Selection indexes for range Rambouillet, Columbia and Targhee lambs

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UMI®
SELECTION INDEXES FOR RANGE RAMBOUILLET, COLUMBIA AND TARGHEE LAMBS

by

Sterling Keith Ercanbrack

A Dissertation Submitted to the Graduate Faculty in Partial Fulfillment of The Requirements for the Degree of

DOCTOR OF PHILOSOPHY

Major Subject: Animal Breeding

Approved:

Signature was redacted for privacy.

In Charge of Major Work

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Dean of Graduate College

Iowa State College

1952
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I. INTRODUCTION

Making the decision regarding which animals to retain for breeding has undoubtedly perplexed animal husbandmen since the beginning of animal domestication. One does not often know with certainty the intrinsic genetic nature of any individual animal. Furthermore, each animal's true breeding value is generally obscured by various environmental and certain physiological factors in conjunction with the oftentimes unpredictable results of gene expression and interaction. Additional complications are introduced when it becomes necessary to choose between animals which are superior for different reasons. The question as to how much credit to allow for superiority in one respect as compared with another must be answered before one can make the most efficient selection of breeding stock and thus help to insure maximum progress in improving production.

Development and use of proper mating systems for producing better animals and efficient and accurate selection of superior breeding stock are perhaps the two most important objectives in the genetic improvement of domestic livestock. The attainment of these objectives requires information concerning a host of subjects which have been and still are the subjects of scientific research.

The purpose of this investigation was to resolve some of the difficulties connected with the selection of sheep. Specifically, its primary objective was to construct weanling indexes for selecting range lambs of Rambouillet, Columbia, and Targhee breeding—indexes that will help answer the questions related to (1) the relative emphasis that should be placed
upon important traits affecting the production of lamb and wool in selecting breeding stock and (2) which animals should be retained for breeding.

During the course of the investigation it was necessary to obtain four important kinds of preliminary information fundamental to the attainment of the primary objective. First, it was necessary to estimate and to correct for the effects of several environmental and a few specific physiological factors* which are likely to confuse one's judgment concerning which animals are truly genetically superior and to bias estimates of heritabilities and correlations for selection purposes. Estimates of phenotypic variation were obtained in this process. Second, estimates of both phenotypic and genetic correlations among the traits were required for determining how and to what extent an improvement in one trait might affect another. Third, information regarding the fraction of an animal's superiority or inferiority (in each trait) which is likely to be heritable (i.e., an estimate of heritability) was essential for estimating the extent to which selection for each trait was likely to be effective. Fourth, estimates of the relative economic values of the traits were required for determining the relative importance of obtaining an improvement in each trait. The joint consideration of these basic factors will permit estimation of the optimum emphasis to be placed upon each trait for securing the maximum benefit from selection.

Inasmuch as range lambs are generally marketed at weaning age, it is economically impracticable to delay beyond that age in making the initial selection of replacement or breeding stock. Of course, one should assure

*The physiological (or genetic) factors included here are age at weaning and sex. Under the proper circumstances one might also include such factors as age at shearing, age at lambing, inbreeding, fertility, and cachexia resulting from poisoning, certain diseases, parasitic infestations, and malnutrition.
that some leeway for additional selection remains after that time. Appraisals of economic characteristics such as unscoured and clean fleece weights, fleece grade, and fertility have not usually been attempted as early as weaning age; and only preliminary estimates are available for various other traits. Selecting by index does assist in reserving some freedom for later selection in nearly all traits. High correlations between most weaning and yearling traits and subsequent production indicate that prudent selection for weanling traits should be worth while.

Hazel and Lush (1942) have shown theoretically that selecting by means of an index which sums the proper credits for all important traits is more efficient than selecting for only one trait at a time or for several traits when each has its own, established culling level. Selecting by index prevents inadvertent over- or under-emphasis of particular traits and allows unusually high merit in one trait to compensate for somewhat inferior merit in another. Hazel and Terrill (1946) observed that selecting by index considerably increased the efficiency of selection among range Rambouillet ewe lambs; and Bernard et al. (1950) found that mean values for several characters of gilts recommended as replacements on the basis of a swine index but not selected were significantly higher than those for gilts selected but not recommended by the index. Thus, it appears that selection indexes, if properly used, should be of considerable assistance to animal husbandmen striving to make the maximum genetic progress from selection as rapidly and economically as possible.
II. REVIEW OF LITERATURE

A. Environmental and Physiological Factors Affecting Selection of Lambs

Certain environmental and physiological (or genetic) factors causing unusual variation in the expression of an animal's phenotype tend to have an important influence upon the selection of breeding stock. These factors, among many others, frequently mislead one's efforts to evaluate properly an animal's real breeding or genotypic value.

For example, Donald and MoLean (1935) reported that 130-day weights of English Leicester and Southdown lambs in New Zealand were smaller among female lambs and among lambs from 2-year-old dams than among males or among lambs from older dams. Bonsma (1939) found that the "weight growth" of purebred and crossbred South African Merino lambs was less for lambs born at a ewe's first parturition (usually at 2 years of age), for lambs with smaller birth weights, and for lambs whose mothers were poor milkers.

Phillips and Dawson (1937, 1940) observed that selection of Hampshire, Shropshire, and Southdown lambs from the United States Department of Agriculture's experimental flock at Beltsville, Maryland, was influenced strongly by whether a lamb was born as a single, twin, or triplet, by the birth weight, and by the birth date of the lamb. Single, heavy, and older lambs were favored. With the possible exception of birth weight, there appeared to be no real justification, from a genetic standpoint, for discriminating among lambs in this manner.
In experiments on suckler-lamb (fat unweaned lambs) production in South Africa, Starke (1944) found that growth rate, conformation (carcass), and finish (degree of fatness) were each influenced significantly by the type of birth (single, twin, etc.) of crossbred Southdown lambs.

Sidwell and Grandstaff (1949) and Sidwell, et al. (1961a, 1961b) observed that weaning weight, body type (conformation), and condition (degree of fatness) of range Navajo and Navajo crossbred lambs in New Mexico were affected significantly by age of dam, type of rearing (i.e., as a single, twin, or twin reared singly), and age at weaning. In addition, staple length, weaning weight, and condition were influenced by the sex of the lamb. The lighter weights, poorer body types and thinner lambs were found among lambs having either relatively young or old dams, among twin lambs reared together, and among the younger lambs. Female lambs generally had longer staples, had lighter weights, and were fatter than ram lambs.

Perhaps the most comprehensive studies of the effects of environmental and other factors upon lamb traits are those of Hazel and Terrill (1945a, 1946a). Their findings are particularly comparable to those of this investigation since they were made on lambs of similar breeding, reared under generally similar environmental conditions. The following traits of 2,163 Rambouillet, 478 Columbia, 238 Corriedale, and 366 Targhee lambs reared under Intermountain range conditions in Idaho and southern Montana were included: weaning weight, staple length, body type, condition, face covering, and neck folds.

Their results indicated that ewe lambs were generally superior to ram lambs in all traits except weaning weight (in which the ram lambs excelled), although differences in condition were consistently of minor importance.
Ewes over 2 years of age reared lambs superior in all traits except face covering and neck folds. Mature Rambouillet ewes, however, reared lambs with slightly but significantly more face covering and more neck folds. Single lambs were consistently superior to twin lambs in all respects except face covering and neck folds. Single lambs had more folds, but differences in staple length and face cover were relatively unimportant. Important differences in favor of older lambs occurred in weaning weight, staple length, and body type. Older lambs were in slightly but significantly better condition at weaning age, and differences in face covering were unimportant. Neck folds in Rambouillets were slightly but significantly more numerous among older lambs, but among the other breeds the younger lambs had the greatest fold development. Inbreeding had important detrimental effects on weaning weight, body type, and condition but either unimportant or no effects on neck folds, face cover, and particularly staple length.

The remarkable agreement among the findings of various investigators working on many different breeds under a variety of environmental conditions accentuates the importance of considering carefully the effects of these factors in attempting to increase the effectiveness of selection. Other more obvious but none the less important factors which may occasionally be overlooked are those causing an impairment of otherwise normal physiological processes with resulting physical debilitation and cachexia. Such factors include poisoning from noxious range plants, certain diseases in special cases, internal or external parasitic infestations, and malnutrition. Failing to account properly for effects which tend to bias
evaluation of an animal's genotype may impede genetic progress seriously because of culling genetically superior or saving genetically inferior breeding animals.

B. Correlations among Lamb Traits

A basic requirement for attaining maximum efficiency when selecting for more than a single trait is a knowledge of the phenotypic and genetic correlations among the traits under selection. Such knowledge allows the geneticist to anticipate to some extent just what effects selection for the various traits will have upon each other and to adjust the emphasis upon individual traits accordingly.

When both phenotypic and genetic correlations are high, it may sometimes be economical to select for a relatively valueless but easily recognized trait with the reasonable expectation of achieving improvement in a highly valuable correlated trait which is difficult, expensive, or impossible to measure. In addition, when the phenotypic correlation is high, one trait may be useful simply in predicting the magnitude of another. A good illustration of this in sheep is the use of staple length and grease fleece weight for predicting clean fleece weight (Terrill et al., 1945; Pohle and Keller, 1943).

The literature contains an abundance of information on phenotypic relationships among various economic traits of ewes but little on genetic relationships. Published data concerning either phenotypic or genetic correlations among weaning traits of lambs are scanty. Details about phenotypic correlations among various fleece and body traits of several
range breeds of ewes may be seen in papers by Hill (1921), Spencer et al. (1928), Pohle and Keller (1943), Jones et al. (1944), and Terrill et al. (1945).

Morley (1950) and Rae (1950) have made comprehensive investigations on relationships among traits of Australian Merino and New Zealand Romney Marsh sheep, respectively, including studies of the genetic correlations. Morley estimated genetic correlations between staple length and folds and body weight and folds to be -0.66 and 0.23, respectively. Rae estimated a genetic correlation of 0.21 ± 0.31 between staple length and body type (mutton conformation as indicated by scores which increased as merit increased).

Some results of unpublished research at the Western Sheep Breeding Laboratory, Dubois, Idaho, are compiled in Tables 1 and 2. The most notable features of Table 1 are that estimates of phenotypic correlations between face cover and each of the other traits are very low and that estimates of those among weaning weight, body type, and condition are relatively high.

Estimates in Table 2 indicate that the genetic correlations involving face cover may be low also.

Comparison of Tables 1 and 2 shows that the phenotypic relationships between weaning weight and staple length and between weaning weight and neck folds seem to be distinctly opposite to the corresponding genetic relationships. Knowledge of only the phenotypic correlations would lead one to believe that a genetic increase in weaning weight would be accompanied by genetic increases in both staple length and number of folds. Here, then, is a good example of the importance of knowing genetic as well as phenotypic relationships among the traits.
Table 1. Phenotypic Correlations among Weanling Traits of Range Rambouillet Lambs

<table>
<thead>
<tr>
<th>Trait</th>
<th>Sex</th>
<th>Staple length</th>
<th>Weaning weight</th>
<th>Body type</th>
<th>Condition</th>
<th>Neck folds</th>
</tr>
</thead>
<tbody>
<tr>
<td>Face cover</td>
<td>Rams</td>
<td>.06</td>
<td>-.01</td>
<td>-.04</td>
<td>.00</td>
<td>.04</td>
</tr>
<tr>
<td></td>
<td>Mixed</td>
<td>.02</td>
<td>-.05</td>
<td>.05</td>
<td>.08</td>
<td>.12</td>
</tr>
<tr>
<td>Staple length</td>
<td>Rams</td>
<td>.21</td>
<td>-.29</td>
<td>-.16</td>
<td>-.08</td>
<td>.24</td>
</tr>
<tr>
<td></td>
<td>Mixed</td>
<td>.15</td>
<td>-.28</td>
<td>-.19</td>
<td>-.12</td>
<td></td>
</tr>
<tr>
<td>Weaning weight</td>
<td>Rams</td>
<td>-.89</td>
<td>-.51</td>
<td>.24</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Mixed</td>
<td>-.49</td>
<td>-.56</td>
<td>.14</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Body type</td>
<td>Rams</td>
<td>.62</td>
<td>-.07</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Mixed</td>
<td>.47</td>
<td>.12</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Condition</td>
<td>Rams</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Mixed</td>
<td></td>
<td></td>
<td></td>
<td>-.08</td>
<td>-.16</td>
</tr>
</tbody>
</table>

*Rams data from Terrill, Kyle, and Hazel (1950) and mixed data from the Western Sheep Breeding Laboratory (1946). Merit in face cover, body type, condition, and neck folds was indicated by scores which increased as merit decreased.*

Table 2. Genetic Correlations among Weanling Traits of Range Rambouillet Lambs

<table>
<thead>
<tr>
<th>Trait</th>
<th>Staple length</th>
<th>Weaning weight</th>
<th>Body type</th>
<th>Condition</th>
<th>Neck folds</th>
</tr>
</thead>
<tbody>
<tr>
<td>Face cover</td>
<td>.08</td>
<td>-.13</td>
<td>-.03</td>
<td>.06</td>
<td>.13</td>
</tr>
<tr>
<td>Staple length</td>
<td>-.26</td>
<td>-.37</td>
<td>.01</td>
<td>-.27</td>
<td></td>
</tr>
<tr>
<td>Weaning weight</td>
<td>-.38</td>
<td>-.14</td>
<td>.14</td>
<td>-.14</td>
<td></td>
</tr>
<tr>
<td>Body type</td>
<td></td>
<td>.61</td>
<td>.48</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Condition</td>
<td></td>
<td></td>
<td>.01</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Unpublished data from the Western Sheep Breeding Laboratory (1946). Merit in face cover, body type, condition, and neck folds was indicated by scores which increased as merit decreased.*
G. Estimates of Heritabilities of Lamb Traits

Attempts to improve genetic merit rapidly will be comparatively ineffectual unless a rather substantial fraction of the phenotypic variation is caused by genetic differences among individuals. One cannot select successfully for superior genes unless they are present in the population and unless they have discernible effects. An important requirement for developing any efficient selection program, therefore, is to estimate the proportion of the apparent variation (in each trait in the specific population under selection) which is caused by the average effects of the genes. This estimate (of heritability) provides an indication of how closely the average individual's phenotype may be expected to resemble its genotype (Hazel, 1943). If the average resemblance is high for a particular trait, the genetic change expected from selection is proportionately large, and proportionate emphasis should be exerted in selecting for that trait (see, however, p. 74, para. 2).

An extensive review of the literature regarding the inheritance of diverse traits in sheep has been completed by Serra (1948). Estimates of heritabilities of several fleece and body traits of yearling or older sheep have been made by Rasmussen (1942), Terrill and Hazel (1943), McMahon (1945), Phillips et al. (1945), Goot (1946), Jones et al. (1946), Rae (1948, 1950), Cookerham (1949), and Morley (1950).

A few attempts have been made to estimate the heritability of prolificacy. Rietz and Roberts (1915) found dam-offspring and sire-offspring correlations of 0.087 ± 0.010 and 0.053 ± 0.010, respectively, between type of birth (single, twin, or triplet) of parent and offspring. Doubling
the correlations gives estimates of 0.17 and 0.11 for heritability. The data consist of approximately 10,000 observations from the American Shropshire Sheep Record and, consequently, are likely to represent a selected population. Also, environmental effects which are similar for sheep in the same flock but different for those in different flocks could have contributed to these correlations. Wentworth and Sweet (1917) made a similar study involving several thousand observations from the American Southdown Record. They calculated correlations of $0.060 \pm 0.018$ and $0.038 \pm 0.018$ between type of birth of maternal grandsire and offspring and maternal granddam and offspring, respectively. These values, as might be expected, are less than those observed above; but they may be compared with corresponding correlations of $0.004 \pm 0.011$ and $0.043 \pm 0.010$ calculated by Riets and Roberts (1915) on Shropshire data.

