

8105  
E24  
no. 105  
Cop. 2

# Estimation of Combining Abilities From a Diallel Cross of Three Inbred Lines Of Suffolk Sheep



Agricultural Experiment Station  
Oregon State University  
Corvallis



Technical Bulletin 105  
November 1968

## Contents

Introduction .....	3
Review of Literature .....	4
Laboratory Animals .....	4
Sheep .....	5
Cattle .....	6
Materials and Methods .....	6
Results and Discussion .....	9
Diallel Scheme Lambs .....	9
Crossbred Lambs .....	15
Summary and Conclusions .....	24
Appendix .....	26
Bibliography .....	33

---

AUTHORS: Prentiss Schilling was a graduate research assistant in the Department of Animal Science at Oregon State University when this study was made. He is now an assistant professor in the Department of Statistics at Louisiana State University. Ralph Bogart is a professor of animal genetics in the Department of Animal Science and the Director of the Genetics Institute at Oregon State University. Kenneth E. Rowe is assistant professor of statistics at Oregon State University.

# Estimation of Combining Abilities From a Diallel Cross of Three Inbred Lines of Suffolk Sheep

PRENTISS SCHILLING, RALPH BOGART, AND KENNETH E. ROWE

## Introduction

Performance of a strain or line in cross combinations may be evaluated in terms of general and specific combining ability. These terms were originally defined by Sprague and Tatum (1942), who utilized a diallel crossing system as the testing procedure.

Upon the crossing of inbred lines, the differences observed in the performance of the offspring of lines when crossed in all possible combinations may be referred to as the differences in general combining ability of the lines. On the other hand, specific crosses that result from the combinations of any lines may appear to be above or below the average performance of the lines involved. This would be referred to as the specific combining abilities of the lines. In addition, reciprocal crosses between two lines may not perform the same, giving rise to what is called the reciprocal effect. The diallel cross mating system has been used to estimate general and specific combining abilities as well as reciprocal effects of lines, as it allows for all possible combinations of lines or partial combinations.

The first part of the present investigation was directed toward evaluating three inbred lines of Suffolk sheep for general and specific combining abilities. The traits considered were birth weight, 120-day adjusted weaning weight, conformation and condition scores at weaning, and yearling wool weight and grade of the lambs produced in a diallel mating scheme.

In addition, the study was designed to estimate the general combining ability and reciprocal effects of crossbred lambs produced by mating the linecross ewe lambs of the diallel to a Southdown or a Hampshire ram. Performance trait measurements, endocrine gland weights, carcass measurements, and organoleptic evaluations were taken on the crossbred lambs.

The three inbred lines used in this experiment were all started from the same parental stock and were bred as one-sire and 15-ewe lines. To produce the material for starting the three lines, a ram selected on the basis of the performance of his offspring was mated to 75 unrelated ewes. Ewe lambs produced from this mating were ran-

domly allotted to the three lines. The three top ram lambs also were randomly allotted to each of the lines. Thus there was not much likelihood for initial genetic diversity among the three lines. Selection of replacement rams and ewes in all three lines was based on 120-day adjusted weaning weight, conformation score at weaning, and condition score at weaning. No selection was practiced for the other traits considered in this study. Therefore, it was possible to investigate the effects of genetic drift in the lines for the traits that were not under selection pressure and at the same time evaluate the lines for possible changes in the traits that were under selection pressure.

## Review of Literature

In the last several years the concept of combining ability has become increasingly important in plant and animal breeding. It is especially useful in testing procedures in which it is desired to study and compare the performances of lines in hybrid combination. The terms "general combining ability" and "specific combining ability" were originally defined by Sprague and Tatum (1942) in connection with a diallel crossing system. They defined the terms as follows: "The term 'general combining ability' is used to designate the average performance of a line in hybrid combination . . . . The term 'specific combining ability' is used to designate those cases in which certain combinations do relatively better or worse than would be expected on the basis of the average performance of the lines involved."

A diallel crossing system is one in which a set of  $p$  lines is chosen and crosses among these lines are made. This procedure gives rise to a maximum of  $p^2$  combinations. Data from such combinations can be most conveniently set out in a  $p \times p$  table in which  $x_{ii}$  represents the mean value for the  $i^{\text{th}}$  inbred,  $x_{ij}$  the mean value for the  $F_1$  resulting from crossing the  $i^{\text{th}}$  and the  $j^{\text{th}}$  inbreds, and  $x_{ji}$  represents its reciprocal. Thus the  $p^2$  combinations can be divided into three groups: (1) the  $p$  parental lines themselves, (2) one set of  $1/2p(p-1)$   $F_1$ 's, and (3) the set of  $1/2p(p-1)$  reciprocal  $F_1$ 's (Griffing, 1956a). Statistical methods and the genetic basis for analysis of the data from the diallel mating plan have been presented by Dickinson and Jinks (1956), Griffing (1956a,b), Hayman (1954a,b, 1957, 1958, 1960), Kempthorne (1956), and Gilbert and Jinks (1964).

### *Laboratory animals*

Some of the material on laboratory animals is reviewed because most of the animal studies in which diallel crossing has been employed as a means of estimating combining ability have been done with laboratory animals.

The effects on litter size of crossing lines of mice inbred without selection was investigated by Roberts (1960). He used 30 lines of mice inbred up to an inbreeding coefficient of .50 with only natural selection. The mean litter size of the linecross mice did not exceed that of the outbred population from which the inbred lines were derived. The estimates of variance components associated with general and special (specific) combining abilities were very small, especially those relating to special (specific) combining ability.

All possible crosses and reciprocals were made among four lines of mice by Carmon (1962) in an attempt to evaluate heterosis, combining ability, and maternal effects for body weight at 21 and 45 days of age. Heterosis measured as a comparison between linebreds and crossbreds was highly significant for weight at both ages. The line with the lowest performance produced offspring that were the best in crosses, while the better performing lines produced offspring in crosses that were the poorest in performance. General combining ability effects, maternal effects, and sex-linked effects were highly significant for weights at both ages. Specific combining ability effects were nonsignificant.

Kidwell and others (1960) mated four inbred lines of rats in all 16 possible ways, including reciprocal crosses, in order to estimate the effects of sex, heterosis, lines, general and specific combining ability, sex linkage, and maternal effects on 28- and 70-day body weight. Effects of sex, lines, and maternal ability were highly significant at 28 and 70 days. Heterotic effects were significant at 70 days but not at 28 days. General combining ability effects were highly significant at 28 days but not significant at 70 days. There was no evidence of specific combining ability or sex linkage effects.

The inheritance of litter size, body weight, and litter weight in diallel crosses between six inbred strains of rats was investigated by Jinks and Broadhurst (1963). They found litter size to be maternally determined at birth and there were no differences in survival to maturity among litters. There was no heterosis for litter size and almost none for body weight and total litter weight. For all characters, the best litter from the inbred strains was not exceeded by any outcross.

### *Sheep*

In an investigation to measure the combining ability of Western and Down breeds of sheep for economically important traits, Bailey (1960) concluded that first-cross lambs have no advantage over straightbred Hampshires for market purposes, but the crossbred ewe lambs may show heterotic advantages in lamb production and be useful as flock replacements. The crosses were Suffolk, Corriedale, Columbia, and Targhee rams on grade Hampshire ewes.

Performance data, seven live body measurements, and live animal and carcass condition and conformation scores were obtained by Busch and others (1962) to evaluate four inbred lines of Suffolk sires. Differences were noted between groups in 120-day weight and average daily gain. Lambs in the sire line with the lowest daily gain were the smallest per unit of body weight in all body measurements except loin width. Also, they scored the lowest in conformation and condition.

### *Cattle*

Damon and others (1961) presented a genetic analysis of the data resulting from an experiment designed to evaluate breeds of beef cattle and crosses in the Gulf Coast region. Angus, Brahman, Brangus, Charolais, Hereford, and Shorthorn breeds were included. A significant or highly significant heterosis effect was found for 180-day weight, slaughter grade, rate of gain on feed, and weight per day of age, but not for slaughter calf grade. General combining ability effects were found to be significant for all five traits. Specific combining ability effects were found to be significant or highly significant for all traits except slaughter calf grade. Maternal effects were found to be highly significant for all traits except slaughter grade.

Reporting on results obtained from crossing four inbred lines of Hereford cattle, Bogart (1965) concluded that, in general, lines showing superiority, when mated within the line, produced calves showing superiority when combined with a common population of grade females, or when these lines were crossed in all possible ways. Also, a line which possessed an outstanding trait tended to transmit this trait to its offspring when used for crossing within the breed. There appeared to be more heterosis expressed in females than in males when lines were crossed within a breed.

