females nursing F_3 generation progeny was evaluated in three-, four-, and five or more yr old females. Traits evaluated included 12-hr milk yield, estimated 200-day milk yield, 200-day weight of progeny, and 200-day weight of progeny adjusted to a common estimated milk yield (Table 12). Milk yield was estimated using the weigh/nurse/weigh procedure at intervals of 5 wk when calf age averaged 8, 13, and 18 wk. The effects of heterosis on milk yield were significant for each of the composite populations. Average effects of retained heterosis for the three composite populations on 12-hr milk yield was 1.48 lb (14.5%) and on 200-day weight was 34 lb (6.9%). Adjusting 200-day weight of progeny to a common estimated 200-day milk yield resulted in mean retained heterosis in the three composite populations of 14 lb suggesting that approximately 59% of the retained heterosis effects observed for 200-day weight of progeny was accounted for through retained heterosis effects on milk yield.

Genetic and Phenotypic Variation. Estimates of heritability (h^2) and their standard errors and phenotypic standard deviations (σ_p) were computed separately for purebreds combined and for composite populations combined for all traits evaluated. Estimates of h^2 were computed using the sire within breed-component of variance. Phenotypic standard deviations were computed by extracting the square root of the sum of the between and within sire components of variance. Generally, the differences between purebreds combined and composite populations combined were small and were not consistent for estimates of both h^2 and σ_p. There was no tendency for h^2's or σ_p to be greater for composite populations combined than for contributing purebreeds combined. Thus, greater genetic and phenotypic variation expected for composite populations combined than for purebreeds combined was not observed.

Composite Breed Formation

Concepts and Considerations. The distribution of numbers by herd size in the U.S. beef breeding herd is as follows: 35% represented by herds of 50 cows or fewer; 55% represented by herds of 100 cows or fewer, and 87% represented by herds of 500 cows or fewer. Further, of farms and ranches that have beef cows, 80% have 50 cows or fewer, 93% have 100 cows or fewer and more than 99% have 500 cows or fewer.

With 55% of the U.S. beef breeding herd and 93% of the farms and ranches that have beef cows represented by units of 100 cows or fewer, there are obvious limitations on feasible options for optimum crossbreeding systems. The limitations are most significant if female replacements are produced within the herd and natural service breeding is used. Further, fluctuation between generations in additive genetic (breed) composition in breed-rotation crossbreeding systems restricts the extent to which breed differences in average additive genetic merit for specific characters can be used to match climatic adaptability and performance characteristics to the climatic and nutritive environment and other resources that may be most economical to provide. Thus, the formation of composite breeds based on a multibreed foundation is an attractive alternative, or supplement, to continuous crossbreeding systems to use high levels of heterosis on a continuing basis. Once a new composite breed is formed, it can be managed as a straightbred population, and the management problems that are associated with small herd size and with fluctuations between generations in additive genetic (breed) composition in rotational crossing systems are avoided provided there is a source of seedstock (bulls) of the composite breed desired.

Retention of initial heterozygosity after crossing and subsequent random (*inter sè*) mating within the crosses is proportional to (n-1)/n, where *n* is the number of breeds involved in the cross. This loss in heterozygosity occurs between the F_1 and F_2 generations. If inbreeding is avoided, further loss of heterozygosity in an *inter sè* mated composite population does *not* occur. This expression [i.e., (n-1)/n] assumes equal contribution of each breed used in the foundation of a composite breed. Where the breeds used in the foundation of a composite breed do not contribute equally, percentage of mean F_1 heterozygosity retained is proportional to $1 - \sum_{i}^{n} P^2_i$, where P_i is the fraction of each of *n* breeds contributing to the foundation of a composite breed, e.g., heterozygosity retained in a three-breed composite formed from 3/8 breed A, 3/8 breed B and 1/4 breed C can be computed as $1 - [(3/8)^2 + (3/8)^2 + (1/4)^2] =$ 65.6%. Obviously, the maximum number of breeds that can be used to contribute to achieving an optimum additive genetic (breed) composition is preferred because retention of heterozygosity is a function of the number of breeds included in the foundation [i.e., (n-1)/n]. However, use of a greater number of contributing breeds should be balanced against the potential loss in average genetic merit of including the additional breeds. Table 3 provides information on level of heterozygosity relative to the F_1 that is retained after equilibrium is reached for two-, three- and four-breed rotation crossbreeding systems and is presented for two-, three-, four-, five-, six-, seven- and eight-breed composites, with breeds contributing in different proportions in several of the composites. Estimates of increase in weight produced per cow exposed to breeding, based on the assumption that retention of heterosis is approximately proportional to retention of heterozygosity, are presented in Table 3 for each mating type.