Johansson and Hansson (1943) found an intra-breed, intra-flock regression of average daughter litter size on average dam litter size of sheep in Sweden to be 0.107, indicating a heritability of 0.214 based on averages of three records per individual. The data included 1,370 pairs of Oxforddown, Shropshire, Cheviot and Landrace breeds and were obtained from registered flocks of the Swedish Sheep Breeders' Association. There apparently was little selection for litter size since all offspring from every animal supposedly were recorded; but it is doubtful that the daughters themselves were unselected. Using the method of intra-sire regression, Cockerham (1949) estimated litter size to have a heritability of 0.10 $\pm 0.05$. The data were obtained from several breeds, principally Hampshires, reared under farm flock conditions in North Carolina and contained just 135
degrees of freedom. The estimate was adjusted for averaging several litters of each individual and is therefore lower than an unadjusted estimate based on average litter size. A comparable estimate calculated from Johansson's and Hansson's data is 0.144.

The only known estimates of heritabilities of lamb (weanling) traits are those of Nelson and Venkatachalam (1949), Hazel and Terrill (1946b, 1946c) and, Terrill and Hazel (1946). Nelson and Venkatachalam studied heritability of weaning weight among five breeds in the Michigan State College flock. Estimates of 0.29 ± 0.14 and 0.42 ± 0.21 were obtained via parent-offspring regression (348 pairs) and paternal half-sib correlation methods, respectively. A weighted average of the two methods yielded the value 0.33 ± 0.12.

Other estimates of heritabilities are compiled in Table 3. It is evident from this table that heritabilities of different traits within the same breed may vary considerably and that selection for improvement in body type, for example, is less likely to be immediately effective than selection for face covering. Another significant observation is that sizeable population (breed) differences may occur in the heritabilities of the same traits, weaning weight for example. This emphasizes the importance of estimating heritabilities which apply to the particular population under selection.

It seems appropriate to point out in conclusion that a knowledge of heritability is important not only because of the reasons already discussed, but also because it may help in choosing the most desirable mating system for a particular circumstance, in deciding on the most efficient basis for selecting each trait, and in estimating the optimum intensity
for selection among young animals with records of performance still incomplete (Wright, 1939; Lush, 1940, 1949; Dickerson and Hazel, 1944a, 1944b).

Table 3. Estimates of Heritabilities of Weanling Traits for Several Breeds of Range Sheep

<table>
<thead>
<tr>
<th>Trait</th>
<th>Rambouilleta</th>
<th>Columbiaa</th>
<th>Targheea</th>
<th>Corriedalea</th>
<th>Averageb</th>
</tr>
</thead>
<tbody>
<tr>
<td>Face cover</td>
<td>.60±.07</td>
<td>.48</td>
<td>.56</td>
<td>.42</td>
<td>.46±.06</td>
</tr>
<tr>
<td>Staple length</td>
<td>.39±.08</td>
<td>.46</td>
<td>.49</td>
<td>.40</td>
<td>.43±.06</td>
</tr>
<tr>
<td>Weanling weight</td>
<td>.34±.08</td>
<td>.21</td>
<td>-.01</td>
<td>.45</td>
<td>.17±.05</td>
</tr>
<tr>
<td>Body type</td>
<td>.07±.07</td>
<td>.17</td>
<td>-.07</td>
<td>.11</td>
<td>.07±.04</td>
</tr>
<tr>
<td>Condition</td>
<td>.14±.06</td>
<td>.11</td>
<td>.16</td>
<td>.41</td>
<td>.21±.05</td>
</tr>
<tr>
<td>Neck folds</td>
<td>.45±.08</td>
<td>.06</td>
<td>.15</td>
<td>-.06</td>
<td>.08±.04</td>
</tr>
</tbody>
</table>

aCompiled from results of parent-offspring regression methods used by Hazel and Terrill (1945b, 1946b, 1946c) and Terrill and Hazel (1946). The number of dam-offspring pairs for each breed in order of listing are 892, 404, 254, and 140, respectively.

bWeighted averages of both half-sib and dam-offspring methods, including all breeds except Rambouillet. Averages are based on 1711 lambs and 798 dam-offspring pairs (Hazel and Terrill, 1946c).

D. Relative Economic Values of Traits of Ewes and Lambs

The relative economic values of the various traits indicate the relative increase in net profit to be expected from a comparable genetic improvement in each trait. Rigorous methods for determining these values have not been developed, and it appears that few estimates other than Winters' et al. (1946) have been published. They calculated that the
average price per pound for four top grades of wool at Boston was 3.4 times that per pound of top lambs at South St. Paul during the period 1920-39.

A few empirical estimates of the relative economic values of various ewe and lamb traits, obtained from unpublished data, are included here for reference. Morley (1950) used the following tentative estimates for traits of Australian Merino ewes: one pound of clean wool, 10 units; one centimeter of staple length, 1 unit; one pound of body weight, 1 unit; one grade of skin folds, minus 5 units; one crimp per inch (as an indication of fineness), 2 units. Rae (1950) estimated that traits of New Zealand Romney Marsh ewes had these relative values: one pound of unsecured wool, 15 units; one count unit (visual estimate of spinning count), 4 units; one unit of fleece quality (visual impression of evenness, crimping, luster, etc.), 3 units; one centimeter of staple length, 2 units; one unit in body type score (mutton conformation), 4 units; one unit decrease in hairiness (log scale), 3 units.

The Western Sheep Breeding Laboratory (1946) used the following preliminary estimates of economic values in calculating an index for Rambouillette lambs (values are expressed in dollars per unit change in each trait): face covering score, 1.440; centimeters of staple length, 1.720; pounds of weaning weight, 0.112; body type score (conformation), 0.470; condition score (degree of fatness), 0.470; and neck folds score, 0.750.

It is apparent from the comparative lack of information in this particular sphere of animal breeding research that additional accurate and detailed investigations would be useful. The rate of progress to be expected from selecting simultaneously for several traits, under even the
most optimum circumstances, is so slow that selecting for traits in disregard of their relative economic importance seems exceedingly wasteful.

E. Selection Indexes for Sheep

An increasing awareness of the importance of precise and reliable criteria upon which to base selection has stimulated investigators to renewed efforts in developing selection indexes. Among those recently developed were a few for sheep. Winters et al. (1946) compared various systems for rating ewes on their productivity. The index which they accepted as most practicable for rating ewes reared under farm flock conditions was based on the production per 100 pounds of ewe when the lambs were 23 weeks old:

\[
\left( \frac{3.4 \times \text{pounds of wool}}{\text{weight of ewe in pounds}} \right) + \frac{\text{pounds of lamb at 23 weeks}}{100}
\]

Another index which also included the wool production and the lamb production at 23 weeks was adjusted by calculated requirements for maintenance of ewe and lamb. The maintenance requirements were increased in accordance with the 0.73 (cf. Winters, 1940) power of body weight. This index was considered the most accurate of seven, but was criticized because of the difficulty involved in its computation and interpretation.

Morley (1950) constructed an index for Australian Merino sheep with emphasis primarily on wool production. Using the technique of discriminant functions applied to information regarding phenotypic and genetic correlations, phenotypic variation, heritabilities, and relative economic values of several traits, he developed the following index:
\[ I = 100 + 1.54X_1 - 1.26X_2 + 0.01X_3 - 0.75X_4 + 0.13X_5 \]

where

- \( X_1 \) = clean fleece weight in pounds
- \( X_2 \) = staple length in centimeters
- \( X_3 \) = body weight in pounds
- \( X_4 \) = skin fold score
- \( X_5 \) = crimps per inch.

Morley estimated that selection on the basis of this index would permit substantial improvement in clean fleece weight and folds accompanied by trivial decreases in staple length and fineness.

Rae (1950) constructed similar indexes for New Zealand Romney Marsh ewes. Among three indexes, the two chosen as most satisfactory were

\[ I_2 = 1.70L + 1.13F_1 + 2.46F.W. + 0.32H + 0.59B + 2.82C \]

and

\[ I_3 = 0.61L + 0.79F_1 + 1.92F.W. + 1.89H + 0.61B \]

where

- \( L \) = staple length in centimeters
- \( F_1 \) = fleece quality score
- \( F.W. \) = fleece weight (grease) in pounds
- \( H \) = hairiness in logarithmic units
- \( B \) = body type score
- \( C \) = spinning count score.

Index \( I_2 \) was considered most desirable for instances when the optimum count is finer than the flock average; \( I_3 \) was considered useful when the reverse condition is true. Although the rate of improvement as a result of using the indexes was expected to be slow, it seemed evident that index selection would be superior to ill-defined and haphazard methods.
For selecting Rambouillet rams, an index which also considers heritability, economic importance, and phenotypic and genetic relationships among the traits was described by Terrill (1948). The index, based in part upon statistics determined incompletely and therefore subject to revision, is

\[ I = W - 3G + 11Cl + L + 7T + 4C - 7F - 5N \]

where
- \( W \) = body weight in pounds
- \( G \) = grease fleece weight in pounds
- \( Cl \) = clean fleece weight in pounds
- \( L \) = staple length in centimeters
- \( T \) = body type score
- \( C \) = condition score
- \( F \) = face covering score
- \( N \) = neck folds score.

Emphasis is placed upon both wool and lamb production. Terrill pointed out that occasional departures from strict adherence to the index were necessary to permit considering certain traits or physical defects not included in the index.

Finally, an index developed for selecting range Rambouillet lambs (Hazel and Terrill, 1946d; Phillips, 1947) at the Western Sheep Breeding Laboratory is

\[ I = 75 - 15F + 7L + W + 0.4T + 7C - 11N \]

where
- \( F \) = face covering score
- \( L \) = staple length in centimeters
- \( W \) = weaning weight in pounds
- \( T \) = body type score
C = condition score

N = neck fold score.

The multiple regression technique described by Hazel (1943) was used in its construction. Selection based on this index resulted in larger selection differentials for most traits than selection based on personal judgment. However, the superiority of index selection was greater when a large fraction of the lambs were selected than when only a few were selected. It is generally more difficult to select subjectively for a large proportion of individuals, since one cannot easily evaluate relative merit in the many animals which are superior in some respects and inferior in others. It is not so perplexing to choose the few individuals which are superior (or inferior) in all respects. In addition, Hazel and Lush (1942) noted in their theoretical study that index selection was relatively more advantageous than selection based on independent culling levels (for each trait) when the intensity of selection was lower.
III. ORIGIN AND NATURE OF DATA

A. Foundation and Experimental Animals

In the spring of 1944, the Utah Agricultural Experiment Station pur-
chased 900 yearling ewes of predominantly Rambouillet breeding and estab-
lished them on station range and pasture facilities in southern Utah
adjacent to Cedar City. The ewes were obtained from three native range
flocks, and some selection for open faces and smooth bodies was made at
the time. Rambouillet, Columbia, and Targhee sires were obtained from the
Utah State Agricultural College at Logan, the Branch Agricultural College
at Cedar City, the U. S. Sheep Experiment Station at Dubois, Idaho, and
from private breeders in Utah.

In the fall of 1944, the foundation ewes were randomly divided into
two groups and bred to Rambouillet and Columbia rams. During subsequent
years the breed of rams was alternated for each group so that the same
ewes were never mated to the same breed of rams in successive years. The
female progeny from these matings became the dams used in this investigation
and were designated as either first-cross Rambouillets or first-cross
Columbias.

At maturity the first-cross Rambouillets were mated to Rambouillet
rams and the first-cross Columbias were divided at random and mated to
either Columbia or Targhee rams. The unselected progeny of both sexes
from these matings during the years 1947-49 constitute the offspring
included in the investigation. For the sake of convenience and to prevent
misunderstanding concerning their ancestry, the progeny are subsequently
referred to by the symbols Ramc, Cole or Tar whichever is appropriate.
They may be considered as reasonably typical of the lambs produced on many
western ranches, especially on those where it is customary to raise grade
female replacements and to purchase purebred white-faced rams.

B. Management and Environment

The ewes were bred each fall during November in alfalfa and perennial
grass (principally crested wheat grass, _Agropyron cristatum_) pastures on
the experimental farm just west of Cedar City. Animals within the various
breeding groups were mated at random so that whatever inbreeding occurred
was of little consequence. Ewes were first mated at about 18 months of age.

The herd was trailed to the winter range during early December each
year and usually remained there until approximately March 1st. This range
is located about 60 miles west of Cedar City at elevations ranging from
4,000 to 6,000 feet. The region is characteristic of the píñon-juniper
areas of the West, with various species of sagebrush constituting the prin-
cipal undergrowth. During the last 40 days on the range the sheep custom-
arilly were fed a supplement of one-fifth of a pound of 43 per cent cotton-
seed cake per head daily. However, exceptionally deep snows in the winter
of 1948-49 required the feeding of both hay and concentrates during most of
that winter.

In early March the ewes were returned to the experimental farm and
were fed alfalfa hay and concentrates until lambing was completed in May.
The sheep were shorn several days before lambing, which commenced near the last week in March each year. Parturition occurred in an open corral, but each ewe was then immediately removed to an adjacent shed where she was placed with her offspring in an individual pen. Here she usually remained for one or two days. This procedure provided optimum opportunity for the acceptance and survival of the new born lambs. Lambs were ear-tagged with tags containing individual lamb numbers, and birth weights and dates were recorded soon after birth. The ewes and lambs were removed to alfalfa, crested wheatgrass, and fall-planted rye pastures as soon after docking and castration as forage development would permit.

In early June the herd was taken to the summer range located 12 miles east of Cedar City at elevations ranging from 6,000 to 9,000 feet. This range is of the aspen-fir type and is covered with an abundance of native grasses, forbs, and shrubs. The entire range is fenced and free from predators, so practically no herding was necessary during the summer months. The lambs were removed from the summer range and weaned either in late August or mid-September depending upon the moisture received during the summer. The long-time average annual precipitation is 15-20 inches for the summer range and 7-12 inches for the winter range. Annual temperatures commonly range from 100°F. during the summer down to 0°F. and below during the winter. The ewes usually remained on the summer range until they were returned to the farm pastures in October preparatory to breeding in November.

Death losses among very young lambs were considered to be normal in amount and were caused principally by pneumonia and dirt-eating. Every precaution was taken to reduce losses to a minimum. Principal known causes of death among older lambs and ewes were dirt-eating and bloat,
respectively. Undoubtedly a few losses occurred from plant poisoning and from starvation of lambs due to abandonment or separation from dams. Parasites are usually of minor importance in range herds. Losses from other causes among both ewes and lambs may be ascribed chiefly to the rigors of their winter environment and to straying.

C. The Observations

The observations on the several traits investigated were obtained at weaning time after the lambs had been separated from their dams from 12 to 24 hours. The lambs were generally corralled in the evening and the observations were taken during the following day. The data included observations on a total of 1,156 offspring (524 Ram₂, 307 Col₂, and 325 Tar₁) and 561 dams (264 first-cross Rambouillets and 297 first-cross Colombias). Complete records were available on 1,080 dam-offspring pairs (485 Ram₂, 291 Col₂, and 304 Tar₁) for computing genetic correlations and heritabilities. The average age of all lambs when the traits were observed was 149 days.

In order to gain some of the advantages of repeated observations on the same individual and to make final evaluation of the traits as objective as possible, all traits except weaning weight were measured or scored independently by either two or three individuals. Averages of the various individual evaluations were then used as the assigned values for each trait. It was also possible through this system to detect and rectify gross errors of evaluation. Traits evaluated on the basis of scores were face covering, body type (mutton conformation), condition (degree of fatness), and folds (neck and body wrinkles). Traits which were measured
objectively were weaning weight and staple length. To investigate any possible association between type of birth and prolificacy, the lambs were also classified according to the size of litter in which they were born (i.e., as singles, twins, or triplets).

