INHERITANCE AND INTERACTION OF IMMUNE TRAITS IN BEEF CALVES¹

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ABSTRACT

Three sets of blood samples were obtained from beef calves of two experimental populations and assayed for various immunological measurements. The first set of samples was taken between 24 and 48 h after birth and quantified for IgG₁ concentration. A second set was taken immediately prior to vaccination for infectious bovine rhinotracheitis virus (IBRV; at an average age of 164 d) and a third set taken 60 d post-vaccination. These later samples were quantified for antibodies specific to IBRV. Level of complement C3 was also quantified in the samples taken immediately prior to vaccination. Three hundred sixty-seven calves were from four Hereford lines; three lines were previously selected for growth traits and the fourth was a randomly selected control line. There were no consistent differences in immune traits among these lines. The second group of 165 animals were Angus, Hereford and Red Poll calves. While Angus calves had a higher mean IgG₁ concentration at 24 to 48 h of age than Hereford or Red Poll calves, no differences among breeds were found for the other immune traits measured. Calves from older dams (>3 yr old) tended to have higher mean IgG₁ concentrations, pre-vaccination IBRV antibody titers and complement C3 levels than calves from 2- and 3-yr-old cows. However, these calves had lower 60-d post-vaccination IBRV titers than calves from the younger cows ($P < .05$). As pre-vaccination IBRV antibody titer increased, post-vaccination IBRV antibody titer decreased ($P < .05$). All pooled heritability estimates did not differ significantly from 0 (range $-.06 \pm .08$ to $.21 \pm .12$), nor were there significant phenotypic associations between the immune traits and growth performance.

(Key Words: Cattle, Genetics, Colostral Immunity, IBR/IPV Virus, Antibodies, Complement.)

Introduction

To provide immune protection to the ungulate neonate, maternal immunoglobulins from colostrum are actively absorbed across the intestinal wall during the first 24 to 36 h after birth (Bush and Staley, 1980). Estimates of heritability for neonatal immunoglobulin levels in cattle (Norman et al., 1981) and sheep (Berggren-Thomas, 1985; Gilbert et al., 1986) range from $.16 \pm .06$ to $.69 \pm .30$.

Selection for components of disease resist-

ance may decrease livestock losses due to disease. Studies in cattle (Lie, 1979), sheep (Nguyen, 1984; Berggren-Thomas, 1985) and swine (Buschmann et al., 1974; Rothschild et al., 1984a,b) have investigated genetic variation for immune response against an antigen. In these studies, heritability estimates ranged from $.05 \pm .20$ to $.70 \pm .13$.

This study was designed to examine genetic variation among and within genetic groups for: serum IgG₁ concentration at 24 to 48 h of age, IBRV (infectious bovine rhinotracheitis virus) antibody titers immediately prior to IBRV vaccination as well as 60 d post-vaccination, and complement C3 level immediately prior to vaccination. Some potential environmental sources of variation affecting these immune traits (e.g., sex of calf, age of calf and of dam, inbreeding of calf and of dam and birth weight) also were examined, and phenotypic associations among immune traits and between immune traits and growth were studied.

Materials and Methods

Populations. At three times in 1982, blood

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samples were obtained from beef calves at the Roman L. Hruska U.S. Meat Animal Research Center (MARC) in Clay Center, Nebraska. Calves from the Selection Experiment Hereford population (367) and 165 calves (79 Angus, 40 Herefords and 46 Red Pools) from the Germ Plasm Utilization (GPU) herd were used. Selection Experiment Herefords were from four separate lines, established in 1960 and maintained as one population at MARC since 1971. These lines had been selected for weaning weight (WWL), yearling weight (YWL) or an index of yearling weight and muscling score (IXL). Each of the selection lines was composed of 130 cows and six sires. The fourth line was a randomly selected 215-cow, 10-sire control line (CNL). A more detailed report of the population and of management and selection procedures was presented by Buchanan et al. (1982). The GPU calves were part of a larger project designed to evaluate heterosis retention and selection response in composite populations of beef cattle. Angus, Hereford and Red Poll calves included in the study were straightbred controls of those breeds included in the composites and represented offspring from 10 Angus, six Hereford and seven Red Poll sires.