## **Materials and Methods**

A diallel mating system involving three inbred lines of Suffolk sheep was initiated in 1961. The three inbred lines used in the diallel matings had been maintained as closed flocks since 1952. Management of the lines was similar from year to year, with all three lines being exposed to the same type of pasture and care. In the extreme months of January and February, supplemental hay and concentrates were given the ewes, but as soon as grass was available the ewes and lambs were maintained solely on pasture. Selection of replacement ewes and rams was based on an index giving equal emphasis to 120-day adjusted weaning weight and the combination of conformation score and condition score at weaning. The three inbred lines were maintained as one-sire lines.

The data for the study were obtained over a period of five years of diallel mating, 1961 through 1965. The breeding scheme for the diallel crossing is shown in the following breeding arrangement:

Line of ram	Line of ewe		
	1	2	3
1	1 x 1	1 x 2	1 x 3
2	2 x 1	2 x 2	2 x 3
3	3 x 1	3 x 2	3 x 3

There were six ewes involved in each type of cross; consequently, a total of 18 ewes of each line was included in this investigation each year. Six ewes of each line were exposed to a ram of each line.

The number of lambs born over the five-year period for each cell of the diallel scheme is given in Table 1.

Data were obtained starting with birth weights in February of 1961. Ram lambs were left intact. Weights during the preweaning period were taken at four-week intervals for the first three weighings and at two-week intervals thereafter. Lambs were weaned when they reached 85 pounds. All lambs not reaching 85 pounds by June 15 were weaned regardless of weight. At weaning, conformation and condition scores were taken on each lamb. Weaning weight was adjusted to a 120-day age basis. All ewe lambs and part of the ram lambs were kept and sheared as yearlings the last week in March each year. Wool weights and grades were taken on each fleece. The lamb measurements included in this study were: birth weight, 120-day adjusted weaning weight, conformation and condition scores<sup>1</sup> at weaning, and yearling wool weight and grade.

The linecross ewes produced in the diallel were mated as yearlings and two-year-olds to produce two lamb crops for evaluation of lamb-producing ability of the linecross ewes. The first group of linecross ewes were bred in the fall of 1962 to lamb in 1963. The first year of evaluating the linecross ewes a Southdown ram was used, but during the last three years of the study one-and-the-same Hampshire ram was used for breeding. A total of 95 crossbred lambs was born over the four-year period (1963-1966). Performance traits measured on these crossbred lambs were birth weight, 120-day adjusted weaning weight,

<sup>1</sup> Each lamb was scored by three persons, with each one placing his evaluation independently of the other two. The score for each lamb was the average of the scores given by each of the three judges. Scores were on the basis of 90-100 = Prime; 80-90 = Choice; and 70-80 = Good.

Table 1. NUMBER OF LAMBS BORN BY LINE OF EWE AND LINE OF RAM

Line of ram	Line of ewe			Total
	1	2	3	
1	54	23	35	112
2	32	33	40	105
3	36	21	66	123
Total	122	77	141	340

and conformation and condition scores at weaning. At weaning, which was at 85 pounds liveweight, the crossbred lambs were slaughtered in a commercial abattoir. Weights of the right and left adrenal, the entire pituitary, and the thyroid glands were taken at time of slaughter.

Carcass data were taken on each lamb after one week of aging. The carcass traits considered were cold carcass weight, carcass grade, carcass length, average fat thickness over the 12th rib, and rib-eye area. The various cuts of the carcass were expressed as a percent of the cold carcass weight and included: brisket-flank-and-shank, shoulder and neck, seven-rib rack, fat trim, trimmed loin, kidney knob, and trimmed legs.

Organoleptic evaluations were taken on a seven-rib rack of each carcass. A trained panel composed of eight members made the evaluations. The measurements taken were percent loss in cooking, percent drip in cooking, tenderness, juiciness, flavor of lean, flavor of fat, and overall score. The scoring scale for tenderness, juiciness, flavor of lean, flavor of fat, and overall score was from one to nine, with nine being the most pronounced.

All performance data were adjusted for type of birth (twin or single) and sex, as deviations from the means of type of birth-sex subclasses.

Least squares analyses were carried out for birth weight, 120-day adjusted weaning weight, conformation and condition scores at weaning, and yearling wool weight and grade to determine the effect of line of sire and line of dam on level of performance of the straight line and linecross lambs produced in the diallel. The effect of the line of sire was assumed to be equal to the general combining ability of the line. The interaction between line of sire and line of dam was assumed to be equal to the specific combining ability of the line. The following mathematical formula was used:

$$X_{ijk} = u + S_i + D_j + SD_{ij} + e_{ijk}$$

Where,  $X_{ijk}$  = The performance of the  $k^{\text{th}}$  individual from the  $j^{\text{th}}$  line of dam and the  $i^{\text{th}}$  line of sire,

$u$  = an effect common to all individuals,

$S_i$  = the effect of line of sire,

$D_j$  = the effect of line of dam,

$SD_{ij}$  = the interaction between line of sire and line of dam, and

$e_{ijk}$  = random error.

Likewise, least squares analyses were used to determine year effects, general combining ability effects, and reciprocal genotypic effect on the performance traits, endocrine gland weights, carcass characteristics, and organoleptic evaluations of the crossbred lambs. The mathematical model used for the analyses was derived from a model outlined by Griffing (1956a). The following mathematical model was used:

$$X_{hijk} = u + Y_h + g_i + g_j + r_{ij} + e_{hijk}$$

Where,  $X_{hijk}$  = The performance of the  $k^{\text{th}}$  individual from a dam of  $i^{\text{th}}$  and  $j^{\text{th}}$  breeding in the  $h^{\text{th}}$  year,

$u$  = an effect common to all animals,

$Y_h$  = the effect of year ( $h = 63-66$ ),

$g_i$  and

$g_j$  = the general combining ability effects,

$r_{ij}$  = the reciprocal genotypic effect such that  $r_{ij} = r_{ji}$ , and

$e_{hijk}$  = random error.

## Results and Discussion

### *Diallel scheme lambs*

Estimates of general and specific combining abilities were obtained on lambs produced in a diallel mating scheme involving three inbred lines of Suffolk sheep. The traits considered were birth weight, 120-day adjusted weaning weight, conformation and condition scores at weaning, and yearling wool weight and grade. A total of 340 lambs was born in the diallel over a five-year period, 1961 through 1965. The means for all six traits studied on lambs born in the diallel were adjusted for type of birth (twin or single) and sex (Table 2). The means are arranged according to the particular linecross or inbred group. The number of observations used in each case to determine the mean also is presented. When line 2 ewes were used either for linecrossing or for breeding within the line, there were smaller numbers of lambs. This is in part due to a shortage of line 2 ewes compared

Table 2. MEANS OF INBRED AND LINECROSS LAMBS PRODUCED BY DIALLEL MATINGS ADJUSTED FOR TYPE OF BIRTH AND SEX

	Overall	1x1	1x2	1x3	2x1	2x2	2x3	3x1	3x2	3x3
Birth weight (lbs.) .....	9.07	8.51	9.80	9.18	9.36	9.45	9.37	8.96	9.82	8.53
No. of observations .....	340	54	23	35	32	33	40	36	21	66
120-day adjusted weaning weight (lbs.)	74.90	73.74	74.21	78.72	74.21	66.31	75.91	79.47	74.06	75.39
No. of observations .....	263	41	14	32	25	26	36	29	17	43
Score of conformation <sup>1</sup> .....	82.90	82.61	82.64	83.66	82.44	79.19	82.81	86.68	82.63	82.93
No. of observations .....	260	41	14	31	25	26	36	28	16	43
Score of condition <sup>1</sup> .....	82.91	82.68	83.14	83.39	82.20	79.06	82.22	87.63	82.96	82.94
No. of observations .....	260	41	14	31	25	26	36	28	16	43
Yearling wool weight (lbs.) .....	4.30	4.37	3.91	5.07	4.58	3.60	4.65	4.64	3.91	3.84
No. of observations .....	140	23	6	14	12	17	23	13	9	23
Yearling wool grade <sup>2</sup> .....	56.61	54.43	55.78	56.90	57.18	57.34	57.40	55.52	57.40	57.38
No. of observations .....	127	20	6	14	10	15	22	11	8	21

<sup>1</sup> Conformation and condition scores were 90-100 = Prime, 80-90 = Choice, 70-80 = Good.

<sup>2</sup> Wool grades were the average spinning counts.

with the numbers available in the other two lines. This line was also lower in fertility level, but it did not appear advisable to include fertility as one of the dependent variables in the study.

*Birth weight.* The overall average birth weight was 9.07 pounds. Inbred line 1 had the lowest birth weight (8.51 pounds), followed by line 3 (8.53 pounds), while line 2 (9.45 pounds) compared favorably with the linecrosses. All linecrosses involving line 2 were above the overall mean, with linecross 3 x 2 having the heaviest birth weight (Table 2).