The scoring system developed by the U. S. Sheep Experiment Station was used. Scoring units ranged from 1 to 5 with the most superior animals being scored 1 and the most inferior being scored 5. As a result of averaging the individual evaluations, thirteen different scores were possible for face cover, body type, and folds, respectively; and nine different scores were possible for condition.

The traits were evaluated in the following manner: staple length was measured in the center of each lamb's right side midway between the longer wool on the britch and the shorter wool on the shoulder. Two men independently obtained measurements of the unstretched staple to the nearest eighth of an inch. Immediately subsequent to this, each animal was scored on its condition by both feeling and scrutinizing appropriate parts of its body. It was then weighed individually on enclosed scales, the weaning weight being recorded to the nearest pound. The lamb was next released from the scales into a small arena where it was scored by three experienced observers, working independently, for face covering, body type, and folds, respectively.

Animals most superior for face covering had no wool in front of the poll and those least superior had wool almost down to the nostrils. Terrill (1949b) shows photographs which correspond closely to the degrees of face covering associated with the scores used for this trait. Body type was evaluated on the basis of the estimated carcass conformation, a
of type of pattern.

An attempt was made to estimate the energy absorption for each of 229 dams of mixed breed
successive lamping records for each of 229 dams of mixed breed.

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subsequent examination of the pattern of the lamp was
been. A sereology, the pattern of the lamp in which the lamp was
made that be obtained from the site of the lamp in which the lamp was
mean time, a somewhat more but nevertheless useful indication of this
examination or pattern. It is clear that at least the examination of each lamp's position in the pattern, to have some order and sense reflected in the examination of each lamp. The examination reflected the idea of examination, however, a word of examination reflected the idea of the examination.

The importance of each trait is discussed in detail in a later chapter.

were then removed.

were considered important. The conclusion was that patterns are passed from
were next, and these make up a photograph of the first to the next, although
absence of order were considered most supported. In some cases, these were
by a mutation type that permitted...
IV. ANALYTICAL METHODS

A. Estimation and Consideration of Effects Which Can Reduce the Accuracy of Selection

Estimating the effects of the environmental and physiological factors which have important influences on phenotypic variation and correcting the data for these effects were basic problems which had to be considered before more accurate estimates of phenotypic and genetic parameters could be obtained. The proper applications of these improved estimates can increase significantly the effectiveness of selection for desired characteristics.

A priori information coupled with an examination of ranges of observations in the diverse subclasses indicated that it would be advisable to obtain separate estimates of the effects (and correction factors) for the Ram₂ offspring. Because of an obvious similarity among Col₂ and Tar₁ lambs, both in phenotype and maternal ancestry, combined (joint) estimates were obtained for these two groups. These combined estimates will more nearly approach, in accuracy, the estimates for the Ram₂ group, since that group contained nearly double the number of observations in either the Col₂ or the Tar₁ group.

Variances of all Ram₂ traits were distinctly different from those of corresponding Col₂ and Tar₁ traits. With the possible exception of variances for face cover and staple length, variances of all Col₂ and Tar₁ traits were homogeneous. Variations in face cover and in staple length
in the Col₂ group differed significantly from those in the Tar₁ group just at the 5 and 1 per cent levels of probability, respectively. Although the same correction factors for environmental and physiological effects were used on the Col₂ and Tar₁ data, all three groups subsequently were analyzed separately in obtaining estimates of correlations and heritabilities.

1. The mathematical model

The following linear function of the several effects for which corrections were to be made was adopted as a reasonable hypothesis for the composition of individual observations in the Col₂ and Tar₁ data:

\[ Y_{ijklmr} = u + s_i + b_j + y_k + d_l + t_m + ax_{ijklmr} + e_{ijklmr} \]

where

\[ i = 0, 1; j = 1, 2; k = 7, 8, 9; l = 2, 3, 4; \]
\[ m = 1, 2, 3; r = 1, 2, \ldots, n_{ijklm} \]

and

\[ u = \text{a convenient constant, characteristic of all observations, from which the effects may be expressed as deviations. The composition of } u \text{ depends upon the restrictions imposed upon the other parameters and the } e_{ijklmr}'s \text{ in the model.} \]

\[ s_i = \text{an effect of sex; that is, an effect of differences between female and castrated male (wether) lambs.} \]

*With the omission of the \( b_j \), this hypothesis is identical to the one for Ram₂ data.*

**In each case only the most apparent causes of the effects have been specified. Obviously, any influence common to all individuals in a given class and different for individuals in other classes may contribute to a particular estimated effect.*
\( b_j^* \) = an effect of differences between Tar\(_1\) and Col\(_2\) lambs.

\( y_k^* \) = an effect of differences among lambs born in different years. Presumably, these differences were caused by annual variations in environmental factors such as temperature, rainfall, wind, forage supply, and management methods. Other factors, such as changes in the average annual genetic composition of the sires or dams and yearly variations in scoring standards, also might have contributed.

\( d_l^* \) = an effect of differences in age among two-, three-, and four-year-old dams.

\( t_m^* \) = an effect of type of rearing presumably caused by differences in the pre-weaning environment afforded to lambs born and reared as singles, born and reared as twins, and born as twins but reared singly.

\( a \) = the linear regression of \( Y \) on the age of the lamb (in days) at weaning.

\( x_{ijklmr}^* \) = the difference between the age of the \( r^{th} \) lamb in the \( ijkml^{th} \) subclass and the average age of all Tar\(_1\) and Col\(_2\) lambs.

\( e_{ijklmr}^* \) = the amount by which the predicted value (using the parameters just described) of an observation on the \( r^{th} \) lamb in the \( ijkml^{th} \) subclass differs from the observed value. This

*In each case only the most apparent causes of the effects have been specified. Obviously, any influence common to all individuals in a given class and different for individuals in other classes may contribute to a particular estimated effect.*
difference or "error" arises because the mathematical model
describes only a few of the innumerable sources of variation
which affect individual observations and because even those
few may be described imperfectly by this completely additive
model.

Because the effects within the a, b, d, and t classifications, respectively,
cannot logically be considered as random samples from respective popula-
tions of effects, they are assumed to be "fixed" effects or constants.
Although under some circumstances year (y) effects might well be random
samples from the "population" of years, they also are treated as constants.
Year effects are attributable principally to physical environmental dif-
ferences, and it is well known that such differences are cyclic. In
addition, management practices in consecutive years tend to be similar.
Therefore, it is improbable that the three consecutive years represented
in these data constitute a random sample of years. The assumptions regard-
ing the effects alter neither the method of estimation nor the mechanics
of tests of significance. However, they do influence the nature of infer-
ences which can be made about the effects. For example, the d's are not
regarded as a random sample of all possible ages of dams. Hence, the
variance associated with the d's is an estimate of that in a selected
segment of the population. Likewise, the years are not random; and the
mean square associated with years is unlikely to provide an unbiased
estimate of a component of variance for the population of years. In this
investigation the mean squares due to parameter differences will actually
be linear functions of variance components and "mean squares" of "fixed
deviations" instead of simply linear functions of variance components
(cf. Eisenhart, 1947).
(a) Adequacy of the model. The adequacy of the proposed model as a
description of the population in question should be examined. At present,
mathematical, economical, and intellectual limitations prevent one from
including in the model all sources of variation. In addition, the prac-
tical applications of estimates of variances, correlations, and heritabil-
ities make it undesirable, in most instances, to include all sources of
variation even if that were possible. It appears that one should first be
familiar with the nature of the data and the circumstances under which the
estimates are likely to be applied. Then, one can develop a model which is
reasonably in harmony with the known facts and which is also suitable for
the purpose for which it is intended.

In general, the data under investigation may be considered a reason-
ably good example of the observations as they occur in the population.
There were no dams older than four years; but in herds of range sheep,
young dams are nearly always greatly in the majority. Hence, this small
deviation from natural conditions seems unlikely to be of real consequence.
Mass selection practiced on the foundation stock and possibly among the
dams was perhaps more intense than is customary in some range sheep popula-
tions. This probably reduced the variation within these groups a small
amount, but it is unlikely to influence seriously estimates concerning the
offspring. The offspring included were not consciously subjected to any
form of artificial selection, although typical natural selective forces
were, of course, in operation.

In constructing the mathematical model, which was used simply to
obtain correction factors for important "non-genetic" sources of pheno-
typic variation, attention was given primarily to those sources which
likely would be controlled in practice* either physically or statistically. Theoretically one might account statistically for all sources of variation (if they could be identified) which were not genetic. If that were done and if dominance and epistasis were not important, estimates of heritabilities subsequently obtained would approach unity. In most cases these estimates would have rather limited practical applications because such complete statistical (or physical) control could or would rarely be exercised in practice. Improper use of such estimates could actually impede rather than advance genetic improvement. Therefore, in any particular investigation, one should be prudent about the extent to which statistical control is used. The circumstances under which the resulting estimates are likely to be applied may not be so ideal as those of the investigation.

Because it is neither possible nor always desirable to correct fully for all sources of variation, it is well to consider briefly the consequences of ignoring some sources of variation. The estimate of any particular parameter (effect) included in the model is expected to equal the true value of the parameter, plus the average effect of the ignored sources of variation within the main class characterized by the parameter, plus the mean of the errors within that class. This expectation may be expressed mathematically as

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*Occasional circumstances arise when it is desirable to include in the model a non-random source of variation simply to avoid biasing estimates of particular effects, even though this variation should or would remain uncontrolled in practice. An example is the inclusion of terms for parental birth year (when contemporary parents may be considered random variables from the same genetic population) to eliminate non-random parental effects on estimates of other effects in the model (cf. Koch, 1950).
\[ E(\tilde{\beta}_i) = \beta_i + \tilde{\nu}_i + \tilde{\mu}_i \]

where \( i \) indicates the particular main class to which the estimate applies.

If the effects of the ignored sources of variation are randomly distributed throughout each class, the expectation of the errors will be zero; and the average effect of the ignored sources (which will be the same in every class) will have been included in the estimate of \( \mu \).

Thus, estimates of parameters will be unbiased; and the variation associated with the ignored sources will be included as part of the error variance. Ignoring random effects merely defines them operationally as contributing to the "error" in each observation.

If the effects of the ignored sources of variation are not randomly distributed throughout each class, the average effect will be different in various classes. Differences among the class parameters will have changed, and the variation attributable to the parameters will have changed. The parameters actually will have been redefined operationally to include some of the effects (or all of the effects if they are perfectly correlated with the parameters) caused by the ignored sources of variation. Hence, the parameters and errors will have biological interpretations differing somewhat from those which would be appropriate if the ignored sources of variation were included in the model.

In view of the previously noted influence of individual differences in birth weights of lambs and milking abilities of dams upon selection of weanling offspring, one might question the desirability of ignoring these sources of variation.

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*A circumflex (\(^\wedge\)) placed above the symbol for a parameter distinguishes an estimate of the parameter from the parameter itself (except as otherwise noted in the text). A bar (\(-\)) distinguishes a mean value.*
However, under most practical range conditions little accurate information will be available on either of these sources. In addition (and of perhaps greater importance), to the extent that the variation in birth weights and milking abilities is genetic, it seems desirable to permit them to influence selection. In this way one actually will be selecting for genetic improvements in birth weights and milking qualities, with resultant improvements in viability and in some weanling traits.

Finally, a limited amount of a priori information in conjunction with a comparison of appropriate series of subclass means indicated that interactions among the effects were likely to be negligible. Consequently, interactions were not included in the model. The greatly increased complexity of the calculations would have made it unusually difficult to include all interactions, and there seemed to be no clear-cut reason for including any particular set of them. To the extent that interactions did occur, variation caused by them is included in the estimate of the error variance; and estimates of uncomplicated main effects and their sampling errors and tests of hypotheses are only approximate.

(b) Underlying conditions and assumptions. For one to make the most useful inferences on the basis of an analysis of variance, not only must the mathematical model suitably describe the observations, but the parameters (or effects) in the model and the observations themselves must satisfy certain conditions made necessary by present mathematical (or practical) limitations. The "necessary" conditions (or assumptions) have been discussed in detail by Eisenhart (1947) and briefly by Kempthorne
Briefly, the conditions specify that the e's (errors) be normally and independently distributed with a common (homogeneous) variance around a mean of zero and that "treatment" effects (parameters) be additive. If the conditions are not strictly fulfilled, certain alternative procedures sometimes permit either satisfaction of the conditions (in cases of non-normality or non-additivity) or extraction of the maximum information from the observations under the pertaining conditions (in cases of correlations or heterogeneity among the errors). It is desirable, therefore, to examine how closely these conditions are actually approximated in any particular investigation in order to avoid using the less efficient procedures and to avoid making erroneous inferences.

Normality in the distribution of errors is necessary if tests of hypotheses are to be exact. There is some assurance that the distributions in this investigation (with the exception of those for folds and type of birth) approximated the normal. Mean values were generally near the center of the ranges, and a priori information has revealed that observations on similar biological material were usually almost normally distributed. Although no rigorous statistical tests of normality were made actually, the distribution of fold scores for each breeding group probably is skewed toward the high score side. The distribution of type of birth is, of course, not normal.

Statisticians have found evidence that moderate departures from normality do not seriously bias F-tests or two-tailed t-tests of hypotheses, although the true probabilities of making a type I error (i.e., rejecting
the null hypothesis when it is true) are often slightly larger (but may be smaller) than the tabular probabilities indicate. In addition, there is likely to be some loss of efficiency in estimating "treatment" effects, although this loss probably is not often large. Any loss of efficiency is accompanied by a corresponding loss of power in the F- and t-tests (Cochran, 1947).

It is assumed that correlations among the errors were negligible* because the offspring in the investigation were unselected, sires and dams were mated at random, and all lambs were maintained in the same herd under comparable environmental conditions (known non-random environmental influences were considered in the model, of course). In addition, correlations (among the errors) arising because of individual differences among persons measuring and scoring the traits were at least partially avoided by requiring two or three persons to make independent observations on each trait (except weaning weight) and each person to observe the trait on all animals. Correlations among the parameters, introduced by the disproportionality of the data, were circumvented by using the least squares method of fitting constants (to be described briefly later) in the statistical analysis. To the extent that the errors were not independently distributed and that this was not accounted for in the analysis, estimates of standard errors and variances may be biased in either direction, depending upon the sign of the covariance terms. Resulting estimates of parameters will not be biased, however.

*That is, errors were independently distributed. Correlations among the errors might arise, for example, if the herd contained several different inbred lines or if lambs came from several different flocks affected by distinctly different environments and these factors were not considered in the statistical analysis.
To avoid the consequences of heterogeneity of errors (or variances), the Ram¿ data were analyzed separately from the Col¿ and Tar¿ data in obtaining estimates of parameters and correction factors (parameter differences). Joint (combined) estimates were obtained for the Col¿ and Tar¿ groups. One should perhaps point out here that even if variances in face cover and staple length in the Col¿ and Tar¿ groups were not homogeneous (as might be suspected according to the tests), joint intra-group estimates of effects on these traits were unlikely to be biased on that account alone. Also, because differences between corresponding variances of these traits in the two breeding groups were relatively small and because a much larger number of observations was available for obtaining joint estimates, the efficiencies of the joint estimates were greater (notwithstanding possible heterogeneous variances) than those of any individual estimates. The joint estimates could have been made still more efficient, however, had separate estimates of the effects been obtained for each group. These separate estimates could then have been combined by weighting each with the reciprocal of its own variance. This was not done because of the questionable nature of the heterogeneity, because of the increased computational labor, and because any further increase in efficiency would have been comparatively small (less than 5 per cent).