Management. During the 1982 spring calving season (March 23 to April 28), blood samples were collected from 532 calves between 24 and 48 h of age. Blood samples were taken again from these same calves at an average age of 164 d. Also at this time, they were weighed and a modified live vaccine of IBRV and parainfluenza type 3 (PI₃) virus was administered intramuscularly. Thirty days post-vaccination, calves were weaned, weighed and placed in the MARC feedlot. Final blood samples were obtained from the calves approximately 30 d after weaning, at an average age of 224 d.

Laboratory Analyses. Blood samples were allowed to clot at room temperature and centrifuged at $1,100 \times g$ for 10 min. Serum was removed and stored at -20°C .

The 24- to 48-h serum samples were assayed for IgG₁ concentration by a single radial immunodiffusion (SRID) gel procedure (Fahey and McKelvey, 1965). Five dilutions of an IgG₁ protein standard were included on each plate of the assay, allowing estimation of mg IgG₁/ml serum for each sample.

The later serum samples were assayed for titers of antibodies specific to IBRV virus by a kinetic-based, enzyme-linked immunosorbent

assay (k-ELISA; Barlough et al., 1983). Five serum standards previously quantified for serum neutralization titer to IBRV using serum neutralization techniques, were included on each plate of the assay. A standard curve was constructed for each plate and a predicted serum neutralization titer (expressed as the reciprocal of the dilution of serum-virus neutralization antibodies) was determined for each sample. Linear quantitative data were collected using the k-ELISA technique and converted to a continuous scale of titers, circumventing serial dilutions of test sera as used in the serum neutralization technique.

Serum samples taken at an average age of 164 d were assayed also for complement C3 component by SRID gel procedures (Gewurz and Suyehira, 1980). In addition to the sample sera, five dilutions of a serum standard were assayed on each plate. The level of C3 in each test serum was expressed in serum units (SU) relative the serum standard. The amount of C3 in the serum standard was defined as 100 serum units (SU).

An intra-assay coefficient of variation (CV) was obtained for each assay as the average of the CV among sample duplicates (SRID assay for IgG₁ level) or among sample quadruplicates (k-ELISA assay for IBRV-specific antibodies and SRID assay for complement C3 level). An inter-assay serum standard was included on each plate of each assay. Each assay's repeatability over time was evaluated by the CV of this standard.

Statistical Analyses. The distributions of IgG₁ at 28 to 48 h of age, IBRV antibody titer prior to vaccination, IBRV antibody titer 60 d post-vaccination and complement C3 level prior to vaccination did not differ from normality. Statistical analyses for these immune traits were done by analysis of variance (Harvey, 1975). Data from Selection Experiment and GPU populations were analyzed separately.

In preliminary analyses, all two-factor interactions among line or breed of calf, sex and age of dam were tested for statistical significance. However, none was important. In additional analyses of serum IgG₁ concentration, linear and curvilinear effects of birth weight were analyzed within line or breed as potential sources of variation. In the analyses for IBRV titers prior to vaccination and 60 d post-vaccination and complement C3 level, factors included as potential sources of vari-

ation were linear and curvilinear effects of birth weight within line or breed, serum IgG₁ concentration within line or breed and age of calf. Linear, quadratic and cubic effects of inbreeding of dam and calf on all immune traits were analyzed as covariates in the Selection Experiment Hereford population. All regression polynomials were sequentially tested and eliminated if not significant.

The final mathematical model for each immune trait within each population included line or breed of calf, sire within line or breed, sex, age of dam and terms through the highest order of polynomial that was significant for each covariate. All effects were assumed fixed except sire within line or breed. The mean square for sire within line or breed was the error term for line or breed, respectively. The residual mean square was used for testing all other sources of variation. Mean squares from analyses of the final model for each immune trait within each population were used to compute sire and residual variance components for deriving paternal half-sib heritability estimates for each population. To determine pooled heritability estimates (across populations), pooled sire and residual mean squares for each immune trait were obtained by adding the respective degrees of freedom and sums of squares from the separate analyses of the two populations. Standard errors of heritabilities were approximated using the method of Dickerson (1969).

Phenotypic and genetic correlations among the immune traits were determined in a single analysis within each population. The model included the effects of line or breed, sire within line or breed, sex of calf and age of dam.

Weights at time of vaccination and at weaning and average daily gains from birth to these two weights were included as dependent variables in additional analyses to obtain phenotypic correlations and genetic correlation estimates between the immune traits and growth.