Analysis of variance for birth weight is presented in Appendix Table 1. The interaction between line of sire and line of dam was considered as a measure of the specific combining ability effect. Since this interaction was nonsignificant, it was concluded that specific combining ability effects among lines are not important for birth weight. A significant difference was noted between dam lines but not between sire lines. The effect of line of dam included any maternal influences and indicates there was a maternal effect on birth weight. The weight of the young at birth was dependent on the uterine environment of the dam, and a maternal influence could exist. Any effects of sex-linkage would be included in the line of sire source of variation. The variance component estimate for sire line was negative and therefore assumed to be zero, indicating a lack of general combining ability effect.

*Weaning weight.* Weaning weights adjusted to a basis of 120 days of age were taken on 263 lambs. The overall mean for all inbred lines and linecrosses was 74.90 pounds (Table 2). Inbred line 2 had the lowest 120-day adjusted weaning weight (66.31 pounds), with line 1 the next lowest (74.21 pounds), while line 3 (75.39 pounds) was above the overall mean. The crosses between line 1 and line 2 were below the overall mean (74.21 pounds), indicating that lines 1 and 2 were not only low in weaning weight as straight lines but also were ineffective when crossed together. On the other hand, linecross 3 x 1 was highest in weaning weight (79.47 pounds), followed by its reciprocal cross 1 x 3 (78.72 pounds), indicating that line 1 combined well with line 3.

Results of the analysis of variance for 120-day adjusted weaning weight are shown in Appendix Table 2. Lack of statistically significant differences between lines of sire or lines of dam justifies the conclusion that general combining ability effects were unimportant for weaning weight. This is contrary to the findings of Busch and others (1962), who noted differences between three inbred lines of Suffolk sires in 120-day weight when lambs of these lines were mated to grade Columbia ewes. The variance component due to line of dam was larger

than the line of sire variance component, suggesting that maternal influences affected weaning weight. Specific combining ability as measured by the interaction between line of sire and line of dam was also nonsignificant. Therefore, it appears that the lines did not segregate as far as 120-day adjusted weaning weight was concerned.

Numerous experiments with various species of animals have been reported concerning general and specific combining ability effects on weaning weight. Hetzer and others (1961) reported a significant general combining ability effect but no specific combining ability effect for 56-day weight in swine. In a similar study Bradford and others (1958) observed maternal effects to be more important than general combining ability for 56-day pig weight. They also observed a lack of evidence for specific combining ability. Studying rats, Kidwell and others (1960) obtained a highly significant general combining ability effect for 28-day weight but no specific combining ability or sex-linked effects. Damon and others (1961) crossed six breeds of beef cattle and obtained significant general and specific combining ability effects for 180-day weaning weight.

*Conformation and condition scores.* Conformation and condition scores at weaning were taken on 260 lambs produced in the diallel scheme. The overall mean for conformation score was 82.90 and for condition score was 82.91 (Table 2). Line 1 and line 2 were below the overall average for both scores, while line 3 was equal to the overall mean for both scores. As was observed with 120-day adjusted weaning weight, linecross 3 x 1 was superior for both conformation and condition scores, followed by its reciprocal cross 1 x 3. Since linecross 2 x 1 and the reciprocal 1 x 2 were below average for conformation score and 1 x 2 was only slightly above average for condition score, it was deduced that lines 1 and 3 combine better than lines 1 and 2 for conformation and condition scores. Linecrosses 2 x 3 and 3 x 2 were very near the overall average for both scores.

The mean squares for the interaction between line of sire and line of dam (Appendix Tables 3 and 4) were smaller than the error mean square for both conformation and condition scores. Since this resulted in a negative variance component for the interaction between line of sire and line of dam, the variance component was assumed to be equal to zero, indicating no specific combining ability effects for conformation or condition scores. Also the mean square for line of dam for conformation score was smaller than the error mean square, and for condition score was approximately equal to the error mean square. The effects due to line of sire were nonsignificant for both conformation and condition scores, which indicates that general combining ability among the lines was not important. Since selection in all

these lines was made for conformation and condition scores at weaning, there was no segregation between lines for these two traits.

Busch and others (1962) found similar results while investigating the performance of four inbred lines of Suffolk sires. They found no differences between line of sire for conformation score or for condition score. In crosses among Hampshires, Shropshires, and Targhees, Bailey (1960) drew the general conclusion that the first-cross lambs had no advantage over the straightbred Hampshires for market grade.

*Yearling wool weight.* A total of 140 yearling wool weights were recorded for individuals produced by the diallel matings. The average weight observed for the 140 fleeces was 4.30 pounds (Table 2). Straight line 2 and line 3 yearlings had the lowest wool weights, and the average yearling wool weight of line 1 was approximately equal to the overall mean. Linecross 1 x 3 had the heaviest fleece (5.07 pounds), followed by linecrosses 2 x 3 (4.65 pounds) and 3 x 1 (4.64 pounds). Linecrosses 2 x 3 and 2 x 1 both had heavier fleeces (4.65 and 4.58 pounds) than the overall mean, while linecrosses 3 x 2 and 1 x 2 both had a yearling wool weight much lighter than the overall mean (3.91 pounds). This tended to indicate that for yearling wool weight line 2 combined fairly well as line of sire but poorly as line of dam.

The same order of linecross performance was observed for wool weight as for 120-day weaning weight, where linecrosses 1 x 2 and 3 x 2 had the lowest average weaning weights as well as lowest wool weights for the linecrosses. Linecrosses 1 x 3 and 3 x 1 had greater average fleece weights than linecrosses 1 x 2 and 2 x 1, which again demonstrated that line 1 combined better with line 3 than with line 2.

A significant specific combining ability effect was observed for yearling wool weight, as shown by a significant line of sire by line of dam interaction (Appendix Table 5). As a result we would assume that the lines were diverging for wool weight. Effect of line of dam was found highly significant, while the mean square for line of sire was smaller than the error mean square. This suggested a lack of general combining ability, while indicating a possibility of maternal effects. It is conceivable that a maternal influence may exist for yearling wool weight, since the dam giving more milk generally produces a heavier lamb at weaning with more body surface for wool production. This larger body size could be carried on through the postweaning period, resulting in a greater wool weight as a yearling. Wool weight and 120-day adjusted weaning weight followed nearly the same trend, with the linecrosses having the heaviest weaning weights also having the heaviest fleeces.

The results of this investigation did not agree completely with the results of Ragab and others (1956). After crossing two breeds of

Egyptian sheep, they concluded that the fleece of the crossbreds was intermediate in staple length and weight between the two parent breeds. They surmised that crossing of breeds did not improve wool weight or staple length.

*Yearling wool grade.* Yearling wool grades were obtained on 127 of the fleeces. The average wool grade was 56.61. Straight line 1 had the lowest wool grade, but line 2 and line 3 had wool grades higher than the overall average. Linecross 3 x 1 had the lowest wool grade of all the linecrosses, followed by linecross 1 x 2 with the next to lowest (Table 2). No consistent trends between crosses and reciprocals were shown for yearling wool grade.

The analysis of variance presented in Appendix Table 6 shows that the mean square for interaction between line of sire and line of dam was less than the error mean square. This indicated there was not a specific combining ability effect for wool grade. The mean squares for effect of line of sire and line of dam were larger than the error mean square but were not significant, indicating an absence of general combining ability. The dam variance component was slightly larger than the variance component due to line of sire, but the difference was not large enough to assume any appreciable maternal effects. Estimates of the components of variance of the sex traits measured on the animals produced by the diallel mating are presented in Table 3.

Table 3. SUMMARY OF VARIANCE COMPONENT ESTIMATES OF THE SIX TRAITS MEASURED ON ANIMALS PRODUCED BY THE DIALLEL MATINGS

Trait	$\sigma^2_g$	$\sigma^2_s$	$\sigma^2$
Birth weight .....	.24	.23	3.37
120-day adjusted weaning weight .....	10.98	4.99	241.02
Conformation score at weaning .....	.70	0 (-2.18)	99.73
Condition score at weaning .....	2.65	0 (-0.73)	103.28
Yearling wool weight .....	.27	.39	.91
Yearling wool grade .....	1.68	0 (-0.65)	10.17

There was very little evidence of general or specific combining ability for the six traits studied. There was only a significant specific combining ability effect for yearling wool weight and significant line of dam effects for birth weight and yearling wool weight. The small

amount of general and specific combining ability indicates that the lines used in the diallel crosses were genetically similar. This small amount of genetic diversity between lines may be attributed to the fact that all three lines were started from a common genetic base in 1952. Females and males were assigned at random at that time from the common base population to one of the three lines. Since 1952 the lines have been maintained as closed lines, but the possibility of the lines diverging has been kept to a minimum by using the same selection index in all three lines.

