United States Department of Agriculture

Agricultural Research Service

Technical Bulletin Number 1875

October 1999

Composite Breeds To Use Heterosis and Breed Differences To Improve Efficiency of Beef Production

In cooperation with the Institute of Agriculture and Natural Resources, University of Nebraska-Lincoln

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Abstract

Gregory, K.E., L.V. Cundiff, and R.M. Koch. 1999. Composite Breeds To Use Heterosis and Breed Differences To Improve Efficiency of Beef Production. U.S. Department of Agriculture Technical Bulletin No. 1875, 81 pp.

This report is a summary of results from a long-term experiment of 15 years conducted with beef cattle at the Roman L. Hruska U.S. Meat Animal Research Center. The study estimated the retention of heterosis for major bioeconomic traits in composite populations (established with contributions by four or five purebreeds) and evaluated the potential of using these composite populations to achieve and maintain optimum performance levels and to maintain high levels of heterosis. At least 13 scientific papers were published from this project, resulting in numerous conclusions, presented here.

This publication will be of use to scientists, students, and extension specialists interested in beef cattle breeding and genetics; beef cattle breeders; and others with interests in the beef cattle industry.

Keywords: beef cattle breeding, breed composition, breeding, calves, cattle, crossbreeding, composite breeds, genetics, genotype, heritability, heterosis, heterosis retention, heterozygosity, inbreeding, phenotype

While supplies last, single copies of this publication may be obtained at no cost from Keith Gregory, USDA–ARS, Roman L. Hruska U.S. Meat Animal Research Center, P.O. Box 166, Clay Center, NE 68933.

Copies of this publication may be purchased from the National Technical Information Service, 5285 Port Royal Road, Springfield, VA 22161; telephone 703–605–6000.

Issued October 1999

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Executive 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 percent. Crossbred cows remain in the herd 1.3 yr longer and have a 30 percent greater lifetime production than straightbred cows.

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. These are traits where the optimum is determined by production environment and by market requirements.

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

4. Crossbreeding systems can 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 in level of performance among cows and calves 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 to optimize average genetic merit for major bioeconomic traits. This includes traits such as growth rate and size, carcass composition, milk yield, and age at puberty.

7. Composite breeds offer the opportunity to (a) use high levels of heterosis on a continuing basis if population size in seedstock herds is sufficiently large or if periodic introduction of new genetic material is made to avoid inbreeding, (b) achieve and maintain optimum breed (additive genetic) composition needed to match performance characteristics of different 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. 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 is important, that is, the level of heterosis for traits may vary among breed crosses.

3. Generally, retained heterosis in advanced generations was equal to or greater than expected based on retained heterozygosity in the three composite populations.

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

5. Even though results suggest that specific cross heterosis is 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, the

use of average values for F_1 heterosis and of retained heterosis based on genetic expectation in advanced generations of *inter se* mated composite populations is suggested for *Bos taurus* breeds.

6. These results, generally, support the hypothesis that heterosis in cattle can be accounted for by dominance effects of genes. Thus, heterosis in breed crosses involving *Bos taurus* breeds can likely be accounted for by recovery of accumulated inbreeding depression that has occurred in breeds since their formation.

7. Estimates of genetic standard deviations and phenotypic coefficients of variation were similar for parental purebreds combined and for composite populations combined for most bioeconomic traits. Estimates of heritability were similar for parental purebreds and composites. Thus, no increase in genetic variation was observed in composite populations relative to contributing purebreeds. The similarity of genetic variation for composites and contributing purebreds is believed to result from the large number of genes affecting major bioeconomic traits. Composite populations (breeds) have a high degree of uniformity both within and between generations.

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

9. 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 growth rate and size, composition of gain, milk production, climatic and nutritive adaptability, and age at puberty.

10. Large differences among parental breeds were observed for growth rate and size; dystocia; age at puberty; scrotal circumference; maternal traits, including milk production; and carcass composition.

11. Composites were generally intermediate to parental breeds for carcass composition and more nearly approached the optimum carcass composition, for example, Hereford, Angus, and Red Poll (British breeds) had more carcass fat than is optimum, whereas the continental breeds tended to have less carcass fat than is optimum to meet current market requirements in U.S. beef production systems.

12. There is limited opportunity to select among or within breeds to achieve high levels of marbling or high levels of fat in the longissimus muscle simultaneously with achieving a high percentage of retail product in the carcass. These results suggest that the most logical approach to resolution of the genetic antagonism between favorable carcass composition and less favorable carcass quality grade (that is, marbling) is to form composite breeds with breed contributions organized to achieve a balance between favorable carcass composition and desirable carcass quality grade at optimum slaughter weights.

13. Factors favoring the use of composite breeds are (a) it is a simple procedure that results in high levels of retained heterosis, (b) it is a highly effective procedure that makes use of breed complementarity, (c) it achieves a relatively high level of uniformity both within and between generations, and (d) it makes use of high levels of heterosis and breed complementarity simultaneously, regardless of herd size.

Introduction

Heterosis achieved through continuous crossbreeding can be used to increase weight of calf weaned per cow exposed to breeding by 20 percent (Gregory and Cundiff 1980). Heterosis can also increase longevity of cows by 1.3 yr and can increase the total calf weight weaned per cow by 30 percent over the life span of a dam (Cundiff et al. 1992).

Comprehensive programs of breed characterization revealed large differences among breeds for most bioeconomic traits (Gregory et al. 1982; Cundiff et al. 1986). Optimum crossbreeding systems are difficult to adapt in herds having fewer than four bulls (Gregory and Cundiff 1980). Further, fluctuation in breed composition between generations in rotational crossbreeding systems can result in considerable variation among cows and calves in the level of performance for major bioeconomic traits unless breeds used in the rotation are of similar biological type. Use of breeds with similar performance characteristics restricts the use that can be made of breed differences in average genetic merit for bioeconomic traits to meet requirements for specific production and marketing situations (Gregory and Cundiff 1980). The potential of composite breeds as an alternative to continuous crossbreeding for using heterosis and for using genetic differences among breeds (that is, breed complementarity) to achieve and maintain a more optimum additive genetic (breed) composition needed to be investigated in a comprehensive experiment. Retention of initial (F_1) heterozygosity after crossing and subsequent random (*inter se*) mating within crosses is proportional to $(n-1)/n$ when n breeds contribute equally to the foundation (Wright 1922; Dickerson 1969, 1973). When breeds used in the foundation of a composite breed do not contribute equally, the percentage of F_1 heterozygosity retained is proportional to $1 - \Sigma P_i^2$, 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 se* mated populations does not occur (Wright 1922; Dickerson 1969, 1973).

The large differences that exist among breeds for most bioeconomic traits are the result of different selection goals in different breeds. Results from the Germplasm Evaluation Program at the U.S. Meat Animal Research Center (Cundiff et al. 1986) provide evidence that genetic variation between breeds is similar in magnitude to genetic variation within breeds for many bioeconomic traits. The heritability of breed differences approaches 100 percent, whereas the heritability of differences within breeds for major bioeconomic traits varies from less than 10 percent to about 50 percent, depending on the trait. The heritability of breed differences approaches 100 percent because estimates of breed differences are based on the means of a large number of individuals from a representative sample. This tends to average within-breed genetic variation. Estimates of the heritability of differences within breeds are generally based on single observations of individuals for a specific trait. Thus selection among breeds is much more effective than selection within breeds.

Breed differences in bioeconomic traits are an important genetic resource and can be used to achieve and maintain performance levels that are optimum for different production and marketing situations for traits such as growth rate and size, milk production, carcass composition, age at puberty, and climatic and nutritive adaptability. Large breed differences exist for these traits and breed differences may be used to achieve and maintain optimum additive genetic (breed) composition through the formation of composite breeds.

The focus of this bulletin is to present a summary of results from a major experiment that was conducted to accomplish the following objectives: (1) to estimate the retention of combined individual and maternal heterosis ($H^i + H^m$) for major bioeconomic traits in advanced generations of *inter se* mated composite populations established with contributions by either four or five purebreeds and (2) to evaluate the potential of composite breeds as a procedure to use breed differences, or breed complementarity, to achieve and maintain optimum performance levels for major bioeconomic traits on a continuing basis in harmony with the production environment and market requirements.

Experimental Procedure

Populations

Matings were made to establish three composite populations (MARC I, MARC II, and MARC III) as indicated in table 1. In this experiment the F_1 generation is defined as the first generation that reflects the final breed composition of a composite population. As indicated in table 1, the F_1, F_2, and F_3 generations were mated *inter se* to produce, respectively, F_2-, F_3-, and F_4-generation progeny. Five breeds contributed to the MARC I population (1/4 Charolais, 1/4 Limousin, 1/4 Braunvieh, 1/8 Hereford, and 1/8 Angus—a 75:25 ratio of continental breeds to British breeds). Four breeds contributed to the MARC II population (1/4 Gelbvieh, 1/4 Simmental, 1/4 Hereford, and 1/4 Angus—a 50:50 ratio of continental breeds to British breeds). Four breeds contributed to the MARC III population (1/4 Pinzgauer, 1/4 Red Poll, 1/4 Hereford, and 1/4 Angus—a 25:75 ratio of continental breeds to British breeds).

Composite populations were formed from the same sires and dams that were represented in the nine contributing parental breeds shown in table 1. Genetic expectations for individual (H^i) heterosis and maternal (H^m) heterosis for each generation are provided in table 1. The numbers of sires used and individuals born each year for each contributing

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

	Dam	Progeny	Composite populations: MARC I	MARC II	MARC III	Mean
Parents of F_1 generations†			(C × LH) × (B × LA) or (C × LA) × (B × LH) Reciprocals	(GH) × (SA) or (GA) × (SH)	(PA) × (RH) or (PA) × (HR) Reciprocals	
Breed composition of F_1 and subsequent generations			0.25B, 0.25C, 0.25L 0.125H, 0.125A	0.25G, 0.25S 0.25H, 0.25A	0.25P, 0.25R 0.25H, 0.25A	
F_1 Heterozygosity‡			0.94§	1	1	0.98
F_2 Heterozygosity			0.78	0.75	0.75	0.76
F_3 Heterozygosity			0.78	0.75	0.75	0.76
Heterosis‖	F_1	F_2	$0.78\ H^i + 0.94\ H^m$	$0.75\ H^i + 1\ H^m$	$0.75\ H^i + 1\ H^m$	$0.76H^i + 0.98\ H^m$
Heterosis	F_2	F_3	$0.78\ H^i + 0.78\ H^m$	$0.75\ H^i + 0.75\ H^m$	$0.75\ H^i + 0.75\ H^m$	$0.76H^i + 0.76\ H^m$
Heterosis	F_3	F_4	$0.78\ H^i + 0.78\ H^m$	$0.75\ H^i + 0.75\ H^m$	$0.75\ H^i + 0.75\ H^m$	$0.76H^i + 0.76\ H^m$

†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.

‡Retention of initial F_1 heterozygosity following crossing and subsequent random mating within the crosses (*inter se*) is proportional to $1 - \sum P_i^2$, 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.

§0.94 instead of 1 because both sires and dams of the F_1 generation were one-fourth Limousin.

‖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.

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

Breed group	No. of sires	Total no. of indiv. born	Individuals born													
			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	Retained heterozygosity relative to F_1† (%)	Estimated increase in weight weaned per cow exposed‡ (%)
Pure breeds	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		
F_3—1/2A, 1/2B	50.0	11.6
F_3—5/8A, 3/8B	46.9	10.9
F_3—3/4A, 1/4B	37.5	8.7
Three-breed composite		
F_3—1/2A, 1/4B, 1/4C	62.5	14.6
F_3—3/8A, 3/8B, 1/4C	65.6	15.3
Four-breed composite		
F_3—1/4A, 1/4B, 1/4C, 1/4D	75.0	17.5
F_3—3/8A, 3/8B, 1/8C, 1/8D	68.8	16.0
F_3—1/2A, 1/4B, 1/8C, 1/8D	65.6	15.3
Five-breed composite		
F_3—1/4A, 1/4B, 1/4C, 1/8D, 1/8E	78.1	18.2
F_3—1/2A, 1/8B, 1/8C, 1/8D, 1/8E	68.8	16.0
Six-breed composite		
F_3—1/4A, 1/4B, 1/8C, 1/8D, 1/8E, 1/8F	81.3	18.9
Seven-breed composite		
F_3—3/16A, 3/16B, 1/8C, 1/8D, 1/8E, 1/8F, 1/8G	85.2	19.8
Eight-breed composite		
F_3—1/8A, 1/8B, 1/8C, 1/8D, 1/8E, 1/8F, 1/8G, 1/8H	87.5	20.4

†Retention of initial F_1 heterozygosity after crossing and subsequent random (*inter se*) mating within the 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 $1 - \Sigma P_i^2$, 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 se* mated populations does not occur.

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

purebreed and for each generation of each composite population are shown in table 2. Table 3 shows the retained heterozygosity relative to the F_1 generation for different mating types and the estimated increase in cow productivity assuming that retained heterosis is proportional to retained heterozygosity.

Contributing purebred contemporaries have been maintained for the Pinzgauer breed since 1982 and for all other breeds since 1978. The first 3/4 Pinzgauer was produced in 1980, and the first 7/8 Pinzgauer (purebred for female animals in breed registry) was produced in 1982. The 15/16 Pinzgauer (purebred for registry of male animals) were produced after 1984. Pinzgauer females (7/8) producing (15/16) Pinzgauer progeny were included in the data analyses.

The Braunvieh population averaged 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 females. The females were obtained as calves from dairy herds in Wisconsin and Minnesota 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 females bred to produce 7/8 Gelbvieh progeny was purchased in 1977 to augment the Gelbvieh population. The females had been graded up from a female population of Charolais × 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 females in 1977 and was augmented by Charolais graded up from an Angus × Hereford base started in 1967 at the research center. Charolais sires were sampled from a broad genetic base.

The Red Poll population was established from registered females purchased from several sources in 1966, 1967, and 1968, with sires sampled from a broad genetic base.

The Hereford and Angus breeds were 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 were 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 to natural service by 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 were used on yearling heifers because of late puberty in both sexes of these breeds. Females 2 or more yr old were mated by artificial insemination (AI) for 28 days, followed by natural-service exposure for 28 days, for a total mating season of 56 days. More than 80 percent of sires were 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 it was from the first of June until late July. Since 1985 the mating season for yearling heifers was from late May until near mid-July, and for dams 2 or more yr old it was from mid-June until almost 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 until 1985, unless they were not pregnant for 2 successive yr. Since 1985, all nonpregnant animals were removed each year from all breed groups. Nonperformance criteria, such as age, color, and extremes in skeletal size, were used to remove excess cows to maintain population size for each breed group. No females were removed from the project before being exposed to breeding. An attempt was 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 were used to identify sires for breeding use in all populations. The intent was to avoid extremes in weight, condition, and muscular and skeletal anatomy. Reducing dystocia was considered in identifying sires for use in all breed groups. Larger scrotal circumference also was favored, particularly in breeds that are late to reach puberty (that is, Hereford and Limousin). Polledness and color patterns of red or red with white markings were 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 (that is, "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), however, 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. The general plan was to group females in three fully integrated management units under the day-to-day supervision of a 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 as follows:

- Group 1: All generations of the composite MARC I population plus Braunvieh, Charolais, and Limousin.
- Group 2: All generations of the composite MARC II population plus Simmental, Gelbvieh, and Pinzgauer.
- Group 3: All generations of the composite MARC III population plus Hereford, Angus, and Red Poll.

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 the composite MARC II population for two reasons: (1) the three management groups had to contain similar numbers of animals and (2) the feed and management requirements of Pinzgauer females are similar to those of Simmental and Gelbvieh. Even though the populations were in three management groups, uniform management protocols were followed for 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 where the three management groups were maintained were contiguous; different management groups used the same pastures at different times. All groups received the same feed but the amounts varied to be consistent with requirements.

Two-yr-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 the winter feeding period.

Feeding of Young Heifers and Young Bulls

The mean birth date was April 7, and calves were weaned the first week of October in most years at an average age of 180 days. After an adjustment feeding period (28 days), heifers were fed diets of corn silage, alfalfa haylage, and a protein-mineral-vitamin supplement for three consecutive time periods of approximately equal length. Diets provided 2.34 megacalories of metabolizable energy per kilogram of dry matter (Mcal of ME/kg of DM) and 11.62 percent crude protein (CP) during period 1, 2.24 Mcal of ME/kg of DM and 12.34 percent CP during period 2, and 2.18 Mcal of ME/kg of DM and 11.70 percent CP during period 3. Heifers received these diets until they were placed on an improved cool-season grass pasture from mid- to late April, depending on adequacy of pasture to meet nutritive requirements.

After an adjustment feeding period of 28 days after weaning, intact males were fed a diet of corn silage, rolled corn, and protein-mineral-vitamin supplement (2.69 Mcal ME/kg of DM, 12.88 percent CP) for 140 days.

Data Collection

Calves were weighed at birth, in the middle of the breeding season (end of AI breeding period), at weaning, and at 28, 84, 140, and 168 days after weaning. Yearling heifers were weighed at the beginning and end of the mating season and when they were palpated for pregnancy. Thereafter, females were weighed, measured for height, and scored for condition three times a year at the following times: (1) before calving, (2) at the start of the breeding season, and (3) 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 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 score was subjectively evaluated using the following descriptive scores:

1 = no difficulty,

2 = little difficulty by hand,

3 = little difficulty with a calf jack,

4 = slight difficulty with a calf jack,

5 = moderate difficulty with a calf jack,

6 = major difficulty with a calf jack,

7 = caesarean birth, and

8 = abnormal presentation.

Percentage of calving difficulty was analyzed (scores 1 and 2 = 0; scores 3, 4, 5, 6, and 7 = 1; and scores of 8 were excluded from the analyses). Scores of 8 also were excluded from the analysis of calving difficulty score.

Growth, Feed Efficiency, and Carcass and Meat Data of Castrate Males

The castrate males included in this study were the unselected male progeny of 21 Red Poll, 22 Hereford, 23 Angus, 24 Limousin, 26 Braunvieh, 27 Pinzgauer, 27 Gelbvieh, 19 Simmental, 25 Charolais, 39 MARC I, 30 MARC II, and 24 MARC III sires. The steers were F_3-generation progeny in the three composite populations. Animals included in this part of the study were born in 1988, 1989, 1990, and 1991 from dams that were 2, 3, 4, and 5 or more yr old.

Feeding and Management

The mean birth date of animals included in this part of the experiment was April 13. In the last 3 yr, animals were weaned at an average age of approximately 150 days on September 7 or 11. Because of drought, animals were weaned on August 18 in 1988 at an average age of 127 days. Animals were initially placed on a weaning diet that provided 2.65 Mcal of ME/kg of DM and 15.4 percent CP and that was composed of ground alfalfa hay, rolled corn, corn silage, and protein-mineral supplement. After the animals adjusted to weaning over a period of about 30 days, corn silage gradually replaced the ground alfalfa hay and a portion of the rolled corn so that the diet provided 2.69 Mcal of ME/kg of DM and 12.88 percent CP and consisted of corn silage

(66 percent), rolled corn (22 percent), and protein-mineral supplement (12 percent). At an average age of 203 days (between October 30 and November 15) over the 4 yr, animals of each breed group were stratified by weight and randomly assigned to a treatment. Before assigning animals to a treatment, seven to nine males in each breed group were identified as candidate replacement sires. These sires represented a broad pedigree base and were near the mean weight of their respective breed group. Two finishing diets varying in dietary energy content were used for each year-breed-group subclass. Feed level 1 (finishing diet) consisted of 2.82 Mcal of ME/kg of DM and 11.50 percent CP. Feed level 2 (finishing diet) consisted of 3.07 Mcal of ME/kg of DM and 11.50 CP. The diet (on a dry-matter basis) for feed level 1 consisted of corn silage (59.77 percent), rolled corn (32.77 percent), and protein-mineral supplement (7.46 percent). The diet (on a dry-matter basis) for feed level 2 consisted of corn silage (18.00 percent), rolled corn (75.24 percent), and protein-mineral supplement (6.76 percent). Immediately after the animals were assigned to a treatment, they were castrated.

The animals were kept on the backgrounding diet (2.69 Mcal of ME/kg of DM and 12.88 percent CP) for different periods in different years before they were put on the finishing diet. The average age at which the animals were placed on a finishing diet in each birth year was as follows: 1988, 319 days; 1989, 293 days; 1990, 264 days; and 1991, 212 days. Feed-consumption data in each year were recorded for each pen starting on the following dates: 1988, November 9; 1989, 1990, and 1991, December 4.

Slaughter and Processing Procedures

Animals were serially slaughtered at four end points, with 20, 21, or 22 days between slaughter dates and 63 days between the first and fourth slaughter. The initial slaughter date was between May 21 and 26 in each of the 4 yr. The number of days between initial weight (203 days) to final weight averaged 204, 224, 245, and 267 days for the four slaughter groups. Thus, the mean feeding period from initial to final weight was 235 days and the mean slaughter age was 438 days. Steers were assigned to slaughter groups on a random basis stratified by weight, based on the last weight taken before the start of the serial slaughter schedule. The final weight of each animal was recorded at 7 a.m. after the animals were given access to feed and water the previous night. All steers remaining were weighed at each slaughter date. Weights of steers slaughtered at the first three slaughter dates were approximately the same as weights of steers remaining in a pen.

Steers were slaughtered in a commercial facility. Following a chill period of 24 hr, data on fat thickness at the 12th rib, perirenal fat percentage, and longissimus muscle area were obtained, and the right side of each carcass was returned to the U.S. Meat Animal Research Center to obtain carcass cut-out, chemical composition, and sensory panel data. For animals born in 1988, 1989, and 1990, limitations on carcass processing capability forced random sampling of sides for detailed cut-out and sensory data. Cut-out data were obtained on all but 65 carcasses in the 3 yr.

Carcasses were processed into wholesale cuts of round, loin, rib, chuck, plate, flank, and brisket plus shank. Each wholesale cut was processed further by cutting it into boneless steaks, roasts, lean trim, and fat trim to 0.3 inches, except that the dorsal and lateral vertebral processes were left in the short loin and dorsal vertebral processes and ribs were left in standing rib roasts. Lean trim was targeted to contain 20 percent fat and was adjusted to this fat level based on chemical analysis of the lean trim. Further processing removed all subcutaneous and accessible intermuscular fat (0 inches fat trim) from any surface, and the remaining bone was removed from the short loin and from the standing rib roasts. The 9–10–11th rib cut was removed and processed by the procedures described for wholesale cuts and kept separate from the remainder of the rib. Soft tissue (lean and fat) from the 9–10–11th rib cut was ground and sampled for determination of water and fat.