To estimate pooled phenotypic correlations among immune traits and between immune traits and growth traits, pooled among-sire and residual covariances among traits, as well as pooled among-sire and residual mean squares for each trait were determined. In obtaining pooled covariances, respective degrees of freedom and crossproducts for the Selection Experiment Herefords and the GPU population were added.

Genetic correlations were unestimable due to negative sire components or not valid because of very large standard errors.

Pairwise comparisons among breeds, selection lines and dam age groups were made using Bonferroni *t* statistics (Gill, 1978).

Results and Discussion

The intra- and inter-assay coefficients of variation for the IgG₁, SRID, the IBRV-specific k-ELISA and the complement C3 SRID assays were 7 and 10%, 4 and 20%, and 8 and 15%, respectively, indicating satisfactory assay repeatability between sample replicates and over time. The average coefficients of determination (r^2) for standard curves of each assay were .96, .96 and .94, respectively.

The overall least-squares means of each immune trait, as well as the least-squares means for the genetic groups, both sexes and the age of dam groups are presented for the Selection Experiment Herefords in table 1 and for the GPU population in table 2. Coefficients of significant regressions are given in tables 3 and 4 for the Selection Experiment Herefords and the GPU herd, respectively.

Perinatal IgG₁. Among the Selection Experiment Hereford lines, the randomly selected control line had the highest mean perinatal (24 to 48 h of age) IgG₁ concentration, and was significantly higher than the yearling weight line. In the Germ Plasm Utilization herd, breeds differed in calf IgG₁ level, with Angus calves having a higher mean concentration than Red Poll and Hereford calves ($P < .05$). Angus calves were observed to be more active during the first 24 h after birth than calves of the other two breeds. Perhaps this increased activity decreased the time of birth to colostrum ingestion, and so increased immunoglobulin absorption in the Angus calves.

Male and female calves did not differ in perinatal IgG₁ levels. Calf IgG₁ level at 24 to 48 h of age increased as age of the dam increased. However, this difference was significant only in the Selection Experiment Herefords. In the GPU population as birth weight increased, IgG₁ level increased in Angus calves ($P < .10$) but decreased in Hereford calves ($P < .10$). Level of IgG₁ in Red Poll calves was not affected by birth weight. Birth weight did not affect level of IgG₁ in the Selection Experiment Hereford calves.

IBRV Antibody Titer. The randomly selected

TABLE 1. LEAST-SQUARES MEANS AND STANDARD ERRORS FOR LINE, SEX AND AGE OF DAM EFFECTS ON IMMUNE TRAITS IN SELECTION EXPERIMENT HEREFORDS

Effect	n	Perinatal IgG ₁ , mg/ml	Pre-vaccination IBRV titer ^a	Post-vaccination IBRV titer ^a	Complement C3, SU ^b
Overall	367	26.0 ± .59	4.8 ± .15	13.8 ± .39	82.3 ± .74
Line ^c					
WWL	86	25.7 ± 1.17 ^{fg}	4.5 ± .30 ^{de}	12.4 ± .77 ^d	83.4 ± 1.46 ^d
YWL	88	22.4 ± 1.16 ^f	4.7 ± .31 ^{de}	13.9 ± .77 ^{de}	82.8 ± 1.48 ^d
IXL	69	26.8 ± 1.30 ^{fg}	4.4 ± .34 ^d	15.1 ± .85 ^e	81.6 ± 1.63 ^d
CNL	124	28.9 ± 1.01 ^g	5.4 ± .26 ^e	13.7 ± .68 ^{de}	81.6 ± 1.36 ^d
Sex					
Male	190	25.3 ± .83 ^d	4.8 ± .22 ^d	13.9 ± .55 ^d	78.9 ± 1.03 ^f
Female	177	26.6 ± .83 ^d	4.7 ± .21 ^d	13.7 ± .54 ^d	85.8 ± 1.04 ^g
Age of dam					
2 yr	97	20.3 ± 1.13 ^f	4.3 ± .32 ^d	17.1 ± .80 ^f	80.7 ± 1.40 ^d
3 yr	92	26.6 ± 1.15 ^g	4.6 ± .30 ^d	14.4 ± .76 ^g	81.4 ± 1.43 ^{de}
4-9 yr	178	31.0 ± .84 ^h	5.4 ± .23 ^e	9.9 ± .58 ^h	84.9 ± 1.04 ^e

^aTiter of serum-virus neutralization antibodies to IBRV.