The linecross ewes produced by the diallel matings were bred as yearlings and two-year-olds to produce two lamb crops from each ewe for evaluation of the lamb-producing ability of the linecross ewes. The straight-line females were not evaluated for lamb-producing ability since they were required as replacements in the diallel scheme. As a result, only general combining ability effects and reciprocal effects were estimated. Effect of year was removed before estimates of general combining ability and reciprocal effects were obtained. The first year a Southdown ram was used to sire the lambs, but during the last three years of the study one-and-the-same Hampshire ram was used. Any sire effects that might have existed due to the use of the Southdown ram were removed with the year effect since the Southdown was used only one year. That is, the sire effect of the Southdown was confounded with year effect. This study was not concerned with estimating year effects and sire effects but was directed toward estimating general combining ability effects and reciprocal effects.

### *Crossbred lambs*

A total of 95 crossbred lambs was born over the four-year period that linecross ewes were mated (1962-1965). Performance traits measured on the resulting crossbred lambs were birth weight, 120-day adjusted weaning weight, and conformation and condition scores at weaning. The following endocrine gland weights were taken: right and left adrenal, pituitary, and thyroid. The weights of the two adrenal glands were obtained separately because the glands on the two sides differ in size in some species. The carcass traits considered were cold carcass weight, carcass grade, carcass length, average fat thickness over the 12th rib, and rib-eye area. The weights of brisket-flank-and-shank, shoulder and neck, seven-rib rack, fat trim, trimmed loin, kidney knob, and trimmed legs were expressed as a percent of the cold carcass weight. Organoleptic and cooking evaluations were recorded for percent total loss in cooking, percent drip in cooking, tenderness, juiciness, flavor of lean, flavor of fat, and overall score. The number of observations for each of the traits by linecross of dam is presented in Table 4. The least squares constants for the various characters studied

Table 4. NUMBER OF OBSERVATIONS FOR EACH OF THE TRAITS STUDIED ON THE LAMBS PRODUCED BY THE LINECROSS EWES OF THE DIALLEL MATINGS

Traits	Total	Number of observations					
		Type of dam					
		1x2	2x1	1x3	3x1	2x3	3x2
Birth weight .....	95	11	12	11	16	34	11
Performance traits <sup>1</sup> ..	84	9	11	11	14	29	10
Endocrine gland weights .....	82	8	11	11	13	29	10
Carcass characteristics .....	78	8	11	10	12	27	10
Test panel evaluations .....	76	8	11	9	12	26	10

<sup>1</sup> Includes 120-day adjusted weaning weight and conformation and condition scores at weaning.

are shown in Appendix Table 7. The overall mean and mean by linecross of ewe for each trait are shown in Appendix Table 8.

Year effects were found to be significant for 120-day adjusted weaning weight, right adrenal weight, left adrenal weight, thyroid weight, carcass length, percent brisket-flank-and-shank, and juiciness score. Year effects were highly significant for pituitary weight, rib-eye area, percent shoulder and neck, percent rack, percent total loss in cooking, flavor of lean, and flavor of fat. These year effects were removed in order to obtain a more accurate estimate of general combining ability effects and reciprocal effects.

*Birth weight.* Birth weight was recorded on a total of 95 crossbred lambs. The overall average birth weight was 9.57 pounds (Appendix Table 8). Linecross ewes 2 x 3 produced lambs with the lowest birth weight (8.98 pounds), while linecross ewes 2 x 1 had the heaviest crossbred lambs (9.88 pounds). All linecross ewes possessing line 1 breeding produced lambs heavier at birth than the overall mean. Line 1 was superior when brought in through the maternal side rather than the paternal side. That is, linecross ewes 2 x 1 and 3 x 1 produced lambs with the heaviest birth weights (Appendix Table 8).

The analysis of variance for birth weight is shown in Appendix Table 9. Neither a general combining ability effect nor reciprocal effects were found for birth weight. The mean squares for both general

combining ability and reciprocal effects were smaller than the error mean square.

*Weaning weight.* The overall mean for 120-day adjusted weaning weight on the 84 crossbred lambs was 81.67 pounds. Linecross 3 x 1 and 1 x 3 ewes produced lambs with the heaviest weaning weights (Appendix Table 8). Among the lambs produced in the diallel, linecross lambs 3 x 1 and 1 x 3 had the heaviest 120-day adjusted weaning weights (88.92 and 82.96 pounds). Therefore, the linecross ewe lambs with the heaviest weaning weights produced crossbred lambs with the heaviest weaning weights. Linecross 3 x 2 and 2 x 3 ewes raised lambs with the lowest 120-day adjusted weaning weights (75.88 and 79.33 pounds). As a result it was observed that line 2 performed better in combination with line 1 than with line 3, while at the same time line 1 performed better with line 3 than with line 2 (Appendix Table 8).

The analysis of variance (Appendix Table 9) shows no significant general combining ability or reciprocal effects for 120-day adjusted weaning weight. The mean square for general combining ability was larger than the error mean square, while the mean square for reciprocal effects was smaller. Therefore, it was concluded that the lines had not diverged sufficiently in genetic make-up to produce significant differences in 120-day adjusted weaning weight.

*Conformation and condition scores.* Linecross 1 x 3 ewes produced lambs with the highest conformation and condition scores at weaning (91.61 and 90.67). The lowest conformation and condition scores were recorded for lambs produced by 1 x 2 linecross ewes (79.29 and 82.99).

No general combining ability or reciprocal effects were observed for either conformation score or condition score (Appendix Table 9). The mean squares for general combining ability and reciprocal effects were both larger than the error mean square for conformation score, indicating a positive variance component for both. For condition score the variance component for reciprocal effects was assumed to be zero, since the mean square for reciprocal effects was smaller than the error mean square. Consequently, it appears that the genetic make-up is the same for all three lines in regard to these two traits.

*Endocrine gland weights.* A total of 82 crossbred lambs was slaughtered and the endocrine glands removed and weighed. Adjustments for differences in body size were made in analysis of the data. The largest adrenals (right and left) were recorded for lambs produced by linecross 1 x 3 ewes (Appendix Table 8). Lambs from linecross 3 x 1 and 3 x 2 ewes had the heaviest pituitary gland weights,

followed by lambs from 1 x 3 ewes. Thyroid weight was greatest for lambs from 3 x 1 and 1 x 3 ewes. The lambs from linecross 3 x 1 and 1 x 3 ewes had the heaviest 120-day adjusted weaning weights and also exhibited the heavier right and left adrenal, pituitary, and thyroid weights. This would indicate that the more rapidly gaining lambs (those having the heavier weaning weights) possessed the largest endocrine glands. However, it should be noted that lambs from the 3 x 2 linecross ewes were the lightest in 120-day adjusted weaning weight but had heavier pituitary weights (Appendix Table 8).

The analyses of variance for endocrine gland weights are shown in Appendix Table 10. No significant general combining ability effects or reciprocal effects were noted for the weights of the four glands. It was noted that a positive general combining ability variance component was present for all four gland weights. On the other hand, the mean squares for reciprocal effects for all four gland weights were below the error mean squares, indicating that variance components for reciprocal effects were unimportant.

*Carcass traits.* Detailed carcass information was obtained on 78 of the crossbred lambs. The average cold carcass weight was 37.22 pounds, average carcass grade was 6.28 (high good), average carcass length was 56.19 centimeters, average fat thickness over the 12th rib was 3.83 millimeters, and the average rib-eye area was 1.89 square inches (Appendix Table 8). Lambs from 1 x 3 linecross ewes exhibited the heaviest cold carcass weight, highest carcass grade, thickest fat covering, and largest rib-eye area. Lambs from the 1 x 2 linecross ewes had the longest carcasses. Lambs of linecross 3 x 1 ewes were second in cold carcass weight, carcass grade, carcass length, and fat thickness over the 12th rib, as well as being third in rib-eye area. These results indicated that line 1 and line 3 combined better than line 1 and line 2 or line 2 and line 3 for all five of these traits. Linecross 2 x 3 and 3 x 2 ewes produced lambs showing the lowest mean for all five of the carcass traits (Appendix Table 8).

The analyses of variance for cold carcass weight, carcass grade, carcass length, fat thickness, and rib-eye area are presented in Appendix Table 11. A significant general combining ability effect was observed for carcass grade and a highly significant general combining ability effect was found for fat thickness over the 12th rib, while general combining ability effects for cold carcass weight were approaching significance. This indicated that the inbred lines had drifted apart in those traits that had not been under selection pressure. Line 1 was superior in combining ability for carcass grade, followed by line 3; line 3 was the highest in combining ability for fat thickness, followed by line 1 (Appendix Table 7). No significant reciprocal effects were

found for any of these five traits. With the exception of carcass grade, the mean squares for reciprocal effects were smaller than the error mean squares.

Contrary to these results, in a study involving outbred and inbred sires of cattle, Tallis and others (1959) observed a lack of line differences for various carcass characteristics. However, Hetzer and others (1961) observed significant general combining ability effects for several carcass traits in swine, including backfat thickness.