Existing breeds of cattle are mildly inbred lines, and because heterosis seems to result primarily from the dominance effects of genes, heterosis can be accounted for as recovery of accumulated inbreeding depression that has occurred in breeds since their formation. Deviation of heterosis from linear association with heterozygosity results from epistatic effects of genes. For loss of favorable epistatic combinations that may either have become fixed or are maintained by either natural or deliberate selection in parental breeds, the deviation from linearity of loss in heterosis with loss in heterozygosity is negative (greater). However, for loss of unfavorable epistatic combinations that may have become fixed through chance, the deviation from linearity of loss in heterosis with loss in heterozygosity obviously is likely to be positive (less). Both genetic situations may exist, but the likelihood is greater for favorable than for unfavorable epistatic combinations in parental breeds, particularily for fitness traits. Also, heterosis may deviate from heterozygosity in a positive direction if a threshold effect (nonlinear) of heterozygosity relative to heterosis should exist.

Other than for characters affected by natural or automatic selection (i.e., fitness), the likelihood is small that fixed favorable epistatic combinations are important because of changing selection goals that have characterized beef cattle breeding.

Because retention of heterosis is, generally, linearly associated with retention of heterozygosity, composite breed formation offers much of the same opportunity as rotational crossbreeding for retaining individual and maternal heterosis, in addition to heterosis in male reproductive performance (Table 3). Further, composite breeds offer the opportunity to use genetic differences among breeds to achieve and maintain the performance level for such traits as climatic adaptability, growth rate and size, carcass composition, milk production, and age at puberty that is optimum for each of a wide range of production environments and to meet different market requirements. Further, composite breeds provide herds of any size with an opportunity to use heterosis and breed differences simultaneously.

A specific composite breed does not permit the use of different genotypes (complementarity) for male and female parents. However, specialized paternal and maternal composite breeds may be developed for use in production systems in which the production resource base and market requirements favor the exploitation of complementarity. Between-breed selection is highly effective for achieving and maintaining an optimum additive genetic composition (performance level) for such specialized breeds by using several breeds to contribute to the foundation population for each specialized composite breed. There is opportunity to develop general purpose composite breeds through careful selection of fully characterized candidate breeds to achieve an additive genetic (breed) composition that is better adapted to the production situation than is feasible through continuous crossbreeding or through intrabreed selection.

The maintenance of effective population size sufficiently large that the initial advantage of increased heterozygosity is not dissipated by re-inbreeding is essential for retention of heterozygosity (heterosis) in composite breeds. *Thus, the resource requirement for development and use of composite breeds as seedstock herds is high, and from an industry standpoint requires a highly viable and creative seedstock segment.* Early re-inbreeding and a small number of inadequately characterized parental breeds contributing to the foundation of composite breeds have likely been major causes for limited success of some previous efforts at composite breed development.

For the seedstock segment that develops composite breeds, it is suggested that the number of females be appropriate for the use of not less than 25 sires per generation. Use of 25 sires per generation would result in a rate of increase in inbreeding of about .5% per generation. With an average generation interval of 5 years, the accumulated inbreeding in a composite breed after 50 years (e.g., 10 generations) would be about 5%. Further, a large number of sires (i.e., 15-20) of each purebreed contributing to a composite breed should be sampled in order to minimize the rate of inbreeding in subsequent generations of *inter sè* mating. Because some of the foundation sires used from each contributing breed are not likely to leave sons, the genetic base will likely be reduced in the first generation. *Inbreeding may be viewed as the "other side of the coin" to heterosis and must be avoided in order to retain high levels of heterozygosity (heterosis) in composite breeds.*

The development of composite breeds may now be viewed as a predictable procedure when contributions are limited to *Bos taurus* breeds. However, because of the dynamic nature of the beef cattle industry, characterization of candidate breeds is needed on a continuing basis in a range of production environments. This information is needed to provide the basis for effective choices of contributing breeds in order to approach the most favorable additive genetic (breed) composition consistent with the role perceived for each composite. *The most appropriate source of this information should be records from perfor-*

mance programs of breed associations that will provide estimates of breed means for major bioeconomic traits on a continuing basis.

Heterosis in crosses of *Bos indicus* breeds with *Bos taurus* breeds is considerably greater (perhaps two fold) than crosses among *Bos taurus* breeds. We do not believe that results from composite populations with contributions limited to *Bos taurus* breeds in regard to linearity of association of heterosis with heterozygosity should be extrapolated to composite breeds that have contributions from both *Bos taurus* and *Bos indicus* breeds. Rather, we believe that a large scale, comprehensive experiment is needed to estimate retention of heterosis in advanced generations of *inter sè* mated composite populations with contributions from both *Bos taurus* and *Bos indicus* breeds.