^bSerum units.

^cLine abbreviations are weaning weight (WWL), yearling weight (YWL), index of yearling weight and muscling score (IXL) and randomly selected control (CNL).

^{d,e}Means within the same trait and effect with no superscript in common differ (P<.05).

^{f,g,h}Means within the same trait and effect with no superscript in common differ (P<.01).

TABLE 2. LEAST-SQUARES MEANS AND STANDARD ERRORS FOR BREED, SEX AND AGE OF DAM EFFECTS ON IMMUNE TRAITS IN GERM PLASM UTILIZATION CALVES

Effect	n	Perinatal IgG ₁ , mg/ml	Pre-vaccination IBRV titer ^a	Post-vaccination IBRV titer ^a	Complement C3, SU ^b
Overall	165	33.6 ± 1.27	4.6 ± .40	8.8 ± .40	77.2 ± 1.37
Breed					
Angus	79	38.9 ± 1.83 ^c	4.3 ± .55 ^d	8.9 ± .53 ^d	79.7 ± 1.98 ^d
Hereford	40	28.4 ± 2.35 ^d	5.2 ± .70 ^d	8.9 ± .78 ^d	75.1 ± 2.49 ^d
Red Poll	46	33.4 ± 2.46 ^d	4.4 ± .69 ^d	8.6 ± .72 ^d	76.6 ± 2.62 ^d
Sex					
Male	89	33.3 ± 1.68 ^d	4.5 ± .46 ^d	8.3 ± .54 ^d	74.4 ± 1.75 ^c
Female	76	33.8 ± 1.82 ^d	4.8 ± .49 ^d	9.3 ± .60 ^d	79.9 ± 1.88 ^d
Age of dam					
3 yr	56	33.4 ± 2.05 ^d	4.0 ± .52 ^d	9.9 ± .67 ^e	74.1 ± 2.04 ^c
4-7 yr	109	35.2 ± 1.61 ^d	5.0 ± .44 ^d	8.0 ± .51 ^f	79.2 ± 1.63 ^d

^aTiter of serum-virus neutralization antibodies to IBRV.

^bSerum units.

^{c,d}Means within the same trait and effect with no superscript in common differ (P<.05).

^{e,f}Means within the same trait and effect with no superscript in common differ (P<.01).

control line had the highest mean titer of IBRV antibodies prior to vaccination and was significantly higher than the line selected for an index of yearling weight and muscling score. Sixty days post-vaccination, the index line was highest in mean IBRV titer and differed significantly from the line selected for weaning weight.

Levels of pre-vaccination IBRV antibodies did not differ among Angus, Hereford and Red Poll calves, nor did the breeds differ in antibody titer 60 d post-vaccination.

Male and female calves did not differ in IBRV antibody titers at either time of measurement. Calves from older cows tended to have

TABLE 3. REGRESSION COEFFICIENTS^a AND STANDARD ERRORS OF IMMUNE TRAITS ON VARIOUS EFFECTS FOR SELECTION EXPERIMENT HEREFORDS

Y	X	b_1	b_{11}
Pre-vaccination IBRV titer ^b	Perinatal IgG ₁ (mg/ml)	.03 ± .02	-.0012 ± .006
Post-vaccination IBRV titer ^b	Perinatal IgG ₁ (mg/ml)	-.07 ± .04 [†]	.004 ± .002*
Post-vaccination IBRV titer ^b	Pre-vaccination IBRV titer ^b	-.30 ± .14*	NS ^c
Post-vaccination IBRV titer ^b	Age of calf (d)	.12 ± .05*	NS
Post-vaccination IBRV titer ^b	Inbreeding of dam (%)	-.08 ± .18	-.10 ± .04*
Complement C3 (SU) ^d	Inbreeding of calf (%)	-1.3 ± .6*	-.44 ± .22*

$$^a Y = b_0 + b_1 (X) + b_{11} (X)^2.$$

^b Titer of serum-virus neutralizing antibodies to IBRV.

^c Nonsignificance determined in previous analyses so effect was not included in this model.

^d Serum units.

[†] $P < .10$.

* $P < .05$.