Brisket-flank-and-shank, shoulder and neck, rack, fat trim, trimmed loin, kidney knob, and trimmed leg weights were recorded, and the percent of each of these of the cold carcass weight was calculated. The more desirable cuts were the rack, trimmed loin, and trimmed legs, which means the crossbred lambs showing the greatest percent of these cuts would be the most desirable. Lambs from 3 x 1 linecross ewes had the greatest percent of shoulder and neck, rack, and trimmed loin but had the lowest percent of trimmed legs (Appendix Table 8). The lowest percent brisket-flank-and-shank was observed for lambs produced by 1 x 2 and 1 x 3 linecross ewes, while the largest percent of brisket-flank-and-shank resulted from carcasses of lambs from 3 x 2 linecross ewes. The lowest percent of shoulder and neck was found for lambs produced by 2 x 1 linecross ewes, followed by lambs from 1 x 3 linecross ewes. Lambs from 2 x 1 ewes exhibited the smallest percent of rack. Percent fat trim, which was undesirable, was greatest for lambs produced by 1 x 3 ewes and smallest for lambs produced by 1 x 2 ewes. The greatest percent kidney knob was observed in lambs produced by 1 x 3 cross ewes, whereas the smallest percent of kidney knob came from lambs produced by 3 x 2 ewes. Since all lambs were run on pasture with their dams and had no creep feed, one must conclude that differences in fat trim or in kidney fat reflect the inherent tendency of certain groups to store more fat. The least percent of trimmed loin came from lambs produced by 2 x 1 ewes (Appendix Table 8).

The analyses of variance for all the various carcass percentages are given in Appendix Table 12. Significant general combining ability effects were recorded for percent fat trim, percent kidney knob, and percent trimmed legs. These traits were not under selection pressure and as a result the lines appear to have separated with respect to them. Line 3 was the highest in combining ability for percent fat trim, which was considered an undesirable trait, followed by lines 1 and 2 in that order. Line 1 was greatest in combining ability for percent kidney knob fat, also considered undesirable, followed by line 3 and line 2, respectively (Appendix Table 7). These findings indicate that line 2 had the lowest combining ability for increasing the percent of waste fat in the carcass. On the other hand, line 2 was the best in general combining

ability for percent trimmed legs, followed by line 1 and line 3. Significant reciprocal effects were not found for any of the seven carcass characteristics.

In a related study involving six inbred lines of swine crossed in all possible ways, Hetzer and others (1961) observed significant general combining ability effects for all carcass traits measured except dressing percent. They measured dressing percent, percent yield of lean cuts, percent yield of bacon, percent yield of preferred cuts (sum of lean cuts and bacon), percent yield of fat cuts, and backfat thickness. Specific combining ability effects were significant only for percent bacon, indicating that specific combining ability effects were very small, if present at all.

*Test panel evaluations.* A seven-rib rack was removed from the carcass of 76 of the crossbred lambs for cooking and organoleptic evaluations. A trained test panel of eight members evaluated a portion of lean and fat from each rack. Percent total loss in cooking was greatest for lambs produced by linecross 2 x 3 ewes and lowest for lambs of 2 x 1 ewes. Percent drip in cooking (which is an indicator of the amount of intra- and intermuscular fat) was lowest for lambs from 3 x 2 linecross ewes and highest for lambs from 1 x 3 linecross ewes (Appendix Table 8). This was to be expected, since it was noted earlier that lambs produced by 1 x 3 linecross ewes had the greatest percent fat trim and percent kidney knob fat. Likewise, it was previously observed that lambs from 3 x 2 linecross ewes had the second from lowest percent fat trim and the smallest percent kidney knob.

No consistent trends were established for the taste panel evaluations. The variations between lines for the five evaluations were fairly small. Lambs from 1 x 3 linecross ewes were evaluated as the most tender, whereas lambs from 3 x 1 linecross ewes exhibited the least amount of tenderness. The 2 x 1 linecross ewes produced lambs with carcasses having the greatest amount of juiciness, while 1 x 2 ewes produced lambs with the least amount of juiciness. Lambs from 1 x 2 linecross ewes were scored the most desirable for flavor of lean, flavor of fat, and overall score of the rack; lambs from 1 x 3 ewes were lowest in flavor of lean and overall score. Linecross 3 x 2 ewes produced lambs with the least desirable flavor of fat (Appendix Table 8).

No significant general combining ability effects or reciprocal effects were observed for any of the cooking or taste panel evaluations (Appendix Table 13). Obviously the lines had not drifted apart in these traits. The mean squares for reciprocal effects for all seven traits were smaller than the error mean squares. The general combining ability effects for percent total cooking loss and percent drip in cooking were the only traits even approaching significance.

*Estimates of variance components.* The expected mean squares for all the traits studied on the crossbred lambs are presented in Table 5. Expected mean squares for year were not included, since it was not the intention to estimate variance components for years. Estimates of variance components for the traits measured on the lambs produced by the linecross ewes of the diallel matings are shown in Table 6. Variance components for reciprocal effects were negative and therefore assumed equal to zero for all traits except conformation score at weaning, carcass grade, percent rack, and juiciness. General combining ability variance components were all greater than zero except for birth weight, carcass length, percent of carcass in shoulder and neck, percent of carcass in trimmed loin, tenderness, juiciness, and overall score of organoleptic evaluations.

The lack of sufficient genetic diversity between the three lines to obtain general combining ability, specific combining ability, and reciprocal effects was generally demonstrated throughout the study. Since the lines were developed from a common genetic base and the same direction of selection was applied in all three lines, genetic diversity was held to a minimum. For some of the traits to which no direct selection was applied, such as carcass traits, sufficient diversity between lines was developed to the point where significant general combining ability effects were detected. On the other hand, even though no direct selection was applied to increase or decrease endocrine gland weights or taste panel and cooking evaluations, general combining ability and reciprocal effects were not significant for them.

The biological implication brought out by this study is that to have general combining ability, specific combining ability, and reciprocal effects, genetic diversity between lines must be present in the initial material. This has been shown by the research of Rowe and Cock-erham (1964) with *Drosophila*. They found that the amount of heterosis was closely associated with the expected amount of heterozygosity in the linecrosses. Even though the three inbred lines used in the present study were kept as closed lines, the selection for the same characters in each line maintained them very similar genetically. Probably even with more intensive inbreeding but rigid selection within lines, genetic separation of the lines would not be accomplished. In this case, the inbreeding coefficient of the line would be increasing, but the changes in gene frequencies would likely be in the same direction and at about the same rate in each of the lines. It is also possible that selection is maintaining heterozygosity to the point that homozygous loci in the lines are not being increased even though the calculated inbreeding coefficients are being increased. That is, the calculated inbreeding coefficient may be much greater than the actual inbreeding because the

Table 5. EXPECTED MEAN SQUARES FOR THE TRAITS MEASURED ON LAMBS PRODUCED BY LINECROSS EWES OF THE DIALLEL MATINGS

Source of variation	Expected mean squares				
	Birth weight	120-day adjusted weaning weight, conformation and condition scores	Endocrine gland weights	Carcass measurements	Taste panel evaluations
General combining ability	$\sigma^2 + 8.629 \sigma_g^2$	$\sigma^2 + 7.734 \sigma_g^2$	$\sigma^2 + 7.516 \sigma_g^2$	$\sigma^2 + 7.266 \sigma_g^2$	$\sigma^2 + 7.265 \sigma_g^2$
Reciprocal effects	$\sigma^2 + 6.809 \sigma_r^2$	$\sigma^2 + 6.077 \sigma_r^2$	$\sigma^2 + 5.913 \sigma_r^2$	$\sigma^2 + 5.702 \sigma_r^2$	$\sigma^2 + 5.573 \sigma_r^2$
Error	$\sigma^2$	$\sigma^2$	$\sigma^2$	$\sigma^2$	$\sigma^2$

Table 6. ESTIMATES OF VARIANCE COMPONENTS FOR THE TRAITS MEASURED ON LAMBS PRODUCED BY LINECROSS EWES OF THE DIALLEL MATINGS

Trait	$\sigma_p^2$ *	$\sigma_r^2$ *	$\sigma^2$ *
Birth weight .....	0 (-.093)	0 (-.279)	2.918
120-day adjusted weaning weight	25.719	0 (-27.203)	266.255
Conformation score .....	11.309	10.441	105.667
Condition score .....	9.974	0 (-6.284)	94.323
Right adrenal weight .....	.0040	0 (-.002)	.0176
Left adrenal weight .....	.0010	0 (-.0021)	.0258
Pituitary weight .....	.0003	0 (-.0004)	.0065
Thyroid weight .....	.0182	0 (-.0194)	.1325
Cold carcass weight .....	13.163	0 (-5.488)	50.421
Carcass grade .....	1.478	.265	4.294
Carcass length .....	0 (-.163)	0 (-.835)	6.098
Brisket, flank, and shank weight <sup>†</sup> ..	.0016	.0009	.0192
Fat thickness .....	2.868	0 (-.353)	4.612
Shoulder and neck weight <sup>†</sup> .....	0 (-.0013)	0 (-.0005)	.0104
Rack weight <sup>†</sup> .....	.0015	.0001	.0112
Rib-eye area .....	.0175	0 (-.0141)	.0987
Weight of fat trim <sup>†</sup> .....	.0153	0 (-.0038)	.0428
Trimmed loin weight <sup>†</sup> .....	0 (-.0004)	0 (-.0005)	.0078
Kidney knob weight <sup>†</sup> .....	.0026	0 (-.0007)	.0056
Trimmed legs weight <sup>†</sup> .....	.0103	0 (-.0018)	.0203
Percent total loss in cooking.....	.384	0 (-.393)	2.895
Percent drip in cooking .....	.404	0 (-.235)	2.092
Tenderness .....	0 (-.113)	0 (-.149)	.8729
Juiciness .....	0 (-.008)	.032	.229
Flavor of lean .....	.007	0 (-.023)	.148
Flavor of fat .....	.012	0 (-.019)	.118
Overall score .....	0 (-.0419)	0 (-.0566)	.3656

\* Estimated variance.