SUMMARY

Rationale for Development of Composite Breeds

1. Heterosis (hybrid vigor) for major bioeconomic traits including reproduction, calf survival, maternal ability, growth rate and longevity of beef cattle is important. Heterosis can be used to increase weight of calf weaned per cow exposed to breeding by 20%.

2. Large differences exist among breeds of beef cattle for major bioeconomic traits including growth rate and size, composition of gain, milk production, dystocia, (calving difficulty), age at puberty and climatic and nutritive adaptability.

3. About 55% of the cows in U.S. beef breeding herd are in units of 100 or fewer cows. This involves about 93% of the farms and ranches that have beef cows.

4. Crossbreeding systems may be used to achieve high levels of heterosis. However, optimum crossbreeding systems are difficult to adapt in herds that use fewer than four bulls.

5. Fluctuation in breed composition between generations in rotation crossbreeding systems can result in considerable variation among cows and calves in level of performance for major bioeconomic traits unless breeds used in the rotation are similar in performance characteristics.

6. Use of breeds with similar performance characteristics restricts the use that can be made of breed differences in average genetic merit for bioeconomic traits. This includes traits such as: (a) growth rate and size, (b) carcass composition, (c) milk yield, and (d) age at puberty.

7. Composite breeds offer opportunity to: (a) use high levels of heterosis on a continuing basis if population size in seedstock herds is sufficiently large to avoid inbreeding, (b) achieve and maintain optimum breed (additive genetic) composition needed to match performance characteristics of the composite breeds to each of a wide range of production situations and to different market requirements, and (c) achieve and maintain uniform performance levels from one generation to the next.

Conclusions from Experimental Results

1. Generally, high levels of heterosis were observed for growth rate, reproduction, and maternal traits including milk production.

2. Heterosis differed among composite populations for some major bioeconomic traits. Results suggest that specific cross heterosis may be important, i.e., level of heterosis for some traits may vary among specific breed crosses.

3. Generally, retained heterosis in advanced generations was equal to, or greater, than expectation based on retained heterozygosity in the three composite populations. Retained heterosis for reproductive traits did not differ from genetic expectation based on retained heterozygosity in composites MARC I and MARC II. There was no heterosis (individual and maternal combined) for fetal survival in composites MARC I and MARC II.

4. Fetal survival between pregnancy diagnosis and calving was less for composite MARC III than for the average of contributing purebreeds. For composite MARC III results suggest that combinations of genes with favorable epistatic effects on fetal survival have evolved in either the Red Poll or the Pinzgauer breed, or possibly in both, that are distinctly different from those that have evolved in Hereford, Angus or the other breeds that contributed to composites MARC I or MARC II. The basis for this suggestion is that the Hereford and Angus breeds contributed to all three composite populations, whereas, the Red Poll and Pinzgauer breeds contributed only to composite MARC III.

5. Results suggest that although there is, generally, a high relationship between retained heterosis and retained heterozygosity the relationship is not linear for all situations; i.e., for some traits and in some breed combinations, retained heterosis *may be greater* or *may be less* than expectation based on retained heterozygosity.

6. Even though results suggest that specific cross heterosis may be of some importance, it is not feasible to have estimates of F_1 heterosis and of heterosis retained in advanced generations of a large number of specific breed combinations in order to choose breeds as contributors to specific composite populations (breeds). Thus, use of *average* values of F_1 heterosis and of retained heterosis in advanced generations of *inter sè* mated composite populations is suggested.

7. These results, generally, support the hypothesis that heterosis in cattle is primarily due to dominance effects of genes. Thus, heterosis in breed crosses can be accounted for as recovery of accumulated inbreeding depression that has occurred in breeds since their formation.

8. Estimates of heritability and phenotypic standard deviations were similar for parental purebreeds combined and for composite populations combined for most bioeconomic traits. Thus, increased genetic variation that may be expected in composite populations relative to contributing purebreeds was not observed.

9. Composite populations (breeds) offer an alternative breeding system that is *generally* competitive with crossbreeding for using heterosis and is easier to manage regardless of size of herd.

10. Composite populations (breeds) offer a procedure that is more effective than continuous crossbreeding for

using genetic differences among breeds to achieve and maintain *optimum* performance levels for major bioeconomic traits on a continuing basis. This includes traits such as: (a) growth rate and size, (b) composition of gain, (c) milk production, (d) climatic and nutritive adaptability, and (e) age at puberty.