TABLE 4. REGRESSION COEFFICIENTS^a AND STANDARD ERRORS OF IMMUNE TRAITS ON VARIOUS EFFECTS FOR GERM PLASM UTILIZATION CALVES

Y	X	b_1	b_{11}
Perinatal IgG ₁ (mg/ml)	Birth wt (kg)		
Angus		.15 ± .08 [†]	NS ^b
Hereford		-.19 ± .13 [†]	NS
Red Poll		.07 ± .11	NS
Pooled		.01 ± .06	NS
Pre-vaccination IBRV titer ^c	Perinatal IgG ₁ (mg/ml)	.02 ± .02	-.003 ± .001*
Post-vaccination IBRV titer ^c	Perinatal IgG ₁ (mg/ml)	-.10 ± .03*	.003 ± .001*
Complement C3 (SU) ^d	Birth wt (kg)		
Angus		.25 ± .08*	NS
Hereford		.00 ± .13	NS
Red Poll		-.15 ± .11 [†]	NS
Pooled		.03 ± .06	NS

$$^a Y = b_0 + b_1 (X) + b_{11} (X)^2.$$

^b Nonsignificance determined in previous analyses so effect was not included in this model.

^c Titer of serum-virus neutralization antibodies to IBRV.

^d Serum units.

[†] $P < .10$.

* $P < .05$.

higher mean titers of pre-vaccination IBRV antibodies than calves from younger cows. In the Selection Experiment Hereford population, mean titers 60 d post-vaccination decreased as age of dam increased from 2 to 4 yr and greater ($P < .01$). Similarly, within the GPU herd, calves from 4- to 7-yr-old cows had lower mean post-vaccination titers than calves from 3-yr-old cows ($P < .01$).

The quadratic regressions of IBRV titers at pre-vaccination and 60 d post-vaccination on perinatal IgG₁ were significant in both populations. As perinatal IgG₁ concentration increased to 50 mg/ml, pre-vaccination IBRV antibody titer increased and IBRV antibody titer 60 d post-vaccination decreased. As perinatal IgG₁ increased above 50 mg/ml, pre-vaccination antibody titer decreased while antibody titer 60 d post-vaccination increased.

Several regressions involving IBRV titer 60 d post-vaccination were significant in the Selection Experiment Hereford population. As prevaccination IBRV titer increased, a linear decrease in post-vaccination titer occurred ($P < .05$). Post-vaccination titer increased as calf age increased ($P < .01$). As dam inbreeding increased to 4%, a very slight increase in IBRV titer 60 d post-vaccination was found. Dam inbreeding greater than 4% and up to 12% was associated with a decrease in post-vaccination antibody titer.

Interactions of Antibody Levels. Existing antibodies immediately prior to vaccination may have been of colostral origin or from previous subclinical infections. Several observations support the interpretation that maternal antibodies probably were present at vaccination. In both populations, as perinatal IgG₁ concentration increased, an increase in titer of prevaccination IBRV antibodies was found. Both IgG₁ and IBRV antibodies are components of colostral immunoglobulins, the former being antibodies of a specific subclass and the latter being antibodies to a specific antigen (IBRV). It may be that calves obtaining high levels of colostral IgG₁ acquired high colostral titers specific to IBRV as well. These IBRV antibodies may not have been completely catabolized, leaving some still present at vaccination.

Age of dam influenced all the immune traits measured. As age of dam increased, perinatal IgG₁ level increased. This may reflect an increase in immunoglobulin concentration in colostrum of older cows (Frerking and Aeikens, 1978; Norman et al., 1981), more total colostrum produced by the older cows or better

mothering by the older, more experienced dams, decreasing the time from birth to colostrum ingestion. Calves from older cows had higher titers of pre-vaccination IBRV antibodies than calves from younger cows. It is possible that more colostral antibodies were present immediately prior to vaccination in calves from older cows because higher titers of IBRV antibodies, as well as higher levels of IgG₁, were available to them at birth. The age of dam effect also was significant for post-vaccination IBRV antibody titer, with calves from older cows having lower titers than calves from younger cows. If calves from older cows, those with higher titers of residual pre-vaccination IBRV antibodies, had greater neutralization of the vaccine, a lower vaccination response would occur and lower titers 60 d later would result.