<sup>†</sup> Expressed as a percent of cold carcass weight.

heterozygous individuals may have been selected for replacements each time.

In view of these findings it might be of advantage to select one line for one trait or group of traits, a second line for a second trait or group of traits, and a third line for a third trait or group of traits. This practice would maximize genetic diversity between lines and greatly improve general as well as specific combining abilities between lines. In any event divergence between the inbred lines must be present before general and specific combining abilities will be obtained. It is evident that the only practical value inbred lines possess is the use that can be made of them to obtain general or specific combining ability. Therefore, it would be advisable that workers wishing to make use of general and specific combining abilities should first test the lines to be

used for their genetic diversity and potential combining abilities. Then the material showing better combining ability could be developed into lines that would be useful for the production of superior linecrosses.

### Summary and Conclusions

A complete diallel cross among three inbred lines of Suffolk sheep was conducted over a five-year period, 1961 through 1965. Birth weight, 120-day adjusted weaning weight, conformation and condition scores at weaning, and yearling wool weight and grade were recorded on the lambs resulting from this cross. In the development of the lines no selection was applied for birth weight, wool weight, or wool grade; however, selection was applied for 120-day weight and scores for conformation and condition. Data on these traits were analyzed in order to detect differences due to line of sire, line of dam, and sire x dam interaction. The line of sire effect was assumed to be a measure of the general combining ability effect of the line, while the sire x dam interaction was assumed to be a measure of the specific combining ability. The line of dam effect was also a measure of general combining ability plus any maternal effects present.

No significant general combining ability effects were observed for any of the six traits studied on the individuals born from the diallel matings. Significant line of dam effects were observed for birth weight and yearling wool weight, indicating a possibility of maternal effects for these two traits. Significant specific combining ability effects were observed only for yearling wool weight. Thus, it appears that any genetic drift that occurred for the traits under selection was insufficient to provide any significant combining ability effects. Yearling wool weight, which was not under selection pressure, was the only trait which showed line divergence sufficient to give a significant specific combining ability effect.

The linecross ewe lambs produced by the diallel matings were bred as yearlings and two-year-olds to a common sire to determine the lamb-producing ability of the linecross ewes. No straight-line ewe lambs were evaluated for lamb-producing ability. Estimates of general combining ability and reciprocal effects were obtained on the lambs produced by the linecross ewes. Year effects were removed before estimates of general combining ability and reciprocal effects were obtained. A total of 95 lambs was evaluated over a four-year period, 1963-1966. Observations were made on birth weight, 120-day adjusted weaning weight, conformation and condition scores at weaning, endocrine gland weights, detailed carcass information, and organoleptic and cooking evaluations. General combining ability and reciprocal effects were not significant for any of the four performance traits studied. Also, there

were no significant general combining ability or reciprocal effects noted for the four endocrine gland weights.

No reciprocal effects were observed, but a significant general combining ability effect was observed for carcass grade and a highly significant general combining ability effect was found for fat thickness over the 12th rib. There were also significant general combining ability effects for percent fat trim, percent kidney knob, and percent trimmed legs, indicating that divergence between lines had occurred with respect to these traits that were not under selection pressure. It is of interest to mention that line 2 was noted for rapid growth and was the lowest of the lines in fertility. It also was outstanding for combining with other lines to give a high yield of trimmed legs and lacked the ability to combine for heavy fat trim or high kidney knob fat. One might consider the implication that rapid growth is associated with more lean and less fat but less fertility. However, with only a few lines it is possible that traits may have gone together by random drift.

No significant general combining ability effects or reciprocal effects were observed for any of the cooking or taste panel evaluations. There was very little variation between groups for taste panel evaluations.

Development of the three lines from the same genetic foundation and selection within each of the lines for the same traits tended to keep the lines genetically similar, which resulted in little general or specific combining ability being obtained from crossing the lines. There was somewhat more combining ability expressed in the traits not under direct selection during the development of the lines, but even such traits as wool weight and grade and endocrine weights failed to show marked combining ability effects. The study indicates that lines of breeding which are started from the same foundation material and kept under the same selection pressures are not likely to diverge greatly. Lines started from the same foundation may diverge rather strongly for traits not under selection pressure. For lines to have the greatest ability to give heterosis in crossing, they should be from divergent original material and/or selected for different traits.

## Appendix

Appendix Table 1. ANALYSIS OF VARIANCE OF BIRTH WEIGHT OF LAMBS PRODUCED BY DIALLEL MATINGS

Source of variation	D.F.	Mean square	Expected mean square	Variance components
Line of sire ....	2	2.47	$\sigma^2 + 27.48 \sigma_s^2$	$\sigma_s^2 \doteq 0$
Line of dam ....	2	14.52 <sup>†</sup>	$\sigma^2 + 21.44 \sigma_d^2$	$\sigma_d^2 \doteq .52$
S x D .....	4	6.86	$\sigma^2 + 14.88 \sigma_{s,d}^2$	$\sigma_{s,d}^2 \doteq .23$
Error .....	331	3.37	$\sigma^2$	$\sigma^2 \doteq 3.37$
Total .....	339			

<sup>†</sup> Significant at  $p < .05$ .

Appendix Table 2. ANALYSIS OF VARIANCE OF 120-DAY ADJUSTED WEANING WEIGHT OF LAMBS PRODUCED BY DIALLEL MATINGS

Source of variation	D.F.	Mean square	Expected mean square	Variance components
Line of sire .....	2	399.99	$\sigma^2 + 23.55 \sigma_s^2$	$\sigma_s^2 \doteq 6.75$
Line of dam ....	2	494.32	$\sigma^2 + 16.65 \sigma_d^2$	$\sigma_d^2 \doteq 15.21$
S x D .....	4	297.42	$\sigma^2 + 11.32 \sigma_{s,d}^2$	$\sigma_{s,d}^2 \doteq 4.99$
Error .....	254	241.02	$\sigma^2$	$\sigma^2 \doteq 241.02$
Total .....	262			

Appendix Table 3. ANALYSIS OF VARIANCE OF SCORE FOR CONFORMATION AT WEANING OF LAMBS PRODUCED BY DIALLEL MATINGS

Source of variation	D.F.	Mean square	Expected mean square	Variance components
Line of sire ....	2	135.27	$\sigma^2 + 23.24 \sigma_s^2$	$\sigma_s^2 \doteq 1.53$
Line of dam ....	2	97.60	$\sigma^2 + 16.02 \sigma_d^2$	$\sigma_d^2 \doteq 0.00$
S x D .....	4	75.36	$\sigma^2 + 11.21 \sigma_{s,d}^2$	$\sigma_{s,d}^2 \doteq 0.00$
Error .....	251	99.73	$\sigma^2$	$\sigma^2 \doteq 99.73$
Total .....	259			

Appendix Table 4. ANALYSIS OF VARIANCE OF SCORE FOR CONDITION AT WEANING OF LAMBS PRODUCED BY DIALLEL MATINGS

Source of variation	D.F.	Mean square	Expected mean square	Variance components
Line of sire ....	2	224.14	$\sigma^2 + 23.24 \sigma_s^2$	$\sigma_s^2 \doteq 5.20$
Line of dam ....	2	104.79	$\sigma^2 + 16.02 \sigma_d^2$	$\sigma_d^2 \doteq 0.09$
S x D .....	4	95.06	$\sigma^2 + 11.21 \sigma_{sd}^2$	$\sigma_{sd}^2 \doteq 0.00$
Error .....	251	103.28	$\sigma^2$	$\sigma^2 \doteq 103.28$
Total .....	259			

Appendix Table 5. ANALYSIS OF VARIANCE OF YEARLING WOOL WEIGHT OF LAMBS PRODUCED BY DIALLEL MATINGS

Source of variation	D.F.	Mean square	Expected mean square	Variance components
Line of sire ....	2	0.90	$\sigma^2 + 12.46 \sigma_s^2$	$\sigma_s^2 \doteq 0.00$
Line of dam ....	2	5.41 <sup>1</sup>	$\sigma^2 + 8.22 \sigma_d^2$	$\sigma_d^2 \doteq 0.55$
S x D .....	4	3.12 <sup>2</sup>	$\sigma^2 + 5.74 \sigma_{sd}^2$	$\sigma_{sd}^2 \doteq 0.39$
Error .....	131	0.91	$\sigma^2$	$\sigma^2 \doteq 0.91$
Total .....	139			

<sup>1</sup> Significant at  $p < .01$ .