For greater detail see:

1. Keith E. Gregory, L. V. Cundiff, and R. M. Koch. 1991. Breed effects and heterosis in advanced generations of composite populations for preweaning traits of beef cattle. J. Anim. Sci. 69:947.
2. Keith E. Gregory, L. V. Cundiff, and R. M. Koch. 1991. Breed effects and heterosis in advanced generations of composite populations for growth traits in both sexes of beef cattle. J. Anim. Sci. 69:3202.
3. Keith E. Gregory, D. D. Lunstra, L. V. Cundiff, and R. M. Koch. 1991. Breed effects and heterosis in advanced generations of composite populations for puberty and scrotal traits of beef cattle. J. Anim. Sci. 69:2795.
4. Keith E. Gregory, L. V. Cundiff, and R. M. Koch. 1991. Breed effects and heterosis in advanced gen birth weight, birth date, dystocia, and survival as traits of dam in beef cattle. J. Anim. Sci. 69:3574.
5. Keith E. Gregory, L. V. Cundiff, and R. M. Koch. 1992. Breed effects and heterosis in advanced generations of composite populations for reproduction and maternal traits of beef cattle. J. Anim. Sci. 70:656.
6. Keith E. Gregory, L. V. Cundiff, and R. M. Koch. 1992. Breed effects and heterosis in advanced generations of composite populations on actual weight, adjusted weight, hip height, and condition score of beef cows. J. Anim. Sci. 70:1742.
7. Keith E. Gregory, L. V. Cundiff, and R. M. Koch. 1992. Effects of breed and retained heterosis on milk yield and 200-day weight in advanced generations of composite populations of beef cattle. J. Anim. Sci. 70:2366.

Table 1—Matings to establish composites, retention of heterozygosity and expected retention of heterosis

			Composite Populations			
	Dam	Progeny	MARC I	MARC II	MARC III	Mean
Parents of F_1 generation[a]			(C x LH) x (B x LA) OR (C x LA) x (B x LH) Reciprocals	(GH) x (SA) OR (GA) x (SH)	(PA) x (RH) OR (PA) x (HR) Reciprocals	
Breed composition of F_1 and subsequent generations			.25B, .25C, .25L .125H, .125A	.25G, .25S .25H, .25A	.25P. .25R .25H, .25A	
F_1 Heterozygosity[b]			.94[d]	1	1	.98
F_2 Heterozygosity			.78	.75	.75	.76
F_3 Heterozygosity			.78	.75	.75	.76
Heterosis[c]	F_1	F_2	$.78 H^i + .94 H^m$	$.75 H^i + 1 H^m$	$.75 H^i + 1 H^m$	$.76 H^i + .98 H^m$
Heterosis	F_2	F_3	$.78 H^i + .78 H^m$	$.75 H^i + .75 H^m$	$.75 H^i + .75 H^m$	$.76 H^i + .76 H^m$
Heterosis	F_3	F_4	$.78 H^i + .78 H^m$	$.75 H^i + .75 H^m$	$.75 H^i + .75 H^m$	$.76 H^i + .76 H^m$

[a] Composite populations were established from same animals used in purebred foundation where C = Charolais, L = Limousin, H = Hereford, B = Braunvieh, A = Angus, G = Gelbvieh, S = Simmental, P = Pinzgauer, and R = Red Poll.

[b] Retention of initial (F_1) heterozygosity following crossing and subsequent random mating within the crosses (*inter sè*) is proportional to 1 - $\sum_{i}^{n}$ P2i, where P_i is the fraction of each of *n* breeds contributing to the foundation of a composite population. Loss of heterozygosity occurs between the F_1 and F_2 generations. If inbreeding is avoided, further loss of heterozygosity does not occur.

[c] H^i denotes individual heterosis expressed by progeny of a given generation and H^m denotes maternal heterosis expressed by their dams assuming that retention of heterosis is proportional to retention of heterozygosity. F_2 progeny express the maternal heterosis (H^m) of their F_1 dam.

[d] .94 instead of 1 because both sires and dams of F_1 generation were one-fourth Limousin.