As age of Selection Experiment Hereford calves increased, IBRV antibody titer 60 d post-vaccination also increased. A possible explanation for this may be that younger calves had less time to catabolize colostral immunoglobulins. Therefore, more maternal IBRV antibodies may have been present to neutralize the IBRV vaccine. A lower vaccination response would result and lead to lower levels 60 d later. Older calves may have had less residual maternal antibodies at time of vaccination, less interference with the vaccine, a greater vaccine response and higher titers 60 d later.

Titers of IBRV-specific antibodies at 24 to 48 h after birth also were quantified for approximately 18% of the calves. The mean titers were $27.4 \pm .6$ and 37.9 ± 3.2 in the Selection Experiment Hereford and GPU populations, respectively. If calves had lost these IBRV colostral antibodies at the rate of one-half their remaining antibody titers every 82 d, the pre-vaccination titers found in this study ($4.8 \pm .15$ and $4.6 \pm .40$, respectively) would have been expected. However, if the half-life of these proteins was that long, the antibodies must be extremely resistant to proteolytic decay. In the study by Brar et al. (1978), a half-life of 21 d was estimated for IBRV-specific antibodies in calves known to be free from natural infection of IBRV. If 21 d were the half-life for antibodies in calves of this study, colostral antibodies would be at a very low level by 84 d of age, and responses to IBRV infections would have begun. Multiple exposures to IBRV can be expected in cattle herds as large as the Selection Experiment Hereford and GPU populations. Thus, the antibodies existing immediately prior

to vaccination may have been produced in response to natural infection. Yet regardless of the origin of IBRV antibodies present immediately prior to vaccination, they appear to have inhibited vaccination response.

Antibodies measured 60 d post-vaccination may have been synthesized in response to the vaccination, or they have been uncatabolized antibodies remaining in the body since before the vaccination. The design of the experiment did not allow us to differentiate easily among maternal antibodies, antibodies generated in response to infection and those generated in response to the vaccination.

Complement C3 Level. When activated, complement proteins of the blood interact in an ordered sequence and mediate an inflammatory response as well as cause irreversible membrane lesions and lysis of invading cells (Douglas, 1984). Complement C3 is the major protein of the complement system. No differences were found in levels of complement C3 among lines of the Selection Experiment Hereford population or breeds of the GPU herd.

Female calves were significantly higher in mean complement C3 level than male calves in both populations. The reason for this sex difference is not obvious. Calves from younger cows (2 and 3 yr of age in the Selection Experiment Hereford and the GPU populations, respectively) were significantly lower in mean C3 level than calves from older cows (4 to 9 yr

old in the Selection Experiment Herefords and 4 to 7 yr old in the GPU herd).

Inbreeding of the calf significantly affected C3 levels in the Selection Experiment Herefords. As inbreeding increased to 5%, there was a slight increase in complement C3 level (5 SU). As inbreeding increased above 5% and to 9%, C3 level decreased (18 SU). Within the GPU herd, as birth weight increased, C3 level increased in Angus calves ($P < .05$) but decreased in Red Poll calves ($P < .10$). Level of C3 was not affected by birth weight in Hereford calves.

Heritabilities. Pooled heritability estimates for the immune traits are presented as the diagonal elements of table 5. All estimates were low and nonsignificant.

The heritability estimate for perinatal IgG₁ level was much lower than the heritabilities obtained by Normal et al. (1981) for calf IgG₁ level at 24 and 36 h of age ($.52 \pm .28$ and $.69 \pm .30$, respectively). Muggli et al. (1984) estimated heritabilities of $.23 \pm .17$ and $-.07 \pm .27$ (in Selection Experiment Herefords and the GPU population, respectively) for IgG₁ level at 24 and 48 h of age when IgG₁ level was considered a trait of the dam rather than a trait of the calf. These estimates were calculated using maternal grandsire variance components and included data from some additional calves for whom later immunological traits were not available.

The heritability estimate for IBRV antibody titer 60 d post-vaccination was lower than the

TABLE 5. HERITABILITY ESTIMATES (DIAGONAL CELLS) AND PHENOTYPIC CORRELATIONS INVOLVING IMMUNOLOGICAL AND GROWTH TRAITS POOLED ACROSS SELECTION EXPERIMENT HEREFORD AND GERM PLASM UTILIZATION POPULATIONS

	Perinatal IgG ₁	Pre-vaccination IBRV titer	Post-vaccination IBRV titer	Complement C3 level
Perinatal IgG ₁ level	$.09 \pm .10$			
Pre-vaccination IBRV titer	.03	$.21 \pm .12$		
Post-vaccination IBRV titer	$-.10^*$	$-.11^*$	$-.06 \pm .08$	
Complement C3 level	$-.03$	.05	$-.03$	$.04 \pm .10$
Birth wt	ND ^a	.00	$-.09^*$	ND ^a
164-d wt	.11*	$-.01$	$-.02$	.10*
Birth to 164-d gain	.18**	.01	.02	.05
Weaning wt	.14**	.01	$-.01$	.08
Birth to weaning gain	.19**	.04	.02	.07

^aFinal model for immune trait included birth weight so the phenotypic correlation was not determined.