The retail product included trimmed (0.3 inches or 0 inches of fat trim) steaks and roasts plus lean trim adjusted to 20 percent fat based on chemical analysis of the lean trim. Lean trim was ground and sampled for water and fat determinations to provide a basis for adjusting individual animal yields more precisely to 80 percent lean and 20 percent fat in the lean trim.

Carcass lean was calculated by adding the total of boneless roasts and steaks trimmed to 0 inches of subcutaneous and accessible intermuscular fat, and lean trim with all fat subtracted based on chemical analysis of the lean trim. Carcass fat was calculated as the sum of the physically removed perirenal, subcutaneous, and accessible intermuscular fat plus fat mathematically removed from the lean trim based on chemical analysis of the lean trim. Carcass bone included all bone from the carcass.

Three measures of composition resulted from these procedures: (1) retail product, fat trim, and bone; (2) carcass lean, carcass fat, and carcass bone; or (3) estimated lean, fat, and bone from the 9–10–11th rib and the wholesale rib.

Three longissimus muscle steaks, cut 1-inch thick from the 5th and 6th and from the 12th ribs, were frozen on day 9 after slaughter and used for chemical determination of water and fat in the longissimus muscle and for shear force and sensory panel evaluation of the longissimus muscle. Sample preparation followed AMSA (1978) guidelines.

Analysis of Data

Data were analyzed by least squares mixed model procedures (Harvey 1985). 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 as a random effect for analysis of all traits. 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. Studentized Range as described by Snedecor and Cochran (1980) was computed to obtain approximations of differences required for significance among breed group means. For greater detail on data analyses, experimental procedures, and experimental results, see Gregory et al. (1991a–d; 1992a–c; 1994a–c; 1995a–c).

Results and Discussion

Heterosis and Heterosis Retention

Heterosis for Growth Traits in Both Sexes

Heterosis effects on 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 of the three composite populations (tables 4 and 5). Combined individual and maternal heterosis ($H^i + H^m$) 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 ($p>0.05$) from genetic expectation for other traits. The effects of heterosis on muscling score in males was not important. These results support the hypothesis that heterosis in cattle for traits related to growth and size can be accounted for by dominance effects of genes (tables 4 and 5).

Heterosis for Puberty Traits in Females and Scrotal Circumference in 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.

Table 4. Effects of heterosis on growth traits of females

Linear contrasts	Birth weight (lb)	200-day weight (lb)	368-day weight (lb)	368-day height (inches)	368-day condition score†
Heterosis					
MARC I					
F_1 minus purebreds	5.3**	40.1**	64.6**	0.8**	0.8**
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‡	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‡	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‡	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‡	2.0**	2.2	8.4*	.1	–.1

†Evaluated on a scale of 1–9, 9 = highest, 1 = lowest.

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

*$p<0.05$.

**$p<0.01$.

Table 5. Effects of heterosis on growth traits of males

Linear contrasts	Birth weight (lb)	200-day weight (lb)	368-day weight (lb)	368-day height (inches)	368-day condition score†	368-day muscling score†
Heterosis						
MARC I						
F_1 minus purebreds	2.2*	32.8**	58.2**	0.7**	0.4**	0.10
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‡	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‡	3.1**	–11.2**	15.4*	–.1	.1*	–.02
MARC III						
F_1 minus purebreds	4.0**	37.0**	57.6**	.9**	.4**	
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‡	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‡	2.6**	–0.4	11.5*	.0	–.1	–.07

†Evaluated on a scale of 1 to 9, 9 = highest, 1 = lowest.

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

*$p<0.05$.

**$p<0.01$.

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

Linear contrasts	Percent reaching puberty in: 368 days	410 days	452 days	Adjusted age at puberty[†] (days)	Adjusted weight at puberty[†] (lb)	Scrotal circumference (cm)
Heterosis						
MARC I						
F_1 minus purebreds	24.2**	23.6**	10.8**	–22**	22**	0.9**
F_2 minus purebreds	22.5**	23.9**	10.2**	–22**	20**	1.1**
$F_{3\&4}$ minus purebreds[‡]	19.5**	21.3**	6.1**	–21**	18**	1.4**
Observed minus expected[§]	.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[‡]	19.9**	17.7**	2.0	–20**	15**	1.3**
Observed minus expected[§]	–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	10.0**	9.5**	1.9	–11**	29**	.7**
Observed minus expected[§]	–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[‡]	16.5**	16.1**	3.3*	–17**	20**	1.1**
Observed minus expected[§]	–3.3	–2.0	–2.4	1	4	.1

[†]Adjusted to 100 percent puberty basis.
[‡]F_4 generation for scrotal circumference only.
[§]Linear contrasts of observed and expected heterosis to test hypothesis that retained heterosis is proportional to retained heterozygosity.
*$p<0.05$.
**$p<0.01$.

Heterosis was significant for scrotal circumference in each generation of each composite population and for the mean of the three composite populations. Results from a separate analysis showed that heterosis effects on scrotal circumference are mediated through heterosis effects on growth rate and through factors that are independent of growth rate. There was close agreement in heterosis retained for puberty traits in females and for scrotal circumference in males with genetic expectation based on retained heterozygosity. These results support the hypothesis that puberty traits in females and scrotal circumference in males can be accounted for by dominance effects of genes (table 6).

Heterosis for Birth Weight, Birth Date, Dystocia, and Survival as Traits of the Dam

Heterosis effects were evaluated as traits of the dam in F_2-generation progeny of F_1-generation dams and combined F_3- and F_4-generation progeny of combined F_2- and F_3-generation dams in each of the three composite populations and for the mean of the three composite populations. Traits included birth weight; birth date (Julian); percentage calving difficulty; and percentage survival at birth, 72 hr after birth, 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 (dystocia) were not significant. Effects of heterosis were significant for date of birth (earlier) in 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 ($p>0.05$) from genetic expectation based on retained heterozygosity. These results support the hypothesis that heterosis in cattle for these traits can be accounted for by the dominance effects of genes (table 7).

Heterosis for Reproductive 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 of dams pregnant, percentage calf crop born, percentage calf crop weaned, 200-day calf weight per female exposed to breeding, and 200-day calf weight (table 8). Also, breed group means and estimates of the effects of heterosis on the percentage of fetal death loss based on females palpated while pregnant are presented (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 each generation 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 ($p<0.01$) 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 the MARC I and MARC II populations, heterosis retained for reproductive traits in combined F_2- and F_3-generation dams producing F_3 and F_4 progeny did not differ ($p>0.05$) from genetic expectation based on retained heterozygosity. In the MARC III population, loss of heterosis for reproductive traits (other than for 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-than-expected heterosis loss was the result of a higher rate of fetal death between the diagnosis of pregnancy and parturition (tables 9 and 10).

In another major experiment involving Angus, Hereford, and Shorthorn, there was no evidence that heterosis (H^i) had an effect on either embryonic or fetal survival. However, maternal heterosis (H^m) was important for early embryonic survival but not for fetal survival between the diagnosis of pregnancy and parturition (Wiltbank et al. 1967; Cundiff et al.

Table 7. Effects of heterosis on birth and survival traits for calves born from dams of all ages

Linear contrasts	Birth weight (lb)	Birth date (Julian)	Calving difficulty (%)	Survival		
				At birth (%)	At 72 hr (%)	At weaning (%)
Heterosis						
MARC I						
F_1 minus purebreds†	6.0**	–2.3**	0.4	–0.9	0.0	1.2
F_2 & F_3 minus purebreds†	6.0**	–2.4**	1.6	.3	.5	2.5
Observed minus expected‡	.4	.3	1.2	.5	—	1.4
MARC II						
F_1 minus purebreds†	5.7**	–2.7**	1.4	.6	.6	1.8
F_2 & F_3 minus purebreds†	5.7**	–1.8**	3.3*	.7	.9	2.6*
Observed minus expected‡	.9	–.5	2.1	.2	.4	1.0
MARC III						
F_1 minus purebreds†	4.2**	–1.8**	–3.2*	1.2	2.3*	3.3**
F_2 & F_3 minus purebreds†	4.4**	–2.7**	–.4	.3	1.0	.1
Observed minus expected‡	.9	1.2	–2.4**	–.7	–1.0	–2.7
Mean heterosis, all composites						
F_1 minus purebreds†	5.3**	–2.3**	–.5	.3	1.0	2.1**
F_2 & F_3 minus purebreds†	5.3**	–2.3**	1.5	.4	.8	1.7
Observed minus expected‡	.7	.3	1.9	.1	–.1	–.1

†F_1-generation females producing F_2-generation progeny and combined F_2- & F_3-generation females producing F_3- & F_4-generation progeny.

‡Linear contrasts of observed and expected heterosis to test the hypothesis that retained heterosis is proportional to retained heterozygosity.

*$p<0.05$.

**$p<0.01$.

Table 8. Effects of heterosis on reproductive and maternal traits of dams of all ages

Linear contrasts	Pregnant (%)	Calves born (%)	Calves weaned (%)	200-day calf weight per female exposed to breeding (lb)	200-day calf weight (lb)
Heterosis					
MARC					
F_1 minus purebreds†	7.5**	7.9**	7.8**	65**	36**
F_2 & F_3 minus purebreds†	7.3**	6.4**	6.6	60**	37**
Observed minus expected‡	.8	–.5	–.2	4	5
MARC II					
F_1 minus purebreds†	3.6**	4.0**	5.0*	45**	28**
F_2 & F_3 minus purebreds†	1.0	1.2	2.2	40**	40**
Observed minus expected‡	–1.9	–2.0	–1.8	4	16**
MARC III					
F_1 minus purebreds†	5.5**	4.2**	6.2**	56**	36**
F_2 & F_3 minus purebreds†	1.9	–2.6	–2.5	9	31**
Observed minus expected‡	–2.6	–6.0	–7.5**	–36**	1
Mean heterosis, all composites					
F_1 minus purebreds†	5.5**	5.4**	6.3**	55**	33**
F_2 & F_3 minus purebreds†	3.4**	1.7**	2.1	37**	36**
Observed minus expected‡	–1.2	–2.8*	–3.1*	–9	7**

†F_1-generation females producing F_2-generation progeny and combined F_2- & F_3-generation females producing F_3- & F_4-generation progeny.

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

*$p<0.05$.

**$p<0.01$.

1974). Results from the current experiment do not indicate a heterosis effect in either the F_1 generation or the combined F_2 and F_3 generations for fetal survival between the diagnosis of pregnancy and parturition in MARC I and MARC II populations (table 10).

Subsequent to completion of this experiment and in two other populations developed through the use of composite MARC III bulls, fetal death loss between pregnancy diagnosis and parturition has not differed from other populations including composites MARC I and MARC II. Thus the lower fetal survival observed in composite MARC III in this experiment seems to have been a chance event or possibly resulted from an epistatic combination that was restored with relative ease.

For MARC I and MARC II populations, these results support the hypothesis that heterosis for reproductive and maternal traits in cattle can be accounted for by the dominance effects of genes. The same conclusion can be made for maternal traits in MARC III populations (for example, 200-day calf weight).

Table 9. Breed group means for fetal death loss based on females palpated pregnant

Breed group	Fetal death: 2-yr-old dams Number	%	5-yr-old dams Number	%	Dams of all ages Number	%
Overall mean	4,744	3.8	5,153	3.6	16,820	3.7
Red Poll	305	4.9	338	3.9	1,127	6.1
Hereford	260	2.8	461	1.9	1,200	3.3
Angus	476	3.2	601	3.7	1,736	4.2
Limousin	254	2.9	422	.9	1,207	1.9
Braunvieh	316	3.2	338	2.4	1,130	3.1
Pinzgauer	285	2.8	94	3.4	759	3.0
Gelbvieh	344	2.8	185	3.3	941	2.4
Simmental	344	1.4	297	3.4	1,110	2.7
Charolais	306	7.0	330	1.2	1,173	2.9
Parental breed mean		3.4		2.7		3.3
D.05† for parental breeds		4.9		4.2		5.0
MARC I						
F_1‡	175	4.0	523	.9	1,070	2.2
F_2 & F_3‡	394	3.2	145	2.8	946	3.7
MARC II						
F_1‡	242	3.5	640	2.7	1,369	2.5
F_2 & F_3‡	461	4.0	273	3.2	1,282	3.0
MARC III						
F_1‡	202	3.4	440	6.4	989	5.4
F_2 & F_3‡	380	8.5	66	14.4	781	9.3
D.05† for all breed groups		5.4		4.7		5.5

†D.05 = the approximate difference between means required for significance.

‡F_1-generation females producing F_2-generation progeny or combined F_2- & F_3-generation females producing F_3- & F_4-generation progeny.

Heterosis for Actual Weight, Adjusted Weight, Hip Height, and Condition Score in Females

Heterosis effects were evaluated in the three composite populations in the F_1, F_2, and F_3 generations separately and combined. Because heterosis did not differ ($p>0.05$) between generations, only the results from analysis of combined (F_1, F_2, and F_3) generations of females 2 yr old or older are presented in table 11. Traits included actual weight, weight adjusted to a common condition score, hip height, and condition. The effects of heterosis were generally important ($p<0.05$) for all traits in F_1, F_2, and F_3

Table 10. Effects of heterosis on fetal death based on females palpated pregnant

Linear contrasts	Fetal death loss (%) in dams that were: 2 yr old	5 or more yr old	All ages
Heterosis			
MARC I			
F_1 minus purebreds†	0.0	1.0	0.7
F_2 & F_3 minus purebreds†	.8	–1.0	–.8
Observed minus expected‡	.8	–1.9	–1.4
MARC II			
F_1 minus purebreds†	–1.0	.3	.7
F_2 & F_3 minus purebreds†	–1.4	–.2	.1
Observed minus expected‡	–.6	–.4	–.5
MARC III			
F_1 minus purebreds†	0	–3.2**	–1.3
F_2 & F_3 minus purebreds†	–5.1**	–11.2**	–5.1**
Observed minus expected‡	–5.1**	–8.6**	–4.0**
Mean heterosis, all composites			
F_1 minus purebreds†	–.3	–.6	0
F_2 & F_3 minus purebreds†	–1.9*	–4.1**	–2.0**
Observed minus expected‡	–1.6§	–3.6**	–2.0**

†F_1-generation females producing F_2-generation progeny and combined F_2- & F_3-generation females producing F_3- & F_4-generation progeny.

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

§$p<0.10$.

*$p<0.05$.

**$p<0.01$.

generations separately and combined in the three composite populations. Although the estimates of heterosis for these traits in 1-yr-old females are not presented, generally the magnitude of heterosis observed at 1 yr did not differ from that observed at 2–7 or more yr old. Thus, heterosis effects on weight did not change after the females were 1 yr old.

Adjusting weight to a common condition score resulted in an average reduction by about one-fourth of heterosis effects on actual weight. In other words, about one-fourth of the effects of heterosis on weight resulted from the effects of heterosis on condition score. Although estimates of heterosis are not presented separately for each of the three generations of 1-yr-old females or females age 2 and greater and for

Table 11. Effects of heterosis on actual weight, adjusted weight, hip height, and condition score in females 2–7 or more yr old with composite generations combined

Linear contrasts	Actual weight (lb)	Adjusted weight‡ (lb)	Hip height (inches)	Condition score§
Heterosis†				
MARC I				
F_1, F_2, & F_3 minus purebreds	46**	34**	0.4**	0.4**
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**

†Heterosis effects did not differ between generations.
‡Adjusted to a common condition score.
§Evaluated on a scale of 1 to 9, 9 = highest, 1 = lowest.
*$p<0.05$.
**$p<0.01$.

the mean of the three populations, retained heterosis in the F_3 generation did not differ ($p>0.05$) from genetic expectation based on retained heterozygosity. These results support the hypothesis that the effects of heterosis on actual weight, adjusted weight, hip height, and condition score of females can be accounted for by the dominance effects of genes.

Retained Heterosis for Milk Yield and 200-Day Weight of Progeny

Retained heterosis in F_2-generation females nursing F_3-generation progeny was evaluated in females ages 3, 4, and 5 or more yr old. As indicated in table 1, for F_2-females nursing F_3-generation progeny the genetic expectation for retained heterosis averages 0.76 of the F_1 level. 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 three composite populations. Average effects of retained heterosis for the three populations on 12-hr milk yield was 1.48 lb (14.5 percent), and on 200-day calf weight it was 34 lb (6.9 percent). Adjusting 200-day weight of progeny to a common estimated 200-day milk yield resulted in mean retained heterosis in the three populations of 14 lb, suggesting that about 59 percent of the retained heterosis effects observed for 200-day weight of progeny was accounted for through retained heterosis effects on milk yield.

Retained Heterosis for Growth, Carcass, and Meat Traits

Retained heterosis for growth, carcass, and meat traits was evaluated in castrate males from the F_3 generation (tables 13–16). As indicated in table 1, genetic expectation for retained heterosis in the F_3 generation of the three composites averages 0.76 of the F_1 level. Retained heterosis was important in each of the three composites and for the mean of the three composites for initial weight, final weight, average daily gain (ADG), carcass weight, rib-eye

Table 12. Effects of heterosis on milk yield and 200-day weight of progeny (F_2-generation females nursing F_3-generation progeny)

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

†Adjusted to a common estimated milk yield.

*$p<0.05$.

**$p<0.01$.

area, and estimated kidney, pelvic, and heart fat (table 13). Retained heterosis was significant for marbling score in the MARC II population but not in either of the other two composites (table 13). There was no retained heterosis for adjusted fat thickness at the 12th rib or for dressing percentage.

Retained heterosis was significant for weight of totally trimmed retail product, fat trim, and bone at 0.0 inches fat trim (table 14) and for weight of carcass lean, carcass fat, and carcass bone in the three composites (table 15). When evaluated on an age constant basis, the MARC II and MARC III populations had a significantly smaller percentage of retail product and percentage of carcass lean and a significantly greater percentage of fat trim and carcass fat than the mean of parental purebreds. In contrast, the MARC I population did not differ from parental purebreds in carcass composition. When carcass composition was adjusted for the effects of carcass weight, MARC II and MARC III populations did not differ from the mean of contributing purebreds in carcass composition. Thus, the effects of retained heterosis on carcass composition in MARC II and MARC III populations were through heterosis effects on carcass weight. Generally, the composites had a smaller percentage of bone and greater bone weight than the mean of contributing purebreds.

Effects of retained heterosis on traits relating to carcass and meat quality are presented in table 16. Table 13 shows that the MARC II population had a significantly higher marbling score than contributing purebreds, and table 16 shows significantly more fat in the longissimus muscle, as determined by chemical analysis. Results reveal the higher percentage of fat in MARC II and MARC III populations than in contributing purebreds, whereas composite MARC I populations did not differ ($p>0.05$) from contributing purebreds.

Generally, the effects of retained heterosis on carcass and meat quality traits were not important (table 16). For the MARC III population, however, the

Table 13. Effects of retained heterosis on growth and carcass traits of F_3-generation progeny

Linear contrasts	Initial weight (lb)	Final weight (lb)	Average daily weight gain (lb)	Carcass weight (lb)	Dressing percent-age (%)	Adjusted fat[†] (inches)	Rib-eye area[‡] (inches^2)	Kidney, pelvic, and heart fat[§] (%)	Marb-ling score
Heterosis									
MARC I minus purebreds	30.2**	45.9**	0.07*	29.5**	0.08	–0.05	0.54**	0.29**	–0.03
MARC II minus purebreds	51.2**	67.7**	.06	42.3**	.13	.08	.43**	.33**	.15**
MARC III minus purebreds	22.9**	37.0**	.06	26.2**	.29	.08	.48**	.28**	.04
Mean heterosis	34.8**	50.3**	.06**	32.6**	.17	.02	.48**	.30**	.05

[†]Adjusted fat thickness at 12th rib.

[‡]Area of the longissimus muscle.

[§]Estimate of kidney, pelvic, and heart fat.

[‖]$p<0.10$.

*$p<0.05$.

**$p<0.01$.

Table 14. Effects of retained heterosis on carcass composition of F_3-generation progeny

Linear contrasts	Retail product[†]		Fat trim[‡]		Bone	
	%	lb	%	lb	%	lb
Heterosis						
MARC I minus purebreds	–0.11	18.1**	0.49	9.3**	–0.38**	1.5
MARC II minus purebreds	–1.90**	12.6**	2.35**	26.7**	–.44**	3.1**
MARC III minus purebreds	–.89**	10.1*	1.00**	14.1**	–.1	3.3**
Mean heterosis	–.97**	13.7**	1.28**	16.5**	–.31**	2.6**

[†]Totally trimmed retail product (0.0 inches fat) includes steaks and roasts plus lean trim adjusted to 20-percent fat based on chemical analysis of lean trim.

[‡]All subcutaneous (0.0 inch) and accessible intermuscular fat removed.

*$p<0.05$.

**$p<0.01$.

Table 15. Effects of retained heterosis on carcass lean, carcass fat, and carcass bone of F_3-generation progeny

Linear contrasts	Lean[†]		Fat[‡]		Bone	
	%	lb	%	lb	%	lb
Heterosis						
MARC I minus purebreds	–0.12	16.0**	0.50	11.3**	–0.38**	1.6
MARC II minus purebreds	–1.68**	11.4**	2.12**	27.8**	–.44**	3.0**
MARC III minus purebreds	–.77**	9.4**	.87*	14.9**	–.10	3.3**
Mean heterosis	–.86**	12.3**	1.16**	18.0**	–.31**	2.6**

[†]Carcass lean includes steaks and roasts to 0 inches of fat cover plus fat-free lean trim based on chemical analysis of lean trim.

[‡]Carcass fat includes fat trim plus fat in lean trim (estimated by chemical analysis of lean trim).

*$p<0.05$.

**$p<0.01$.

Table 16. Effects of retained heterosis on carcass and meat quality traits of F_3-generation progeny

Linear contrasts	Adjusted fat (inches)	Marbling score[†]	Long. muscle fat (%)[‡]	Fat in 9–11 rib cut (%)[§]	Shear force (lb)	Sensory panel scores Tenderness	Sensory panel scores Juiciness	Sensory panel scores Flavor
Heterosis								
MARC I minus purebreds	–0.01	–0.03	–0.08	0.05	–0.33	0.16	0.00	0.01
MARC II minus purebreds	.01	.15**	.29*	2.28**	–.35	.02	–.02	.08*
MARC III minus purebreds	.01	.04	.04	1.37**	.97**	–.24**	–.07	–.02
Mean heterosis	.00	.05	.08	1.23**	.09	–.02	–.03	.02

[†]A marbling score of 4.00–4.90 = slight, 5.00–5.90 = small.