No valid assumptions can be made about possible heterogeneity of errors within subclasses. To the extent that such heterogeneity occurs, main effects will usually be estimated less efficiently and tests of significance will be less sensitive. To the extent that any heterogeneity exists between main classes (errors within each main class being
homogeneous), tests of significance and standard errors of particular main
class effects and correction factors may be biased in either direction.
With the exception of the previously noted heterogeneity among breeding
groups, variances within other classifications were assumed to be homo-
geneous inasmuch as ranges of observations within them were reasonably
similar and because there appeared to be no substantial reason for the
opposite assumption.

It is probable that any assumption of additivity of effects in these
data should, in reality, be regarded simply as a reasonable approximation.
Deviations from additivity in the form of interactions are unlikely to be
of major importance. Morley (1950) did point out some evidence of multi-
plicative effects on body weight and possibly on greasy fleece weight and
staple length of yearling sheep; but he found no suitable transformations
for achieving additivity. One might suggest that, in general, departures
from additivity are probably unimportant in comparison to possible errors
in the observations arising from subjectivity in scoring and measuring.

If departures from additivity occur, one should expect a decrease in
efficiency of estimation. Any loss in information is likely to be smaller,
however, when effects are small. Cochran (1947) states that this loss
should be negligible when effects do not exceed 20 per cent of some basic
observation, provided that there is neither a serious departure from
additivity nor a small error term. The variance caused by any interactions
not considered in the model will be included in the residual (error)
variance with a resultant overestimation of errors and loss in sensitivity
(power) of tests of significance. In addition, estimates of parameters
(effects) will be biased except in cases where observations in the sample subclasses are distributed exactly in the same proportions as they occur in the population. The general effect of non-additivity is similar to that produced by heterogeneity of errors.

One might summarize by pointing out that the observations (or errors) and the parameters obviously do not adhere rigidly to the conditions governing the most effective use of the statistical techniques. In general, departures from the conditions in these data probably are not serious; nevertheless, one should regard tests of significance and measures of reliability as approximate rather than exact.

2. Analysis of non-orthogonal data

When disproportionate numbers of observations appear in the various subclasses of a multiple classification table, differences in the unadjusted marginal means of the classes do not usually constitute unbiased estimates of true mean differences between classes. The data in such a multiple classification table are commonly termed non-orthogonal. They are not amenable to the usual abbreviated methods of analyzing orthogonal data, because such methods do not permit estimates of parameters in one classification to be independent of the effects of parameters in another. However, the least squares method of fitting constants (Yates, 1934; Hazel, 1946; Henderson, 1948) enables one to obtain unbiased estimates of parameters and sampling errors and to make valid tests of hypotheses. Least squares solutions will be both efficient and unbiased if the mathematical model is adequate and the underlying conditions previously described are satisfied.
(a) **Method of fitting constants.** Least squares estimates of the parameters (constants) in a linear model are those which minimize the sum of the squared errors. Such estimates were obtained by taking the partial derivatives of the expression

$$\sum e_{ijklmr}^2 = \sum (y_{ijklmr} - u - s_i - b_j - y_k - d_l - t_m - ax_{ijklmr})^2$$

with respect to each of the parameters in turn, setting these derivatives equal to zero, and solving simultaneously the resulting set of normal equations.

The normal equations obtained by this process may be represented as follows:

\[ u: \ N:\:\:\:\hat{u} + \sum_{i} N_{i}\hat{s}_{i} + \sum_{j} N_{j}\hat{b}_{j} + \sum_{k} N_{k}\hat{y}_{k} + \sum_{l} N_{l}\hat{d}_{l} \]

\[ + \sum_{m} N_{m}\hat{t}_{m} + \hat{a}x = y \]

\[ s_i: \ N_i \hat{u} + N_i \hat{s}_i + \sum_{j} N_{ij}\hat{b}_j + \sum_{k} N_{ik}\hat{y}_k + \sum_{l} N_{il}\hat{d}_l \]

\[ + \sum_{m} N_{mi}\hat{t}_m + \hat{a}x_i = y_i \]

\[ b_j: \ \vdots \ \vdots \ \vdots \ = y_j \]

\[ a: \ x \vdots \vdots \hat{u} + \sum_{i} x_i \hat{s}_i + \sum_{j} x_j \hat{b}_j + \sum_{k} x_k \hat{y}_k + \sum_{l} x_l \hat{d}_l \]

\[ + \sum_{m} x_m \hat{t}_m + \hat{a} \sum_{ijklmr} x_{ijklmr} = \sum y_{ijklmr} x_{ijklmr} \]
where \( N \) equals the number of observations obtained by including only those common to the particular main class(es) indicated by letter subscripts and otherwise summing over all classifications indicated by dot (.) subscripts. A separate equation was obtained for each of the \( s_i \)'s, \( b_j \)'s, \( y_k \)'s, \( d_l \)'s, and \( t_m \)'s. Careful inspection of the formulas will show that each equation actually may be written in a straightforward manner without the necessity of taking the partial derivatives formally.

It was impossible to obtain unique solutions of the equations without first imposing some restriction upon the model parameters, since the \( s, b, y, d, \) and \( t \) equations were not independent. The equations within each of these classifications summed to the \( u \) equation. Among three commonly used restrictions, that

\[
\sum_{i=1}^{N} s_i = \sum_{j=1}^{N} b_j = \sum_{k=1}^{N} y_k = \sum_{l=1}^{N} d_l = \sum_{m=1}^{N} t_m = 0
\]

or that \( \sum_{i=1}^{N} s_i = \sum_{j=1}^{N} b_j = \sum_{k=1}^{N} y_k = \sum_{l=1}^{N} d_l = \sum_{m=1}^{N} t_m = 0 \) or that

\( s_i = b_j = y_k = d_l = t_m = 0 \), the simplest was chosen. Thus, it was required that

\[
\hat{s}_1 = \hat{b}_2 = \hat{y}_9 = \hat{d}_4 = \hat{t}_1 = 0.
\]

The equations corresponding to these parameters consequently were deleted from the set, leaving a set of now independent equations. In a sense, the population is now defined as one in which \( s_1, b_2, y_9, d_4, \) and \( t_1 \) are common to all members of the population; and estimates of these parameters are thus included in the estimate of \( u \) (which, incidentally, also contains the intrinsic mean of the \( e \)'s because of the requirement that errors be distributed around a mean of zero). The remaining parameters were estimated as deviations from \( \hat{u} \).
Although different restrictions result in different estimates of the parameters themselves, estimates of the parameter differences (correction factors) within each classification, the sampling errors of these differences, and the error or residual phenotypic variance* remain the same. The restriction, in reality, simply defines $u$ as a particular value thus permitting one to obtain unique estimates of the remaining parameters. Since the differences among parameters within a given classification are identical under all three restrictions, one may easily calculate the estimates of parameters which would be obtained under either of the restrictions not imposed. One simply equates differences in the estimates to be calculated to differences in the corresponding estimates already obtained under the imposed restriction. The resulting set of simultaneous equations may then be solved by making use of the relationships (among groups of parameters) defined by the pertinent restriction. However, estimates of the parameters themselves are usually important only in so far as they permit estimation of differences among parameters.

After the dependencies among the normal equations had been eliminated, the equations were solved simultaneously, using the technique of matrix inversion. This technique, in brief, involves equating the matrix of known coefficients of the unknown parameters to the unit matrix and solving to obtain the inverse matrix. Any parameter ($p$) may then be estimated by obtaining the sum of the products ($\sum G_i a_{ij}$) of the sums ($G$'s) on the right-hand side of the normal equations and the elements ($a_{ij}$'s) in the

*The residual phenotypic variance is that remaining in the observations after correcting for the sources of variation included in the model.
particular row of the inverse matrix corresponding to the parameter to be estimated. The inverse matrix was obtained by using the Abbreviated Doolittle method described by Dwyer (1941). Using matrix notation, the relationships among the various matrices may be expressed as follows:

\[
\begin{align*}
//a_{ij}// & \cdot //p_i// = //g_i//, \\
//c_{ij}// & \cdot //s_i// = //s_i//, \\
//c_{ij}// & \cdot //s_i// = //s_i//,
\end{align*}
\]

where

\[
a_{ij} = a_{ji}; c_{ij} = c_{ji}; i, j = 1, \ldots, n;
\]

and \(//a_{ij}//\) represents the symmetric matrix of coefficients, \(//p_i//\) the vector of unknown parameters, \(//g_i//\) the vector of sums on the right-hand side, \(//c_{ij}//\) the inverse (reciprocal) of the coefficient matrix, and \(//I//\) the unit matrix.

An estimate of the residual phenotypic variance, \(\hat{e}^2\), was obtained by subtracting the reduction in the total sum of squares due to fitting constants (parameters),

\[
\sum \hat{p}_i g_i,
\]

from the total sum of squares,

\[
\sum y_{ijklmr}^2,
\]

and subsequently dividing the remainder by the appropriate degrees of freedom (\(N\ldots\ldots\) minus the number of independent equations). Since the variance of \(\hat{p}_i\) equals \(a_{ii} \sigma_e^2\) and the covariance of \(\hat{p}_i\) and \(\hat{p}_j\) equals \(c_{ij} \sigma_e^2\), the variance of an estimated difference, \(\hat{p}_i - \hat{p}_j\), equals \((a_{ii} + a_{jj} - 2a_{ij}) \sigma_e^2\). Sampling errors of the differences (correction
factors) consequently were estimated by

\[ \sqrt{c_{ii} + c_{jj} - 2c_{ij}} \]

where \( c_{ii}, c_{jj}, \) and \( c_{ij} \) are appropriate elements of the inverse matrix.

However, the peculiar circumstance that \( (\hat{p}_i - \hat{p}_j) = \hat{p}_i \) occurred in those instances where the imposed restriction defined \( \hat{p}_j \) as zero. In such instances, therefore, the sampling error of \( (\hat{p}_i - \hat{p}_j) \) was estimated by

\[ \sqrt{c_{ii}} \]

Given any linear contrast of the \( \hat{p} \)'s, say

\[ \phi' = k_1\hat{p}_1 + k_2\hat{p}_2 + \ldots + k_q\hat{p}_q, \]

where the \( k \)'s are known constants, the sum of squares associated with that contrast may be estimated by

\[ \frac{\phi'^2}{\sum k_i k_j c_{ij}} \]

with 1 d.f. (Lucas, ca. 1948).

For example, when given the contrast

\[ \phi'_1 = \hat{p}_1 - 1/2 (\hat{p}_2 + \hat{p}_3), \]

the mean square is estimated by

\[ \frac{\hat{p}^2_1 - \hat{p}_1\hat{p}_2 - \hat{p}_1\hat{p}_3 + 1/4 \hat{p}_2^2 + 1/2 \hat{p}_2\hat{p}_3 + 1/4 \hat{p}_3^2}{c_{11} - c_{12} - c_{13} + 1/4 c_{22} + 1/2 c_{23} + 1/4 c_{33}}. \]

When \( \hat{p}_3 \), say, is zero, the above estimator reduces to

\[ \frac{\hat{p}^2_1 - \hat{p}_1\hat{p}_2 + 1/4 \hat{p}_2^2}{c_{11} - c_{12} + 1/4 c_{22}}. \]
Using this method, the test of the hypothesis that \((p_1 - p_2) = 0\) was accomplished by calculating the ratio

\[
\frac{(\hat{p}_1 - \hat{p}_2)^2}{(\hat{c}_{11} - 2\hat{c}_{12} + \hat{c}_{22})\hat{\sigma}_e^2}
\]

or

\[
\frac{\hat{p}_1^2}{\hat{c}_{11}\hat{\sigma}_e^2}
\]

(when \(\hat{p}_2 = 0\))

and by comparing the result with values of \(F^*\) corresponding to appropriate degrees of freedom. The test of the hypothesis that \(p_1 - \frac{1}{2}(p_2 + p_3) = 0\) was accomplished by obtaining the mean square as described above, dividing it by \(\hat{\sigma}_e^2\), and comparing the quotient with appropriate values of \(F^*\).

(b) Adjusting the observations. The sums, sums of squares, sums of products, and coefficients of parameters required for the normal equations were obtained by coding the data on punch cards and summarizing with International Business Machines equipment. Subsequently, the basic statistics were calculated from the summarized data using semi-automatic calculating machines.

After the various environmental effects and correction factors had been estimated, variation among the observations due to the effects was removed by adjusting all observations to a common basis. For example, all Ram \(_2\) observations were adjusted to the basis of a single, wether lamb, 149 days old, born to a four-year-old dam in 1949. This also was accomplished with the assistance of IBM equipment. The only variation thus remaining in the observations was that ascribable to differences among the \(e\)'s (i.e., the residual phenotypic variation). These adjusted observations were used in the important process of obtaining estimates of the phenotypic and genetic parameters required for completing the selection indexes.
B. Estimation of Phenotypic and Genetic Correlations

Once the adjusted observations were obtained, the data, unaffected by measurable extraneous sources of variation, could be analyzed in a straightforward manner. The next step was to obtain both phenotypic and genetic correlations among the important economic traits.

1. Phenotypic correlations

Phenotypic correlations among the traits were obtained by calculating the familiar product-moment coefficient of correlation. To facilitate obtaining the many sums, sums of squares, and sums of products required for the different correlations among the six traits, the adjusted observations were coded on IBM cards and summarized with IBM machines.

Tests of the hypothesis that \( r = 0 \) were accomplished in the manner described by Snedecor (1946, p. 149). A test of the hypothesis that \( \hat{r}_1, \hat{r}_2, \) and \( \hat{r}_3 \), say, were simply different estimates of the same \( r \) was accomplished by transforming each estimate to

\[
z = \frac{1}{2} \log_e(1 + \hat{r}) - \frac{1}{2} \log_e(1 - \hat{r})
\]

and subsequently proceeding in the manner described by Snedecor (1946, p. 151 ff.) A combined estimate of \( r \) was obtained in this process.

2. Genetic correlations

Because correlations among different traits of the same individual each usually contain an appreciable environmental component in addition to a genetic component, they do not ordinarily provide accurate indications of probable genetic relationships among the traits. Hazel (1943) suggested
that genetic correlations could be obtained by correlating trait $x$ in one individual with trait $y$ in a close relative, thus circumventing the environmental component. It is desirable to have the relationship as high as possible to reduce sampling errors of estimates to a minimum. However, one must take care that the advantages gained by the high relationship are not nullified by possible environmental correlations between related individuals.

It was convenient in this investigation to use dam-offspring pairs for estimating genetic correlations inasmuch as they also were used for estimating heritabilities. The correlation between any two traits was estimated by evaluating the expression

$$\sqrt{\frac{\text{Cov } x_d^o \text{Cov } x_o^O \text{Cov } x_y^o \text{Cov } y_o^O}{\text{Cov } x_d^d \text{Cov } y_o^o}}$$  (Hazel, 1943)

where $x$ and $y$ represent adjusted observations on the two traits and the subscripts $d$ and $o$ distinguish observations measured on dam and offspring, respectively. The formula has a logical biometrical origin; and it yields estimates which are unbiased by the selection of dams, since the effects of selection appear in both numerator and denominator and tend to cancel out.

Unfortunately, there were a few occasions, especially when covariances were small, in which sampling errors caused the terms in the numerator to have opposite signs. Such circumstances might be anticipated in instances where the population parameter has a low value, unless the data are unusually accurate or extensive. On these occasions, the arithmetic rather than the geometric mean of the covariances in the numerator was calculated.
Any possible bias resulting from this substitution seems unlikely to be important in comparison to the already large sampling errors which appear to be a usual, although regrettable, consequence of the method.

(a) **Standard errors of genetic correlations.** Using large-sample methods, Rae (1950) obtained standard errors appropriate for genetic correlations which were estimated by

\[
\frac{\text{Cov } x_d y_o + \text{Cov } x_o y_d}{2 \sqrt{\text{Cov } x_d x_o \text{ Cov } y_d y_o}}.
\]

Inasmuch as only a few of the genetic correlations in this investigation were estimated in the above manner, it was desirable to obtain standard errors which were suitable for the primary method of estimation. Accordingly, a formula for the variance of a genetic correlation estimated by

\[
\sqrt{\frac{\text{Cov } x_d y_o \text{ Cov } x_o y_d}{\text{Cov } x_d x_o \text{ Cov } y_d y_o}}
\]

was developed, using the method outlined by Rae (1950, p. 64 ff.). The derivation of the formula is described in the next few pages.