* $P < .05$.

** $P < .01$.

moderate heritability ($.56 \pm .33$) for the immune response in bovine against human serum albumin estimated by Lie (1979). As mentioned earlier, IBRV antibodies measured 60 d post-vaccination may have included antibodies due to a natural infection as well as those synthesized in response to vaccination.

Lie et al. (1983) estimated a heritability of $.69 \pm .15$ for serum haemolytic complement activity in immunized cattle. A nonsignificant heritability was estimated in this study for C3, one of the components of the haemolytic complement pathway. The nonsignificant heritability estimates obtained for all immune traits examined indicate that improvement of these traits through genetic selection would be difficult.

Correlations Among Immune Traits. Pooled phenotypic correlation coefficients among the immune traits are presented in table 5. All correlations were small or nonexistent.

Correlations Between Immune Traits and Growth Traits. Pooled phenotypic correlations between humoral immune traits and weights at approximately 164 d of age and at weaning and average daily gains from birth through approximately 164 d of age and from birth through weaning were determined (table 5). All pooled phenotypic correlations between perinatal IgG₁ level and growth traits were significant and ranged from .11 to .19. These modest positive correlations suggest that a calf receiving greater amounts of colostral IgG₁ might continue to receive greater nourishment throughout the suckling period and so grow more rapidly. It may also be that the increased IgG₁ level results in a healthier calf that is better able to express its growth potential. Phenotypic correlations of the other immune traits and production traits were small and generally nonsignificant.

Conclusions

As previously mentioned, the design of the experiment did not allow determination of the origin of IBRV antibodies measured at various times. Better monitoring of the levels by more frequent bleedings might allow detection of the decline of maternal antibodies and the increase due to the calf's own antibody synthesis. Another way to avoid the inherent problems of maternal antibodies and natural infections interfering with the vaccination response and its measurement would be to immunize

the calves with an antigen to which their immune systems were naive. True antibody response due to vaccination could then be determined.

Another improvement on the experimental design might be to sample the animals earlier than 60 d post-vaccination. Measurement 28 d post-vaccination might be more suitable because peak level of antibodies against IBRV antigen occurs around 28 d post-vaccination (Gerber et al., 1978). In this study, persistence of antibodies may have been measured rather than peak response.

Biozzi et al. (1979) successfully selected mice for increased antibody titer against sheep and pigeon red blood cells given in alternating generations. Yet these same mice were less efficient at catabolizing the antigen within phagocytic cells called macrophages, and the antigen was more persistent within the body. These mice were more susceptible to classes of pathogens for which immunological defense is primarily by phagocytic means. There is an important lesson from the finding of Biozzi et al. (1979): before sound recommendations can be made concerning selection for improved disease resistance, associations among immune traits must be known. The results of this experiment suggest the existence of intricate associations among the antibody-mediated immune traits measured. However, complement C3 level was not shown to interact with the other immune traits.

Literature Cited

- Barlough, J. E., R. H. Jacobson, D. R. Downing, K. L. Marcella, T. J. Lynch and F. W. Scott. 1983. Evaluation of a computer-assisted, kinetics-based enzyme-linked immunosorbent assay for detection of coronavirus antibodies in cats. *J. Clin. Microbiol.* 17:202.
- Berggren-Thomas, P. L. 1985. Inheritance of active and passive immune responses in sheep. M. S. Thesis. Oregon State Univ., Corvallis.
- Biozzi, G., D. Mouton, O. A. Sant'Anna, H. C. Passos, M. Gennari, M. H. Reis, V.C.A. Ferreira, A. M. Heumann, Y. Bouthillier, O. M. Ibanez, C. Stiffel and M. Siqueira. 1979. Genetics of immunoresponsiveness to natural antigens in the mouse. *Curr. Top. Microbiol. Immunol.* 85:31.
- Brar, J. S., D. W. Johnson, C. C. Muscoplat, R. E. Shope and J. C. Meiske. 1978. Maternal immunity to infectious bovine rhinotracheitis and bovine viral diarrhea viruses: Duration and effect on vaccination in young calves. *Amer. J. Vet. Res.* 39:241.
- Buchanan, D. S., M. K. Nielsen, R. M. Koch and L. V. Cundiff. 1982. Selection for growth and muscling