[‡]Chemical fat in longissimus muscle.

[§]Chemical fat in 9–11 rib cut.

[‖]Force required to shear a 0.5-inch core.

*$p<0.05$.

**$p<0.01$.

effects of retained heterosis were significant for greater shear force and lower sensory panel score for tenderness. Table 37 shows that two parental breeds of the MARC III population (Red Poll and Pinzgauer) may have been primarily responsible for these significant differences since these breeds had among the lowest values for shear force and the highest values for tenderness. These differences are unlikely to be the result of sampling error among steaks because shear force and sensory panel tenderness scores were evaluated on different steaks from the longissimus muscle.

Retained Heterosis for Different Measures of Gain Efficiency

The effects of retained heterosis on different measures of gain efficiency are presented in table 17 for F_3-generation castrate males. Serial slaughter of castrate males at average ages of 407, 427, 448, and 470 days, with an overall average age of 438 days, permitted adjustment by regression to evaluate efficiency of gain to different end points. Retained heterosis was not consistent among the composite populations for the different measures of gain efficiency. Because of their higher initial weight, the MARC I and MARC III populations were less efficient than the mean of parental purebreds in the time constant period (0 to 207 days). To fat constant end points of marbling score and percentage fat in the longissimus muscle (table 17), the MARC II population was more efficient and the MARC I and MARC III populations less efficient than the mean of parental purebreds in liveweight gain.

Generally, more favorable levels of retained heterosis were observed for the composite MARC II population than for composite MARC I and MARC III populations for different measures of gain efficiency. The generally lower gain per megacalories of metabolizable energy in composites relative to the mean of parental purebreds in some measures of gain efficiency is due to higher initial weights and thus to higher maintenance requirements during the evaluation period. The higher initial weights resulted from retained individual (H^i) and maternal (H^m) heterosis. Although retained individual heterosis affected postweaning gain (table 13), it was not sufficient to offset the higher maintenance requirement associated with higher initial weight for most measures of gain efficiency.

Differences Among Parental Breeds

Differences in Growth Traits (Males and Females)

Differences among parental breeds include the sum of the additive direct and additive maternal genetic effects ($G^i + G^m$). The effects of breed group were important (p<0.01) for all growth traits evaluated in females (table 18) and males (table 19). Weights were adjusted to a mean age of dam of 3.5 yr.

The approximate differences between means, of parental breeds and of all breed groups, required for statistical significance (D.05) are presented in table 18 for females and table 19 for males. Means for birth weight of females ranged from 71.9 lb in Angus to 97.7 lb in Pinzgauer and of males from 77.0 lb in Angus to 108.0 lb in Pinzgauer. Means for 200-day weight of females ranged from 392 lb in Hereford to 536 lb in Gelbvieh and of males from 419 lb in Hereford to 571 lb in Gelbvieh. Means for 368-day weight of females ranged from 631 lb in Hereford to 787 lb in Simmental and Charolais and of males from 842 lb in Hereford to 1,052 lb in Simmental. Means for hip height of females at 368 days ranged from 44.1 inches in Hereford to 48.8 inches in Braunvieh, Gelbvieh, Simmental, and Charolais and of males from 45.7 inches in Hereford to 50.8 inches in Simmental. For condition score at 368 days, means for females ranged from 3.7 in Limousin to 5.9 in Angus and for males from 3.3 in Limousin to 5.6 in Hereford and Angus. Means for muscle score of males at 368 days ranged from 4.0 in Red Poll to 6.9 in Limousin. Muscle score was not recorded in females at 368 days.

Differences for each sex among parental breeds in birth weight, 200-day weight, and 368-day weight suggest great opportunity to select among breeds for growth traits in combined additive direct (G^i) and additive maternal (G^m) genetic effects.

Differences in Female Puberty Traits and Male Scrotal Circumference

Differences among parental breeds reported here include the sum of additive direct and additive maternal genetic effects ($G^i + G^m$).

Table 17. Retained heterosis for different measures of gain efficiency of F_3-generation castrate males

Linear contrasts	Live-weight gain (LWG) and retail product gain (RPG) per Mcal of ME						
	Time constant 0 to 207 days		Gain constant From 684 to 1,191 lb	To a carcass weight of 734 lb	To a retail product wt. of 463 lb (0 inches fat trim)	To a marbling score of 5.00	To a longissimus muscle fat content of 4%
	LWG	RPG	LWG	LWG	RPG	LWG	LWG
Heterosis	grams						
MARC I minus purebreds	–2.37**	–0.90*	0.14	–1.23*	1.13*	–2.71**	–3.12**
MARC II minus purebreds	.12	.29	2.57**	1.54*	.35	.98†	1.64*
MARC III minus purebreds	–1.00†	–.84*	.34	–.10	.28	–.69	–.91
Mean heterosis	–1.08**	–.48†	1.02*	.07	.59†	–.81*	–.80†

†$p<0.1$.
*$p<0.05$.
**$p<0.01$.

Puberty in females. Means for different measures of puberty are presented by breed group in table 20. The approximate difference required for statistical significance (D.05) of parental breeds and of all breed groups is also listed. The percentage of parental breeds reaching puberty by 368 days (the end of the feeding period), 410 days (the start of the breeding season), and 452 days (the end of the breeding season) was, respectively, 65.3 (range from 31.7 in Hereford to 89.7 in Braunvieh), 72.9 (range from 39.9 in Hereford to 94.2 in Braunvieh), and 92.6 (range from 79.3 in Limousin to 100 in Braunvieh). Parental breed differences in adjusted age at puberty ranged from 350 days in Braunvieh to 411 days in Hereford, with a mean of 376 days. This range of 61 days between breed group means is of major importance when females are exposed to mating as yearlings in a restricted 42-day mating season. Of equal interest and significance is the difference observed among breeds in the percentage that reached puberty at the start of the breeding season (410 days). This parental breed difference (39.9 percent vs. 94.2 percent) is more than twice as great as the heterosis effect on percentage reaching puberty at the start of the breeding season (410 days). These results suggest a high relationship among breeds between age at puberty and breed history of selection for milk production.

The parental breed differences in adjusted age and weight at puberty reported here are likely underestimated because observations on date of first estrus were not started until March 1. We can assume that a higher percentage of breed groups that reach puberty at younger ages had already reached puberty before observations for estrus were started than for breed groups that reached puberty later. Cumulative percentages of groups that reached puberty by 368, 410, and 452 days are not as likely to be underestimated. Thus, greater attention should focus on differences among cumulative percentages of groups that reached puberty by 368, 410, and 452 days than on differences in adjusted age at puberty.

Table 18. Breed group means for growth traits of females

Breed group	Number	Birth weight (lb)	200-day weight (lb)	368-day weight (lb)	368-day hip height (inches)	368-day condition score†
Overall mean	7,785	87.8	490	750	47.2	5.2
Red Poll	521	80.7	445	675	45.7	5.0
Hereford	537	76.5	392	631	44.1	5.6
Angus	780	71.9	423	681	44.5	5.9
Limousin	526	82.9	450	692	47.2	3.7
Braunvieh	490	94.8	525	776	48.8	4.6
Pinzgauer	282	97.7	520	776	48.4	4.6
Gelbvieh	439	92.2	536	785	48.8	4.8
Simmental	506	91.3	527	787	48.8	4.6
Charolais	538	95.0	512	787	48.8	4.7
D.05‡		2.6	11.5	17.4	.4	.2
MARC I						
F_1	239	92.2	514	794	48.0	5.5
F_2	430	92.4	512	785	48.0	5.2
F_3 & F_4	304	93.0	514	789	48.4	5.1
MARC II						
F_1	331	85.6	518	778	47.2	6.1
F_2	536	88.4	494	765	46.8	5.8
F_3 & F_4	436	87.3	500	770	47.2	5.7
MARC III						
F_1	243	85.6	476	741	46.4	5.7
F_2	394	85.6	478	743	46.1	5.8
F_3 & F_4	253	86.2	472	736	46.1	5.6
D.05§		3.3	14.1	21.4	.5	.3

†Evaluated on a scale of 1 to 9, 9 = highest, 1 = lowest.

‡D.05 is the approximate difference between means of parental breeds required for significance.

§D.05 is the approximate difference between means of breed groups required for significance.

Results from a separate analysis indicate that breed group differences in age at puberty are largely independent of breed group differences in weight at 368 days.

Scrotal circumference in males. Means of scrotal circumference are presented by breed group in table 20, along with the difference (D.05) required for statistical significance between means of parental breeds and of all breed groups. Mean scrotal circumference adjusted for age of dam by regression (linear, 0.434; quadratic, –0.084) (3.6 yr) and for date of birth by regression (linear, –0.043) (354 days) was 32.4 cm for all parental breeds. Scrotal circumference at 368 days ranged from 29.0 cm in Limousin to 34.1 cm in Gelbvieh.

Table 19. Breed group means for growth traits of males

Breed group	Number	Birth weight (lb)	200-day weight (lb)	368-day weight (lb)	368-day hip height (inches)	368-day condition score†	368-day muscling score†
Overall mean	7,055	94.2	523	986	48.8	4.9	5.3
Red Poll	419	86.2	487	902	47.6	5.0	4.0
Hereford	489	81.8	419	842	45.7	5.6	4.6
Angus	754	77.0	450	882	46.1	5.6	5.1
Limousin	477	90.0	481	911	49.2	3.3	6.9
Braunvieh	454	102.1	556	1,019	50.4	4.2	5.0
Pinzgauer	222	108.0	560	1,039	49.6	4.8	4.8
Gelbvieh	377	98.1	571	1,036	50.4	4.3	5.6
Simmental	451	98.1	562	1,052	50.8	4.6	5.7
Charolais	421	102.3	542	1,034	50.4	4.1	5.9
D.05‡		3.1	12.8	22.0	.4	.2	.2
MARC I							
F_1	242	95.7	536	1,014	49.6	4.7	5.8
F_2	448	97.7	538	1,008	49.6	4.5	5.7
F_3 & F_4	247	97.9	534	990	49.6	4.4	5.6
MARC II							
F_1	344	91.9	567	1,028	49.6	5.5	5.2
F_2	555	95.0	529	1,008	48.8	5.6	5.3
F_3 & F_4	403	94.4	538	1,025	49.2	5.5	5.2
MARC III							
F_1	237	92.4	516	975	48.4	5.7	4.9
F_2	381	92.8	518	986	48.0	5.6	4.7
F_3 & F_4	134	93.5	512	988	48.0	5.4	4.8
D.05§		3.7	15.4	26.5	.5	.3	.2

†Evaluated on a scale of 1 to 9, 9 = highest, 1 = lowest.
‡D.05 is the approximate difference between means of parental breeds required for significance.
§D.05 is the approximate difference between means of breed groups required for significance.

Significant differences among breed groups remained in scrotal circumference after adjusting by regression for differences in weight at 368 days. This result suggests that differences among breed groups in scrotal circumference are influenced only in part by breed group differences in weight at 368 days.

Correlations. Correlation coefficients between group means for puberty traits in females and scrotal circumference in males were 0.88 ($p<0.01$) or higher (table 21). Correlation coefficients between breed group means for puberty traits in females and percentage of yearlings pregnant were 0.87 ($p<0.01$) or higher (table 22).

Table 20. Breed group means for puberty traits in females and scrotal circumference in males

Breed group	Number of females	Puberty traits in females: Percent reaching puberty by: 368 days	410 days†	452 days‡	Adjusted age§ (days)	Adjusted weight§ (lb)	Number of males	Scrotal circumference‖ (cm)
Overall mean	6,034	72.4	79.8	94.8	370	736	6,649	32.8
Red Poll	450	83.7	88.6	97.4	359	650	410	33.1
Hereford	427	31.7	39.9	82.8	411	695	472	30.3
Angus	670	46.1	57.4	93.3	393	697	738	32.1
Limousin	403	36.1	44.0	79.3	408	743	464	29.0
Braunvieh	359	89.7	94.2	100.0	350	732	444	33.7
Pinzgauer	246	85.8	92.1	96.6	360	739	215	33.0
Gelbvieh	330	86.3	92.9	99.1	353	745	366	34.1
Simmental	358	77.4	86.8	98.0	363	758	437	33.7
Charolais	406	50.7	60.6	86.5	391	814	406	32.2
Parental breed mean		65.3	72.9	92.6	376	730		32.4
D.05¶		11.0	10.0	6.2	8.1	20.7		.7
MARC I								
F_1	182	78.0	85.5	99.2	366	767	240	32.5
F_2	332	76.3	85.8	98.7	366	765	405	32.7
F_3 & F_4††	190	73.4	83.0	94.6	367	763	201	33.0††
MARC II								
F_1	274	89.8	95.2	97.6	360	745	340	34.1
F_2	410	82.6	89.3	97.4	361	738	502	33.6
F_3 & F_4††	239	80.3	86.9	95.3	360	739	344	33.8††
MARC III								
F_1	243	86.2	91.2	100.0	361	710	233	33.6
F_2	358	77.6	84.0	95.1	368	723	330	32.8
F_3 & F_4††	157	71.8	79.0	94.4	370	723	102	32.8††
D.05‡‡		13.5	12.4	7.7	10.0	25.6		.9

† 410 days = start of breeding season.

‡ 452 days = end of breeding season.

§ Adjusted to a 100-percent puberty basis.

‖ Adjusted to a common age.

¶ D.05 is the approximate difference between means of parental breeds required for significance.

†† F_4-generation for scrotal circumference only.

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

General. These results reveal large differences among breeds in percentage reaching puberty at 368, 410, and 452 days; in age of females at puberty; and in scrotal circumference of males and show a high correlation among breed group means for these traits. Breed differences in these traits provide considerable opportunity to use genetic differences among breeds to optimize additive genetic value to meet a wide range of production situations.

Adjusting female age at puberty for differences in 368-day weight by regression had little effect on breed rank or variation among breeds for age at puberty, suggesting that differences in age at puberty among breeds is largely independent of breed differences in growth rate to 368 days. Adjusting scrotal measurements by regression for differences in weight at 368 days resulted in some reduction in variation among breeds in scrotal circumference (the range was reduced from 5.1 to 3.7 cm). However, significant breed differences in scrotal circumference were still present. Although differences in scrotal circumference among breeds are partially attributable to breed differences in weight at 368 days, there are important differences ($p<0.01$) among breeds in scrotal circumference that are independent of weight.

Differences in Birth Weight, Birth Date, Dystocia, and Survival

Differences among parental breeds include additive direct genetic effects and additive maternal genetic effects ($G^i + G^m$).

Table 21. Correlation coefficients among parental breed means for puberty traits in females and scrotal circumference in males

Female puberty traits	Scrotal circumference (cm)
Percentage in puberty at 368 days	0.88**
Percentage in puberty at 410 days	.91**
Percentage in puberty at 452 days	.95**
Age at puberty (in days)	–.91**
Age at puberty (adjusted for 368-day weight)	–.91**

**$p<0.01$.

Table 22. Correlation coefficients among parental breed means for puberty traits and percentage of females pregnant as yearlings

Female puberty traits	Pregnancy (%)
Percentage in puberty at 368 days	0.87**
Percentage in puberty at 410 days	.89**
Percentage in puberty at 452 days	.97**
Age at puberty (in days)	–.89**
Age at puberty (adjusted for 368-day weight)	–.88**

**$p<0.01$.

Calves with 2-yr-old dams. Table 23 gives birth and survival data for calves from 2-yr-old dams. The mean birth weight of parental breed calves was 83.1 lb. Birth weight ranged from 69.4 lb in Angus to 93.3 lb in Braunvieh. The mean Julian birth date for parental breed calves was 79. The Julian birth date ranged from 74 in Red Poll and Pinzgauer to 88 in Limousin. Breed rank for birth date is highly associated with age at puberty or gestation length or both.

The mean for calving difficulty (percentage of dams requiring assistance) in parental breeds was 52.6 percent. Calving difficulty ranged from 31.8 percent in Angus to 73.8 percent in Braunvieh. Mean calf survival at weaning for parental breeds was 80.4 percent. Survival at weaning ranged from 74.3 percent in Hereford to 85.4 percent in Red Poll. Results from a separate analysis showed that the effects of breed group were important ($p<0.01$) for percentage calving difficulty and survival at birth, at 72 hr, and at weaning, independent of breed group effects on birth weight. The sex of the calf had an important effect ($p<0.01$) on percentage calving difficulty, independent of the effects of sex on birth weight. Sixty-two percent of the male calves and 46 percent of the female calves (adjusted to a common birth weight) required assistance.

Calf weight at birth had an important effect on birthing difficulty and calf survival. Each 1-lb increase in birth weight resulted in a 1.9-percent (linear) increase in the need for assistance at birth. The negative linear and quadratic (curvilinear) regressions ($p<0.01$) of survival percentage at birth, at 72 hr, and at weaning on birth weight reflect the importance of birth weight on calf survival percentage and the curvilinearity of the effect. The significant effect of breed group on percentage calving difficulty and survival at birth, at 72 hr, and at weaning (adjusted to a common birth weight) reflect important differences among breed groups for these traits, independent of the effects of breed group on birth weight. Thus, there appears to be some opportunity to reduce dystocia and to increase calf survival rate by considering factors other than birth weight, such as anatomical characteristics of the dam and the calf. Similarly, the greater percentage of calving difficulty in the birth of males at a common birth weight shows that sex of the calf has an important effect, independent of the effects of sex on birth weight.

Calves with dams 3 yr old or older. The mean birth weight of parental breed calves born from dams 3 or more yr old was 92.6 lb. Birth weight ranged from 76.3 lb in Angus to 104.5 lb in Pinzgauer (table 24). The mean birth date (Julian) of parental breed calves was 105. Julian birth date ranged from 99 in Angus to 109 in Limousin and Braunvieh. The mean calving difficulty of parental breed calves was 8.6 percent. Calving difficulty ranged from 0.9 percent in Angus to 15.9 percent in Pinzgauer. Mean calf survival at weaning of parental breed calves was 92.6 percent. Survival at weaning ranged from 88.1 percent in Simmental to 95.6 percent in Red Poll.

In a separate analysis, gestation length, birth date, birth weight, calving difficulty, and survival at birth and at 72 hr were analyzed for calves born to dams 3 or more yr old. Data on gestation length were not available on calves born from 2-yr-old dams. Breed group effects were significant for gestation length, birth date, birth weight, and calving difficulty but not for survival at birth and at 72 hr. A regression analysis of these traits on gestation length, gestation length within sex, and gestation length within breed group was conducted. The analyses revealed that the linear regressions of all traits on gestation length (days) were significant; that is, birth date, 1 day; birth weight, 0.9 lb; survival at birth, 0.1 percent; and survival at 72 hr, 0.2 percent. Gestation length accounted for 90 percent of the breed group variation in birth date, 14 percent of the breed group variation in birth weight, and 31 percent of the breed group variation in percentage calving difficulty.

Calves with dams of all ages. Mean birth weight of parental breed calves from dams of all ages was 90.2 lb. Birth weight ranged from 74.7 lb in Angus to 101.9 lb in Pinzgauer (table 25). Mean birth date (Julian) of parental breed calves from dams of all ages was 99. Julian birth date ranged from 93 in Angus to 104 in Limousin. Mean calving difficulty of parental breed calves from dams of all ages was 19.7 percent. Calving difficulty ranged from 8.8 percent in Angus to 28.5 percent in Braunvieh. Mean calf survival at weaning of parental breed calves with dams of all ages was 89.7 percent.

Table 23. Breed group means for birth and survival of calves from 2-yr-old dams

Breed group	Number of births	Calf birth weight (lb)	Calf birth date (Julian)	Calving difficulty† (%)	Survival of calves (%) At birth	At 72 hr	At weaning
Overall mean	4,140	83.8	78	52.5	95.5	89.0	81.0
Red Poll	268	76.7	74	54.0	95.7	90.6	85.4
Hereford	242	74.5	84	49.1	93.2	86.2	74.3
Angus	433	69.4	75	31.8	93.0	86.2	81.4
Limousin	210	79.4	88	40.6	96.0	85.1	76.2
Braunvieh	287	93.3	80	73.8	98.2	90.8	81.0
Pinzgauer	250	92.4	74	62.1	95.2	88.9	82.3
Gelbvieh	321	88.4	79	60.5	93.6	88.1	79.2
Simmental	312	85.3	79	52.5	97.9	91.2	80.9
Charolais	261	88.4	78	48.6	98.0	92.8	82.8
Parental breed mean		83.1	79	52.6	95.6	88.9	80.4
D.05‡		3.3	3.3	13.2	5.1	8.0	9.9
MARC I							
F_1§	167	88.4	77	55.5	95.4	89.8	82.1
F_2 & F_3§	308	90.0	79	56.6	96.8	90.7	82.9
MARC II							
F_1§	232	83.8	76	50.6	94.6	86.8	78.4
F_2 & F_3§	393	85.8	75	57.1	95.1	87.8	83.1
MARC III							
F_1§	192	80.9	72	46.2	95.1	89.5	84.4
F_2 & F_3§	264	81.4	76	48.4	95.2	90.1	81.2
D.05¶		3.7	3.7	14.9	5.8	9.1	11.2

† Percentage of dams requiring assistance.

‡ D.05 is the approximate difference between means of parental breeds required for significance.

§ F_1-generation females producing F_2-generation progeny and combined F_2- & F_3-generation females producing F_3- & F_4-generation progeny.