Table 2—Number of sires used and individuals born by birth year and breed group

Breed group	Number sires	Number indiv. born	Year of birth 1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991
Red Poll	51	1,322	47	129	109	114	110	109	109	88	80	84	84	87	87	85
Hereford	68	1,491	142	114	101	118	116	109	113	93	100	104	104	102	102	73
Angus	78	2,076	168	167	227	234	216	225	225	98	85	86	86	84	88	87
Limousin	56	1,478	86	127	117	115	117	121	107	99	106	98	105	96	104	80
Braunvieh	58	1,384	105	107	114	112	115	117	114	95	84	81	85	84	86	85
Pinzgauer	37	816					17	72	115	134	78	75	74	76	86	89
Gelbvieh	51	1,214	19	26	50	93	137	163	116	89	90	89	86	85	84	87
Simmental	67	1,410	145	117	111	110	116	113	111	90	88	80	82	82	84	81
Charolais	57	1,421	90	101	118	104	116	108	117	97	99	96	100	90	94	91
MARC I-F_1	20	583	33	87	141	112	107	103								
MARC I-F_2	24	1,081				38	74	121	147	132	145	121	117	100	86	
MARC I-F_3	45	806							41	65	128	116	122	107	108	119
MARC I-F_4	24	401										37	62	84	105	113
MARC II-F_1	17	730	143	198	183	132	74									
MARC II-F_2	28	1,328			48	100	181	223	199	117	110	105	98	82	65	
MARC II-F_3	42	974						42	99	174	115	116	107	105	103	113
MARC II-F_4	25	533									47	74	77	99	112	124
MARC III-F_1	15	556			115	108	118	113	102							
MARC III-F_2	24	925					42	70	129	174	144	112	100	85	69	
MARC III-F_3	31	694								38	73	119	132	118	97	117
MARC III-F_4	14	307											29	62	93	123

Table 3—Heterozygosity of different mating types and estimated increase in performance as a result of heterosis

Mating type	Heterozygosity % relative to F1[a]	Estimated increase in weight weaned per cow exposed[b] (%)
Purebreeds	0	0
Two-breed rotation	66.7	15.5
Three-breed rotation	85.7	20.0
Four-breed rotation	93.3	21.7
Two-breed composite:		
F3 - 1/2A, 1/2B	50.0	11.6
F3 - 5/8A, 3/8B	46.9	10.9
F3 - 3/4A, 1/4B	37.5	8.7
Three-breed composite:		
F3 - 1/2A, 1/4B, 1/4C	62.5	14.6
F3 - 3/8A, 3/8B, 1/4C	65.6	15.3
Four-breed composite:		
F3 - 1/4A, 1/4B, 1/4C, 1/4D	75.0	17.5
F3 - 3/8A, 3/8B, 1/8C, 1/8D	68.8	16.0
F3 - 1/2A, 1/4B, 1/8C, 1/8D	65.6	15.3
Five-breed composite:		
F3 - 1/4A, 1/4B, 1/4C, 1/8D, 1/8E	78.1	18.2
F3 - 1/2A, 1/8B, 1/8C, 1/8D, 1/8E	68.8	16.0
Six-breed composite:		
F3 - 1/4A, 1/4B, 1/8C, 1/8D, 1/8E, 1/8F	81.3	18.9
Seven-breed composite:		
F3 - 3/16A, 3/16B, 1/8C, 1/8D, 1/8E,1/8F, 1/8G	85.2	19.8
Eight-breed composite:		
F3 - 1/8A, 1/8B, 1/8C, 1/8D, 1/8E, 1/8F, 1/8G, 1/8H	87.5	20.4

[a] Retention of initial (F_1) heterozygosity after crossing and subsequent random (*inter sè*) mating within the crosses is proportional to (n-1)/n when *n* breeds contribute equally to the foundation. When breeds used in the foundationof a composite breed do not contribute equally, percentage of mean F_1 heterozygosity retained is proportional to $1 - \sum_{i}^{n} P^2{}_i$, where Pi is the fraction of each of *n* contributing breeds to the foundation of a composite breed. This loss of heterozygosity occurs between the F_1 and F_2 generations, and if inbreeding is avoided, further loss of heterozygosity in *inter sè* mated populations does not occur.

[b] Based on heterosis effects of 8.5 percent for individual traits and 14.8 percent for maternal traits and assumption that retention of heterosis is proportional to retention of heterozygosity.