<sup>2</sup> Significant at  $p < .05$ .

Appendix Table 6. ANALYSIS OF VARIANCE OF YEARLING WOOL GRADE OF LAMBS PRODUCED BY DIALLEL MATINGS

Source of variation	D.F.	Mean square	Expected mean square	Variance components
Line of sire ....	2	26.10	$\sigma^2 + 12.04 \sigma_s^2$	$\sigma_s^2 \doteq 1.32$
Line of dam ..	2	24.83	$\sigma^2 + 7.19 \sigma_d^2$	$\sigma_d^2 \doteq 2.04$
S x D .....	4	6.80	$\sigma^2 + 5.21 \sigma_{sd}^2$	$\sigma_{sd}^2 \doteq 0.00$
Error .....	104	10.17	$\sigma^2$	$\sigma^2 \doteq 10.17$
Total .....	112			

Appendix Table 7. LEAST SQUARES CONSTANTS FOR THE VARIOUS TRAITS STUDIED ON LAMBS PRODUCED BY LINECROSS EWES OF THE DIALLEL MATINGS

Trait	General combining ability effect			Reciprocal effects <sup>1</sup>					
	Line 1	Line 2	Line 3	$r_{12}$	$r_{21}$	$r_{13}$	$r_{31}$	$r_{23}$	$r_{32}$
Birth weight .....	0.308	-0.102	-0.207	-0.103	0.103	-0.082	0.082	-0.283	0.283
120-day adjusted weaning weight .....	4.067	-4.269	0.202	0.100	-0.100	2.981	-2.981	1.727	-1.727
Conformation score .....	0.582	-3.164	2.582	-4.624	4.624	1.947	-1.947	0.489	-0.489
Condition score .....	2.046	-2.894	0.848	-2.083	2.083	1.853	-1.853	0.318	-0.318
Right adrenal weight .....	0.024	-0.052	0.028	0.009	-0.009	0.028	-0.028	0.010	-0.010
Left adrenal weight .....	0.009	-0.043	0.034	-0.043	0.043	0.018	-0.018	0.002	-0.002
Pituitary weight .....	-0.007	-0.017	0.024	-0.023	0.023	-0.003	0.003	-0.010	0.010
Thyroid weight .....	-0.001	-0.113	0.114	-0.005	0.005	-0.045	0.045	-0.013	0.013
Cold carcass weight .....	2.336	-2.521	0.185	-0.813	0.813	1.435	-1.435	0.222	-0.222
Carcass grade .....	0.611	-0.906	0.295	-0.458	0.458	0.621	-0.621	-0.429	0.429
Carcass length .....	0.480	-0.038	-0.442	0.166	-0.166	-0.300	0.300	0.233	-0.233
Brisket, flank, and shank <sup>2</sup> .....	-0.392	0.272	0.120	-0.250	0.250	-0.094	0.094	-0.455	0.455
Fat thickness .....	0.595	-1.233	0.638	0.443	-0.443	0.439	-0.439	0.023	-0.023
Shoulder and neck <sup>2</sup> .....	0.010	-0.066	0.056	0.290	-0.290	-0.174	0.174	0.068	-0.068
Rack <sup>2</sup> .....	0.242	-0.344	0.102	0.182	-0.182	-0.159	0.159	0.283	-0.283
Rib-eye area .....	0.106	-0.076	-0.030	0.008	-0.008	0.050	-0.050	0.005	-0.005
Fat trim <sup>2</sup> .....	0.444	-0.962	0.518	-0.306	0.306	0.448	-0.448	0.103	-0.103
Trimmed loin <sup>2</sup> .....	-0.120	-0.053	0.172	0.181	-0.181	-0.075	0.075	-0.165	0.165
Kidney knob <sup>2</sup> .....	0.290	-0.335	0.045	0.016	-0.016	0.135	-0.135	0.026	-0.026
Trimmed legs <sup>2</sup> .....	-0.410	0.746	-0.336	-0.040	0.040	0.057	-0.057	-0.320	0.320
Percent total loss in cooking .....	-0.553	0.189	0.364	0.247	-0.247	0.171	-0.171	-0.118	0.118
Percent cooking drip .....	0.365	-0.534	0.170	-0.049	0.049	0.269	-0.269	0.173	-0.173
Tenderness .....	-0.012	0.056	-0.044	0.029	-0.029	0.071	-0.071	0.011	-0.011
Juiciness .....	-0.092	0.073	0.018	-0.194	0.194	-0.126	0.126	-0.085	0.085
Flavor of lean .....	0.022	0.088	-0.110	0.042	-0.042	-0.032	0.032	-0.009	0.009
Flavor of fat .....	0.103	-0.022	-0.081	0.034	-0.034	-0.033	0.033	0.003	-0.003
Overall score .....	0.032	0.032	-0.064	0.057	-0.057	-0.065	0.065	0.015	-0.015

<sup>1</sup> r represents the reciprocal effect of the particular linecross.

<sup>2</sup> Expressed as a percent of cold carcass weight.

Appendix Table 8. MEANS FOR THE VARIOUS TRAITS MEASURED ON LAMBS PRODUCED BY LINECROSS EWES OF THE DIALLEL MATINGS

Trait	Overall mean	Line of ewe					
		1 x 2	2 x 1	1 x 3	3 x 1	2 x 3	3 x 2
Birth weight (lbs.) .....	9.57	9.67	9.88	9.59	9.75	8.98	9.54
120-day adjusted weaning weight (lbs.) .....	81.67	81.57	81.37	88.92	82.96	79.33	75.88
Conformation score .....	86.50	79.29	88.54	91.61	87.72	86.41	85.43
Condition score .....	85.92	82.99	87.15	90.67	86.96	84.19	83.56
Right adrenal weight (g.) .....	.93	.91	.89	1.01	.95	.92	.90
Left adrenal weight (g.) .....	.99	.91	1.00	1.05	1.01	.98	.98
Pituitary weight (g.) .....	.49	.44	.49	.50	.51	.49	.51
Thyroid weight (g.) .....	2.07	1.95	1.96	2.14	2.23	2.06	2.08
Cold carcass weight (lbs.) .....	37.22	36.22	37.85	41.18	38.31	35.11	34.66
Carcass grade .....	6.28	5.53	6.44	7.81	6.56	5.24	6.10
Carcass length (cm.) .....	56.19	56.80	56.47	55.93	56.53	55.94	55.48
Brisket, flank, and shank (%) <sup>1</sup> ..	16.81	16.44	16.94	16.44	16.63	16.75	17.66
Fat thickness (mm.) .....	3.83	3.64	2.75	5.50	4.62	3.26	3.21
Shoulder and neck (%) <sup>1</sup> .....	26.89	27.12	26.54	26.78	27.13	26.95	26.81
Rack (%) <sup>1</sup> .....	9.36	9.44	9.08	9.55	9.86	9.40	8.84
Rib-eye area (sq. in.) .....	1.89	1.93	1.91	2.02	1.92	1.79	1.78
Fat trim (%) <sup>1</sup> .....	4.70	3.88	4.49	6.11	5.21	4.36	4.15
Trimmed loin (%) <sup>1</sup> .....	8.17	8.18	7.82	8.15	8.30	8.12	8.45
Kidney knob (%) <sup>1</sup> .....	2.25	2.22	2.19	2.72	2.45	1.99	1.93
Trimmed legs (%) <sup>1</sup> .....	28.42	28.72	28.80	27.73	27.62	28.51	29.15
Percent total loss in cooking (%) ..	22.46	22.34	21.85	22.44	22.10	22.53	23.13
Percent drip in cooking (%) ..	3.45	3.23	3.33	4.25	3.72	3.26	2.91
Tenderness .....	6.90	6.97	6.91	7.00	6.86	7.01	6.99
Juiciness .....	6.20	5.99	6.38	6.00	6.25	6.21	6.38
Flavor of lean .....	6.20	6.35	6.27	6.08	6.14	6.17	6.19
Flavor of fat .....	6.00	6.12	6.05	5.99	6.05	5.90	5.89
Overall score .....	6.40	6.52	6.41	6.30	6.43	6.38	6.35

<sup>1</sup> Expressed as a percent of cold carcass weight.