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

Table 24. Breed group means for birth and survival of calves from dams 3 or more years old

Breed group	Number of births	Calf birth weight (lb)	Gestation length (days)	Calf birth date (Julian)	Calving difficulty† (%)	Survival of calves (%) At birth	At 72 hr	At weaning
Overall mean	10,710	93.3	287	104	8.1	98.2	96.3	93.3
Red Poll	706	86.2	288	103	3.0	98.7	97.4	95.6
Hereford	818	81.1	288	107	5.1	97.6	95.7	93.9
Angus	1,133	76.3	283	99	.9	98.5	94.9	91.7
Limousin	871	88.6	289	109	7.2	98.3	96.6	93.2
Braunvieh	714	100.1	290	109	13.2	98.2	96.9	91.9
Pinzgauer	391	104.5	287	103	15.9	96.1	94.4	91.6
Gelbvieh	677	97.7	287	107	8.3	99.2	97.6	93.7
Simmental	671	97.0	287	106	14.4	97.0	93.4	88.1
Charolais	784	101.4	286	105	9.8	98.8	97.3	93.4
Parental breed mean		92.6	287	105	8.6	98.0	96.0	92.6
D.05‡		2.4	1.6	2.8	5.1	2.0	2.8	4.0
MARC I								
F_1§	828	98.1	287	106	8.2	97.2	96.2	93.3
F_2 & F_3§	453	97.9	288	104	8.9	98.6	96.5	94.9
MARC II								
F_1§	1,031	94.2	287	102	8.3	98.7	96.9	94.8
F_2 & F_3§	662	93.3	287	104	9.3	98.8	96.5	93.8
MARC III								
F_1§	664	91.5	287	103	3.3	98.9	98.1	96.0
F_2 & F_3§	307	91.7	286	100	6.1	97.9	96.2	93.2
D.05¶		2.9	1.9	3.3	5.8	2.3	3.2	4.7

† Percentage of dams requiring assistance.

‡ D.05 is the approximate difference between means of parental breeds required for significance.

§ F_1-generation females producing F_2-generation progeny and combined F_2- & F_3-generation females producing F_3- & F_4-generation progeny.

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

Survival at weaning ranged from 86.4 percent in Simmental to 93.4 percent in Red Poll.

General. These results show large differences among breeds in percentage calving difficulty, particularly in calves from 2-yr-old dams. While the means are not presented, calves with difficult births from 2-yr-old dams were significantly heavier at birth and had significantly lower survival rates at 72 hr and at weaning than calves from 2-yr-old dams that did not have difficult births. Large differences were observed among breed groups in calving difficulty and calf survival, independent of the effects of breed group on birth weight. This result suggests some opportunity to reduce calving diffi-

Table 25. Breed group means for birth and survival of calves from dams of all ages

Breed group	Number of births	Calf birth weight (lb)	Calf birth date (Julian)	Calving difficulty† (%)	Survival of calves (%) At birth	At 72 hr	At weaning
Overall mean	14,850	91.1	98	19.2	97.6	94.5	90.4
Red Poll	974	83.8	96	15.9	98.0	95.9	93.4
Hereford	1,060	79.4	101	16.5	96.6	93.3	89.2
Angus	1,566	74.7	93	8.8	97.2	92.8	89.3
Limousin	1,081	86.4	104	15.7	97.8	93.8	89.2
Braunvieh	1,001	98.6	102	28.5	98.3	95.5	89.3
Pinzgauer	641	101.9	96	27.4	96.0	92.9	89.0
Gelbvieh	998	95.2	100	21.5	97.9	95.3	90.4
Simmental	983	94.2	99	23.9	97.3	92.9	86.4
Charolais	1,045	98.1	98	19.5	98.7	96.3	90.9
Parental breed mean		90.2	99	19.7	97.5	94.3	89.7
D.05‡		2.2	2.4	5.8	2.2	3.2	4.2
MARC I							
F_1§	995	95.9	98	19.5	97.0	94.7	90.8
F_2 & F_3§	761	96.1	98	20.7	98.2	95.1	92.0
MARC II							
F_1§	1,263	91.7	96	19.1	97.8	94.1	90.6
F_2 & F_3§	1,055	91.7	96	21.0	97.9	94.5	91.4
MARC III							
F_1§	856	89.1	94	13.9	98.1	96.0	93.5
F_2 & F_3§	571	89.3	94	16.7	97.3	94.7	90.3
D.05¶		2.6	2.7	6.6	2.5	3.7	4.8

† Percentage of dams requiring assistance.
‡ D.05 is the approximate difference between means of parental breeds required for significance.
§ F_1-generation females producing F_2-generation progeny and combined F_2- & F_3-generation females producing F_3- & F_4-generation progeny.
¶D.05 is the approximate difference between means of all breed groups required for significance.

culty and to increase calf survival by considering factors other than birth weight such as anatomical characteristics of the dam and calf. Similarly, greater calving difficulty was observed in male calves than in female calves, independent of sex effects on birth weight, indicating that anatomical differences between sexes likely contribute to dystocia. In a separate analysis of births from 2-yr-old females, calf survival at weaning was lowest ($p<0.05$) in the smallest and largest birth weight classes and did not differ ($p>0.05$) among intermediate birth weight classes. These results document that intermediate birth weights are optimum for increased survival.

Differences in Reproductive and Maternal Traits

Differences among parental breeds include additive direct genetic effects and additive maternal genetic effects ($G^i + G^m$).

Because age has an important effect on reproductive and maternal traits of different breeds, results are presented for females of three different ages—2 yr old, 5 or more yr old, and all ages combined.

Females 2 yr old. Means of parental breeds and of all breed groups are presented in table 26, along with the approximate difference between means required for significance.

Large differences ($p<0.01$) were observed among parental breeds for the percentage of females pregnant when bred as yearlings in a 42-day mating season. The means ranged from 54.7 percent in Limousin to 85.6 percent in Gelbvieh. Breed group means for percentage of female yearlings pregnant were highly associated ($p<0.01$) with breed group means in measures of puberty (table 22). Large differences ($p<0.01$) in the percentage of calves born were observed among parental breeds. The differences between the percentage of pregnancies and the percentage of calves born (an average of 2.6 percent) reflect errors in diagnosing pregnancy by rectal palpation and fetal losses between pregnancy diagnosis and parturition. Rank of parental breeds for percentage of calves born was similar to the rank of breeds for percentage pregnant—Limousin had the lowest birth rate (53.0 percent) and Gelbvieh the highest (83.2 percent). Large differences ($p<0.01$) were observed among parental breeds in the percentage of calves surviving to weaning. Differences between the percentage of calves born and the percentage surviving to weaning reflect calf mortality. Calf mortality averaged 13.7 percent and included calves that were dead at birth. Rank of parental breeds for percentage of calf crop weaned was similar to the rank of breeds for calf crop born—Limousin had the lowest percentage (41.8 percent), and Braunvieh the highest (66.4 percent).

Large differences ($p<0.01$) were observed in 200-day calf weight per female exposed to breeding. These values reflect differences among parental breeds in the percentage of calves weaned and 200-day calf weight; that is, reproduction rate, calf survival, and preweaning growth for additive genetic maternal effects (G^m) and additive direct genetic effects (G^i). Because of the importance of fitness traits (that is, reproduction rate and survival) in contributing to this measure of output per female, there was considerable similarity in breed rank for 200-day calf weight per female exposed and measures of fitness. Hereford ranked lowest (178 lb) and Gelbvieh ranked highest (340 lb) in 200-day calf weight per female exposed to breeding.

Large differences ($p<0.01$) were observed in 200-day calf weight. Hereford ranked the lowest (378 lb) and Gelbvieh highest (506 lb). These values include breed differences in additive maternal genetic effects (G^m) and additive direct genetic effects (G^i) for preweaning growth.

Females 5 or more yr old. Means are presented by breed group in table 27, along with the approximate difference required for significance (D.05). Comparisons of differences can be made between parental breeds and between means of all breed groups. Because of the large differences among breeds in reproductive traits of 2-yr-old females associated with age differences at puberty (tables 21 and 22), it was desirable to evaluate breed differences in reproductive and maternal traits after the animals were mature (at an age of 5 to 10 yr old, at parturition).

Parental breed differences were large ($p<0.05$) for 200-day calf weight per female exposed to breeding. Hereford ranked lowest (348 lb) and Charolais highest (477 lb). However, Charolais, Braunvieh, Gelbvieh, Simmental, and Pinzgauer did not differ ($p>0.05$) from each other. The Hereford breed was lighter ($p<0.05$) than all breed groups except Angus,

Table 26. Breed group means for reproductive and maternal traits of females 2 yrs old

Breed group	Number of females	Percentage pregnant†	Calf crop born (%)†	Calf crop weaned (%)†	200-day calf weight per female exposed to breeding (lb)†	200-day calf weight (lb)
Overall mean	6,535	77.3	74.4	60.6	284	463
Red Poll	436	81.0	77.0	66.2	286	432
Hereford	453	64.1	62.3	46.8	178	378
Angus	685	77.9	75.4	61.8	249	402
Limousin	474	54.7	53.0	41.8	179	427
Braunvieh	426	83.0	80.3	66.4	334	500
Pinzgauer	373	81.6	79.3	64.1	314	486
Gelbvieh	458	85.6	83.2	66.2	340	506
Simmental	477	82.4	81.2	66.0	331	498
Charolais	476	72.3	67.2	56.2	269	478
Parental breed mean		75.8	73.2	59.5	276	456
D.05‡		10.5	11.4	11.6	54.0	11.5
MARC I						
F_1§	230	78.2	75.1	62.1	305	487
F_2 & F_3§	551	86.3	83.5	69.0	336	486
MARC II						
F_1§	331	73.9	71.3	56.7	269	472
F_2 & F_3§	714	74.8	71.8	59.1	288	484
MARC III						
F_1§	250	82.2	79.4	66.9	308	460
F_2 & F_3§	501	81.6	74.7	60.5	275	451
D.05ǁ		11.9	13.0	13.2	61.5	13.0

†Based on females exposed to breeding; pregnancy determined by rectal palpation.

‡D.05 is the approximate difference between means of parental breeds required for significance.

§F_1-generation females producing F_2-generation progeny and combined F_2- & F_3-generation females producing F_3- & F_4-generation progeny.

ǁD.05 is the approximate difference between means of all breed groups required for significance.

Table 27. Breed group means for reproductive and maternal traits of females 5 or more years old

Breed group	Number of females	Percentage pregnant†	Calf crop born (%)†	Calf crop weaned (%)†	200-day calf weight per female exposed to breeding (lb)†	200-day calf weight (lb)
Overall mean	7,920	90.8	87.4	83.0	438	528
Red Poll	607	89.6	86.1	84.2	411	489
Hereford	728	86.0	84.4	80.7	348	431
Angus	1,030	91.3	87.9	82.4	384	465
Limousin	736	87.8	87.0	82.6	406	491
Braunvieh	599	90.6	88.4	84.2	476	566
Pinzgauer	188	90.5	87.4	79.3	445	565
Gelbvieh	328	88.5	85.6	82.6	474	571
Simmental	516	87.8	84.8	78.8	453	575
Charolais	569	90.8	89.7	85.2	477	560
Parental breed mean		89.2	86.8	82.2	430	523
D.05‡		5.7	7.6	8.3	44.1	12.3
MARC I						
F_1§	624	92.9	92.1	86.6	473	546
F_2 & F_3§	202	95.2	92.5	88.6	484	546
MARC II						
F_1§	820	93.3	90.7	85.3	448	523
F_2 & F_3§	347	91.3	88.4	84.4	467	553
MARC III						
F_1§	522	92.4	86.5	83.0	427	516
F_2 & F_3§	104	94.4	80.8	77.4	406	525
D.05‖		6.6	8.7	9.5	50.9	14.3

† Based on females exposed to breeding; pregnancy determined by rectal palpation.

‡ D.05 is the approximate difference between means of parental breeds required for significance.

§ F_1-generation females producing F_2-generation progeny and combined F_2- & F_3-generation females producing F_3- & F_4-generation progeny.

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

and this difference approached significance ($p<0.10$).

Large parental breed differences ($p<0.01$) were observed for 200-day calf weight. Hereford (431 lb) was significantly lighter than all other breed groups. Simmental (575 lb) was significantly heavier ($p>0.05$) than the other breeds except for Braunvieh, Gelbvieh, and Pinzgauer.

Females of all ages. Means of reproductive and maternal traits are presented by breed group in table 28, along with the approximate difference (D.05) required for significance. Comparisons of differences can be made between parental breeds and between means of all breed groups.

Large differences ($p<0.01$) in the percentage of females pregnant were observed among parental breeds. Limousin had the lowest percentage (74.8 percent) and Red Poll the highest (86.6 percent). The Limousin and Hereford breeds did not differ ($p>0.05$) from each other, nor did the Red Poll, Braunvieh, Angus, Simmental, Charolais, Gelbvieh, and Pinzgauer. Large differences ($p<0.01$) were observed among parental breeds for calf crop born percentage. Limousin ranked lowest (73.4 percent) and Pinzgauer highest (83.7 percent). Again, the Limousin and Hereford breeds did not differ ($p>0.05$) from each other. The Red Poll, Braunvieh, Angus, Simmental, Charolais, Gelbvieh, and Pinzgauer did not differ ($p>0.05$) significantly. Large differences ($p<0.01$) were observed among parental breeds for calf crop weaned percentage. Limousin ranked lowest (66.0 percent) and Red Poll highest (76.2 percent). The means for Limousin, Hereford, and Simmental did not differ ($p>0.05$) from each other. The means for Red Poll, Braunvieh, Angus, Charolais, Gelbvieh, and Pinzgauer also did not differ ($p>0.05$) from each other. Differences between the calf crop born percentage and the calf crop weaned percentage reflect calf mortality and include calves that were dead at birth. The mean difference for all breeds was 8.0 percent. Simmental had the highest calf mortality rate (10.8 percent) and Red Poll the lowest (5.1 percent).

Large differences ($p<0.01$) were observed among parental breeds in 200-day calf weight per female exposed to breeding. Hereford ranked the lowest (280 lb) and Gelbvieh the highest (413 lb). Hereford ranked lower ($p<0.05$) than all other breed groups except Limousin. The difference between Hereford and Limousin, however, approached significance ($p<0.10$). Gelbvieh did not differ ($p>0.05$) from Pinzgauer, Braunvieh, and Charolais.

Large differences ($p<0.01$) were observed among parental breeds in 200-day calf weight. The Hereford breed was the lightest (407 lb) and was significantly lighter ($p<0.05$) than all other parental breeds. The Simmental and Gelbvieh breeds were the heaviest (544 lb) and were significantly heavier ($p<0.05$) than all parental breeds except Braunvieh.

General. For most of the traits measured for the three age groups, the differences among means for the parental breeds were greater for the 2-yr-old females than for the age groups "5 or more yr old" and "of all ages." Such was the case for pregnancy rate, percentage calf crop born, percentage calf crop weaned, and 200-day calf weight per female exposed to breeding. The large differences in pregnancy rate among parental breed 2-yr-old females can be largely accounted for by differences in measures of puberty (tables 21 and 22). Even though the differences for females of all ages were of lesser magnitude, large differences ($p<0.05$) were observed for pregnancy rate, percentage calf crop born, percentage calf crop weaned, and 200-day calf weight per female exposed to breeding. Pregnancy rates of yearlings were lower and therefore reduced the overall pregnancy rate when averaged over all ages.

Differences for Actual Weight, Adjusted Weight, Hip Height, and Condition Score of Females

Data on 1-yr-old females were collected 168 days after weaning, at the end of the breeding season (452 days) and when the females were palpated for pregnancy (522 days). Data on females 2 yr old and older were collected in February (about 2 mo before calving), in June (before the start of the breeding season), and in October (when the females were palpated for pregnancy). The results presented in tables 29–32 reflect the mean values of observations made within a year. The approximate difference required for significance between means of parental breeds and between means of all breed groups are presented in tables 29–32. Cows from which no calf

Table 28. Breed group means for reproductive and maternal traits of females of all ages

Breed group	Number of females	Percentage pregnant†	Calf crop born (%)†	Calf crop weaned (%)†	200-day calf weight per female exposed to mating (lb)†	200-day calf weight (lb)
Overall mean	24,342	84.7	81.6	73.8	372	502
Red Poll	1,710	86.6	81.3	76.2	356	467
Hereford	1,835	78.9	76.3	68.2	280	407
Angus	2,763	84.6	81.0	72.6	320	439
Limousin	1,958	74.8	73.4	66.0	306	461
Braunvieh	1,696	85.0	82.4	73.9	400	539
Pinzgauer	1,066	86.3	83.7	74.8	401	534
Gelbvieh	1,365	85.2	83.2	75.5	413	544
Simmental	1,718	83.1	80.8	70.0	382	544
Charolais	1,804	83.2	80.8	73.7	387	522
Parental breed mean		83.1	80.3	72.3	361	495
D.05‡		4.6	5.5	5.0	28.2	8.4
MARC I						
F_1§	1,281	88.7	86.7	78.8	414	522
F_2 & F_3§	1,301	88.5	85.2	77.6	409	523
MARC II						
F_1§	1,739	86.5	84.3	76.6	394	512
F_2 & F_3§	1,825	84.0	81.5	73.8	389	523
MARC III						
F_1§	1,202	89.6	84.8	79.2	395	497
F_2 & F_3§	1,079	86.0	78.0	70.5	349	492
D.05‖		5.3	6.2	5.7	32.2	9.7

†Based on females exposed to breeding; pregnancy determined by rectal palpation.
‡D.05 is the approximate difference between means of parental breeds required for significance.
§F_1-generation females producing F_2-generation progeny and combined F_2- & F_3-generation females producing F_3- & F_4-generation progeny.
‖D.05 is the approximate difference between means of all breed groups required for significance.

was weaned in a given year were excluded from the data set for that year.

Differences among parental breeds include additive direct genetic effects and additive maternal genetic effects ($G^i + G^m$).

1-yr-old females. Breed group means for 1-yr-olds are provided in table 29 for actual weight, weight adjusted to a common condition score, hip height, and condition score. Large differences were observed among breed groups for all traits evaluated.

2-yr-old females. Breed group means for 2-yr-olds are provided in table 30 for actual weight, weight adjusted to a common condition score, hip height, and condition score. Large differences were observed among breed groups for all traits evaluated. The magnitude of difference in weight between specific breed groups was reduced considerably as a result of adjusting weight to a common condition score.

6-yr-old females. Breed group means for 6-yr-olds are provided in table 31 for actual weight, weight adjusted to a common condition score, hip height, and overall condition score. Again, large differences were observed among breed groups for all traits evaluated. Similarly, the magnitude of difference in weight was reduced considerably as a result of adjusting to a common condition score.

Females 2–7 or more yr old. Breed group means for females 2–7 or more yr old are provided in table 32 for actual weight, weight adjusted to a common condition score, hip height, and condition score. Large differences were observed among breed groups for all traits evaluated.

Differences for Milk Yield and 200-Day Weight of Progeny

Milk yield data were recorded using the weigh/nurse/weigh procedure for the 12 breed groups when calf age averaged 8, 13, and 18 wk (table 33). Large differences were observed among parental breeds in 12-hr milk yield. Herefords were lowest and Braunvieh produced significantly more than all breed groups except Simmental (though the difference between Braunvieh and Simmental approached significance). The order in which parental breeds ranked for 12-hr milk yield was similar to the order in which they ranked for 200-day weight of progeny. The correlation among breed group means for 12-hr milk yield with 200-day weight of progeny was 0.91.

Differences among parental breeds in 200-day weight adjusted by regression to a common estimated milk yield are expected primarily to reflect differences in additive direct genetic effects (G^i) for 200-day weight. For 200-day weight adjusted to a common milk yield, Red Poll, Hereford, Angus, and Limousin did not differ ($p>0.05$) from each other and all were significantly lighter than Braunvieh, Pinzgauer, Gelbvieh, Simmental, and Charolais, which did not differ ($p>0.05$) from each other (table 33).

Differences in Growth, Carcass, and Meat Traits

Differences among parental breeds reported here include the sum of the additive direct and additive maternal genetic effects ($G^i + G^m$).

Breed group means for growth and carcass traits. Breed group means for contributing purebreds and for composites are presented in table 34. Large differences were observed among breed groups in growth traits and carcass traits measured in the cooler. Initial weight was taken at an average age of 203 days and final weight was taken at slaughter at an average age of 438 days (the average length of the feeding period was therefore 235 days). Steers were serially slaughtered at four end points at average ages of 407, 427, 448, and 470 days.

For initial weight, Herefords were lightest ($p<0.05$) and Gelbvieh, Pinzgauer, Simmental, and Braunvieh were heaviest and did not differ ($p>0.05$) from each other. The initial weight of Charolais approached that of the heaviest breed groups, and Angus, Red Poll, and Limousin had intermediate initial weights. For final weight, Herefords were lightest but did not differ ($p>0.05$) from Angus, Red Poll, and Limousin. Simmental, Charolais, Gelbvieh, and Braunvieh were heaviest but did not differ ($p>0.05$) from each other, whereas Pinzgauer differed ($p<0.05$) only from Simmental among the heavier breed groups. For ADG, Red Poll was lowest but was not significantly different ($p>0.05$) from Angus,

Table 29. Breed group means for actual weight, adjusted weight, hip height, and condition score of 1-yr-old females

Breed group	Number of females	Actual weight (lb)	Adjusted weight[†] (lb)	Hip height (inches)	Condition score[‡]
Overall mean	23,292	807	812	48.6	5.0
Red Poll	1,578	739	743	47.2	5.0
Hereford	1,575	712	694	45.7	5.7
Angus	2,211	743	730	46.1	5.6
Limousin	1,665	756	783	48.4	3.6
Braunvieh	1,488	842	862	50.0	4.6
Pinzgauer	957	831	847	49.6	4.6
Gelbvieh	1,254	851	864	50.0	4.8
Simmental	1,584	860	875	50.4	4.7
Charolais	1,665	866	880	50.0	4.7
D.05[§]		21.2	20.0	.4	.2
MARC I					
F_1, F_2, & F_3	2,973	853	853	49.6	5.2
MARC II					
F_1, F_2, & F_3	3,633	833	820	48.4	5.8
MARC III					
F_1, F_2, & F_3	2,709	803	792	47.6	5.6
D.05[ǁ]		26.0	23.2	.5	.3

[†]Weight adjusted to a common condition score.
[‡]Evaluated on a scale of 1 to 9, 9 = highest, 1 = lowest.
[§]D.05 is the approximate difference between means of parental breeds required for significance.
[ǁ] D.05 is the approximate difference between means of all breed groups required for significance. Heterosis effects did not differ between generations.

Limousin, and Pinzgauer; Simmental and Charolais were higher ($p<0.05$) than all breed groups.