Table 4—Effects of heterosis on growth traits - females

	Birth weight (lb)	200-day weight (lb)	368-day weight (lb)	368-day height (in)	368-day condition score[a]
Heterosis					
MARC I					
F_1 minus Purebreds	5.3**	40.1**	64.6**	.8**	.8**
F_2 minus Purebreds	5.7**	40.0**	57.3**	.9**	.5**
$F_{3\&4}$ minus Purebreds	6.2**	40.0**	60.4**	1.1**	.4**
Observed minus Expected[b]	2.0*	8.4*	9.9	.4**	-.2*
MARC II					
F_1 minus Purebreds	2.4**	49.0**	56.9**	.8**	.8**
F_2 minus Purebreds	5.3**	25.4**	44.1**	.4**	.5**
$F_{3\&4}$ minus Purebreds	4.2**	31.5**	49.8**	.6**	.4**
Observed minus Expected[b]	2.4**	-5.1	7.0	-.1	-.2*
MARC III					
F_1 minus Purebreds	3.7**	30.2**	50.3**	.7**	.4**
F_2 minus Purebreds	3.7**	33.3**	52.7**	.4**	.5**
$F_{3\&4}$ minus Purebreds	4.6**	25.8**	46.1**	.5**	.4**
Observed minus Expected[b]	1.8	3.1	8.4	.0	.1
Mean Heterosis All Composites					
F_1 minus Purebreds	4.0**	39.7**	57.3**	.8**	.7**
F_2 minus Purebreds	4.8**	32.6**	51.4**	.6**	.5**
$F_{3\&4}$ minus Purebreds	5.1**	32.4**	52.0**	.7**	.4**
Observed minus Expected[b]	2.0**	2.2	8.4*	.1	-.1

[a] 9 = highest, 1 = lowest.

[b] Linear contrasts of observed and expected heterosis to test hypothesis that retained heterosis is proportional to retained heterozygosity.

* P < .05.

** P < .01.

Table 5—Effects of heterosis on growth traits - males

	Birth weight (lb)	200-day weight (lb)	368-day weight (lb)	368-day height (in)	368-day condition score[a]	368-day muscling score[a]
Heterosis						
MARC I						
F_1 minus Purebreds	2.2*	32.8**	58.2**	.7**	.4**	.10
F_2 minus Purebreds	4.2**	34.8**	51.8**	.7**	.2**	.02
$F_{3\&4}$ minus Purebreds	4.4**	31.5**	34.4**	.6**	.1 -	.08
Observed minus Expected[b]	2.6*	6.0*	-11.0	.1	-.2*	-.16
MARC II						
F_1 minus Purebreds	3.3**	65.3**	75.0**	1.3**	.4**	.00
F_2 minus Purebreds	6.2**	29.1**	54.7**	.5**	.5**	.04
$F_{3\&4}$ minus Purebreds	5.5**	37.7**	71.7**	.8**	.4**	-.01
Observed minus Expected[b]	3.1**	-11.2**	15.4*	-.1	.1*	-.02
MARC III						
F_1 minus Purebreds	4.0**	37.0**	57.6**	.9**	.4**	.27**
F_2 minus Purebreds	4.6**	38.4**	69.2**	.7**	.4**	.08
$F_{3\&4}$ minus Purebreds	5.1**	32.2**	73.2**	.7**	.2	.14
Observed minus Expected[b]	2.2	4.2	30.0**	.0	-.2	-.06
Mean Heterosis All Composites						
F_1 minus Purebreds	3.1**	45.0**	63.5**	.9**	.4**	.12
F_2 minus Purebreds	5.1**	34.2**	58.6**	.6**	.4**	.04
$F_{3\&4}$ minus Purebreds	5.1**	33.7**	59.8**	.7**	.2**	.02
Observed minus Expected[b]	2.6**	-.4	11.5*	.0	-.1	-.07

[a] 9 = highest, 1 = lowest.

[b] Linear contrasts of observed and expected heterosis to test hypothesis that retained heterosis is proportional to retained heterozygosity.

* P < .05.

** P < .01.

Table 6—Effects of heterosis on puberty traits of females and scrotal circumference of males

	Puberty					
	368 days (%)	410 days (%)	452 days (%)	Adjusted age[a] (days)	Adjusted weight[a] (lb)	Scrotal circumference (cm)
Heterosis						
MARC I						
F_1 minus Purebreds	24.2**	23.6**	10.8**	-22**	22**	.9**
F_2 minus Purebreds	22.5**	23.9**	10.2**	-22**	20**	1.1**
$F_{3\&4}$ minus Purebreds[b]	19.5**	21.3**	6.1**	-21**	18**	1.4**
Observed minus Expected[c]	.6	2.7	-2.3	4	0	.7*
MARC II						
F_1 minus Purebreds	29.4**	26.0**	4.3*	-20**	22**	1.6**
F_2 minus Purebreds	22.2**	20.0**	4.1*	-19**	15**	1.0**
$F_{3\&4}$ minus Purebreds[b]	19.9**	17.7**	2.0	-20**	15**	1.3**
Observed minus Expected[c]	-2.1	-1.8	-1.2	5	0	.1
MARC III						
F_1 minus Purebreds	24.3**	21.7**	7.6**	-20**	15**	1.5**
F_2 minus Purebreds	15.7**	14.5**	2.6	-13**	29**	.7**
$F_{3\&4}$ minus Purebreds[b]	10.0**	9.5**	1.9	-11**	29**	.7**
Observed minus Expected[c]	-8.3	-6.8	-3.8	-4	18	-.4
Mean Heterosis All Composites						
F_1 minus Purebreds	26.0**	23.8**	7.5**	-21**	20**	1.3**
F_2 minus Purebreds	20.2**	19.5**	5.6**	-18**	22**	.9**
$F_{3\&4}$ minus Purebreds[b]	16.5**	16.1**	3.3*	-17**	20**	1.1**
Observed minus Expected[c]	-3.3	-2.0	-2.4	1	4	.1

[a] Adjusted to 100% puberty basis.