- score in beef cattle. I. Selection applied. *J. Anim. Sci.* 55:516.
- Buschmann, H., V. Junge, H. Krausslich and A. Radzikowski. 1974. A study of the immune response to sheep erythrocytes in several breeds of swine. *Med. Microbiol. Immunol.* 159:179.
- Bush, L. J. and T. E. Staley. 1980. Absorption of colostral immunoglobulins in newborn calves. *J. Dairy Sci.* 63:672.
- Dickerson, G. E. 1969. Research in quantitative genetics. In: *Techniques and Procedures in Animal Science Research*. Amer. Soc. of Anim. Sci., Albany, NY.
- Douglas, G. N. 1984. *Complement System* (2nd Ed.). Behring Diagnostisitics, San Diego, CA.
- Fahey, J. L. and E. M. McKelvey. 1965. Quantitative determination of serum immunoglobulins in antibody-agar plates. *J. Immunol.* 94:84.
- Frerking, H. and T. Aeikens. 1978. About the importance of colostrum for the newborn calf. *Ann. Rech. Vet.* 9:361.
- Gerber, J. D., A. E. Marron and C. J. Kucera. 1978. Local and systemic cellular and antibody immune responses of cattle to infectious bovine rhinotracheitis virus vaccines administered intranasally or intramuscularly. *Amer. J. Vet. Res.* 39:753.
- Gewurz, H. and L. A. Suyehira. 1980. Complement and immune complexes. In: N. R. Rose and H. Friedman. *Manual of Clinical Immunology* (2nd Ed.). pp 163-174. Amer. Soc. Microbiol., Washington, DC.
- Gilbert, R. P., C. T. Gaskins, J. K. Hillers, C. F. Parker and T. C. McGuire. 1986. Factors affectng the Immunoglobulin G₁ levels in lamb serum and ewe colostrum. *J. Anim. Sci.* 63 (Suppl. 1):199.
- Gill, J. L. 1978. *Design and Analysis of Experiments in Animal and Medical Sciences*. pp 176-177. Iowa State Univ. Press, Ames.
- Harvey, W. R. 1975. Least-squares analysis of data with unequal subclass numbers. USDA, ARS H-4.
- Lie, O. 1979. Genetic analysis of some immunological traits in young bulls. *Acta Vet. Scand.* 20:372.
- Lie, O., M. Syed and H. Solbu. 1983. The genetic influence on serum haemolytic complement levels in cattle. *Anim. Blood Grp. Biochem. Genet.* 14:51.
- Muggli, N. E., W. D. Hohenboken, L. V. Cundiff and K. W. Kelley. 1984. Inheritance of maternal Immunoglobulin G₁ concentration by the bovine neonate. *J. Anim. Sci.* 59:39.
- Nguyen, T. C. 1984. The immune response in sheep: Analysis of age, sex and genetic effects on the quantitative antibody response to chicken red blood cells. *Vet. Immunol. Immunopathol.* 5:237.
- Norman, L. M., W. D. Hohenboken and K. W. Kelley. 1981. Genetic differences in concentration of Immunoglobulins G₁ and M in serum and colostrum of cows and in serum of neonatal calves. *J. Anim. Sci.* 53:1465.
- Rothschild, M. F., H. L. Chen, L. L. Christian, W. R. Lie, L. Venier, M. Cooper, C. Briggs and C. M. Warner. 1984a. Breed and swine lymphocyte antigen haplotype differences in agglutination titers following vaccination with B. bronchiseptica. *J. Anim. Sci.* 59:643.
- Rothschild, M. F., H. T. Hill, L. L. Christian and C. M. Warner. 1984b. Genetic differences in serum-neutralization titers of pigs after vaccination with pseudorabies modified live-virus vaccine. *Amer. J. Vet. Res.* 45:1216.