For carcass weight, Herefords were lightest but did not differ ($p>0.05$) from Red Poll and Angus. Simmental, Charolais, Gelbvieh, and Braunvieh had the heaviest carcass weights and did not differ ($p>0.05$) from each other. Pinzgauer and Limousin had intermediate carcass weights. For dressing percentage, Limousin was significantly higher than all other breed groups; Angus and Charolais were intermediate. Differences in dressing percentage among other breed groups were relatively small even though some were significant. Adjusted fat thickness at the 12th rib ranged from 0.14 inches for Gelbvieh

Table 30. Breed group means for actual weight, adjusted weight, hip height, and condition score of 2-yr-old females

Breed group	Number of females	Actual weight (lb)	Adjusted weight† (lb)	Hip height (inches)	Condition score‡
Overall mean	13,002	1,024	1,029	52.3	5.3
Red Poll	924	906	930	49.9	5.0
Hereford	714	944	910	49.0	6.0
Angus	1,320	933	924	48.5	5.6
Limousin	723	999	1,038	51.8	4.3
Braunvieh	903	1,052	1,080	52.6	4.8
Pinzgauer	753	1,025	1,047	52.0	5.0
Gelbvieh	879	1,069	1,078	53.2	5.3
Simmental	972	1,085	1,098	53.7	5.2
Charolais	945	1,146	1,146	53.3	5.5
D.05§		30.6	26.9	.4	.2
MARC I					
F_1, F_2, & F_3	1,518	1,069	1,071	52.1	5.4
MARC II					
F_1, F_2, & F_3	1,797	1,041	1,019	51.4	6.0
MARC III					
F_1, F_2, & F_3	1,554	1,019	1,005	50.5	5.8
D.05ǁ		38.6	34.0	.6	.3

†Weight adjusted to a common condition score.

‡Evaluated on a scale of 1 to 9, 9 = highest, 1 = lowest.

§D.05 is the approximate difference between means of parental breeds required for significance.

ǁD.05 is the approximate difference between means of all breed groups required for significance. Heterosis effects did not differ between generations.

and Charolais to 0.46 inches for Hereford and Angus. For marbling score, Limousin was lowest but not lower (p>0.05) than Gelbvieh. Angus was highest but not higher (p>0.05) than Red Poll, Hereford, and Pinzgauer in marbling score. Braunvieh, Simmental, and Charolais had intermediate marbling scores that were not different (p>0.05) from each other. The order in which the breeds ranked for REA and carcass weight was similar except Limousin had the highest REA value, although not significantly higher than the REA of Braunvieh and Gelbvieh. Differences among breed groups in KPH generally were small; Red Poll had significantly higher KPH than the other breed groups.

Table 31. Breed group means for actual weight, adjusted weight, hip height, and condition score of 6-yr-old females

Breed group	Number of females	Actual weight (lb)	Adjusted weight[†] (lb)	Hip height (inches)	Condition score[‡]
Overall mean	4,455	1,301	1,287	52.5	5.7
Red Poll	339	1,200	1,188	51.2	5.8
Hereford	396	1,257	1,173	50.4	6.9
Angus	585	1,230	1,184	50.0	6.4
Limousin	390	1,261	1,294	52.8	4.5
Braunvieh	318	1,318	1,334	53.4	5.2
Pinzgauer	90	1,274	1,290	52.8	5.2
Gelbvieh	201	1,349	1,352	53.9	5.5
Simmental	273	1,341	1,349	54.3	5.3
Charolais	315	1,438	1,431	54.3	5.7
D.05[§]		38.1	33.1	.5	.3
MARC I					
F_1, F_2, & F_3	492	1,358	1,341	52.8	5.9
MARC II					
F_1, F_2, & F_3	672	1,290	1,263	52.4	6.1
MARC III					
F_1, F_2, & F_3	384	1,296	1,248	51.6	6.4
D.05[I]		40.4	36.2	.6	.4

[†]Weight adjusted to a common condition score.
[‡]Evaluated on a scale of 1 to 9, 9 = highest, 1 = lowest.
[§]D.05 is the approximate difference between means of parental breeds required for significance.
[I]D.05 is the approximate difference between means of all breed groups required for significance. Heterosis effects did not differ between generations.

Large differences were observed among breed groups in percentage of carcasses that were equal to or greater than USDA Choice quality grade. The range was from a low of 14 percent in Limousin to a high of 77 percent in Angus. Differences among the Hereford, Angus, and Red Poll (British breeds) were, not significant. Among continental breeds, Pinzgauer had the highest percentage of USDA Choice quality grade (55 percent), but this percentage, was not significantly higher than that of Braunvieh (42 percent). Differences among the continental breeds were significant, ranging from 14 percent to 55 percent.

Table 32. Breed group means for actual weight, adjusted weight, hip height, and condition score of females 2–7 or more yr old

Breed group	Number of females	Actual weight (lb)	Adjusted weight† (lb)	Hip height (inches)	Condition score‡
Overall mean	49,251	1,210	1,208	52.4	5.5
Red Poll	3,447	1,098	1,105	50.8	5.4
Hereford	3,516	1,149	1,091	50.0	6.5
Angus	5,022	1,118	1,094	49.6	6.0
Limousin	3,822	1,175	1,213	52.4	4.4
Braunvieh	3,393	1,241	1,266	53.5	4.9
Pinzgauer	2,184	1,197	1,217	52.8	5.1
Gelbvieh	2,706	1,257	1,266	53.9	5.3
Simmental	3,258	1,261	1,272	54.3	5.3
Charolais	3,618	1,352	1,349	53.9	5.5
D.05§		27.8	24.5	.4	.18
MARC I					
F_1, F_2, & F_3	5,820	1,270	1,263	52.8	5.7
MARC II					
F_1, F_2, & F_3	7,389	1,217	1,193	52.0	6.0
MARC III					
F_1, F_2, & F_3	5,076	1,202	1,171	51.2	6.0
D.05ǁ		26.7	23.6	.4	.17

†Weight adjusted to a common condition score.
‡Evaluated on a scale of 1 to 9, 9 = highest, 1 = lowest.
§D.05 is the approximate difference between means of parental breeds required for significance.
ǁD.05 is the approximate difference between means of all breed groups required for significance. Heterosis effects did not differ between generations.

Differences among composites were significant in percentage of carcasses that were equal to or greater than USDA Choice quality grade, ranging from 42 percent in MARC I to 65 percent in MARC III. The breed composition of the MARC I population is three-fourths continental, and breed composition of the MARC III population is three-fourths British.

Breed composition of the MARC II population is one-half continental and one-half British, and 57 percent of the population was graded USDA Choice or higher—almost as high as the MARC III population.

As expected, differences were small among the breed groups in the percentage of carcasses meeting

Table 33. Breed group means for 12-hr milk yield, estimated 200-day milk yield, and 200-day weight of progeny

Breed group	Number of observations	12-hr milk yield (lb)	No. of cows	Estimated 200-day milk yield (lb)	200-day weight of progeny (lb)	Adjusted 200-day weight of progeny[†] (lb)
Overall mean	1,686	11.5	595	4,604	503	494
Red Poll	118	11.9	46	4,774	478	463
Hereford	122	6.7	45	2,774	408	459
Angus	125	9.3	48	3,735	454	472
Limousin	149	10.2	50	4,114	456	459
Braunvieh	147	14.2	52	5,680	558	520
Pinzgauer	156	12.9	52	5,173	531	505
Gelbvieh	150	12.7	51	5,120	545	520
Simmental	151	13.1	51	5,283	545	516
Charolais	146	10.5	50	4,212	518	518
D.05[‡]		1.3		531	28.4	24.2
MARC I[§]	155	12.5	52	5,034	527	505
MARC II[§]	147	11.7	50	4,732	529	514
MARC III[§]	120	11.6	48	4,613	494	481
D.05[¶]		1.3		560	30.0	25.6

[†]Adjusted to a common estimated milk yield.

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

[§]F_2-generation females nursing F_3-generation progeny.

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

or exceeding the USDA Select quality grade. However, these differences were significant, with Limousin and Gelbvieh the lowest.

Breed group means for carcass composition. Breed group means for carcass composition are presented in table 35. Composition is listed as the percentage and weight of retail product, fat trim, and bone with all subcutaneous and accessible intermuscular fat removed (0 inches of fat trim). Breed group means for carcass lean, carcass fat, and carcass bone (by percentage and weight) are presented in table 36. Percentage of retail product ranged from 60.1 in Herefords to 72.3 in Limousin (table 35). Percentage of carcass lean ranged from 53.8 in Hereford to 64.6 in Limousin (table 36).

The mean liveweight of Gelbvieh, Simmental, and Charolais was 121 lb heavier than that of Limousin (table 34), yet Limousin was equal to Gelbvieh,

Table 34. Breed group means for growth and carcass traits measured in a cooler

Breed group	No. of steers	Weight (lb) Initial	Weight (lb) Final	ADG† (lb)	Carcass weight (lb)	Dressing percentage (%)	Adj. fat‡ (inches)	REA§ ($inches^2$)	Estim. KPH‖ (%)	Marbling score¶	Percentage ≥ USDA Choice	Percentage ≥ USDA Select
Overall mean	1,661	569	1,210	2.74	734	60.58	.26	12.10	2.77	4.97	46	95
Red Poll	114	551	1,158	2.58	694	59.98	.30	10.76	3.30	5.30	71	100
Hereford	146	478	1,118	2.72	675	60.33	.46	10.52	2.41	5.21	60	100
Angus	118	514	1,136	2.64	697	61.32	.46	10.56	2.64	5.41	77	100
Limousin	142	531	1,144	2.61	728	63.43	.17	13.41	2.47	4.43	14	84
Braunvieh	139	602	1,250	2.78	747	59.73	.18	13.21	2.79	4.84	42	94
Pinzgauer	118	608	1,228	2.65	730	59.45	.17	12.26	2.74	5.16	55	98
Gelbvieh	150	611	1,250	2.73	750	59.94	.14	12.97	2.68	4.53	15	85
Simmental	127	604	1,281	2.90	767	59.79	.16	12.56	2.50	4.80	34	92
Charolais	126	586	1,263	2.90	767	60.66	.14	12.49	2.80	4.71	24	96
D.05††		23.6	42.3	.11	27.3	.81	.05	.54	.26	.28	19	8
MARC I–F_3	178	584	1,241	2.81	761	61.24	.23	12.94	2.94	4.79	42	91
MARC II–F_3	148	604	1,263	2.81	765	60.48	.32	12.09	2.88	5.13	57	100
MARC III–F_3	155	560	1,197	2.70	725	60.56	.36	11.52	3.06	5.31	65	98
D.05‡‡		24.2	43.4	.13	28.0	.83	.06	.56	.27	.28	20	9

†ADG = Average daily weight gain.

‡Adjusted fat thickness at the 12th rib.

§REA = Area of longissimus muscle.

‖Estimated KPH = estimate of kidney, pelvic, and heart fat.

¶A score of 4.00–4.90 = slight; a score of 5.00–5.90 = small.

††D.05 is the approximate difference between means of parental breeds required for significance.

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

Table 35. Breed group means for carcass composition after all subcutaneous and accessible intermuscular fat was removed (0 inches of fat trim)

Breed group	Number of carcasses	Retail product† %	Retail product† lb	Fat trim %	Fat trim lb	Bone %	Bone lb
Overall mean	1,596	65.8	459	18.9	133	15.2	106
Red Poll	114	62.6	412	22.4	150	14.9	98
Hereford	132	60.1	386	25.5	166	14.4	92
Angus	117	61.5	406	24.4	164	14.1	93
Limousin	138	72.3	499	13.4	94	14.3	98
Braunvieh	137	67.3	478	16.1	117	16.5	117
Pinzgauer	119	66.8	463	17.0	119	16.1	112
Gelbvieh	147	70.0	499	14.2	104	15.8	112
Simmental	126	68.4	495	15.5	116	16.1	117
Charolais	124	68.7	499	15.0	111	16.2	118
D.05‡		1.5	17.6	1.6	14.1	.4	4.4
MARC I, F_3	157	67.2	486	17.9	131	14.9	108
MARC II, F_3	146	63.1	459	22.3	164	14.7	107
MARC III, F_3	139	61.9	427	23.3	164	14.8	102
D.05§		1.5	18.3	1.7	14.6	.4	4.6

†Retail product includes steaks and roasts plus lean trim adjusted to 20 percent fat based on chemical analysis of lean trim.

‡D.05 is the approximate difference between means of parental breeds required for significance.

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

Simmental, and Charolais in retail product weight and weight of carcass lean (tables 35 and 36). This occurred because Limousin had a higher dressing percentage, higher retail product percentage, and smaller bone percentage than the other three breeds.

Differences in carcass composition were small among the British breeds (Red Poll, Hereford, and Angus) (tables 35 and 36). Differences in carcass composition among the continental breeds were greater than among the British breeds, ranging from 66.8 percent retail product and 59.8 percent carcass lean in Pinzgauer to 72.3 percent retail product and 64.6 percent carcass lean in Limousin.

Differences in carcass composition among composites were important ($p<0.05$) and were associated with breed composition of British breeds relative to continental breeds (tables 35 and 36). The MARC III population had 61.9 percent retail product and 55.3 percent carcass lean, whereas the MARC I population had 67.2 percent retail product and 60.0 percent

Table 36. Breed group means for carcass lean, carcass fat, and carcass bone

Breed group	Number	Lean† %	Lean† lb	Fat‡ %	Fat‡ lb	Bone %	Bone lb
Overall mean	1,596	58.8	410	26.0	182	15.2	106
Red Poll	114	56.0	369	29.1	194	14.9	98
Hereford	132	53.8	345	31.8	207	14.4	92
Angus	117	54.9	362	31.0	207	14.1	93
Limousin	138	64.6	446	21.1	147	14.3	98
Braunvieh	137	60.1	428	23.3	168	16.5	117
Pinzgauer	119	59.8	414	24.1	168	16.1	112
Gelbvieh	147	62.4	445	21.8	158	15.8	112
Simmental	126	61.1	442	22.8	168	16.1	117
Charolais	124	61.2	444	22.5	165	16.2	118
D.05ǁ		1.3	15.6	1.5	13.9	.4	4.4
MARC I, F_3	157	60.0	434	25.1	183	14.9	108
MARC II, F_3	146	56.4	410	29.0	213	14.7	107
MARC III, F_3	139	55.3	382	29.9	209	14.8	102
D.05§		1.4	16.1	1.5	14.6	.4	4.6

†Carcass lean includes steaks and roasts with all subcutaneous and accessible intermuscular fat removed, plus fat-free lean trim based on chemical analysis of lean trim.
‡Carcass fat includes fat trim plus fat in lean trim based on chemical analysis of lean trim.
§D.05 is the approximate difference between means of parental breeds required for significance.
ǁD.05 is the approximate difference between means of all breed groups required for significance.

carcass lean. The MARC II population had 63.1 percent retail product and 56.4 percent carcass lean.

Breed group means for carcass and meat quality traits. Breed group means for factors relating to meat quality are presented in table 37. Differences in marbling score ranged from 4.43 in Limousin to 5.41 in Angus. Differences among the British breeds (that is, Angus, Hereford, and Red Poll) were not significant for marbling score. Differences in marbling score among the continental breeds were greater than differences among the British breeds, ranging from 4.43 in Limousin to 5.16 in Pinzgauer. Pinzgauer did not differ ($p>0.05$) from the British breeds in marbling score. Differences in marbling score among composites were closely associated with their continental breed composition relative to British breed composition; for example, MARC I was 4.79, MARC II was 5.13, and MARC III was 5.31.

Fat in the longissimus muscle, determined by chemical analysis, was highly associated with marbling score but was more variable. The range in longissimus muscle fat was from 2.82 percent in Limousin to 4.80 percent in Angus.

Table 37. Breed group means for carcass and meat quality traits

Breed group	Adj. fat† (inches)	Marb-ling score‡	Long. muscle fat§ (%)	Fat in 9–11 rib cut (%)	Shear force‖ (lb)	Sensory panel Tender.¶	Juici.††	Flavor‡‡	Retail product 0 inches trim (%)
Overall mean	0.26	4.97	3.96	33.01	11.22	5.07	5.17	4.87	65.8
Red Poll	.30	5.30	4.65	38.34	10.41	5.15	5.25	4.96	62.6
Hereford	.46	5.21	4.53	40.09	11.16	5.10	5.25	4.80	60.1
Angus	.46	5.41	4.80	40.01	9.92	5.55	5.38	4.92	61.5
Limousin	.17	4.43	2.82	26.51	12.39	4.88	5.01	4.82	72.3
Braunvieh	.18	4.84	3.67	29.83	11.22	5.06	5.12	4.90	67.3
Pinzgauer	.17	5.16	4.22	30.82	9.86	5.43	5.20	4.96	66.8
Gelbvieh	.14	4.53	3.22	27.60	12.74	4.63	5.04	4.75	70.0
Simmental	.16	4.80	3.72	28.67	12.08	4.80	5.14	4.83	68.4
Charolais	.14	4.71	3.38	28.02	11.38	4.95	5.12	4.88	68.7
D.05§§	.05	.28	.50	2.20	.99	.27	.19	.13	1.5
MARC I, F_3	.23	4.79	3.56	31.15	11.05	5.22	5.14	4.87	67.2
MARC II, F_3	.32	5.13	4.36	36.37	11.14	5.04	5.18	4.90	63.1
MARC III, F_3	.36	5.31	4.59	38.69	11.29	5.06	5.20	4.88	61.9
D.05‖	.06	.28	.52	2.28	1.04	.28	.20	.14	1.5

†Adjusted fat = subcutaneous fat at the 12th rib.
‡A score of 4.00–4.90 = slight, 5.00–5.90 = small.
§Chemical fat in cross section of longissimus muscle.
‖Shear force required to cut a 0.5-inch core from the longissimus muscle.
¶A tenderness score of 4 = slightly tough, 5 = slightly tender, 8 = extremely tender.
††A juiciness score of 4 = slightly dry, 5 = slightly juicy, 8 = extremely juicy.
‡‡A flavor score of 4 = slightly bland, 5 = slightly intense, 8 = extremely intense.
§§D.05 is the approximate difference between means of parental breeds required for significance.
‖D.05 is the approximate difference between means of all breed groups required for significance.

Shear force (the force required to cut a 0.5-inch core from the longissimus muscle) ranged from 9.86 lb in Pinzgauer to 12.74 lb in Gelbvieh. With the exception of Pinzgauer, these values tended to be slightly higher in continental breeds than in British breeds.

Sensory panel scores for tenderness, juiciness, and flavor were less variable than shear force values.

The British breeds tended to have slightly higher scores for tenderness than the continental breeds. The Pinzgauer breed had the most favorable score for tenderness among the continental breeds and generally scored equal to the British breeds. Values for the Braunvieh breed did not differ ($p>0.05$) from those of the Hereford and Red Poll in either shear force or tenderness score.

Differences Among Breed Groups for Different Measures of Gain Efficiency

Breed group means for different measures of gain efficiency are presented in table 38. Adjusting gain efficiency to different end points and with different measures of output was made possible as a result of serial slaughter and collection of data on carcass cut-out. Gain efficiency was evaluated for the following:

- from 0 to 207 days (time-constant period)
- from 684 to 1,191 lb (gain-constant period)
- to a weight of 734 lb (carcass weight constant)
- to a retail product weight of 463 lb

Table 38. Breed group means for different measures of gain efficiency

Breed group	No. of carcasses	Live-weight gain (LWG) and retail product gain (RPG) per Mcal of ME: Time constant 0 to 207 days LWG	Time constant 0 to 207 days RPG	Gain constant From 684 to 1,191 lb LWG	To a carcass weight of 734 lb LWG	To a retail product weight of 463 lb RPG	To a marbling score of 5.00[†] LWG	To a longissimus muscle fat content of 4% LWG
		grams						
Overall mean	1,599	51	38	50	51	40	50	50
Red Poll	114	49	35	48	48	28	51	52
Hereford	133	54	34	48	51	24	57	61
Angus	117	50	35	48	49	26	54	57
Limousin	138	54	47	51	54	57	47	41
Braunvieh	138	50	38	51	51	42	49	48
Pinzgauer	119	50	39	50	50	40	51	51
Gelbvieh	148	48	40	49	49	49	45	43
Simmental	126	51	38	52	52	46	49	48
Charolais	125	52	40	52	53	50	49	46
D.05[‡]		1.9	1.3	2.4	2.0	1.6	1.9	2.3
MARC I, F_3	157	50	39	51	51	45	48	45
MARC II, F_3	146	51	37	52	52	37	52	54
MARC III, F_3	138	50	35	49	50	30	53	54
D.05[§]		2.0	1.3	2.5	2.1	1.7	2.0	2.4

[†]A score of 5.00–5.90 = small.

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

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

- to a marbling score of 5.00
- to a longissimus muscle fat content of 4 percent.

Gain efficiencies are expressed as liveweight gain per megacalories of metabolizable energy (Mcal/ME) and retail product weight per Mcal of ME (table 38). Significant differences were observed among breed groups for all measures of gain efficiency.

Breed groups that had the smallest weight to maintain (for example, Limousin and Hereford) tended to be more efficient in liveweight gain in the time-constant period (0 to 207 days). Even though Angus and Limousin had similar initial weights, Limousin produced 12 g more ($p<0.05$) retail product per Mcal of ME than Angus. With the exception of Limousin, breeds that gained at a higher rate tended to be more efficient in liveweight gain in the gain-constant period (684 to 1,191 lb) because of a shorter period of maintenance. Limousin gained at a slower-than-average rate (table 34) but efficiency of liveweight gain (684 to 1,191 lb) was above average.

Because Limousin had a higher dressing percentage, higher percentage of retail product, and lower percentage of bone than the other breeds, it was the most efficient in measures of efficiency where the end point was retail product weight or where the output was retail product gain.

To marbling score constant or longissimus muscle fat percentage end points, breeds with the lowest marbling scores and lowest percentage of fat in the longissimus muscle (for example, Limousin and Gelbvieh) tended to be less efficient, whereas breeds with the highest marbling scores and the highest percentage of fat in the longissimus muscle (for example, Hereford and Angus) tended to be more efficient. The Pinzgauer breed was most efficient to longissimus muscle fat percentage and marbling score constant end points among the continental breeds.

Inbreeding Coefficients

Inbreeding coefficients are presented in table 39 by year for each breed group.

Genetic and Phenotypic Variances

Genetic standard deviations (σ_g) and phenotypic coefficients of variation (*CV*) for all breed groups, contributing purebreds, and composites are presented in table 40 for growth and carcass traits of castrate males; in table 41 for production traits of intact males; and in table 42 for production traits of females. Phenotypic coefficients of variation are not presented for traits that do not have a normal distribution (for example, categorical traits) or for traits with a finite score.