[b] F_4 generation for scrotal circumference only.

[c] Linear contrasts of observed and expected heterosis to test hypothesis that retained heterosis is proportional to retained heterozygosity.

* P < .05.

** P < .01.

Table 7—Effects of heterosis on birth and survival traits of dam - all ages

				Survival		
	Birth weight (lb)	Birth date (Julian)	Calving difficulty (%)	Birth (%)	72 hrs (%)	Weaning (%)
Heterosis						
MARC I						
F_1 minus Purebreds[a]	6.0**	-2.3**	4	-.9	.0	1.2
F_2 & F_3 minus Purebreds[a]	6.0**	-2.4**	1.6	.3	.5	2.5
Observed minus Expected[b]	.4	.3	1.2	.5	—	1.4
MARC II						
F_1 minus Purebreds[a]	5.7**	-2.7**	1.4.6	.6	1.8	
F_2 & F_3 minus Purebreds[a]	5.7**	-1.8**	3.3*	.7	.9	2.6*
Observed minus Expected[b]	.9	-.5	2.1	2	.4	1.0
MARC III						
F_1 minus Purebreds[a]	4.2**	-1.8**	3.2*	1.2	2.3*	3.3**
F_2 & F_3 minus Purebreds[a]	4.4**	-2.7**	.4.3	1.0		.1
Observed minus Expected[b]	.9	1.2	-2.4	-.7	-1.0	-2.7
Mean Heterosis All Composites						
F_1 minus Purebreds[a]	5.3**	-2.3**	-.5	.3	1.0	2.1**
F_2 & F_3 minus Purebreds[a]	5.3**	-2.3**	.5	.4	.8	1.7
Observed minus Expected[b]	.7	.3	1.9	.1	-.1	.1

[a] F_1 generation females producing F_2 generation progeny and combined F_2 & F_3 generation females producing F_3 & F_4 generation progeny.

[b] Linear contrasts of observed and expected heterosis to test hypothesis that retained heterosis is proportional to retained heterozygosity.

* P < .05.

** P < .01.

Table 8—Effects of heterosis on reproduction and maternal traits - all ages

	Pregnant (%)	Calf crop born (%)	Calf crop weaned (%)	200 day calf wt/ female exposed (lb)	200 day calf wt (lb)
Heterosis					
MARC I					
F_1 minus Purebreds[a]	7.5**	7.9**	7.8**	65**	36**
F_2 & F_3 minus Purebreds[a]	7.3**	6.4**	6.6**	60**	37**
Observed minus Expected[b]	.8	-.5	-.2	4	5
MARC II					
F_1 minus Purebreds[a]	3.6**	4.0**	5.0*	45**	28**
F_2 & F_3 minus Purebreds[a]	1.0	1.2	2.2	40**	40**
Observed minus Expected[b]	-1.9	-2.0	-1.8	4	16**
MARC III					
F_1 minus Purebreds[a]	5.5**	4.2**	6.2**	56**	36**
F_2 & F_3 minus Purebreds[a]	1.9	-2.6	-2.5	9	31**
Observed minus Expected[b]	-2.6	-6.0*	-7.5**	-36**	1
Mean Heterosis All Composites					
F_1 minus Purebreds[a]	5.5**	5.4**	6.3**	55**	33**
F_2 & F_3 minus Purebreds[a]	3.4**	1.7	2.1	37**	36**
Observed minus Expected[b]	-1.2	-2.8*	-3.1*	-9	7**

[a] F_1 generation females producing F_2 generation progeny and combined F_2 & F_3 generation females producing F_3 & F_4 generation progeny.

[b] Linear contrasts of observed and expected heterosis to test hypothesis that retained heterosis is proportional to retained heterozygosity.

+ P < .10.

* P < .05.