Let \( a_{ij} \) and \( a_{kl} \) represent any covariances and \( a_{ii} \), etc., any variances calculated from the data; and let \( \sigma_{ij}, \sigma_{ii} \), etc., signify the corresponding population parameters. In addition, let

1. denote trait \( x \) of the dam (\( x_d \) above),
2. denote trait \( y \) of the dam (\( y_d \) above),
3. denote trait \( x \) of the offspring (\( x_o \) above), and
4. denote trait \( y \) of the offspring (\( y_o \) above).
Thus, i, j, k, and l may equal 1, 2, 3, or 4; and the various sets of observations may be regarded as randomly drawn items from a tetra-variate normal distribution with parameters $\sigma_{ij}$, $\sigma_{kl}$, etc.

Now the pertinent estimator of a genetic correlation ($r_g$) may be written in this notation as

$$\sqrt{\frac{a_{14} \cdot a_{23}}{a_{15} \cdot a_{24}}}$$

which may be expressed in logarithms ($\ln = \log_e$) as

$$\ln \hat{r}_g = \frac{1}{2} \ln a_{14} + \frac{1}{2} \ln a_{23} - \frac{1}{2} \ln a_{15} - \frac{1}{2} \ln a_{24}.$$

Then, by expressing any change in $\hat{r}_g$ in the form of a differential as

$$d(\ln \hat{r}_g) = \frac{d \hat{r}_g}{\hat{r}_g} = \frac{da_{14}}{2a_{14}} + \frac{da_{23}}{2a_{23}} - \frac{da_{15}}{2a_{15}} - \frac{da_{24}}{2a_{24}},$$

by measuring this change from the mean $\hat{r}_g$, and by subsequently squaring and taking expected values, one obtains approximately

$$\text{Var } \hat{r}_g = \frac{\text{Var } a_{14}}{4\sigma_{14}^2} + \frac{\text{Var } a_{23}}{4\sigma_{23}^2} + \frac{\text{Var } a_{15}}{4\sigma_{15}^2} + \frac{\text{Var } a_{24}}{4\sigma_{24}^2}$$

$$+ \frac{\text{Cov } a_{14}a_{23}}{2\sigma_{14}\sigma_{23}} - \frac{\text{Cov } a_{14}a_{15}}{2\sigma_{14}\sigma_{15}} - \frac{\text{Cov } a_{14}a_{24}}{2\sigma_{14}\sigma_{24}}$$

$$- \frac{\text{Cov } a_{23}a_{15}}{2\sigma_{23}\sigma_{15}} + \frac{\text{Cov } a_{23}a_{24}}{2\sigma_{23}\sigma_{24}} + \frac{\text{Cov } a_{15}a_{24}}{2\sigma_{15}\sigma_{24}}.$$

*The theoretical basis for this procedure is discussed by Kendall (1948, p. 208).
There remains, however, the problem of evaluating the variances and covariances in the above expression.

To the degree of approximation ordinarily accepted in large sample theory (division by \( n \) instead of \( n-1 \)),

\[
E(a_{ij}) = \sigma_{ij}
\]

and

\[
E(a_{ij}\bar{a}_{kl}) = E\left(\frac{1}{n}\sum_p z_{ip}z_{jp} \frac{1}{n}\sum_q z_{kq}z_{ql}\right),
\]

where \( E \) denotes the expected value of the term in parentheses, \( z \) represents a normal deviate from a large sample of \( n \) observations, and \( p \) and \( q = 1, 2, ..., n \). When \( p \) and \( q \) are not equal, the various cross-products in the left sum above are uncorrelated with those in the right sum. Consequently, there are \( n(n-1) \) independent pairs of cross-products with an expectation of \( \sigma_{ij}\sigma_{kl} \). The remaining \( n \) pairs occur when \( p \) equals \( q \) and have an expectation, \( E(z_{ip}z_{jp}z_{kp}z_{lp}) \), which may be determined by differentiating the moment generating function (cf. Mood, 1950, p. 184) of a tetra-variate normal distribution. This expectation is \( \sigma_{ij}\sigma_{kl} + \sigma_{il}\sigma_{jk} + \sigma_{ik}\sigma_{jl} \).

Therefore,

\[
E(a_{ij}\bar{a}_{kl}) = \frac{n(n-1)}{n^2} \sigma_{ij}\sigma_{kl} + \frac{n}{n^2}(\sigma_{ij}\sigma_{kl} + \sigma_{il}\sigma_{jk} + \sigma_{ik}\sigma_{jl})
\]

\[
= \sigma_{ij}\sigma_{kl} + \frac{1}{n}(\sigma_{il}\sigma_{jk} + \sigma_{ik}\sigma_{jl}),
\]

and

\[
\text{Cov } a_{ij}\bar{a}_{kl} = E\left\{(a_{ij} - \sigma_{ij}) (a_{kl} - \sigma_{kl})\right\}
\]

\[
= E(a_{ij}\bar{a}_{kl}) - \sigma_{ij}\sigma_{kl}
\]

\[
= \frac{1}{n}(\sigma_{il}\sigma_{jk} + \sigma_{ik}\sigma_{jl}).
\]
Similarly,

\[ \text{Cov} \ a_{ij}a_{ik} = \frac{1}{n}(\sigma_{ij} \sigma_{jk} + \sigma_{ij} \sigma_{ik}) \]

and

\[ \text{Var} \ a_{ij} = \frac{1}{n}(\sigma_{ij} \sigma_{jj} + \sigma_{ij}^2) \]

Thus, after substituting the appropriate variances and covariances into the previous expression, one can obtain

\[
\text{Var} \ \hat{r}_e = \frac{r_e^2}{n} \left[ \frac{1}{4} \left( \frac{\sigma_{11} \sigma_{44}}{\sigma_{14}^2} + \frac{\sigma_{22} \sigma_{33}}{\sigma_{23}^2} + \frac{\sigma_{11} \sigma_{53}}{\sigma_{13}^2} + \frac{\sigma_{22} \sigma_{44}}{\sigma_{24}^2} \right) \\
+ \frac{1}{2} \left( \frac{\sigma_{13} \sigma_{24} + \sigma_{12} \sigma_{34}}{\sigma_{14} \sigma_{23}} + \frac{\sigma_{14} \sigma_{23} + \sigma_{12} \sigma_{34}}{\sigma_{13} \sigma_{24}} \right) \\
- \frac{1}{2} \left( \frac{\sigma_{11} \sigma_{34}}{\sigma_{13} \sigma_{24}} + \frac{\sigma_{44} \sigma_{12}}{\sigma_{33} \sigma_{12}} + \frac{\sigma_{33} \sigma_{12}}{\sigma_{23} \sigma_{13}} + \frac{\sigma_{22} \sigma_{34}}{\sigma_{23} \sigma_{24}} \right) \right]^{-1}.
\]

The formula developed by Ras (notation and order slightly changed) appropriate for genetic correlations estimated as

\[
\frac{a_{14} + a_{23}}{2 \sqrt{a_{13} \cdot a_{24}}}
\]

is

\[
\text{Var} \ \hat{r}_e = \frac{r_e^2}{n} \left[ \left( \frac{\sigma_{11} \sigma_{44} + \sigma_{22} \sigma_{33} + \sigma_{14}^2 + \sigma_{25}^2}{(\sigma_{14} + \sigma_{25})^2} + \frac{\sigma_{11} \sigma_{53}}{4 \sigma_{13}^2} + \frac{\sigma_{22} \sigma_{44}}{4 \sigma_{24}^2} + \frac{1}{2} \right) \\
+ \left\{ \frac{2(\sigma_{13} \sigma_{24} + \sigma_{12} \sigma_{34})}{(\sigma_{14} + \sigma_{25})^2} + \frac{\sigma_{14} \sigma_{25} + \sigma_{12} \sigma_{34}}{2 \sigma_{13} \sigma_{24}} \right\} \right].
\]
Unfortunately, application of the two formulae is accompanied by three rather serious limitations which restrict their usefulness. First, the formulae specify the use of true population parameters which are rarely, if ever, known. Thus, estimates of parameters must be used. In general, one can expect the approximations to be better if \( n \) is larger, but it is questionable just how large \( n \) should be for fairly reliable results.

Second, for strict validity of the logarithmic expansion, \( a_{14}, a_{23}, a_{13}, \) and \( a_{24} \) must always be greater than zero. The last two covariances will nearly always meet this requirement, but either one or both of the preceding covariances can be negative. One may occasionally dodge this issue by omitting all terms in either formula after the first pair of braces, but serious errors can result if the estimated correlation is much larger than 0.05.

A careful scrutiny of 45 actual applications of the formulae, giving due recognition to signs as they naturally occurred, revealed that the formulae apparently gave proper qualitative consideration to changes in sign in spite of the above requirement. Whether or not such consideration was quantitatively precise is not known. However, when both \( a_{14} \) and \( a_{23} \) were negative, the results in nearly every case were identical with those which would have been obtained had all signs been positive. This occurred because other negative signs in the formulae generally caused all negative quantities to become positive. Perhaps the most that one can conclude is
that results of using the formulae seem to be reasonable, regardless of the occurrence of negative terms, in so far as one can judge from the relative magnitudes of the constituent covariances in the estimator of the correlation.

Third, since the exact form of the distribution of estimates is unknown, tests of hypotheses about the correlations and absolute measures of reliability are of questionable value except possibly when \( n \) is very large (cf. Kendall, 1948, section 9.3). Nevertheless, it seems that the standard errors should be useful in providing approximate relative measures of reliability and thus be helpful in combining different estimates of the same parameter. In the light of the above limitations, possibly the best justification for the use of either formula is the absence of a better one. It is assumed, of course, that inferences about the parameters are not actually distorted as a result of such use.

It seems appropriate to conclude with a few additional remarks concerning the use of two different estimators for the same kind of correlation. Ordinarily, one can expect such a procedure to result in some inefficient and possibly biased statistics. In addition, estimates obtained with one estimator may not have the same kind of distribution as estimates obtained with another. Consequently, equal sampling errors of estimates will not necessarily signify equal accuracies of estimation in the two cases. Thus, when the different types of estimates are combined, the component estimates may be improperly weighted.

Unfortunately, in these data there seems to be no alternative to the above procedure if the most logical estimator is to be used whenever possible. The estimates, using either estimator, will be the same if the
covariances in the numerator of the estimator are of like sign and of the same magnitude. The less preferred estimator gives a larger result when the magnitudes are different. In view of the similarity between the two estimators, there seems to be no substantial reason for believing that their distributions are appreciably different. Thus, standard errors should be reasonably comparable; and in view of the approximations involved in using the above formulae, any possible dissimilarity seems likely to be unimportant.

C. Estimation of Heritability

The heritability of a characteristic has been defined in a broad sense as the fraction of the phenotypic variation (in that characteristic) which is caused by the unique effects of individual gene complexes in any particular population. In a narrow sense, heritability is generally regarded as only that fraction of the variation attributable to the average (additive) effects of the genes in that population. This latter fraction, therefore, excludes variation attributable to non-linear gene effects associated with dominance, epistasis, and hereditary and environmental interactions. As defined by Lush (1948, p. 271), heritability may be expressed in the broad sense as

\[
\frac{\sigma^2_H}{\sigma^2_P} = \frac{\sigma^2_G + \sigma^2_D + \sigma^2_I + k\sigma^2_E}{\sigma^2_G + \sigma^2_D + \sigma^2_I + \sigma^2_E + \sigma^2_EH}
\]

and in the narrow sense as
where \( \sigma_H^2 \) is the broadly hereditary portion of the phenotypic variance, \( \sigma_P^2 \) (which equals \( \sigma_G^2 \) in the previous notation); \( \sigma_G^2 \) is the narrowly hereditary portion associated with average gene effects; \( \sigma_D^2 \) is caused by dominance deviations; \( \sigma_I^2 \) is caused by epistatic deviations; \( \sigma_E^2 \) is associated with environmental effects; and \( \sigma_{EH}^2 \) is attributable to non-linear joint effects of heredity and environment (\( k \leq 1 \)).

It is usually desirable in estimating heritability to obtain an estimate in the narrow sense (if mating is random) inasmuch as one can expect only the average effects of the genes to appear consistently in successive generations of offspring. Such an estimate is seldom obtained, however, because of the limitations of present estimating techniques. Lush pointed out that estimates will nearly always contain a little of the epistatic variance and occasionally some of the dominance variance, depending upon the method used. In addition, all, part, or none of the non-linear joint effects may be included. The techniques used in this investigation were based upon resemblances between parent and offspring. The primary method of estimation was the method of dam-offspring regression.

1. **The regression of offspring on dam**

This method is described in detail (on an intra sire basis) by Lush (1940); consequently, only a few pertinent remarks will be included here. The method was chosen because resulting estimates of heritabilities are unbiased by selection among the dams (provided that such selection is
based solely upon the dams' own phenotypes), are less likely to be influenced by environmental correlations than in full or half sib methods, are likely to have smaller sampling errors than in the half sib methods, and are unaffected by dominance deviations.

In addition to the desired additive genetic component, the estimates will contain components caused by any environmental or epistatic correlations between dam and offspring. The environmental component is presumably insignificant in these data because all animals were maintained in the same herd, under comparable environmental circumstances (any possible time trends in management practices were of doubtful importance). However, some (less than one-half) of any epistatic variance will be included; so these estimates, in most cases, will be somewhat higher than those obtained in a strictly narrow sense. Just what portion of any joint effects of heredity and environment is included is unknown. One might expect it to be small, although possibly of more importance in the Col2 than in the Ram2 and Tar1 estimates. Because of the system of mating used, the estimates are unlikely to be seriously affected by departures from random mating.

Lush (1948, p. 277) pointed out that if dominance or over-dominance is important, the real regression of parental breeding value upon phenotype will be curvilinear. Consequently, culling of recessive individuals before they become parents will tend to make the regression of offspring on selected parents less than that occurring in the case of unselected parents. Such a circumstance may partially compensate for the overestimation of heritability in the narrow sense caused by inclusion of any of the above mentioned components in the estimate.
Two additional considerations should be discussed. First, each ewe's record appeared in the estimates in direct proportion to the number of lambs she had. Because many of the dams' records thus appeared more than once, the information provided by the sample corresponds more closely to the number of dams than to the number of offspring but also depends upon the repeatability of the offspring records. The degrees of freedom for sampling errors were based upon the number of dams rather than the number of offspring in each estimate. However, unless repeatability is perfect, one actually obtains more information by including several offspring from each dam than by including only one. Estimates of sampling errors thus are likely to be somewhat too high. Unfortunately, better approximations cannot be obtained without an accurate knowledge of repeatabilities.

Second, in obtaining estimates of the variation among the dams, each dam's record was counted only once. Each dam's record was therefore included in the denominator of the regression only once, although it occurred in the numerator in proportion to the number of offspring she had. If the extra dams in the numerator were a random sample of those in the denominator, any bias in the regressions will be negligible inasmuch as the number of observations was large. However, if the dams having more than one offspring were selected because of their superiority in the particular trait under consideration or if the trait is correlated with prolificacy, the numerator (covariance) is likely to be smaller than if this is not the case, resulting in an underestimation of the regression. In cases where such selection or correlation is suspected, the bias can be

*Regressions were calculated as the ratio of the covariance between daughter and dam to the variance of the dams.
avoided by including each dam's record in the denominator each time it appears in the numerator. One should remember, however, that under these circumstances the variance in the denominator will be an underestimate of the true variance among the dams.