Genetic standard deviations and phenotypic coefficients of variation were similar for composites and contributing purebreds. Thus, greater genetic variation and phenotypic coefficients of variation for composite populations in comparison to contributing purebreds were not observed. Our interpretation of these results is that for bioeconomic traits that are influenced by a large number of genes, genetic standard deviations and phenotypic coefficients of variation are similar for composites and for the average of the contributing purebreds.

Heritabilities

Estimates of heritability (h^2) and their estimated standard errors (*SE*) for all breed groups, contributing purebreds, and composites are presented in table 43 for growth and carcass traits of castrate males, in table 44 for production traits of intact males, and in table 45 for production traits of females. Generally, there was close agreement in h^2 for all breed groups, contributing purebreds, and composites. There was no tendency for h^2 to be higher in composites than in contributing purebreds. Because of similarity of estimates among the three groupings and the smaller standard errors as a result of greater numbers, only estimates of h^2 for all breed groups combined are discussed.

Growth and Carcass Traits of Castrate Males

Heritabilities of traits reflecting carcass composition were intermediate in size and were of a magnitude similar to growth traits (table 43). Heritability of marbling score and of longissimus muscle fat percentage were of the same magnitude (0.48 and 0.49, respectively) and were higher than h^2 for growth traits. Heritability of traits relating to meat palatability generally were low. Muscling score in the live animal, a subjective evaluation, had the highest h^2 among the traits analyzed (0.64 ± 0.10).

Table 39. Inbreeding coefficients by birth year and breed group

Breed group	Inbreeding coefficients (%)													
	Year of birth													
	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	Mean
Red Poll	3.48	3.84	3.18	3.66	4.01	5.02	5.36	5.66	6.34	6.49	7.08	7.79	8.70	5.32
Hereford	4.38	3.95	4.40	4.99	6.03	5.21	5.41	7.27	7.78	7.14	7.83	8.90	9.36	6.25
Angus	2.69	4.71	3.80	5.41	6.12	6.80	7.16	7.87	7.51	7.88	8.21	8.14	8.87	6.08
Limousin	.84	1.01	1.32	2.01	2.32	2.50	2.96	2.98	4.11	3.99	3.95	5.08	5.29	2.90
Braunvieh	.74	1.00	2.21	2.14	1.64	2.39	2.64	3.32	4.28	4.39	4.58	5.46	4.91	2.89
Pinzgauer	—	—	—	—	2.07	1.98	2.18	2.30	5.52	3.23	4.46	3.97	4.51	3.34
Gelbvieh	4.03	1.06	.61	.69	1.22	2.44	1.78	3.52	4.33	3.74	3.80	3.30	4.07	2.62
Simmental	.49	.27	.80	.68	1.00	.82	1.39	1.82	2.45	2.23	2.34	2.81	3.11	1.41
Charolais	.10	1.12	1.24	1.16	1.06	1.36	2.29	2.56	3.01	3.66	3.69	4.19	4.83	2.28
MARC I														
F_1	.32	.40	.17	.16	.24	.30	—	—	—	—	—	—	—	.25
F_2	—	—	—	.90	.75	.49	.54	.76	.70	.77	.86	1.18	.79	.75
F_3	—	—	—	—	—	—	2.31	1.97	2.58	2.31	1.95	2.67	2.87	2.41
F_4	—	—	—	—	—	—	—	—	—	5.36	3.83	4.05	3.42	3.94
MARC II														
F_1	.00	.00	.00	.00	.00	—	—	—	—	—	—	—	—	.00
F_2	—	—	.39	.47	.77	.37	.49	.74	.91	.90	.56	1.22	1.44	.69
F_3	—	—	—	—	—	1.91	1.42	1.25	1.62	1.99	1.72	2.18	2.53	1.78
F_4	—	—	—	—	—	—	—	—	3.90	2.75	2.56	3.18	3.50	3.15
MARC III														
F_1	—	—	.00	.00	.00	.00	.00	—	—	—	—	—	—	.00
F_2	—	—	—	—	1.01	.95	1.17	1.22	1.07	1.31	.87	1.43	1.76	1.19
F_3	—	—	—	—	—	—	—	3.49	2.34	2.04	2.36	2.75	3.49	2.63
F_4	—	—	—	—	—	—	—	—	—	—	7.75	5.74	4.04	5.20

Table 40. Genetic standard deviations (σ_g) and phenotypic coefficients of variation (*CV*) for growth and carcass traits of castrate males

	All breed groups		Purebreds		Composites	
Trait	σ_g	*CV*	σ_g	*CV*	σ_g	*CV*
Birth weight (lb)	6.0	0.12	5.7	0.12	5.7	0.13
200-day weight (lb)	30.6	.10	29.3	.10	31.3	.11
Slaughter weight at 438 days (lb)	51.2	.08	47.8	.08	63.3	.08
Carcass weight at 438 days (lb)	30.2	.08	27.3	.08	39.5	.09
Longissimus muscle area (inches^2)	.6	.10	.5	.10	.8	.10
Retail product (%)	2.2	.05	2.2	.04	2.3	.06
Fat trim (%)	2.2	.20	2.3	.19	1.9	.20
Bone trim (%)	.5	.07	.5	.07	.1	.07
Carcass lean weight (lb)	19.0	.09	17.9	.08	23.6	.09
Carcass fat weight (lb)	17.2	.18	19.0	.18	13.9	.19
Bone weight (lb)	6.0	.09	6.2	.08	4.6	.10
Longissimus muscle fat (%)	.8	.28	.6	.27	1.0	.29
Shear force (lb)	.9	.22	.4	.22	1.3	.21

The low h^2 of shear force (0.12 ± 0.08) suggests that differences in shear force were likely associated with high variance. This estimate of h^2 for shear force is lower than most estimates in the literature; for example, Koch et al. (1982) reported an estimate of 0.31.

Production Traits of Intact Males

Traits associated with size (that is, weight and height) had intermediate heritability (0.35 to 0.48) (table 44). Heritability of scrotal circumference was of a magnitude similar to growth and size traits (0.43 $\pm$ 0.04). Heritability of subjective scores (that is, condition, muscling, trimness, and kind) were of similar magnitude and were at the lower end of the h^2 range for size-related traits (0.30 to 0.35). The h^2 for both expressions of calving difficulty (that is, calving difficulty score and percentage requiring assistance) were of sufficient magnitude (0.27 ± 0.08 and 0.31 ± 0.09, respectively) to suggest response to selection among calves with 2-yr-old dams. The h^2 of calving difficulty—either calving difficulty score or percentage calving difficulty—was greater in calves with 2-yr-old dams than calves with dams 3 yr old or older. This was expected because of the higher frequency of calving difficulty of calves from 2-yr-old dams. The h^2 for gestation length of calves born to females 3 yr old or older was 0.46 ± 0.06.

These estimates of h^2 tend to be higher than those typically reported for 200-day weight but lower than those reported for 368-day weight.

Table 41. Genetic standard deviations (σ_g) and phenotypic coefficients of variation (*CV*) for production traits of intact males

Trait	All breed groups		Purebreds		Composites	
	σ_g	*CV*	σ_g	*CV*	σ_g	*CV*
Birth weight (lb)	7.3	0.12	7.7	0.11	7.1	0.12
Preweaning ADG (lb)	.13	.11	.11	.10	.13	.11
200-day weight (lb)	28.9	.09	24.2	.09	26.0	.09
Postweaning ADG (lb)	.20	.11	.20	.11	.20	.11
368-day weight (lb)	46.5	.08	47.2	.08	44.1	.08
368-day height (inches)	.9	.03	.8	.03	.9	.03
368-day condition score†	.47	—	.47	—	.46	—
368-day muscle score‡	.38	—	.40	—	.33	—
368-day trimness score§	.48	—	.50	—	.42	—
368-day kind score‖	.66	—	.48	—	.70	—
368-day scrotal circumference (cm)	1.60	.08	1.53	.07	1.61	.07
CD score, dams of all ages¶	.43	—	.45	—	.41	—
CD score, dams 2 yr old¶	.70	—	.78	—	.59	—
CD score, dams ≥3 yr old¶	.22	—	.29	—	.06	—
Gestation length, born from dams ≥3 yr old (days)	2.7	.01	2.7	.01	2.6	.01

†Evaluated on a scale of 1 to 9, 9 = very fat, 1 = emaciated.

‡Evaluated on a scale of 1 to 9, 9 = very thickly muscled, 1 = very thinly muscled.

§Evaluated on a scale of 1 to 9, 9 = very lacking in trimness, 1 = very trim.

‖Evaluated on a scale of 1 to 9; scored within breed group on overall anatomical desirability, 9 = very desirable, 1 = very undesirable.

¶CD = calving difficulty, scored on a scale of 1 to 7, 7 = caesarean birth, 1 = no difficulty.

Production Traits of Females

Estimates of heritability of weights, heights, and condition scores for 2, 3, 4, and 5 yr olds are based on means of observations made about 2 mo before the start of calving, immediately before the start of breeding, and when pregnancy status was determined about 1 mo after weaning. Estimates of heritability of weight at 1 yr are based on the mean of weights taken just before the start of breeding (410 days), after breeding (452 days), and when pregnancy was diagnosed (522 days). Estimates of h^2 of hip height and condition score at 1 yr are based on the mean of observations made at 368 days and 522 days. Height and condition score were not recorded at 410 days and 452 days. The h^2 of weights were remarkably similar at all ages (table 45). The h^2 of height and condition score were similar at all ages except 5 yr, when both were lower. Because the number of observations decreased as age increased, standard errors of h^2 tended to increase with age. Higher h^2 were expected

Table 42. Genetic standard deviations (σ_g) and phenotypic coefficients of variation (*CV*) for production traits of females

Trait	All breed groups σ_g	All breed groups *CV*	Purebreds σ_g	Purebreds *CV*	Composites σ_g	Composites *CV*
Birth weight (lb)	6.6	0.12	6.8	0.11	6.4	0.12
200-day weight (lb)	25.6	.09	27.1	.09	21.2	.09
368-day weight (lb)	39.9	.09	41.9	.09	36.8	.09
410-day weight (lb)	36.6	.09	39.9	.08	33.3	.09
452-day weight (lb)	42.6	.08	47.6	.08	35.7	.08
522-day weight (lb)	44.5	.08	49.6	.08	37.9	.08
Weight, 1 yr (lb)	42.1	.08	46.7	.08	37.3	.08
Weight, 2 yr (lb)	60.2	.08	61.5	.07	59.5	.08
Weight, 3 yr (lb)	65.3	.08	69.2	.08	63.1	.08
Weight, 4 yr (lb)	66.6	.08	55.3	.08	78.7	.08
Weight, 5 yr (lb)	69.7	.08	74.7	.07	71.2	.08
368-day height (inches)	.9	.03	.8	.03	.9	.03
Height, 1 yr (inches)	.9	.03	.9	.02	.9	.03
Height, 2 yr (inches)	.9	.02	.9	.02	.9	.02
Height, 3 yr (inches)	.9	.02	.9	.02	.8	.02
Height, 4 yr (inches)	.8	.02	.9	.02	.8	.02
Height, 5 yr (inches)	.7	.02	.7	.02	.8	.02
Gestation length, ≥3 yr old (days)	2.5	.01	2.2	.01	2.8	.01
Puberty age (days)	15.2	.07	15.7	.08	13.6	.07

for weights, heights, and condition scores at 1, 2, 3, 4, and 5 yr old than at 368 days and earlier because these estimates of h^2 were based on means of three observations made in different seasons at 1 yr through 5 yr. The h^2 for weights, heights, and condition scores through 368 days were similar to those reported for males from the same population (table 44).

The h^2 for calving difficulty score for calves born from 2-yr-old dams, for calves born from dams 3 yr old or older, and for calves born from dams of all ages generally were higher than h^2 for percentage calving difficulty. This was expected because percentage calving difficulty is expressed as a binary trait (that is, 0 or 1), whereas calving difficulty score is classified into seven categories.

The h^2 of calving difficulty score and percentage calving difficulty were higher for calves from 2-yr-old dams than for calves from dams 3 yr old or older. This is likely associated with the higher frequency of calving difficulty of calves from 2-yr-old dams. However, the h^2 of calving difficulty of female calves is similar to that of male calves (table 44), and male calves experience a higher frequency of calving difficulty than female calves.

Table 43. Heritabilities (h^2) and standard errors (*SE*) for all breed groups, purebreds, and composites for growth and carcass traits of castrate males

	All breed groups		Purebreds		Composites	
Trait	h^2	*SE*	h^2	*SE*	h^2	*SE*
Birth weight	0.25	0.08	0.24	0.10	0.26	0.17
Preweaning ADG	.35	.09	.35	.10	.30	.17
200-day weight	.34	.09	.33	.10	.31	.17
Postweaning ADG	.36	.09	.33	.10	.48	.18
Slaughter weight, 438 days	.28	.08	.26	.10	.37	.18
Carcass weight	.23	.08	.20	.10	.34	.17
Dressing percentage	.19	.08	.22	.10	.08	.15
Adjusted fat at 12th rib	.25	.08	.20	.10	.39	.18
Marbling score†	.48	.09	.45	.11	.55	.19
Longissimus muscle area	.22	.08	.17	.09	.35	.18
Retail product, 0 inches of fat trim‡ (%)	.47	.09	.51	.11	.42	.18
Fat, 0 inches of fat trim§ (%)	.35	.09	.43	.11	.21	.16
Bone 0 inches of fat trim (%)	.21	.08	.27	.10	.01	.15
Retail product weight, 0 inches of fat trim‡	.28	.08	.26	.10	.39	.18
Fat trim weight, 0 inches of fat trim§	.32	.09	.43	.11	.17	.16
Bone weight	.39	.09	.46	.11	.19	.16

Continued

† A score of 4.00 to 4.90 = slight, 5.00 to 5.90 = small.

‡ Retail product includes steaks and roasts plus lean trim adjusted to 20-percent fat based on chemical analysis of lean trim.

§ All subcutaneous and accessible intermuscular fat removed.

Table 43. Heritabilities (h^2) and standard errors (*SE*) for all breed groups, purebreds, and composites for growth and carcass traits of castrate males—Continued

	All breed groups		Purebreds		Composites	
Trait	h^2	*SE*	h^2	*SE*	h^2	*SE*
Carcass lean weight[I]	.28	.08	.25	.10	.39	.18
Carcass fat weight[¶]	.29	.09	.40	.10	.15	.16
Longissimus muscle fat[††] (%)	.49	.09	.36	.10	.75	.20
9–10–11 rib fat[††] (%)	.26	.08	.33	.10	.13	.16
Shear force[‡‡]	.12	.08	.05	.09	.31	.17
Tenderness score[§§]	.22	.08	.12	.09	.51	.18
Juiciness score[II]	.25	.08	.06	.09	.70	.20
Flavor score[¶¶]	.07	.08	.08	.09	.04	.15
Muscling score[†††]	.64	.10	.64	.12	.82	.20
Fat score[†††]	.27	.08	.30	.10	.29	.17

I Carcass lean includes steaks and roasts trimmed to 0 inches of fat cover plus fat-free lean trim based on chemical analysis of lean trim.

¶ Carcass fat includes fat trim plus fat in lean trim based on chemical analysis of lean trim.

†† Ether-extracted fat.

‡‡ Shear force required to cut through a 0.5-inch core of longissimus muscle.

§§ A tenderness score of 4 = slightly tough, 5 = slightly tender, 8 = extremely tender.

II A juiciness score of 4 = slightly dry, 5 = slightly juicy, 8 = extremely juicy.

¶¶ A flavor score of 4 = slightly bland, 5 = slightly intense, 8 = extremely intense.

††† Scores ranged from 3 to 27, with 6, 15, and 24 reflecting low, average, and high, respectively, for muscle or fat.

The h^2 for gestation length for female calves from dams 3 yr old or older was the same as it was for male calves (0.45 ± 0.06 vs. 0.46 ± 0.06) (table 44). The h^2 for age at puberty was slightly lower (0.31 ± 0.04) than some estimates in the literature.

Genetic Correlations

Estimates of genetic correlations (r_g) between growth and carcass traits of castrate males are shown below the diagonal in table 46. Estimates of production traits of intact males are shown below the diagonal in table 47; production traits of females are shown below the diagonal in table 48. The correlations were estimated from purebred and composite breed groups combined with records adjusted for differences in age and days on feed. It is assumed that correlations do not differ among contributing purebreds and composites.

Growth and Carcass Traits of Castrate Males

Slaughter and carcass weight were highly correlated with weight of all carcass components, that is, bone, lean, and fat (table 46). Adjusted fat thickness at the 12th rib was positively correlated with marbling score, fat trim percentage, fat weight, longissimus fat percentage, tenderness, juiciness, flavor, and fat score and was negatively correlated with retail product and bone percentages, lean weight, shear force, and muscling score. The positive correlations of intramuscular fat, as measured by marbling score or longissimus muscle fat, with fat trim percentage and fat weight and the negative correlation with retail product percentage illustrate the difficulty of genetically increasing intramuscular fat in the longissimus muscle while maintaining a favorable lean-to-fat ratio in the carcass. The r_g of retail prod-

Table 44. Heritabilities (h^2) and standard errors (*SE*) for all breed groups, purebreds, and composites of intact males

Trait	All breed groups (*n*=7,536)		Purebreds (*n*=4,115)		Composites (*n*=3,421)	
	h^2	*SE*	h^2	*SE*	h^2	*SE*
Birth weight	0.44	0.04	0.54	0.06	0.37	0.05
Preweaning ADG	.38	.04	.24	.04	.32	.05
200-day weight	.35	.04	.27	.04	.27	.05
Postweaning ADG	.43	.04	.44	.05	.37	.05
368-day weight	.35	.04	.40	.05	.28	.05
368-day height	.48	.04	.41	.05	.48	.06
368-day condition score†	.34	.04	.36	.05	.30	.05
368-day muscling score‡	.35	.04	.36	.05	.30	.05
368-day trimness score§	.34	.04	.37	.05	.27	.05
368-day kind score‖	.30	.03	.17	.04	.32	.05
368-day scrotal circumference	.43	.04	.40	.05	.43	.06
CD score, dams of all ages¶	.26	.03	.28	.04	.24	.05
CD, dams of all ages†† (%)	.21	.03	.19	.04	.24	.05
CD score, dams 2 yr old¶	.27	.08	.34	.12	.19	.12
CD, dams 2 yr old†† (%)	.31	.09	.30	.12	.33	.13
CD score, dams ≥3 yr old¶	.13	.05	.21	.07	.01	.07
CD, dams ≥3 yr old†† (%)	.07	.05	.12	.07	.00	.00
Gestation length, dams ≥3 yr old‡‡	.46	.06	.44	.09	.44	.10

† Evaluated on a scale of 1 to 9, 9 = very fat, 1 = emaciated.
‡ Evaluated on a scale of 1 to 9, 9 = very thickly muscled, 1 = very thinly muscled.
§ Evaluated on a scale of 1 to 9, 9 = very lacking in trimness, 1 = very trim.
‖ Evaluated on a scale of 1 to 9; scored within breed group on overall desirability, 9 = very desirable, 1 = very undesirable.
¶ Calving difficulty score was rated as follows: 1 = no difficulty, 2 = little difficulty by hand, 3 = little difficulty with calf jack, 4 = slight difficulty with calf jack, 5 = moderate difficulty with calf jack, 6 = major difficulty with calf jack, and 7 = caesarean birth.
†† Calving difficulty (%) was scored as follows: scores 1 and 2 = 0; scores 3, 4, 5, 6, and 7 = 1.
‡‡ Calves conceived by artificial insemination.

uct percentage and marbling score was −0.60 ± 0.20. Longissimus muscle area was positively correlated with measures of carcass lean and with muscle score and negatively correlated with shear force. Shear force was highly correlated with tenderness score, but the standard error was large. Muscle score, which was subjectively evaluated in the live animal, had favorable genetic correlations with carcass composition, suggesting that visual evaluation of differences in muscle thickness can have value in selecting for changes in carcass composition.

Table 45. Heritabilities (h^2) and standard errors (*SE*) for all breed groups, purebreds, and composites of females

	All breed groups		Purebreds		Composites	
Trait	h^2	*SE*	h^2	*SE*	h^2	*SE*
Birth weight (lb)	0.42	0.04	0.48	0.05	0.36	0.06
Preweaning ADG	.33	.03	.35	.04	.24	.05
200-day weight (lb)	.32	.03	.38	.05	.21	.04
Postweaning ADG	.37	.04	.36	.04	.39	.06
368-day weight (lb)	.38	.04	.43	.05	.31	.05
410-day weight (lb)	.32	.03	.40	.05	.24	.05
452-day weight (lb)	.42	.04	.55	.05	.27	.05
522-day weight (lb)	.45	.04	.59	.06	.30	.05
Weight, 1 yr (lb)	.45	.04	.59	.06	.32	.06
Weight, 2 yr (lb)	.52	.06	.58	.07	.47	.08
Weight, 3 yr (lb)	.43	.06	.50	.09	.38	.09
Weight, 4 yr (lb)	.41	.08	.31	.10	.52	.12
Weight, 5 yr (lb)	.43	.10	.57	.15	.41	.14
368-day height (inches)	.43	.04	.43	.05	.43	.06
Height, 1 yr (inches)	.52	.04	.54	.06	.49	.07
Height, 2 yr (inches)	.50	.05	.55	.07	.45	.08
Height, 3 yr (inches)	.42	.06	.52	.09	.32	.09
Height, 4 yr (inches)	.40	.08	.48	.11	.33	.11
Height, 5 yr (inches)	.27	.10	.31	.15	.32	.13
368-day condition score†	.40	.04	.45	.05	.31	.05
Condition score, 1 yr†	.40	.04	.46	.06	.29	.05
Condition score, 2 yr†	.40	.05	.50	.07	.28	.07
Condition score, 3 yr†	.38	.06	.36	.08	.36	.09
Condition score, 4 yr†	.47	.08	.49	.11	.31	.10
Condition score, 5 yr†	.29	.10	.40	.15	.11	.11
CD score, dams 2 yr old‡	.33	.09	.42	.11	.24	.14
CD, dams 2 yr old§ (%)	.26	.09	.26	.11	.29	.14
CD score, dams ≥3 yr old‡	.20	.05	.20	.07	.18	.08
CD, dams ≥3 yr old§ (%)	.13	.05	.16	.07	.04	.07
CD score, dams of all ages‡	.31	.03	.37	.05	.18	.04
CD, dams of all ages§ (%)	.17	.03	.18	.04	.14	.04
Gestation length (days)‖	.45	.06	.34	.08	.58	.10
Age at puberty (days)	.31	.04	.30	.05	.30	.06

† Evaluated on a scale of 1 to 9, 9 = very fat, 1 = emaciated.