Appendix Table 9. ANALYSIS OF VARIANCE FOR BIRTH WEIGHT, 120-DAY ADJUSTED WEANING WEIGHT, CONFORMATION SCORE, AND CONDITION SCORE OF LAMBS PRODUCED BY LINECROSS EWES OF THE DIALLEL MATINGS

Source of variation	D.F.	Mean square		Mean squares		
		Birth weight	D.F.	120-day adjusted weaning weight	Conformation score	Condition score
Year .....	3	7.04	3	973.96 <sup>1</sup>	121.04	31.52
General combining ability .....	2	2.12	2	465.16	193.13	171.46
Reciprocal effects .....	3	1.02	3	100.94	169.12	56.14
Error .....	86	2.92	75	266.26	105.67	94.32
Total .....	94		83			

<sup>1</sup> Significant at  $p < .05$ .

Appendix Table 10. ANALYSIS OF VARIANCE FOR ENDOCRINE GLAND WEIGHTS OF LAMBS PRODUCED BY LINECROSS EWES OF THE DIALLEL MATINGS

Source of variation	D.F.	Mean squares			
		Right adrenal	Left adrenal	Pituitary	Thyroid
Year .....	3	.072 <sup>1</sup>	.091 <sup>1</sup>	.040 <sup>2</sup>	.432 <sup>1</sup>
General combining ability .....	2	.047	.033	.009	.269
Reciprocal effects .....	3	.008	.013	.004	.018
Error .....	73	.018	.026	.007	.133
Total .....	81				

<sup>1</sup> Significant at  $p < .05$ .

<sup>2</sup> Significant at  $p < .01$ .

Appendix Table 11. ANALYSIS OF VARIANCE FOR COLD CARCASS WEIGHT, CARCASS GRADE, CARCASS LENGTH, FAT THICKNESS, AND RIB-EYE AREA OF LAMBS PRODUCED BY LINECROSS EWES OF THE DIALLEL MATINGS

Source of variation	D.F.	Mean squares				
		Carcass weight	Carcass grade	Carcass length	Fat thickness	Rib-eye area
Year .....	3	36.028	8.403	21.366 <sup>1</sup>	5.740	.5015 <sup>2</sup>
General combining ability	2	146.064	15.036 <sup>1</sup>	4.913	25.449 <sup>2</sup>	.2262
Reciprocal effects .....	3	19.128	5.803	1.335	2.597	.0184
Error .....	69	50.421	4.294	6.098	4.612	.0987
Total .....	77					

<sup>1</sup> Significant at  $p < .05$ .

<sup>2</sup> Significant at  $p < .01$ .

Appendix Table 12. ANALYSIS OF VARIANCE FOR VARIOUS PORTIONS OF THE CARCASS EXPRESSED AS A PERCENT OF THE COLD CARCASS WEIGHT OF LAMBS PRODUCED BY LINECROSS EWES OF THE DIALLEL MATINGS

Source of variation	D.F.	Mean squares						
		Brisket, flank, and shank	Shoulder and neck	Rack	Fat trim	Trimmed loin	Kidney knob	Trimmed legs
Year .....	3	.0584 <sup>1</sup>	.0479 <sup>2</sup>	.0784 <sup>2</sup>	.0944	.0128	.0051	.0232
General combining ability .....	2	.0306	.0008	.0222	.1541 <sup>1</sup>	.0049	.0242 <sup>1</sup>	.0951 <sup>1</sup>
Reciprocal effects .....	3	.0242	.0076	.0115	.0209	.0050	.0014	.0102
Error .....	69	.0192	.0104	.0112	.0428	.0078	.0056	.0203
Total .....	77							

<sup>1</sup> Significant at  $p < .05$ .

<sup>2</sup> Significant at  $p < .01$ .

Appendix Table 13. ANALYSIS OF VARIANCE FOR TASTE PANEL EVALUATIONS OF A SEVEN-RIB RACK FROM EACH CARCASS OF THE LAMBS PRODUCED BY LINECROSS EWES OF THE DIALLEL MATINGS

Source of variation	D.F.	Mean squares						
		Percent total loss in cooking	Percent drip in cooking	Tender-ness	Juici-ness	Flavor of lean	Flavor of fat	Overall score
Year .....	3	99.89 <sup>1</sup>	2.36	1.84	.82 <sup>2</sup>	3.28 <sup>1</sup>	1.12 <sup>1</sup>	.39
General combin- ing ability ....	2	5.69	5.03	.05	.17	.20	.21	.06
Reciprocal effects .....	3	.70	.79	.04	.41	.02	.01	.05
Error .....	67	2.90	2.09	.87	.23	.15	.12	.37
Total .....	75							

<sup>1</sup> Significant at  $p < .01$ .  
<sup>2</sup> Significant at  $p < .05$ .

## Bibliography

- Bailey, C. M. 1960. The combining ability of Western and Down breeds of sheep for economically important traits. Ph.D. thesis, University of Wisconsin, Madison. (Abstracted in *Dissertation Abstracts*, 21:395).
- Bogart, R. 1965. Crossing lines of cattle within a breed. Seventh Annual Beef Cattle Day Report, Oregon Agric. Expt. Sta. Special Report 192, pp. 13-16.
- Bradford, G. E., A. B. Chapman, and R. H. Grummer. 1958. Effects of inbreeding, selection, linecrossing and topcrossing in swine. III. Predicting combining ability and general conclusions. *Jour. of An. Sci.*, 17:456-467.
- Busch, R. E., R. Bogart, J. A. B. McArthur, and C. W. Fox. 1962. Performance evaluation of four inbred lines of Suffolk sires. *Proc. West. Sec. Amer. Soc. An. Sci.* (Abs. in *Jour. of An. Sci.*, 21:662).
- Carmon, J. L. 1962. Heterosis, combining ability and maternal effects in mice. *Proc. South. Sec. Amer. Soc. An. Sci.* (Abs. in *Jour. of An. Sci.*, 21:382).
- Damon, R. A., Jr., W. R. Harvey, C. B. Singletary, S. E. McCraine, and R. M. Crown. 1961. Genetic analysis of crossbreeding beef cattle. *Jour. of An. Sci.*, 20:849-857.
- Dickinson, A. G., and J. L. Jinks. 1956. A generalized analysis of diallel crosses. *Genetics*, 41:65-78.
- Gilbert, N., and J. L. Jinks. 1964. Non-additive combining abilities. II. Reciprocals and backcrosses. *Heredity*, 19:96-103.
- Griffing, B. 1956 a. Concept of general and specific combining ability in relation to diallel crossing systems. *Aust. Jour. Biol. Sci.*, 9:463-493.
- Griffing, B. 1956 b. A generalised treatment of the use of diallel crosses in quantitative inheritance. *Heredity*, 10:31-50.
- Hayman, B. I. 1954 a. The analysis of variance of diallel tables. *Biometrics*, 10:235-264.
- Hayman, B. I. 1954 b. The theory and analysis of diallel crosses. I. *Genetics*, 39:789-809.
- Hayman, B. I. 1957. Interaction, heterosis and diallel crosses. *Genetics*, 42:336-355.
- Hayman, B. I. 1958. The theory and analysis of diallel crosses. II. *Genetics*, 43:63-85.
- Hayman, B. I. 1960. The theory and analysis of diallel crosses. III. *Genetics*, 45:156-172.
- Hetzer, H. O., R. E. Comstock, J. H. Zeller, R. L. Hiner, and W. R. Harvey. 1961. Combining abilities in crosses among six inbred lines of swine. USDA Tech. Bull. 1237, 127 pp.
- Jinks, J. L., and P. L. Broadhurst. 1963. Diallel analysis of litter size and body weight in rats. *Heredity*, 18:319-336.

- Kempthorne, O. 1956. The theory of the diallel cross. *Genetics*, 41:451-459.
- Kidwell, J. F., H. J. Weeth, W. R. Harvey, L. H. Haverland, C. E. Shelby, and R. T. Clark. 1960. Heterosis in crosses of inbred lines of rats. *Genetics*, 45:225-232.
- Ragab, M. T., A. A. Asker, and K. Ghoneim. 1956. Effect of crossing two breeds of Egyptian sheep on wool characteristics. *Emp. Jour. Exp. Ag.*, 24:307-311.
- Roberts, R. C. 1960. The effects on litter size of crossing lines of mice inbred without selection. *Genetic Res.*, 1:239-252.
- Rowe, Kenneth E., and C. Clark Cockerham. 1964. Relation between performance and heterozygosity in *Drosophila*. *Genetics*, 49:363-366.
- Sprague, G. F., and L. A. Tatum. 1942. General versus specific combining ability in single crosses of corn. *Jour. Amer. Soc. Agronomy*, 34:923-932.
- Tallis, G. M., E. W. Klosterman, and V. R. Cahill. 1959. A topcross breeding experiment with outbred and inbred Hereford sires. I. Line comparisons and phenotypic correlations. *Jour. An. Sci.*, 18:745-754.