** P < .01.

Table 9—Breed group means for percentage calf crop born based on females palpated pregnant

		Number	Two years old	Number	Five or more years old	Number	All ages
Overall mean		4,744	96.2	5,153	96.4	16,820	96.3
Red Poll		305	95.1	338	96.1	1,127	93.9
Hereford		260	97.2	461	98.1	1,200	96.7
Angus		476	96.8	601	96.3	1,736	95.8
Limousin		254	97.1	422	99.1	1,207	98.1
Braunvieh		316	96.8	338	97.6	1,130	96.9
Pinzgauer		285	97.2	94	96.6	759	97.0
Gelbvieh		344	97.2	185	96.7	941	97.6
Simmental		344	98.6	297	96.6	1,110	97.3
Charolais		306	93.0	330	98.8	1,173	97.1
Parental breed mean			96.6		97.3		96.7
D.05[a]			4.9		4.2		5.0
MARC I	F_1[b]	175	96.0	523	99.1	1,070	97.8
	F_2&F_3[b]	394	96.8	145	97.2	946	96.3
MARC II	F_1[b]	242	96.5	640	97.3	1,369	97.5
	F_2&F_3[b]	461	96.0	273	96.8	1,282	97.0
MARC III	F_1[b]	202	96.6	440	93.6	989	94.6
	F_2&F_3[b]	380	91.5	66	85.6	781	90.7
D.05[c]			5.4		4.7		5.5

[a] D.05 is the approximate difference between means of parental breeds required for significance.

[b] F_1 generation females producing F_2 generation progeny and combined F_2 & F_3 generation females producing F_3 & F_4 generation progeny.

[c] D.05 is the approximate difference between means of all breed groups required for significance.

Table 10—Effects of heterosis on percentage calf crop born based on females palpated pregnant

	Two years old	Five or more years old	All ages
Heterosis			
MARC I			
F_1 minus Purebreds[a]	0	1.0	.7
F_2 & F_3 minus Purebreds[a]	.8	-1.0	-.8
Observed minus Expected[b]	.8	-1.9	-1.4
MARC II			
F_1 minus Purebreds[a]	-1.0	.3	.7
F_2 & F_3 minus Purebreds[a]	-1.4	-.2	.1
Observed minus Expected[b]	-.6	-.4	-.5
MARC III			
F_1 minus Purebreds[a]	0	-3.2**	-1.3
F_2 & F_3 minus Purebreds[a]	-5.1**	-11.2**	-5.1**
Observed minus Expected[b]	-5.1**	-8.6**	-4.0**
Mean Heterosis All Composites			
F_1 minus Purebreds[a]	-.3	-.6	0
F_2 & F_3 minus Purebreds[a]	-1.9*	-4.1**	-2.0**
Observed minus Expected[b]	-1.6+	-3.6**	-2.0**

[a] F_1 generation females producing F_2 generation progeny and F_2 & F_3 generation females producing F_3 & F_4 generation progeny.

[b] Linear contrasts of observed and expected heterosis to test hypothesis that retained heterosis is proportional to retained heterozygosity.

+ P < .10.

* P < .05.

** P < .01.

Table 11—Effects of heterosis on weight, height and condition score – two through seven or more years old with composite generations combined

	Actual weight (lb)	Adjusted weight[a] (lb)	Height (in)	Condition score[b]
Linear contrasts				
Heterosis				
MARC I				
F_1, F_2 & F_3 minus purebreds	46**	34**	.4**	.4**
MARC II				
F_1, F_2 & F_3 minus purebreds	20**	12**	.2*	.2**
MARC III				
F_1, F_2 & F_3 minus purebreds	61**	45**	.4**	.3**
Mean heterosis All composites	42**	30**	.3**	.3**

[a] Adjusted to a common condition score.

[b] 9 = highest, 1 = lowest

* P < .05.

** P < .01.

Table 12—Effects of retained heterosis on milk yield and 200-day weight of progeny

	12-hour milk yield (lb)	Estimated 200-day milk yield (lb)	200-day weight of progeny (lb)	Adjusted 200-day weight of progeny[a] (lb)
<u>Linear contrasts</u>				
<u>Heterosis</u>				
MARC I[b] minus purebreds	1.78**	719**	36**	14*
Percent heterosis	17.1	16.7	7.3	2.7
MARC II[b] minus purebreds	1.25**	504**	41**	22**
Percent heterosis	12.1	11.9	8.2	4.7
MARC III[b] minus purebreds	1.40**	499**	26**	7
Percent heterosis	14.2	12.1	5.1	1.5
<u>Mean heterosis</u>				
<u>All composites</u>				
Composites[b] minus purebreds	1.48**	574**	34**	14*
Percent heterosis	14.5	13.6	6.9	3.0

[a] Adjusted to a common estimated milk yield.

[b] F_2 generation females nursing F_3 generation progeny.

* P < .05.

** P < .01.