‡ Calving difficulty score was rated as follows: 1 = no difficulty, 2 = little difficulty by hand, 3 = little difficulty with calf jack, 4 = slight difficulty with calf jack, 5 = moderate difficulty with calf jack, 6 = major difficulty with calf jack, and 7 = caesarean birth.

§ Calving difficulty (%) was scored as follows: scores 1 and 2 = 0; scores 3, 4, 5, 6, and 7 = 1.

‖ Calves conceived by artificial insemination.

Table 46. Genetic and phenotypic correlations among growth and carcass traits of castrate males[†] (*n*=1,594)

Trait	1.	2.	3.	4.	5.	6.	7.
1. Birth weight		0.36	0.44	0.39	–0.04	–0.10	0.20
2. 200-day weight	0.29±.20		.59	.58	.16	.01	.24
3. Slaughter weight	.27±.21	.40±.17		.92	.25	.12	.36
4. Carcass weight	.18±.25	.42±.18	.92±.04		.28	.13	.40
5. Adjusted fat 12th rib	–.06±.25	.15±.22	.23±.23	.13±.25		.25	–.06
6. Marbling score[‡]	–.08±.20	.12±.17	.27±.18	.31±.20	.44±.18		–.05
7. LMA[‡]	.17±.26	.49±.21	.45±.21	.66±.20	–.06±.27	–.02±.21	
8. Retail product[§] (%)	–.16±.20	–.09±.18	–.28±.21	–.12±.22	–.76±.32	–.60±.20	.32±.19
9. Fat trim[ǁ] (%)	.04±.22	.03±.19	.19±.20	.08±.23	.82±.11	.66±.12	.26±.25
10. Bone trim (%)	.54±.24	.26±.25	.37±.30	.18±.32	–.27±.34	–.28±.25	–.25±.31
11. Carcass bone weight	.39±.17	.47±.14	.81±.08	.75±.11	–.05±.21	.08±.16	.31±.20
12. Carcass lean weight[¶]	.04±.25	.36±.18	.58±.14	.76±.10	–.48±.26	–.12±.19	.86±.14
13. Carcass fat weight[††]	.05±.23	.18±.20	.57±.14	.51±.17	.80±.12	.65±.14	.07±.25
14. Long. muscle fat[‡‡] (%)	.10±.20	.14±.17	.24±.18	.26±.19	.33±.18	.98±.06	.20±.21
15. Shear force[§§]	–.08±.35	–.34±.34	–.05±.34	–.10±.37	–.23±.37	–1.00±.48	–.48±.39
16. Tenderness score[ǁǁ]	.29±.28	.54±.24	.07±.25	.15±.28	.14±.27	.32±.20	.56±.31
17. Juiciness score[¶¶]	.14±.25	.41±.22	.06±.24	.03±.26	.34±.24	.23±.18	.24±.27
18. Flavor score[†††]	–.68±.58	.48±.46	–.34±.44	–.12±.47	.10±.46	.33±.37	.22±.50
19. Muscling score[‡‡‡]	.30±.17	.31±.15	.14±.16	.25±.18	–.38±.19	–.18±.14	.54±.17
20. Fat score[‡‡‡]	.07±.24	–.10±.21	.20±.22	.15±.24	.38±.21	.39±.18	–.04±.26

[†]Genetic correlations and their standard errors are below the diagonal and phenotypic correlations above.

Continued

[‡]LMA = Longissimus muscle area. A score of 4.00 to 4.90 = slight, 5.00 to 5.90 = small.

[§]Retail product includes steaks and roasts plus lean trim adjusted to 20-percent fat based on chemical analysis of lean trim.

[ǁ] All subcutaneous and accessible intermuscular fat removed.

[¶]Carcass lean includes steaks and roasts trimmed to 0 inches of fat cover plus fat-free lean trim based on chemical analysis of lean trim.

[††]Carcass fat includes fat trim plus fat in lean trim based on chemical analysis of lean trim.

[‡‡]Ether-extracted fat from a cross section of the longissimus muscle.

[§§]Shear force required to cut through a 0.5-inch core.

[ǁǁ]A score of 4 = slightly tough, 5 = slightly tender, 8 = extremely tender.

[¶¶]A score of 4 = slightly dry, 5= slightly juicy, 8 = extremely juicy.

[†††]A score of 4 = slightly bland, 5 = slightly intense, 8 = extremely intense.

[‡‡‡]Scores ranged from 3 to 27, with 6, 15, and 24 reflecting low, average, and high, respectively, for muscle or fat.

Table 46. Genetic and phenotypic correlations among growth and carcass traits of castrate males† (*n*=1,594)—Continued

Trait	8.	9.	10.	11.	12.	13.	14.
1. Birth weight	0.05	–0.10	0.21	0.54	0.42	0.11	–0.06
2. 200-day weight	–.12	.13	–.08	.50	.52	.38	.02
3. Slaughter weight	–.25	.28	–.23	.72	.79	.66	.12
4. Carcass weight	–.24	.30	–.32	.66	.81	.67	.13
5. Adjusted fat 12th rib	–.56	.60	–.42	–.06	–.03	.60	.27
6. Marbling score‡	–.43	.46	–.31	–.09	–.07	.38	.63
7. LMA‡	.25	–.18	–.13	.30	.55	.06	–.11
8. Retail product§ (%)		–.96	.37	.04	.29	–.82	–.48
9. Fat trim‖ (%)	–.98±.36		–.60	–.16	–.21	.88	.49
10. Bone trim (%)	–.08±.21	–.14±.29		.44	–.14	–.61	–.26
11. Carcass bone weight	–.20±.16	.03±.19	.79±.16		.70	.20	–.08
12. Carcass lean weight¶	.56±.16	–.59±.26	.19±.28	.54±.13		.24	–.13
13. Carcass fat weight††	–.88±.36	.90±.04	–.07±.30	.35±.18	–.16±.22		.41
14. Long. muscle fat‡‡ (%)	–.55±.20	.64±.11	–.43±.25	.03±.16	.06±.19	.65±.13	
15. Shear force§§	.00±.28	–.04±.31	.18±.37	–.02±.29	–.14±.34	–.05±.34	–.77±.41
16. Tenderness score‖‖	.03±.21	–.07±.23	.18±.30	.27±.23	.24±.26	–.02±.25	.20±.20
17. Juiciness score¶¶	–.20±.21	.15±.21	.22±.28	.18±.21	–.07±.24	.08±.23	.29±.18
18. Flavor score†††	–.16±.39	–.11±.39	–.22±.54	–.16±.39	.09±.44	–.05±.43	.30±.36
19. Muscling score‡‡‡	.32±.13	–.39±.17	.33±.20	.32±.14	.46±.15	–.32±.17	–.15±.14
20. Fat score‡‡‡	–.54±.25	.61±.16	–.34±.33	–.04±.20	–.18±.23	.54±.17	.46±.18

†Genetic correlations and their standard errors are below the diagonal and phenotypic correlations above.

Continued

‡LMA = Longissimus muscle area. A score of 4.00 to 4.90 = slight, 5.00 to 5.90 = small.

§Retail product includes steaks and roasts plus lean trim adjusted to 20-percent fat based on chemical analysis of lean trim.

‖All subcutaneous and accessible intermuscular fat removed.

¶Carcass lean includes steaks and roasts trimmed to 0 inches of fat cover plus fat-free lean trim based on chemical analysis of lean trim.

††Carcass fat includes fat trim plus fat in lean trim based on chemical analysis of lean trim.

‡‡Ether-extracted fat from a cross section of the longissimus muscle.

§§Shear force required to cut through a 0.5-inch core.

‖‖A score of 4 = slightly tough, 5 = slightly tender, 8 = extremely tender.

¶¶A score of 4 = slightly dry, 5= slightly juicy, 8 = extremely juicy.

†††A score of 4 = slightly bland, 5 = slightly intense, 8 = extremely intense.

‡‡‡Scores ranged from 3 to 27, with 6, 15, and 24 reflecting low, average, and high, respectively, for muscle or fat.

Table 46. Genetic and phenotypic correlations among growth and carcass traits of castrate males[†] (*n*=1,594)—Continued

Trait	15.	16.	17.	18.	19.	20.
1. Birth weight	–0.02	–0.04	–0.05	0.00	0.11	0.08
2. 200-day weight	–.06	.03	.02	.05	.10	.18
3. Slaughter weight	–.08	.02	–.01	.11	.12	.40
4. Carcass weight	–.07	.02	.01	.09	.15	.38
5. Adjusted fat 12th rib	–.06	.05	.09	.09	–.09	.33
6. Marbling score[‡]	–.24	.20	.21	.12	–.09	.21
7. LMA[‡]	.02	–.02	–.04	.03	.25	.16
8. Retail product[§] (%)	.16	–.11	–.14	–.14	.23	–.36
9. Fat trim[‖] (%)	–.17	.13	.15	.16	–.19	.41
10. Bone trim (%)	.13	–.11	–.09	–.13	–.05	–.38
11. Carcass bone weight	.02	–.04	–.04	.00	.11	.08
12. Carcass lean weight[¶]	.00	–.01	–.06	.02	.28	.20
13. Carcass fat weight[††]	–.16	.10	.11	.16	–.07	.51
14. Long. muscle fat[‡‡] (%)	–.23	.17	.20	.12	–.10	.13
15. Shear force[§§]		–.57	–.19	–.23	–.01	–.09
16. Tenderness score[‖‖]	–1.00±.77		.60	.17	.02	.04
17. Juiciness score[¶¶]	–.96±.54	.88±.13		–.06	–.02	–.04
18. Flavor score[†††]	–1.00±1.00	.63±.52	.79±.66		–.02	.13
19. Muscling score[‡‡‡]	.06±.24	.07±.19	.06±.18	–.25±.35		.01
20. Fat score[‡‡‡]	–.26±.36	.02±.26	–.17±.24	.21±.44	–.03±.17	

[†]Genetic correlations and their standard errors are below the diagonal and phenotypic correlations above.
[‡]LMA = Longissimus muscle area. A score of 4.00 to 4.90 = slight, 5.00 to 5.90 = small.
[§]Retail product includes steaks and roasts plus lean trim adjusted to 20-percent fat based on chemical analysis of lean trim.
[‖]All subcutaneous and accessible intermuscular fat removed.
[¶]Carcass lean includes steaks and roasts trimmed to 0 inches of fat cover plus fat-free lean trim based on chemical analysis of lean trim.
[††]Carcass fat includes fat trim plus fat in lean trim based on chemical analysis of lean trim.
[‡‡]Ether-extracted fat from a cross section of the longissimus muscle.
[§§]Shear force required to cut through a 0.5-inch core.
[‖‖]A score of 4 = slightly tough, 5 = slightly tender, 8 = extremely tender.
[¶¶]A score of 4 = slightly dry, 5= slightly juicy, 8 = extremely juicy.
[†††]A score of 4 = slightly bland, 5 = slightly intense, 8 = extremely intense.
[‡‡‡]Scores ranged from 3 to 27, with 6, 15, and 24 reflecting low, average, and high, respectively, for muscle or fat.

Production Traits of Intact Males

The r_g among size traits, calving difficulty scores and calving difficulty percentage, and gestation length are presented below the diagonal in table 47 for contributing purebreds and composites combined. Genetic correlations among size traits were highly variable, ranging from -0.02 ± 0.07 between birth weight and preweaning ADG and 0.97 ± 0.01 between preweaning ADG and 200-day weight. The low r_g between preweaning and postweaning ADG (0.04 ± 0.07) is not consistent with other reports (Koch et al. 1982). The r_g of birth weight with calving difficulty score and calving difficulty percentage were similar in calves from dams of all ages, from 2-yr-old dams, and from dams 3 yr old or older, ranging from 0.55 ± 0.13 to 0.82 ± 0.29.

The r_g of 0.62 ± 0.04 between 368-day weight and 368-day height (table 47) suggests that selection for either trait would result in changes in the other. The r_g of 0.65 ± 0.05 between 368-day height and 368-day kind score suggests that selection for taller animals will result in higher scores for kind as kind score was applied in this study. The r_g between muscling score and height was low (-0.10 ± 0.07). The r_g between 368-day weight and 368-day condition score was relatively low (that is, 0.24 ± 0.07). The higher r_g between birth weight and calving difficulty score and percentage calving difficulty (range of 0.55 ± 0.13 to 0.82 ± 0.29) than between birth weight and 368-day weight (that is, 0.36 ± 0.06) suggests that calving difficulty could be reduced by reducing birth weight while maintaining 368-day weight. A similar conclusion was reached by Dickerson et al. (1974) in which a selection index of I = [368-day weight − (3.2 × birth weight)] was suggested. The relatively high r_g of gestation length with calving difficulty score and with percentage calving difficulty (that is, 0.57 ± 0.18 and 0.54 ± 0.26, respectively) suggests that some reduction in gestation length would favor reduced calving difficulty. The relatively low r_g between gestation length and birth weight (0.21 ± 0.11) is noted. The r_g of scrotal circumference with other traits evaluated was generally low.

Production Traits of Females

Estimates of r_g and their standard errors for purebreds and composites combined are presented in table 48 below the diagonal. Separate analyses were run for six different age classes of individuals—ages 1, 2, 3, 3 or older, 4, and 5 yr. Data recorded through 522 days were included in all analyses. The reason for this approach was to use all of the data available in each age class. For example, gestation length was available only for calves conceived by artificial insemination in females 3 yr old or older. Further, many of the females were removed from their population based on nonperformance criteria by the age of 5 yr. Differences in magnitude of standard errors for h^2 in table 45 reflect differences in the number of observations for different traits. The r_g were not estimated for all combinations of the 33 traits shown in table 45. Only the r_g among selected weights, heights, condition scores, calving difficulty scores, gestation length, and age at puberty are presented in table 48. For example, percentage calving difficulty is not included because calving difficulty score is a more descriptive evaluation of differences in the trait than the percentage calving difficulty is.

The r_g between birth weight and subsequent weights were similar for all ages to 2 yr but not at 5 yr (table 48). The high standard error reflects the relatively small number of observations made at 5 yr. The r_g between weight and height generally were high at each age. The r_g for weight and height with condition score were variable at each age but tended to be relatively low. The r_g for 200-day and 368-day weight with subsequent weights were much higher than the r_g for birth weight and subsequent weights. The r_g between height at 368 days and height at subsequent ages were only slightly higher than r_g between weight at 368 days and weight at subsequent ages. The r_g between condition score at 368 days and condition score at subsequent ages were relatively low (for example, 0.30 ± 0.09 and 0.36 ± 0.18). Calving difficulty score of calves from 2-yr-old dams was not correlated with height at 368 days (r_g=0.20 ± 0.16) or at 2 yr (r_g=0.00 ± 0.09). The r_g between calving difficulty score at 2 yr and weight at 2 yr was low (0.09 ± 0.09) and not important.

The r_g between birth weight and calving difficulty score at 2 yr (0.59 ± 0.14) was higher than the r_g between birth weight and calving difficulty score at 3 yr old or older (0.44 ± 0.14). The higher r_g between

Table 47. Genetic and phenotypic correlations† among production traits of intact males

Trait	1.	2.	3.	4.	5.	6.	7.
1. Birth weight		0.15	0.37	0.30	0.42	0.44	0.01
2. Preweaning ADG	–0.02±.07		.97	.20	.73	.46	.17
3. 200-day weight	.24±.07	.97±.01		.25	.78	.54	.16
4. Postweaning ADG	.30±.06	.04±.07	.11±.07		.8	.48	.30
5. 368-day weight	.36±.06	.63±.04	.70±.04	.79±.03		.64	.30
6. 368-day height	.40±.06	.46±.06	.55±.05	.39±.06	.62±.04		–.07
7. 368-day condition score	–.07±.07	.01±.08	–.01±.08	.34±.07	.24±.07	–.23±.07	
8. 368-day muscle score	.31±.07	.05±.08	.13±.08	.24±.07	–.26±.07	–.10±.07	.12±.08
9. 368-day trimness score	–.16±.07	.15±.08	.10±.08	–.08±.07	.01±.08	–.10±.07	.25±.07
10. 368-day kind score	.20±.07	.33±.07	.37±.07	.18±.07	.36±.07	.65±.05	–.27±.08
11. Scrotal circumference	.01±.07	.26±.07	.26±.06	.02±.07	.18±.07	.30±.06	.08±.07
12. CD score, dams of all ages‡	.60±.06	–.09±.08	.06±.08	.21±.08	.19±.08	.24±.07	.04±.08
13. CD, dams of all ages§ (%)	.59±.06	.05±.09	.20±.09	.27±.08	.32±.09	.31±.08	–.04±.09
14. CD score, dams 2 yr old‡	.62±.12	–.08±.13	.00±.14	.11±.14	.07±.15	.14±.13	–.20±.15
15. CD, dams 2 yr old§ (%)	.55±.13	.09±.12	.16±.13	.22±.13	.27±.13	.23±.12	–.08±.14
16. CD score, dams ≥3 yr old‡	.62±.17	–.06±.22	.12±.21	.11±.19	.14±.19	.38±.17	–.29±.21
17. CD, dams ≥3 yr old§ (%)	.82±.29	.15±.30	.17±.25	.30±.26	.54±.26	–.28±.30	–.12±.27
18. Gestation length, dams ≥3 yr old	.21±.11	–.15±.14	–.08±.13	.16±.12	.07±.12	.13±.10	–.08±.13

†Genetic correlations and their standard errors are below the diagonal. Phenotypic correlations are above the diagonal.

Continued

‡Calving difficulty score was rated as follows: 1 = no difficulty, 2 = little difficulty by hand, 3 = little difficulty with calf jack, 4 = slight difficulty with calf jack, 5 = moderate difficulty with calf jack, 6 = major difficulty with calf jack, and 7 = caesarean birth.

§Calving difficulty (%) was scored as follows: scores 1 and 2 = 0; scores 3, 4, 5, 6, and 7 = 1.

Table 47. Genetic and phenotypic correlations† among production traits of intact males—Continued

Trait	8.	9.	10.	11.	12.	13.	14.
1. Birth weight	0.07	0.00	0.24	0.11	0.32	0.26	0.53
2. Preweaning ADG	.11	.08	.31	.31	–.03	–.02	–.02
3. 200-day weight	.12	.08	.34	.32	.04	.04	.09
4. Postweaning ADG	.16	.08	.29	.23	.09	.07	.13
5. 368-day weight	.18	.10	.40	.34	.08	.07	.14
6. 368-day height	–.09	.00	.53	.25	.11	.10	.17
7. 368-day condition score	.10	.26	–.10	.10	.00	–.02	.01
8. 368-day muscle score		–.08	–.01	.00	.04	.05	.06
9. 368-day trimness score	–.20±.08		–.20	.06	–.02	–.04	–.03
10. 368-day kind score	–.03±.08	–.22±.08		.18	.05	.05	.07
11. Scrotal circumference	–.17±.07	.13±.07	.22±.07		–.20	–.20	.01
12. CD score, dams of all ages‡	.12±.08	–.11±.08	.23±.09	–.06±.08		.77	
13. CD, dams of all ages§ (%)	.19±.09	–.09±.09	.19±.09	–.06±.09	.93±.02		
14. CD score, dams 2 yr old‡	.33±.16	–.29±.14	–.06±.16	–.17±.18			
15. CD, dams 2 yr old§ (%)	.44±.15	–.23±.13	.00±.15	–.10±.17			1.00±.05
16. CD score, dams ≥3 yr old‡	–.21±.20	–.31±.20	.34±.19	–.25±.19			
17. CD, dams ≥3 yr old§ (%)	–.23±.27	.21±.25	–.14±.25				
18. Gestation length, dams ≥3 yr old	.19±.12	–.11±.12	.09±.12	–.34±.11			

†Genetic correlations and their standard errors are below the diagonal. Phenotypic correlations are above the diagonal.

‡Calving difficulty score was rated as follows: 1 = no difficulty, 2 = little difficulty by hand, 3 = little difficulty with calf jack, 4 = slight difficulty with calf jack, 5 = moderate difficulty with calf jack, 6 = major difficulty with calf jack, and 7 = caesarean birth.

§Calving difficulty (%) was scored as follows: scores 1 and 2 = 0; scores 3, 4, 5, 6, and 7 = 1.

Continued

Table 47. Genetic and phenotypic correlations[†] among production traits of intact males—Continued

Trait	15.	16.	17.	18.
1. Birth weight	0.42	0.26	0.24	0.27
2. Preweaning ADG	.02	–.06	–.04	.01
3. 200-day weight	.10	.00	.02	.07
4. Postweaning ADG	.12	.06	.05	.04
5. 368-day weight	.14	.04	.04	.07
6. 368-day height	.16	.06	.06	.11
7. 368-day condition score	.00	.00	–.03	.00
8. 368-day muscle score	.06	.05	.04	–.02
9. 368-day trimness score	–.04	–.01	–.02	.01
10. 368-day kind score	.08	.03	.03	.07
11. Scrotal circumference	.02	–.05	–.04	–.02
12. CD score, dams of all ages[‡]				
13. CD, dams of all ages[§] (%)				
14. CD score, dams 2 yr old[‡]	.80			
15. CD, dams 2 yr old[§] (%)				
16. CD score, dams ≥3 yr old[‡]			.79	.11
17. CD, dams ≥3 yr old[§] (%)		1.00±.22		.11
18. Gestation length, dams ≥3 yr old		.57±.18	.54±.26	

[†]Genetic correlations and their standard errors are below the diagonal. Phenotypic correlations are above the diagonal.

[‡]Calving difficulty score was rated as follows: 1 = no difficulty, 2 = little difficulty by hand, 3 = little difficulty with calf jack, 4 = slight difficulty with calf jack, 5 = moderate difficulty with calf jack, 6 = major difficulty with calf jack, and 7 = caesarean birth.

[§]Calving difficulty (%) was scored as follows: scores 1 and 2 = 0; scores 3, 4, 5, 6, and 7 = 1.