An examination of appropriate means revealed (on a basis of weanling record) little detectable evidence of either effective selection or sizeable correlations. Most likely there actually was some selection of the dams permitted to lamb in successive years. Such selection would have been based principally upon mature rather than upon weanling records of the dams, however, since any ewes permitted to lamb in the first place had already been selected upon their weanling records. Any selection subsequent to weaning also would have been relatively mild.

Tests of hypotheses that corresponding regression coefficients in the various breeding groups actually are equal were accomplished as described by Snedecor (1946, p. 326 ff.) and Mather (1947, p. 119). In view of the uncertainty of the true magnitudes of the sampling errors, the tests were rather insensitive. However, this deficiency was partially overcome by making tests with sampling errors known to be too small as well as with those known to be too large. When both tests were in agreement, a more precise inference could be made. The calculation of sampling errors was patterned after the method described by Mather (1947, p. 113 ff.), and estimates were combined by weighting with the reciprocals of the respective sampling variances.
2. Association between type of birth of offspring and dam

For comparisons of heritability of type of birth with heritability of any of the other traits to be reasonably valid, it is necessary to have an appropriate estimate of the association between type of birth of offspring and dam. The most suitable estimator for this purpose seems to be Yule's product-sum correlation (Yule, 1912). According to Yule and Kendall (1937, p. 252), this estimator yields a theoretical value of the product-moment coefficient of correlation for a four-fold (2 x 2) table (i.e., for cases when only two values are possible for each variable). It may be expressed in the form

\[ V = \frac{ad - bc}{\sqrt{(a + b)(a + c)(b + d)(c + d)}} \]

where \(a, b, c,\) and \(d\) are the respective frequencies in each cell of the table (cf. Kendall, 1948, section 13.6).

The two classifications in the four-fold table were based upon the type of birth of dam and of offspring. Because none of the dams and only a very few of the offspring were born in litters of greater size than two individuals, all multiple births were classed as twin births. In this manner only two classes (singles or twins) were obtained for each classification. The significance of any association between attributes in corresponding classes was tested in the manner described by Snedecor (1946, section 9.7).

According to Kendall (1948, p. 313), the variance of \(\hat{V}\) may be estimated as
\[
\frac{1}{N} \left[ 1 - V^2 + \left( V + \frac{1}{2} V^3 \right) \frac{(a - d)^2 - (b - c)^2}{\sqrt{(a + b)(a + c)(b + d)(c + d)}} \right]
\]

\[
- \frac{3}{4} \left[ \frac{(a + b - c - d)^2}{(a + b)(c + d)} - \frac{(a + c - b - d)^2}{(a + c)(b + d)} \right]
\]

where sample statistics are substituted into the formula. It is not entirely clear how closely the distribution of \( \hat{V} \) approaches the normal distribution, so one should be circumspect about inferences based upon the usual interpretation of the standard error. For reasons similar to those discussed in the previous subsection, estimates of standard errors are likely to be too large.

In computing \( \hat{V} \), all available records of 431 ewes (made between the ages of two and four years, inclusive) were included, making a total of 1,086 comparisons. Each parturition constituted one record irrespective of whether single or multiple births occurred. To avoid possible biasing of the estimates, every available record was included whether the offspring lived or died.

There is some reason to believe that correlations between type of birth of ewe and lamb will not be the same in cases where the granddams are of different ages. If this is true, the ewes should be a random sample of offspring from a random sample of granddams in order to obtain unbiased estimates of the average population correlation. Unfortunately, the sample in this investigation cannot be considered strictly random because only those ewes with three- and four-year-old dams could be included. Until additional information is available on this matter, one should regard these estimates as applying only to populations in which all granddams are of ages three and four.
D. Estimation of Relative Economic Values

In an attempt to find some reasonably accurate method for estimating the relative economic values of weanling traits it was necessary first to give some attention to a few basic considerations. These are discussed in the subsection immediately following, and the method adopted is outlined in the second subsection.

1. Basic considerations

To arrive at unique estimates of the economic values being investigated it was necessary to make certain assumptions. Thus, the breeding ewe was accepted as the important producing unit since most of the animals in commercial and purebred herds are females. It was assumed in this connection that a genetic improvement in each trait under consideration is of value only to the extent to which it ultimately influences the annual production* of the females averaged over their entire productive lives. Coherent with this assumption is the implication that animals which are selected because of their superiority in the traits are to be retained for breeding whereas the wool and lambs they produce are to be marketed.

A second consideration involves various attributes of the female's production which have direct economic (market) values. Whenever possible, the following important attributes were given prominent attention in evaluating the effects of improvements in the traits upon production: fineness (i.e., grade), staple length, and secured (clean) weight in the

*Production is defined as the quantity and quality of wool and lamb produced per breeding ewe.
case of wool; and freedom from folds, body type and condition (i.e., market grade), and pounds of lamb weaned in the case of lamb. Other attributes such as variability of fiber fineness and variability of staple length also were considered whenever relevant information concerning them was available. It should be mentioned that, in general, effects on wool weight were actually expressed in terms of the unscoured instead of the scoured weight. This was done simply because more information on unscoured weight was available and because prices paid to wool growers are most often expressed in terms of the value per grease pound. Changes in clean weight were considered, however, in arriving at relative economic values.

It seems desirable, in developing an index, to give first consideration to those attributes or traits which have direct economic values (i.e., traits which have market or sale values that do not depend on correlations with other traits) since those traits completely and directly determine over-all breeding value. In addition, it is often useful to include in the index traits which have no direct values themselves but which are correlated genetically with traits that do. An example in range sheep is face cover, which is included in an index because it is correlated with the average pounds of lamb weaned annually during a ewe's lifetime.

It is assumed that traits of breeding animals can have no direct economic values, however, until they are expressed in producing animals where they directly influence the value of production. Because this direct influence on production continues throughout a producing animal's lifetime and since the genetic expression * of a trait can change with age, the most accurate measure

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*The genetic expression of a trait is defined as the expression caused by the average (additive) effects of the genes. It would be equivalent to the phenotypic expression if there were no dominance, epistasis, or environmental variation.
of genetic merit in a trait is the average genetic expression of the trait throughout the animal's entire productive life. The traits for which one selects, however, usually are measured at some specific time or age. Consequently, the emphasis to be exerted in selecting for a trait should depend, among other things, upon the correlation between the genetic expression of the trait at the time the trait is measured (phenotypically) and the average genetic expression of the trait throughout the entire period in which it has a direct economic value (i.e., throughout the animal's entire productive life).

Traits expressed in weanling lambs which are to be retained for breeding thus have no direct economic values. A weanling animal is not yet a producing animal. Nevertheless, certain weanling traits are correlated genetically with those mature traits which do have direct economic values and which completely determine breeding value. Therefore, the indirect economic value to be assigned to a weanling trait depends (cf. Figure 1) upon the partial regressions of the average genetic expressions throughout maturity of those traits having direct economic values on the genetic expression of the weanling trait at the time this trait is measured. It also depends upon the average effect upon income (for a particular herd or population) of a unit improvement in those traits having direct values. The partial regressions (in genetic standard deviation units) are represented by the secondary paths* in Figure 1. The average effects upon income (per genetic standard deviation improvement) are represented by the primary paths.

*Only those secondary paths on which unequivocal experimental evidence is available have been included.
Figure 1. Path diagram illustrating the basis for assigning indirect economic values to weaning traits. The blocks in column I represent genetic expressions of weaning traits, which have no direct economic values. The blocks in column II represent mean genetic expressions, averaged over the entire productive life of the selected animals, of mature traits which do have direct economic values. The blocks in column III represent aggregate breeding values for wool production and lamb production, the sum of which is equivalent to overall breeding value. For explanation of paths, see the text.
2. Method of evaluation

In the final analysis, the relative economic value of a weanling trait may be estimated by obtaining the product of (a) the indirect economic value of a unit of genetic improvement in the trait times (b) the genetic standard deviation of the trait. The principal obstacle to this procedure lies in the determination of (a). The general principles used in obtaining (a) may be outlined as follows:

(1) For traits affecting quantity of production—find the sum of the average annual increase in pounds of wool per breeding ewe times the net income per pound of wool plus the similar increase in pounds of lamb per breeding ewe times the net income per pound of lamb, for a unit of genetic improvement in the trait.

(2) For traits affecting quality of production—find the sum of the average pounds of wool shorn annually per breeding ewe times the net value (per pound of wool) of the change in wool quality plus the average pounds of lamb weaned annually per breeding ewe times the net value (per pound of lamb) of the change in lamb quality, for a unit of genetic improvement in the trait.

(3) For traits affecting both quantity and quality of production—find the sum of the respective values obtained in steps (1) and (2).

In determining the indirect economic values, it is unnecessary (and at present impossible) actually to measure the genetic expressions of the traits. One can obtain estimates of genetic correlations among the traits. Then one can estimate the desired partial regressions of traits having direct economic values upon the weanling traits by using the usual methods of multiple regression (cf. Snedecor, 1946, chap. 13).
It is important that the change in production corresponding to a unit improvement in each trait be determined under some appropriate standard of environmental circumstances which is the same for all traits. The standard should be typical of the circumstances under which the selected animals are likely to be maintained. It is also important that the change in production for any particular case be computed on a per-breeding-ewe* basis. By so doing one allows adequately for the fact that each year there is nearly always one fleece but seldom exactly one lamb corresponding to each ewe on any particular sheep enterprise. Otherwise, the relative values of traits affecting lamb production are apt to be biased upward under circumstances in which the average number of lambs weaned per breeding ewe is less than one and downward when it is greater than one.

An additional point to consider is that by computing the change in production on an annual basis one implicitly assumes that both wool and lambs are produced each year. Such an assumption is not entirely true because ewes generally are not permitted to lamb as yearlings. Therefore, the yearling fleece should receive special consideration. Assuming the average ewe remains in the herd long enough to produce five fleeces and four lamb crops, the yearling fleece constitutes nearly one-fifth of her life-time wool production. If one considers an improvement in the yearling fleece to be as valuable as that in subsequent fleeces, one should include the factor 1.25 in computing the net income from improvements in wool production. Of course, any factor appropriate for the particular case can be used.

*This includes every ewe of breeding age maintained in the herd whether or not she produces a lamb. When it is customary in a particular case to maintain and shear wethers, they also should be included since each wether as well as each dry ewe produces a fleece.
The net income (or net value) mentioned herein is defined as the gross income ultimately obtained as a result of improving a trait less the direct cost of producing the improvement. In other words, all routine expenses and operating costs which would be incurred regardless of any improvement in production are ignored; and only those additional expenses and costs attributable directly to making the improvement are considered. Inasmuch as the sheep enterprises under consideration are essentially range enterprises, which generally sustain a relatively high percentage of fixed costs, the cost of a genetic improvement in production will probably be negligible in most cases. Any efforts toward improving the traits should, with a few exceptions, simply permit more efficient utilization of facilities and labor already available. Consequently, in this investigation net income was based upon the average price paid to producers for lamb and wool, with no deductions for cost of improvement.

Since the economic value of a unit improvement in a trait is a function of the size of the unit of measurement as well as of the biological and environmental factors involved, it should be multiplied by the genetic standard deviation of the trait. This process renders economic values which are independent of units of measurement and, by so doing, provides a common basis upon which to compare the traits. The relative values of the traits, therefore, were based on the effect of one genetic standard deviation change in each trait, since that change is comparable for all traits having similar genetic distributions.

(a) Limitations. It is difficult to make exact economic comparisons among traits having different genetic distributions, because one genetic
standard deviation change then will not constitute a comparable basis of comparison. The same is true for traits having different phenotypic distributions, because estimates of genetic standard deviations usually must be obtained by calculating the square root of the product of heritability and the phenotypic variance. These limitations probably will be unimportant in practice, however, unless the various distributions differ greatly. In this investigation, they seem most likely to be important in economic comparisons involving type of birth.

Another limitation is that relative values are appropriate only for the specific populations and circumstances for which they are calculated and should not be applied generally. This occurs for two primary reasons. First, the effect on production and net income of improving some traits is distinctly non-linear. For example, reducing the amount of face cover to a score of three results in a noticeable increase in pounds of lamb weaned; but further reduction to a score of one causes only a slight additional increase in pounds of lamb weaned. Also, an appreciable premium is paid for wool if staples are sufficiently long to qualify for combing length; but this premium is the same whether staples are just long enough to qualify or much longer than enough to qualify. Hence, the average value of a unit improvement for these traits depends upon how many animals in a particular population already have open faces or how many have fleeces which do not qualify as combing fleeces. Second, different environmental conditions and management practices cause the number and weight of lambs and the weight of fleeces to vary considerably from herd to herd. In herds where the average weight (pounds) of lamb weaned per ewe is high, for
example, proportionately more emphasis should be given to traits affecting lamb production and less to those affecting wool production than in herds where the average weight is low.

Finally, the relative values need to be recalculated periodically to adjust for changes in the population means of those traits in which improvement has non-linear effects on production and income. Recalculation also is needed to correct for semi-permanent changes in relative economic importance caused by various physiological factors or managerial practices affecting the selected animals or by sudden technological developments affecting the value of the products. Thus, periodic recalculation will assist in keeping the emphasis upon each trait at an optimum level.

E. Construction of a Selection Index

The biometrical and genetic principles underlying the construction of selection indexes have been thoroughly discussed by Smith (1936), Hazel (1948), and Lush (1948, p. 321 ff.) and will therefore be mentioned only incidentally here. Assume that an animal's (or plant's) over-all breeding value is determined by some linear function of its respective additive genetic values for each of the important economic traits. Then, because genetic values ordinarily cannot be observed, a linear function of phenotypic values of traits, which would predict the over-all breeding value as accurately as possible, is needed. Smith undertook this problem using the method of discriminant functions, and Hazel subsequently used the method of multiple regression. The results achieved by the two methods are identical. Which one is used is a matter of convenience. The technique
described by Hazel (1943) was used in this investigation and is outlined in the following paragraphs.