Table 48. Genetic and phenotypic correlations[†] among production traits of females

Trait	1.	2.	3.	4.	5.	6.	7.
1. Birth weight		0.40	0.42	0.42	0.40	0.44	0.46
2. 200-day weight (kg)	0.34±.06		.82	.61	.50	.56	.50
3. 368-day weight (kg)	.33±.06	.84±.02		.76	.64	.63	.58
4. Weight, 2 yr	.36±.07	.74±.05	.85±.03			.58	.69
5. Weight, 5 yr	.08±.21	.66±.12	.83±.08			.48	
6. 368-day height	.35±.06	.66±.04	.70±.04	.68±.06	.51±.15		.77
7. Height, 2 yr	.49±.07	.63±.06	.67±.05	.74±.04		.92±.02	
8. Height, 5 yr	.25±.24	.44±.18	.48±.46		.47±.16	.88±.10	
9. 368-day condition score[‡]	−.02±.07	.14±.07	.25±.07	.15±.08	.24±.16	−.15±.07	−.03±.09
10. Condition score, dams 2 yr old[‡]	.03±.09	.32±.09	.36±.08	.48±.07		.01±.10	.10±.09
11. Condition score, dams 5 yr old[‡]	−.20±.25	−.02±.21	.34±.20		.56±.16	−.14±.24	
12. CD score, dams 2 yr old[§]	.59±.14	.06±.15	.09±.16	.09±.09		.20±.16	.00±.09
13. CD score, dams ≥3 yr old[§]	.44±.14	.36±.17	.24±.16			.12±.15	
14. Gestation length (days)	.30±.10	−.23±.12	−.14±.12			−.14±.11	
15. Puberty age (days)	.03±.08	−.14±.09	−.05±.08	.11±.12	−.05+.10	−.11±.08	.17±.12

Continued

[†]Genetic correlations and their standard errors are below the diagonal. Phenotypic correlations are above the diagonal.

[‡]Evaluated on a scale of 1 to 9, 9 = very fat, 1 = emaciated.

[§]Calving difficulty score was rated as follows: 1 = no difficulty, 2 = little difficulty by hand, 3 = little difficulty with calf jack, 4 = slight difficulty with calf jack, 5 = moderate difficulty with calf jack, 6 = major difficulty with calf jack, and 7 = caesarean birth.

Table 48. Genetic and phenotypic correlations[†] among production traits of females—Continued

Trait	8.	9.	10.	11.	12.	13.	14.	15.
1. Birth weight	0.42	0.02	0.03	–0.03	0.43	0.12	0.29	0.05
2. 200-day weight	.39	.19	.20	.08	.10	.04	.06	–.12
3. 368-day weight (kg)	.49	.32	.27	.13	.14	.05	.07	–.11
4. Weight, 2 yr		.11	.47		.09			.00
5. Weight, 5 yr	.70	.10		.41				.01
6. 368-day height	.71	–.05	–.04	–.12	.18	.03	.08	–.06
7. Height, 2 yr		–.11	.02		.10			.02
8. Height, 5 yr		–.17		–.02				.03
9. 368-day condition score[‡]	–.23±.21		.26	.21	–.02	–.03	.04	–.09
10. Condition score, dams 2 yr old[‡]		.30±.09			.00			–.02
11. Condition score, dams 5 yr old[‡]	–.14±.26	.36±.18						–.06
12. CD score, dams 2 yr old[§]		.09±.13	–.14±.10					
13. CD score, dams ≥3 yr old[§]		.09±.18					.05	
14. Gestation length (days)		.06±.13				–.07±.14		
15. Puberty age (days)	.02±.11	–.02±.08	–.09±.14	–.17±.11				

[†]Genetic correlations and their standard errors are below the diagonal. Phenotypic correlations are above the diagonal.

[‡]Evaluated on a scale of 1 to 9, 9 = very fat, 1 = emaciated.

[§]Calving difficulty score was rated as follows: 1 = no difficulty, 2 = little difficulty by hand, 3 = little difficulty with calf jack, 4 = slight difficulty with calf jack, 5 = moderate difficulty with calf jack, 6 = major difficulty with calf jack, and 7 = caesarean birth.

birth weight and calving difficulty score at 2 yr (0.59 $\pm$ 0.14) than between birth weight and 368-day weight (0.33 $\pm$ 0.06) suggests some opportunity to reduce calving difficulty score by reducing birth weight while maintaining 368-day weight. A similar conclusion was reached by Dickerson et al. (1974) in which a selection index of I = [368-day weight − (3.2 × birth weight)] was suggested. These estimates of r_g for females are similar to the r_g for males from the same population (table 47), with the exception of r_g between gestation length and calving difficulty score of calves from females 3 yr old or older, which was considerably higher in males than females (0.57 $\pm$ 0.18 vs. –0.07 $\pm$ 0.14) (table 48).

Phenotypic Correlations

Estimates of phenotypic correlations (r_p) for all breed groups are presented above the diagonal in table 46 for growth and carcass traits of castrate males, above the diagonal in table 47 for production traits of intact males, and above the diagonal in table 48 for some production traits of females. These phenotypic correlations are presented for purebred and composite breed groups combined.

Growth and Carcass Traits of Castrate Males

Phenotypic correlations of marbling score and percentage longissimus muscle fat with palatability attributes (tenderness, juiciness, and flavor) were below 0.30 (table 46). Although marbling score is the primary factor determining carcass quality grade in cattle of the age in this study, it is not very useful for predicting palatability. This is consistent with the findings of other studies at the U.S. Meat Animal Research Center with cattle of similar age and nutritional background.

Production Traits of Intact Males

Phenotypic correlations among size traits for intact males were intermediate to high (table 47). The r_p between 368-day height and 368-day kind score (0.53) was higher than for any other combination. The r_p of 368-day kind score and 368-day scrotal circumference with different measures of growth were low to intermediate. The r_p among different anatomical scores generally were low. As expected, a high r_p between calving difficulty score and percentage calving difficulty was observed in females of different age classes (0.77, 0.80, and 0.79) . The r_p of calving difficulty score and percentage calving difficulty with gestation length were low (0.11 and 0.11) and the r_g were 0.57 and 0.54.

Production Traits of Females

The r_p followed the pattern of the r_g but generally were lower (table 48). The r_p between weights at different ages and between heights at different ages and between weights and heights at the same age were relatively high. The r_p of calving difficulty score at the ages presented, gestation length, and age at puberty with weight, height, and condition score at 368 days generally were low and not important.

Adjustment Factors for Age of Dam

Adjustment factors for age of dam are provided in table 49 for each sex of all breed groups.

Composite Breed Formation

The distribution of numbers by herd size in the U.S. beef breeding herd is as follows: 35 percent represented by herds of 50 cows or fewer, 55 percent represented by herds of 100 cows or fewer, and 87 percent represented by herds of 500 cows or fewer (U.S. Department of Agriculture 1987). On farms and ranches that have beef cows, 80 percent have 50 cows or fewer, 93 percent have 100 or fewer, and more than 99 percent have 500 or fewer.

With 55 percent of the U.S. beef breeding herd and 93 percent 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 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

Table 49. Adjustment factors for adjusting age of dam to a mature basis by sex and breed group

		Females			Intact males		
Breed group	Age of dam (yr)	Birth weight (lb)	Preweaning ADG (lb)	Postweaning ADG (lb)	Birth weight (lb)	Preweaning ADG (lb)	Postweaning ADG (lb)
Red Poll	2	8.1129	0.1742	–0.1014	10.7804	0.2050	–0.0397
	3	3.8360	0.1257	–0.0460	5.6658	0.1213	0.0044
	4	–2.8439	0.0132	–0.0088	1.1464	0.0243	0.0507
Hereford	2	8.4215	0.1962	–0.0728	10.0750	0.2712	–0.0220
	3	3.9903	0.1168	–0.0463	7.0547	0.1830	0.0331
	4	2.5794	0.0639	–0.0022	2.9541	0.0860	0.0353
Angus	2	5.8642	0.2116	–0.0705	8.2011	0.2778	–0.0198
	3	2.4912	0.1411	–0.0220	3.3289	0.1653	0.0309
	4	0.0000	0.0705	–0.0132	0.7275	0.0661	0.0000
Limousin	2	10.6261	0.2249	0.0309	12.3457	0.1962	–0.1345
	3	5.4894	0.1675	0.0331	7.6279	0.1367	0.0110
	4	0.5732	0.0926	0.0220	2.4691	0.0573	0.0044
Braunvieh	2	9.4136	0.2513	–0.0132	7.5617	0.2337	–0.0397
	3	5.9965	0.1587	0.0265	5.2469	0.1279	–0.0044
	4	0.7055	0.0353	0.0022	1.4330	0.0375	0.0353
Pinzgauer	2	15.9171	0.3571	–0.0044	22.5750	0.4563	0.0309
	3	6.3933	0.1918	0.0309	9.3474	0.2910	0.0705
	4	3.1746	0.0397	0.0507	4.7619	0.1235	0.0705
Gelbvieh	2	13.3818	0.2579	–0.0265	11.0009	0.2998	–0.0309
	3	8.4215	0.1565	0.0220	4.2328	0.2160	–0.0088
	4	3.3289	0.0816	0.0265	-1.2566	0.0772	0.0287

Continued

Table 49. Adjustment factors for adjusting age of dam to a mature basis by sex and breed group—Continued

Breed group	Age of dam (yr)	Females			Intact males		
		Birth weight (lb)	Preweaning ADG (lb)	Postweaning ADG (lb)	Birth weight (lb)	Preweaning ADG (lb)	Postweaning ADG (lb)
Simmental	2	12.5882	0.1918	–0.0772	13.3157	0.3175	–0.0309
	3	7.5838	0.1036	–0.0066	6.5035	0.2028	–0.0022
	4	0.0441	0.0044	–0.0044	0.3968	0.0904	0.0375
Charolais	2	13.4700	0.2756	–0.0176	18.6728	0.3175	–0.0088
	3	4.0564	0.2160	–0.0287	7.0547	0.2513	0.0000
	4	1.1464	0.0617	–0.0485	2.0062	0.0948	0.0375
MARC I	2	12.4339	0.2116	–0.0265	12.0811	0.2535	–0.0287
	3	6.7019	0.1455	–0.0132	6.6799	0.1477	0.0353
	4	2.4030	0.0353	–0.0309	1.4550	0.0287	0.0309
MARC II	2	7.4515	0.2072	–0.0750	10.0529	0.2690	–0.0485
	3	0.5071	0.1190	–0.0595	0.6393	0.1764	0.0176
	4	–0.5291	–0.0132	–0.0551	–0.4850	0.0441	–0.0022
MARC III	2	13.3818	0.2006	–0.0617	12.0811	0.2734	–0.0353
	3	3.5714	0.1279	–0.0683	1.2787	0.1455	–0.0287
	4	1.8519	–0.0110	–0.0132	0.6614	0.0683	0.0220

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. The management problems associated with small herd size and wide 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 se*) mating within the crosses is proportional to $(n-1)/n$, where n is the number of breeds involved in the initial cross (Wright 1922, Dickerson 1969, 1973). This loss in heterozygosity occurs between the F_1 and F_2 generations. If inbreeding is avoided, further loss of heterozygosity in an *inter se* mated composite population does not occur. This expression [that is, $(n-1)/n$] 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 $1 - \Sigma P_i^2$, where P_i is the fraction of each of n breed's contributing to the foundation of a composite breed; for example, 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 $1 - [(3/8)^2 + (3/8)^2 + (1/4)^2] = 65.6$ percent. 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 contributing to the foundation [that is, $(n-1)/n$]. 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 in cattle can be accounted for by dominance effects of genes, heterosis involving *Bos taurus* breeds 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 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 is likely to be positive (less). Both genetic situations may exist, but the likelihood would seem to be greater for favorable than for unfavorable epistatic combinations in parental breeds, particularly for fitness traits (for example, reproduction and survival). Also, heterosis may deviate from heterozygosity in a positive direction if a threshold effect (nonlinear) of heterozygosity relative to heterosis should exist. Results from the comprehensive experiment reported in this bulletin show that heterosis in composite populations, generally, is retained in proportion to retained heterozygosity and thus can be accounted for by dominance effects of genes. Other than for characters affected by natural or automatic selection (for example, 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 the same opportunity as rotational crossbreeding for retaining high levels of individual and maternal heterosis, in addition to heterosis for male reproductive performance (table 3). Composite breeds offer the opportunity to use genetic differences among breeds (that is, breed complementarity) 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 specific market requirements. Further, composite breeds provide herds of any size with an opportunity to use heterosis and breed complementarity simultaneously.

A specific composite breed does not permit the use of different genotypes (complementarity) for male and female parents (Cartwright 1970). 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. This may be the case when the slaughter animal is finished under more favorable environmental conditions than the environment where breeding herds are maintained. 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 for each specialized composite breed. There is opportunity to develop both general purpose and specialized maternal and paternal 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 limited the success of some previous efforts in 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 should result in a rate of increase in inbreeding of about 0.5 percent per generation. With an average generation interval of 5 yr, the accumulated inbreeding in a composite breed after 50 yr (that is, 10 generations) would be about 5 percent. Further, a large number of sires (that is, 15–20) of each purebreed contributing to the foundation of a composite breed should be sampled in order to minimize the rate of inbreeding in subsequent generations of *inter se* 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 alternative to heterosis and must be avoided in order to retain high levels of heterozygosity and thus heterosis in composite breeds.

An alternative procedure for keeping rate of inbreeding low in a composite population or breed is to keep the composite open to the introduction of new germplasm. This may be from new samples of the same breeds contributing initially to the composite or by including contributions from additional breeds. In addition to providing an effective procedure for keeping inbreeding at a low level, an "open concept" in maintaining a composite breed allows for continuing use of breed differences to adjust bioeconomic traits closer to the optimum level in harmony with changes in production resource base and with market requirements. Thus an "open concept" has greater flexibility and is generally favored by the authors of this bulletin. An "open concept" does not lessen the need to sample a large number of sires and to use a large number of sires per generation. Inbreeding "bottle necks" can develop unless a large number of sires are used in each generation.

The development of composite breeds may now be viewed as a predictable procedure when contributions to a composite 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. Experimental comparisons involving adequate samples of each breed of interest provide the most reliable estimates of breed differences.

Heterosis from crosses of *Bos indicus* breeds with *Bos taurus* breeds is considerably greater (perhaps twofold) than crosses among *Bos taurus* breeds. We do not believe that these experimental results on heterosis retention in composite populations with contributions limited to *Bos taurus* breeds should be extrapolated to include 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 se* mated composite populations with contributions by both *Bos taurus* and *Bos indicus* breeds. However, from the limited information available, results suggest that heterosis from breed crosses of *Bos taurus* with *Bos indicus* breeds can be accounted for by dominance effects of genes because heterosis in advanced generations seems to be retained in proportion to retained heterozygosity.

In summary, the following factors favor the use of composite breeds:

- It is simple and provides a high level of heterosis or hybrid vigor.
- It is highly effective for using breed differences or breed complementarity to <u>achieve</u> and <u>maintain</u> an optimum additive genetic (breed) composition for production and carcass traits.
- It provides a high degree of uniformity within and between generations.
- It offers small herds an opportunity to use high levels of heterosis and breed complementarity, assuming seedstock herds exist to provide bulls on a continuing basis.

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Glossary

Additive genetic value: The average performance or average breeding value of individuals within a breed for bioeconomic traits resulting from the average effects of all alleles (favorable and unfavorable) on a specific trait in the breed. Additive individual or additive direct genetic effects (G^i) are the result of genotype of the individual, whereas additive maternal genetic effects (G^m) are the result of genotype of the dam, that is, reproductive traits and maternal ability. Thus, additive genetic value = $G^i + G^m$. Differences among breeds are large for additive genetic value for most bioeconomic traits.

Allele: A different form of the same gene that maintains identity, except for rare mutations, in successive generations. Each allele has a specific unique sequence of nucleotides or base pairs.

Backcross: The progeny resulting from mating a cross such as AB to either parent breed such as A×AB or B×AB.

Bioeconomic trait: Any biological trait of economic importance.

Coefficient of variation (*CV*): An expression of variation relative to the mean. The *CV* is usually expressed as a percentage and is calculated as 100 $\sigma/\overline{X}$, where σ is the standard deviation and $\overline{X}$ is the mean.

Complementarity: The use of breed differences to achieve a more optimum additive and nonadditive breed composition for production and carcass traits of economic value. Another use of the word in specific crossbreeding systems (for example, terminal sire systems) is the organization of matings to maximize the influence of desired characteristics and minimize the influence of undesired characteristics of each breed used.

Composite: A new breed or population that is established with contribututions from two or more existing breeds and is generally mated *inter se* to animals of the same breed composition. Composites may be closed or open to the introduction of genes from the same breeds or additional breeds. Such introductions may be made to adjust additive genetic value of the composite for specific traits or to reduce the rate of inbreeding. The primary objectives of composite breeds are (1) it is a simple procedure to use high levels of heterosis, (2) it is a highly effective procedure to use breed differences or breed complementarity, and (3) it results in a high level of uniformity both within and between generations.

Dominance: The result of one gene "A" producing the same phenotype whether paired with "A" or its allele "a." In such a situation, "a" is recessive to "A." Dominance effects result from the interaction of alleles from the same locus. For example, for coat color, black (B) is dominant to red (b), because heterozygotes (Bb) express black coat color the same as homozygotes for the black allele (BB). Red coat color is expressed in animals that are homozygous for red coat color (bb). In a population sense, dominance is the deviation from the average effects of genes "A" and "a" in the population.

Epistasis or epistatic effects: The result of interaction of genes from different loci. The effects of specific gene combinations (epistasis) may be favorable or unfavorable.

F_1 generation: The first generation resulting from the crossing of two breeds such as A×B or B×A. Generally, the sire breed is listed first. The F_1 generation of a composite resulting from three or four or more breeds is the first generation that reflects the "final" breed composition such as results from mating breeds A×BC or AB×CD.

F_2, F_3, and F_4 generations: Generations resulting from mating two individuals from the F_1 generation to produce F_2 progeny, two individuals from the F_2 generation to produce F_3 progeny, and two individuals from the F_3 generation to produce F_4 progeny, respectively.

Gene: The basic unit of inheritance occupying a specific location (locus) on a chromosome. Genes are segments of deoxyribonucleic acid (DNA) molecules connected in double-helix strands of DNA that make up chromosomes.

Genetic correlation (r_g): An estimate of the degree to which genetic variation in one trait is associated with genetic variation in another. Values can range from –1 to +1.

Genotype: The expression of the genetic makeup of an individual.

Heritability (h^2): An estimate of the percentage of the total variation observed that is due to additive effects of genes, that is,

$$h^2 = \frac{\sigma_g^2}{\sigma_g^2 + \sigma_e^2} \text{ or } \frac{\text{additive genetic variance}}{\text{additive genetic variance + environmental variance}}$$

Heritability also is the proportion of differences among individuals, measured or observed, that is transmitted to their offspring. Heritability for a trait can vary between 0 and 1 but is generally expressed in percentage units.

Heterosis (also referred to as hybrid vigor): The difference between the cross and the average of the parental breeds, weighted by their contribution. Observed heterosis is determined by summing heterosis for individual traits (H^i) and heterosis for maternal traits (H^m).

Individual or direct heterosis (H^i): Heterosis expressed as a result of genotype of the individual. This includes heterosis for growth traits. Heterosis for reproductive traits, other than for age at puberty, is generally classified as maternal heterosis because it is evaluated in progeny of crossbred dams.

Maternal heterosis (H^m): Heterosis expressed as a result of genotype of the dam that is in addition to individual or direct heterosis. Heterosis for reproductive and maternal traits expressed either in the dam (that is, reproductive traits) or in progeny (that is, maternal ability) is normally classified as maternal heterosis. Individual heterosis relative to maternal heterosis is individual expression relative to expression as a result of maternal environment.

Paternal heterosis (H^p): Heterosis expressed as a result of genotype of the sire. Heterosis effects in the percentage of calves born that may be attributable to increased libido and/or fertility of F_1 sires compared with the average of parental purebred sires.

Heterozygosity: The result of having different alleles from the same allelic series at a given locus or location on a chromosome pair, for example, Aa.

Homozygosity: The result of having two copies of the same allele at a given locus or location on a chromosome pair, for example, AA or aa.

Inbreeding: The result of mating animals that are more closely related than the average in the population or breed. Inbreeding increases homozygosity (for example, AAbb...× or aaBB...×), whereas crossing increases heterozygosity (AaBb). Because A may produce a more favorable effect and is dominant to its allele a, and B may produce a more favorable effect and is dominant to its allele b, dominance effects of genes can account for heterosis among crosses of *Bos taurus* breeds. In the example given, only two loci are indicated. The number of loci where dominance may be involved in the expression of a bioeconomic trait is believed to be large. Because of chance segregation and recombination of genes from both parents, it is not feasible to achieve homozygosity of all favorable alleles with dominance effects such as AABB....×. All breeds that have been established for an extended period are mildly inbred, and heterosis can likely be accounted for as recovery of accumulated inbreeding depression that has occurred in breeds since their formation, that is, AaBb is superior to either AAbb or aaBB. Inbreeding results in loss of vigor, particularly for fitness traits (that is, survival and reproduction) and crossing restores vigor.

***Inter se* mating:** Mating of animals of the same breed composition to each other.

Mean: The arithmetic average of all individuals in a given group or population.

Nonadditive gene effects: Effects determined by specific pairs of genes at the same location on a chromosome (that is, dominance) or by specific combinations of genes at different locations on chromosomes (that is, epistasis). Nonadditive gene effects cause heterosis or the opposite—inbreeding depression.

Phenotype: The appearance or performance of an animal. The expression of genotype plus environmental factors that affect appearance or performance level for any trait. Phenotypic, *adjective.*

Phenotypic correlation (r_p): An estimate of the degree to which phenotypic variation in one trait is associated with phenotypic variation in another. Phenotypic correlation values can range from –1 to +1.

Rotational cross or rotational crossing: The continuous crossing of breeds in a given sequence generation after generation, such as ABABA or ABCABCA.

r_p: See *phenotypic correlation.*

Standard deviation: The square root of variance or σ. Symbolized by σ (the Greek letter sigma). For traits that have a normal distribution characterized by a bell-shaped curve, 68 percent of the population are bracketed by the mean ± 1 standard deviation, 95 percent of the population are bracketed by the mean ± 2 standard deviations, and 99.6 percent of the population are bracketed by the mean ± 3 standard deviations.

Variance: The measure of variation among individuals in a given group or population. Symbolized by σ^2 (the Greek letter sigma squared).