1. Statistical methods

Suppose the over-all breeding value, $H$, of an animal is determined completely by the function

$$H = a_1G_1 + a_2G_2 + a_3G_3 + \ldots$$

where the $a$'s are the economic values of all traits contributing directly to breeding value (i.e., all traits having direct economic values), and the $G$'s are the average (additive) genetic values of the animal with regard to these same traits. The problem is to find some function (or index),

$$I = b_1X_1 + b_2X_2 + b_3X_3 + \ldots,$$

of the observable phenotypic values ($X$'s) of the traits which is as highly correlated with $H$ as pertinent biological and physical circumstances will allow. Thus, $H$ becomes the dependent variable of multiple regression (cf. Snedecor, 1946, chap. 13). The partial regression coefficients, the $b$'s, are to have whatever values will permit the best estimation of $H$, that is, whatever values will make $R_{IH}$ a maximum $(I = \hat{H})$. The $r$'s involved in the usual normal equations, which are to be solved for the standard partial regression coefficients, are the phenotypic correlations among the traits. The only special difficulty encountered is that of obtaining the correlations between each trait and the dependent variable, the $r_{X_iH}$'s on the right-hand side of the equations.
Hazel (1943) has shown that

\[ r_{X_1H} = r_{X_1G_1} (d_1 r_{G_1G_1} + d_2 r_{G_2G_1} + \ldots + d_n r_{G_nG_1}) \]

where \( r_{X_1G_1} \) (which equals the square root of heritability in the narrow sense) is the correlation between an animal's phenotypic and genetic expressions for a particular trait, \( d_1 \) equals \( a_1 \sigma_{G_1} / \sigma_H \), and \( r_{G_iG_j} \) is the genetic correlation between two traits. For any particular trait, \( \sigma_{G_1} \) may be estimated as the square root of the product of heritability and the phenotypic variance for that trait; and \( \sigma_H \) is equal to the square root of

\[ \sigma_H^2 = a_1^2 \sigma_{G_1}^2 + a_2^2 \sigma_{G_2}^2 + \ldots + 2a_1a_2 \sigma_{G_1} \sigma_{G_2} r_{G_1G_2} + \ldots \]

It was necessary to modify the above technique slightly for this investigation because the weanling traits which compose the index are not the mature traits which directly determine overall breeding value. Figure 2 illustrates the biometrical relations between the weanling traits and overall breeding value. It may be shown from Figure 2 that

\[ r_{X_{W_1}H} = r_{G_{W_1}X_{W_1}} \left\{ r_{G_{W_1}G_{W_1}} (\nu_{11} d_1 + \nu_{12} d_2 + \nu_{13} d_3) + r_{G_{W_1}G_{W_2}} (\nu_{21} d_1 + \nu_{22} d_2 + \nu_{23} d_3) \right\} \]

where \( r_{G_{W_1}X_{W_1}} \) is the square root of the heritability of a weanling trait, \( r_{G_{W_i}G_{W_j}} \) is the genetic correlation between two weanling traits, \( \nu_{ij} \) is the standard partial regression of trait \( G_j \) which contributes directly to breeding value upon weanling trait \( G_{W_i} \) which contributes indirectly to breeding value, and \( d_j \) is the relative economic value of trait \( G_j \). The
Figure 2. Path diagram showing biometrical relations between the phenotypic values of weanling traits and over-all breeding value. The Xw's and Gw's are the phenotypic and genetic expressions, respectively, of weanling traits. The G's are the average genetic expressions throughout maturity of traits contributing directly to over-all breeding value (H). For explanation of other symbols, see the text.
relative economic value of weaning trait \( G_{w1} \) is

\[ v_{11}d_1 + v_{12}d_2 + v_{13}d_3 = \frac{\sigma_{G_{w1}}(e_{11}a_1 + e_{12}a_2 + e_{13}a_3)}{\sigma_H} \]

where \( e_{ij} \) equals \( \frac{\sigma_{G_{1j}}}{\sigma_{G_{w1}}} \) and is the partial regression of trait \( G_j \) upon trait \( G_{w1} \); and \( a_j \) equals \( \frac{\sigma_H}{\sigma_{G_j}} \) and is the direct economic value of trait \( G_j \).

Because \( \sigma_H \) appears equally in the denominator of all relative economic values, it may be ignored. Omitting \( \sigma_H \) from the relative economic value as expressed above leaves the value as it is defined in the previous section. The indirect economic value as defined previously is equivalent to the expression enclosed in parentheses. For the sake of convenience, this expression (i.e., the indirect economic value) will be indicated hereinafter by the letter \( g \).

Because the data provided no information about the \( \sigma_G \)'s or the \( r_{G_{1j}}G_{1j} \)'s, a precise evaluation of \( \sigma_H \) was not possible in this investigation. As a consequence, it was impossible to obtain estimates of \( r_{Xw1H}^2 \), of the standard partial regression coefficients (\( B \)'s), of \( R_{IH} \), and of sampling errors of the \( b \)'s. However, estimates of the quantities \( \sigma_Hr_{Xw1H}^2, \sigma_HB_i, \) and \( \sigma_HR_{IH} \) were obtained.

The normal equations involving the phenotypic correlations, the \( r_{Xw1Xw_j} \)'s, among the weaning traits were solved simultaneously using the inverse matrix technique described earlier. The right-hand sides of these equations actually were equated to the products of \( \sigma_H \) and the \( r_{Xw1H}^2 \)'s.
Solutions of the equations yielded, therefore, the products of $\sigma_H$ and the B's. The b's were obtained from the $\sigma_{HI}$'s by dividing the latter by the phenotypic standard deviations of the weanling traits.

If, once the normal equations have been solved, it is suspected that a particular trait is contributing little to $R_{IH}$, that trait may readily be eliminated from the index. The procedure for dropping a variable (trait) is described by Snedecor (1946; sections 13.13, 13.15). The relative efficiency of the new index may be determined by recalculating $R_{IH}$ and by comparing it with the value obtained when all traits were included in the index. In this study it was necessary to recalculate $\sigma_R R_{IH}$ and compare that quantity with the value obtained when all traits were included.

(a) Estimating progress. If I is normally distributed and selection is entirely on the basis of I, the improvement in over-all breeding value to be expected from using the index may be computed as

$$E(H - \bar{H}) = \frac{\text{Cov}_{IH}}{\sigma_I^2}(I - \bar{I})$$

$$= \frac{z}{P} \frac{\text{Cov}_{IH}}{\sigma_I}$$

where $(I - \bar{I})$ is the selection differential, and $z$ is the ordinate of the normal curve at the point of truncation which delimits an area $p$ corresponding to the portion of individuals selected. Now let $G_{ij}$ and $P_{ij}$ represent additive genetic and phenotypic variances (of weanling traits), respectively, when $i = j$ and covariances when $i \neq j$. Then,

$$\text{Cov}_{IH} = q_1 b_1 \text{Cov}_{Gw_1}X_{w_1} + q_2 b_2 \text{Cov}_{Gw_2}X_{w_2} + \ldots + q_1 b_2 \text{Cov}_{Gw_1}X_{w_2} + \ldots$$
\[ = q_1 b_1 G_{11} + q_2 b_2 G_{22} + \ldots + q_1 b_2 G_{12} + \ldots \]
\[ = \sum_{ij} q_1 b_j G_{ij} \]

since, in the same individual, dominance and epistatic deviations are uncorrelated with additive genetic deviations (Lush, 1948, pp. 33, 105) and since any correlations between heredity and environment in these data are negligible. In addition,

\[ \sigma^2 = b_1^2 p_{11} + b_2^2 p_{22} + \ldots + 2b_1 b_2 p_{12} + \ldots \]
\[ = \sum_{ij} b_1 b_j p_{ij} \]

The expected genetic gain for any particular trait, then, is

\[ E(G_i - \bar{G}_i) = \frac{z \text{ Cov } IG_i}{p} \]
\[ = \frac{z}{p} \frac{\sum b_j G_{ij}}{\sqrt{\sum_{ij} b_1 b_j p_{ij}}} \]

when the above conditions are met, as pointed out by Morley (1950).

Similarly, the expected selection differential for any trait is

\[ E(X_i - \bar{X}_i) = \frac{z}{p} \frac{\sum b_j p_{ij}}{\sqrt{\sum_{ij} b_1 b_j p_{ij}}} \]
2. Limitations

A foremost consideration in evaluating the adequacy of an index constructed in the above manner concerns the hypothesis that a simple linear model is appropriate for describing over-all breeding value or net merit. Such a model is usually proposed in the interests of simplicity and practicality as indicated by Lush (1948) but may not be strictly accurate in every case. If interactions between genes affecting different traits are common, then a linear model will be somewhat in error for indexes including those traits. For example, a particular gene substitution affecting trait A may have different effects on over-all breeding value in the presence of different gene complexes affecting trait B. The index for a particular animal may thus be biased in either direction, depending upon the particular combination of genes the animal possesses. This bias is perhaps no more important, however, than that caused by epistatic and dominance deviations (within particular traits) which can distort any specific estimate of net merit notwithstanding possible additivity of the genetic values for different traits.*

Because the index places maximum emphasis upon characters with high heritability, certain important but lowly heritable characters may occasionally be mistakenly neglected. Wright (1939) pointed out that the importance of estimating the relative significance of hereditary and envi-

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*Lush (1948, p. 330) has pointed out in this regard that selection indexes based entirely on an individual's own phenotype tend to be less useful when non-linearity in the form of overdominance and epistasis is important. In such cases the index should be based more upon the merit of progeny and close relatives and less upon an individual's own phenotype.
Environmental variation is not in setting limits to possible achievement (but in indicating the most effective plan for achievement). For example, heritability could be low in special cases simply because favorable alleles were rare instead of abundant. In these cases heritability might be greatly increased by selecting vigorously for the favorable alleles, consequently increasing gene frequency and genetic variability. Such cases could possibly be distinguished by the occasional appearance of a group of closely related individuals each of whom has exceptional merit in a particular trait of low heritability. It might then be desirable to select more intensively for this trait than the index suggests.

A similar consideration is that the index does not necessarily lead to progress in the desired direction for every trait, since it is $E(H - \bar{H})$ and not $E(G_i - \bar{G}_i)$ that is maximized by using the index. As a result average merit in some traits may actually decline because of sizeable negative genetic correlations. Of course, the decline will be the smallest attainable under circumstances which lead to the maximum gain in overall merit. A continual decline in any one trait might eventually have serious consequences unless selective emphasis is shifted in time to prevent such consequences. This shift will occur automatically if relative economic values are periodically recalculated. Any decline could be retarded by making compensatory (negative assortive) matings among the selected animals, as suggested by Winters (1940).

Since neither relative economic values nor heritability can be expected to remain unchanged over long periods of time, especially if selection is effective, the entire index should be recalculated periodically. This will insure maximum progress at all times. Paradoxically,
the more effectively the index improves genetic merit the more frequently it should be re-evaluated, since the parameters upon which it is based will have been changed more rapidly by selection. It is expected, however, that any one index will be appropriate for several animal generations, barring the occurrence of sudden permanent shifts in relative economic values resulting from new technological developments or changes in managerial practices.
V. RESULTS

A. Magnitude and Significance of Environmental and Physiological Effects on Variation of Weanling Traits

Because of the particular way in which certain parameters in the mathematical models (which were used to describe the observations) are defined, estimates of parameters other than \( y \) are also estimates of parameter differences or correction factors. It was for these parameter differences that the observations were corrected. The differences or correction factors, along with the experimental mean and standard deviation for each trait, are summarized in Tables 4 and 5. Although all possible differences within each group of parameters have been included in the tables, it was of course unnecessary to correct for the third difference in each group of three. It is apparent from the standard errors that many of the estimates have a low accuracy and consequently should be interpreted with discretion.

In addition to estimating the size and accuracy of the correction factors, it was also desirable to test as many hypotheses about the various parameters as sound statistical principles would permit. After some consideration, it seemed that the hypotheses set forth in Tables 6 and 7 were of predominant interest and should be tested. The results are depicted statistically in Tables 6 and 7 and are summarized verbally in the succeeding paragraphs.

Sex differences were significant in all \( \text{Ram}_2 \) traits except body type and condition. Among the \( \text{Col}_2-\text{Tar}_1 \) traits, only staple length was not influenced significantly by sex. Ewe lambs were superior to wether lambs
**Table 4. Means, Standard Deviations, and Correction Factors for Environmental and Physiological Effects on Variation of Ram₂ Weanling Traits**

<table>
<thead>
<tr>
<th>Effects</th>
<th>Differencea</th>
<th>Face cover</th>
<th>Staple lghth.</th>
<th>Weaning wt.</th>
<th>Body type</th>
<th>Condition</th>
<th>Folds</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(score)</td>
<td>(16ths inch)</td>
<td>(pounds)</td>
<td>(score)</td>
<td>(score)</td>
<td>(score)</td>
<td></td>
</tr>
<tr>
<td>Sex</td>
<td>s₀ - s₁</td>
<td>-23±0.06</td>
<td>1.12±0.33</td>
<td>-3.11±0.77</td>
<td>-02±0.03</td>
<td>-03±0.05</td>
<td>-32±0.07</td>
</tr>
<tr>
<td>Year</td>
<td>y₇ - y₉</td>
<td>-37±1.15</td>
<td>1.70±0.82</td>
<td>3.71±1.39</td>
<td>-34±0.08</td>
<td>-01±0.11</td>
<td>.11±.18</td>
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<tr>
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<td>y₈ - y₉</td>
<td>-09±1.12</td>
<td>0.54±0.64</td>
<td>-0.87±1.50</td>
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<td>-09±0.09</td>
<td>.12±.14</td>
</tr>
<tr>
<td></td>
<td>y₇ - y₈</td>
<td>-27±1.11</td>
<td>1.16±0.59</td>
<td>4.56±1.37</td>
<td>-20±0.06</td>
<td>08±0.08</td>
<td>00±.13</td>
</tr>
<tr>
<td>Age of dam</td>
<td>d₂ - d₄</td>
<td>-26±1.10</td>
<td>-0.62±0.57</td>
<td>-6.28±1.32</td>
<td>.10±0.05</td>
<td>.27±0.08</td>
<td>-11±.12</td>
</tr>
<tr>
<td></td>
<td>d₃ - d₅</td>
<td>-16±0.09</td>
<td>-0.40±0.52</td>
<td>-1.74±1.20</td>
<td>-01±0.05</td>
<td>.12±.07</td>
<td>-05±.11</td>
</tr>
<tr>
<td></td>
<td>d₂ - d₃</td>
<td>-10±0.08</td>
<td>-0.12±0.42</td>
<td>-4.54±0.98</td>
<td>.10±.04</td>
<td>.14±.06</td>
<td>-06±.09</td>
</tr>
<tr>
<td>Type of rearing</td>
<td>t₂ - t₁</td>
<td>-14±0.07</td>
<td>-1.55±0.40</td>
<td>-11.38±0.92</td>
<td>.15±.04</td>
<td>.42±.05</td>
<td>-44±.09</td>
</tr>
<tr>
<td></td>
<td>t₃ - t₁</td>
<td>-05±1.12</td>
<td>-1.52±0.64</td>
<td>-2.01±1.49</td>
<td>.09±.06</td>
<td>-.04±.09</td>
<td>-13±.14</td>
</tr>
<tr>
<td></td>
<td>t₂ - t₃</td>
<td>-09±1.12</td>
<td>-0.02±0.67</td>
<td>-9.37±1.55</td>
<td>.06±.06</td>
<td>.46±.09</td>
<td>-31±.15</td>
</tr>
<tr>
<td>Age of lamb</td>
<td>a</td>
<td>.000±.004</td>
<td>0.04±0.021</td>
<td>0.18±0.048</td>
<td>-.001±.002</td>
<td>-.002±.003</td>
<td>.005±.004</td>
</tr>
<tr>
<td>Mean</td>
<td></td>
<td>3.99</td>
<td>21.71</td>
<td>76.95</td>
<td>3.05</td>
<td>3.27</td>
<td>1.76</td>
</tr>
<tr>
<td>Standard deviation</td>
<td></td>
<td>0.69</td>
<td>3.76</td>
<td>8.73</td>
<td>0.36</td>
<td>0.51</td>
<td>0.82</td>
</tr>
</tbody>
</table>

a The parameters constituting each difference are distinguished as follows: s₀ = ewe lamb; s₁ = wether lamb; y₇ = 1947; y₈ = 1948; y₉ = 1949; d₂ = 2-year-old dam; d₃ = 3-year-old dam; d₄ = 4-year-old dam; t₁ = single lamb reared singly; t₂ = twin lamb reared with twin; t₃ = twin lamb reared singly; a = regression of trait upon age of lamb in days.
Table 5. Means, Standard Deviations, and Correction Factors for Environmental and Physiological Effects on Variation of Co₇₁-Tar₁ Weanling Traits

<table>
<thead>
<tr>
<th>Effects</th>
<th>Difference</th>
<th>Face cover (score)</th>
<th>Staple lgth. (16ths inch)</th>
<th>Weaning wt. (pounds)</th>
<th>Body type (score)</th>
<th>Condition (score)</th>
<th>Folds (score)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sex</td>
<td>s₀ - s₁</td>
<td>-14.04</td>
<td>0.70 ± 0.39</td>
<td>-5.82 ± 0.31</td>
<td>-13 ± 0.03</td>
<td>-10 ± 0.05</td>
<td>-11 ± 0.03</td>
</tr>
<tr>
<td>Breeding group</td>
<td>b₁ - b₂</td>
<td>19.04</td>
<td>-1.99 ± 0.39</td>
<td>0.05 ± 0.32</td>
<td>0.05 ± 0.03</td>
<td>-12 ± 0.05</td>
<td>0.01 ± 0.03</td>
</tr>
<tr>
<td>Year</td>
<td>y₇ - y₉</td>
<td>0.04 ± 0.11</td>
<td>2.38 ± 0.97</td>
<td>5.52 ± 2.04</td>
<td>-15 ± 0.08</td>
<td>-31 ± 0.08</td>
<td>22 ± 0.07</td>
</tr>
<tr>
<td>Year</td>
<td>y₈ - y₉</td>
<td>31 ± 0.09</td>
<td>0.27 ± 0.81</td>
<td>-5.43 ± 1.69</td>
<td>0.02 ± 0.07</td>
<td>-29 ± 0.10</td>
<td>16 ± 0.06</td>
</tr>
<tr>
<td>Year</td>
<td>y₇ - y₈</td>
<td>2.71 ± 0.08</td>
<td>2.09 ± 0.71</td>
<td>8.95 ± 1.49</td>
<td>-13 ± 0.06</td>
<td>-02 ± 0.09</td>
<td>0.06 ± 0.05</td>
</tr>
<tr>
<td>Age of dam</td>
<td>d₂ - d₄</td>
<td>0.02 ± 0.07</td>
<td>-0.51 ± 0.65</td>
<td>-9.35 ± 1.37</td>
<td>15 ± 0.06</td>
<td>31 ± 0.08</td>
<td>-05 ± 0.05</td>
</tr>
<tr>
<td>Age of dam</td>
<td>d₃ - d₄</td>
<td>0.05 ± 0.07</td>
<td>0.63 ± 0.51</td>
<td>-1.59 ± 1.28</td>
<td>0.01 ± 0.05</td>
<td>-04 ± 0.07</td>
<td>0.00 ± 0.04</td>
</tr>
<tr>
<td>Age of dam</td>
<td>d₂ - d₃</td>
<td>0.08 ± 0.05</td>
<td>-1.14 ± 0.48</td>
<td>-7.77 ± 1.00</td>
<td>14 ± 0.04</td>
<td>35 ± 0.06</td>
<td>-04 ± 0.05</td>
</tr>
<tr>
<td>Type of rearing</td>
<td>t₂ - t₁</td>
<td>0.17 ± 0.05</td>
<td>-0.51 ± 0.44</td>
<td>-15.02 ± 0.92</td>
<td>25 ± 0.04</td>
<td>57 ± 0.05</td>
<td>-10 ± 0.03</td>
</tr>
<tr>
<td>Type of rearing</td>
<td>t₃ - t₁</td>
<td>0.11 ± 0.08</td>
<td>-0.56 ± 0.75</td>
<td>-7.66 ± 1.57</td>
<td>0.08 ± 0.07</td>
<td>19 ± 0.09</td>
<td>-09 ± 0.05</td>
</tr>
<tr>
<td>Type of rearing</td>
<td>t₂ - t₃</td>
<td>0.28 ± 0.08</td>
<td>-0.15 ± 0.75</td>
<td>-7.36 ± 1.67</td>
<td>0.17 ± 0.07</td>
<td>38 ± 0.09</td>
<td>0.00 ± 0.05</td>
</tr>
<tr>
<td>Age of lamb</td>
<td>a</td>
<td>-0.015 ± 0.003</td>
<td>0.078 ± 0.027</td>
<td>0.200 ± 0.057</td>
<td>-0.06 ± 0.002</td>
<td>-0.001 ± 0.003</td>
<td>-0.06 ± 0.002</td>
</tr>
</tbody>
</table>

Mean

- 3.07
- 29.00
- 80.22
- 2.54
- 3.04
- 1.12

Standard deviation

- 0.55
- 4.86
- 10.19
- 0.42
- 0.59
- 0.35

*Symbols characterizing the various differences have the same meaning as in Table 4. In addition, b₁ = Tar₁ breeding group; b₂ = Co₇₁ breeding group.*
Table 6. Tests of Hypotheses Concerning Environmental and Physiological Effects on Variation of Ram<sub>2</sub> Weanling Traits

| Hypothesis<sup>a</sup> | d.f. | Face cover | Staple lgth. | Weaning wt. | Body type | Condition | Folds  
|------------------------|------|------------|--------------|-------------|-----------|-----------|--------
| s<sub>0</sub> - s<sub>1</sub> = 0 | 1    | 6.59**     | 162.72**     | 1,240.72**  | 0.06      | 0.11      | 13.43**
| d<sub>2</sub> - \(\frac{1}{3}(d<sub>3</sub> + d<sub>4</sub>)\) = 0 | 1    | 2.46*      | 7.95         | 2,245.64**  | 0.80*     | 3.20**    | 0.54
| d<sub>3</sub> - d<sub>4</sub> = 0 | 1    | 1.36       | 8.63         | 161.51      | 0.00      | 0.81      | 0.11
| t<sub>2</sub> - t<sub>3</sub> = 0 | 1    | 0.27       | 0.02         | 2,804.53**  | 0.11      | 6.91**    | 3.05*
| t<sub>1</sub> - \(\frac{1}{3}(t<sub>2</sub> + t<sub>3</sub>)\) = 0 | 1    | 0.76       | 191.88**     | 5,546.61**  | 1.09**    | 2.96**    | 6.58**
| a = 0 | 1    | 0.00       | 78.13*       | 1,142.29**  | 0.01      | 0.20      | 0.26

Error variance 515 0.47 14.17 76.28 0.13 0.26 0.68

Per cent of total variation accounted for  8 13 32 11 12 10

<sup>a</sup>See footnote for Table 4.

**Hypothesis rejected with probability of error less than 1 per cent.

*Hypothesis rejected with probability of error less than 5 per cent.
Table 7. Tests of Hypotheses Concerning Environmental and Physiological Effects on Variation of Col2-Tar1 Weaning Traits

<table>
<thead>
<tr>
<th>Hypothesis*</th>
<th>d.f.</th>
<th>Face cover</th>
<th>Staple lgth.</th>
<th>Weaning wt.</th>
<th>Body type</th>
<th>Condition</th>
<th>Folds</th>
</tr>
</thead>
<tbody>
<tr>
<td>( s_0 - s_1 = 0 )</td>
<td>1</td>
<td>3.15**</td>
<td>77.06</td>
<td>2,262.82**</td>
<td>2.67**</td>
<td>1.71*</td>
<td>2.06**</td>
</tr>
<tr>
<td>( b_1 - b_2 = 0 )</td>
<td>1</td>
<td>5.52**</td>
<td>613.67**</td>
<td>0.41</td>
<td>0.37</td>
<td>2.25*</td>
<td>0.01</td>
</tr>
<tr>
<td>( d_2 - \frac{1}{2}(d_3 + d_4) = 0 )</td>
<td>1</td>
<td>0.24</td>
<td>68.41</td>
<td>7,403.90**</td>
<td>2.03**</td>
<td>10.84**</td>
<td>0.19</td>
</tr>
<tr>
<td>( d_3 - d_4 = 0 )</td>
<td>1</td>
<td>0.19</td>
<td>25.45</td>
<td>159.42</td>
<td>0.01</td>
<td>0.11</td>
<td>0.00</td>
</tr>
<tr>
<td>( t_2 - t_3 = 0 )</td>
<td>1</td>
<td>3.31**</td>
<td>0.92</td>
<td>2,262.60**</td>
<td>1.22**</td>
<td>6.12**</td>
<td>0.00</td>
</tr>
<tr>
<td>( t_1 - \frac{1}{2}(t_2 + t_3) = 0 )</td>
<td>1</td>
<td>0.08</td>
<td>19.07</td>
<td>12,611.47**</td>
<td>2.79**</td>
<td>14.07**</td>
<td>0.88**</td>
</tr>
<tr>
<td>( a = 0 )</td>
<td>1</td>
<td>5.19**</td>
<td>190.91**</td>
<td>1,270.80**</td>
<td>1.02*</td>
<td>0.34</td>
<td>1.21**</td>
</tr>
<tr>
<td>Error variance</td>
<td>622</td>
<td>0.30</td>
<td>23.60</td>
<td>103.76</td>
<td>0.18</td>
<td>0.34</td>
<td>0.13</td>
</tr>
</tbody>
</table>

Per cent of total variation accounted for | 11 | 13 | 38 | 14 | 22 | 7 |

*See footnotes for Tables 4 and 5.

**Hypothesis rejected with probability of error less than 1 per cent.

*Hypothesis rejected with probability of error less than 5 per cent.
in all traits except weaning weight. These findings are in close agree-
ment with those of Hazel and Terrill (1946a, 1946a).

Age of dam caused significant differences in weaning weight, body type,
and condition for both the Ram2 and Col2-Tar1 groups. Differences in face
cover were significant, also, in the Ram2 group. Differences between the
two-year-old and the older dams, with respect to these traits, were more
important than those between three- and four-year-old dams. Differences
between three- and four-year-old dams were not significant for any traits.
In the Ram2 group, the two-year-old dams reared lambs superior in face
cover and fold score but inferior in all other traits. In the Col2-Tar1
group, lambs from two-year-old dams were inferior in all traits for which
differences were significant. These findings, also, are in close agree-
ment with those of Hazel and Terrill. A two-year-old ewe seems to be
either insufficiently mature or insufficiently experienced to rear off-
spring comparable to those of older ewes.

Type of rearing seems to have an important influence upon weaning
weight, condition, body type, and folds. The effect upon body type appears
to be somewhat more important in the Col2-Tar1 group than in the Ram2
group, whereas the reverse is true concerning the effect upon folds. In
general, lambs born and reared as singles were superior in all traits
except face cover and folds. Single lambs were significantly inferior in
fold score. Lambs born as twins and reared as singles were usually
intermediate in merit between lambs born and reared as singles and those
born and reared as twins. It appears that differences in prenatal environ-
ment may be partly responsible for lambs born as twins but reared as
singles being inferior in some respects to lambs both born and reared as
singles. Also, in some instances one twin lamb could have died because the dam was incapable of supporting both. Consequently, the average post-natal environment afforded the surviving twin likely was inferior to that afforded single lambs.

Age of lamb had significant effects in the Ram2 group only on staple length and weaning weight. In the Col2-Tar1 group it influenced significantly all traits except condition. In general, merit in all traits increased with age, although folds were slightly (but not significantly) more numerous among older Rambouillet lambs. Hazel and Terrill (1945a, 1946a) obtained results similar to these with regard to changes in merit with age.

The standard errors in Tables 4 and 5 show that many of the yearly differences were significant. It is noteworthy that year effects may be unimportant in some years, yet very important in others. In view of this uncertainty, it seems advisable to take year effects into consideration invariably in order to insure optimum accuracy in interpretation of results.

The only factor which might be ignored safely in a subsequent investigation is the distinction between ages among dams which are all older than two years. In this regard, however, Sidwell and Grandstaff (1949) and Sidwell et al. (1951a) found that dams of eight or more years in age reared lambs inferior in weaning weight, body type, and condition to those reared by the younger dams (except two-year-olds).

The differences between Col2 and Tar1 lambs (Tables 5 and 7) were relatively small for all traits as compared to differences between the Ram2 and Col2-Tar1 groups (note the means in Tables 4 and 5). The Tar1 lambs were significantly inferior in face covering and staple length but
The Col2-Tar 1 group apparently was superior in all traits to the Ram2 group.

The bottom row in Tables 6 and 7 shows that the environmental and physiological effects under consideration caused a reasonable share of the variation in weaning weight but only a small share of the variation in most other traits, particularly face cover and folds. Apparently, the latter two traits are the ones for which the above corrections are least likely to be needed. Condition was affected to a much greater extent among the Col2-Tar 1 lambs than among the Ram2 lambs. Hazel and Terrill (1945a, 1946a) obtained results somewhat similar to these, although effects on body type were more important in their data than in these. They also found that effects on staple length were relatively more important for Rambouillet lambs and effects on condition relatively less important for Columbia and Targhee lambs than these data indicate.

It is apparent that only a small fraction of the total variation in each trait (except weaning weight) has been accounted for in detail. Perhaps a diligent search for other non-genetic factors influencing variation would reveal important effects which are being ignored at present. If these effects could be controlled practically, the effectiveness of selection could be improved still further.

B. Phenotypic and Genetic Correlations among Weanling Traits

Since it was not clear how seriously non-homogeneity of variances would affect estimates of correlations obtained from pooled data, and since it was not known to what extent corresponding correlations in the
three breeding groups were actually comparable, separate estimates of correlations were obtained for each group. As was mentioned earlier, estimates of phenotypic correlations were combined in the manner described by Snedecor (1946, section 7.6). Genetic correlations were combined by weighting estimates with the reciprocals of their variances. In most instances the combined estimates are likely to be improved estimates of particular correlations. In a few cases, however, they are probably nothing more than averages of correlations which in reality are different. In interpreting the correlations one should remember that for traits evaluated by scoring, merit increases as score decreases.

1. Phenotypic correlations

Estimates of the various phenotypic correlations among the traits are presented in Table 8. Correlations among traits of Ram₂ lambs indicate that lambs having fewer folds tend to be inferior in weight, in body type, and in condition to those having more folds. Otherwise, the correlations show that phenotypic merit in any Ram₂ trait is positively associated with merit in the other Ram₂ traits. In the Col₂ and Tar₁ groups there seem to be no important conflicts among the traits with regard to phenotypic merit. Although folds and weaning weight appear to be negatively correlated (with regard to merit), the association is too slight to be significant.

There seem to be no important contradictions between the results obtained in this investigation and those presented in Table 1, page 9. It is noteworthy, however, that all correlations involving face cover are somewhat larger (cf. Table 8) than other results suggest. This probably
Table 8. Phenotypic Correlations among Ram₂, Col₂, and Tar₁ Weanling Traits

<table>
<thead>
<tr>
<th>Trait</th>
<th>Group</th>
<th>Staple length</th>
<th>Weaning weight</th>
<th>Body type</th>
<th>Condition</th>
<th>Folds</th>
</tr>
</thead>
<tbody>
<tr>
<td>Face cover</td>
<td>Ram₂</td>
<td>- .12**</td>
<td>- .10*</td>
<td>.13**</td>
<td>.12**</td>
<td>.29**</td>
</tr>
<tr>
<td></td>
<td>Col₂</td>
<td>- .02</td>
<td>- .28**</td>
<td>.20**</td>
<td>.20**</td>
<td>.18**</td>
</tr>
<tr>
<td></td>
<td>Tar₁</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Col₂-Tar₁</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Ram₂-Col₂-Tar₁</td>
<td>- .07*</td>
<td>- .15a</td>
<td>.14*</td>
<td>.15*</td>
<td>.23**</td>
</tr>
<tr>
<td>Staple length</td>
<td>Ram₂</td>
<td></td>
<td>- .15**</td>
<td>- .36**</td>
<td>- .13**</td>
<td>- .28**</td>
</tr>
<tr>
<td></td>
<td>Col₂</td>
<td></td>
<td>- .05</td>
<td>- .33**</td>
<td>- .05**</td>
<td>- .12**</td>
</tr>
<tr>
<td></td>
<td>Tar₁</td>
<td></td>
<td>- .12*</td>
<td>- .37**</td>
<td>- .20**</td>
<td>- .17**</td>
</tr>
<tr>
<td></td>
<td>Col₂-Tar₁</td>
<td></td>
<td>- .06</td>
<td>- .35**</td>
<td>- .13**</td>
<td>- .15**</td>
</tr>
<tr>
<td></td>
<td>Ram₂-Col₂-Tar₁</td>
<td></td>
<td>- .11**</td>
<td>- .36**</td>
<td>- .13**</td>
<td>- .21a</td>
</tr>
<tr>
<td>Weaning wt.</td>
<td>Ram₂</td>
<td></td>
<td>- .53**</td>
<td>- .61**</td>
<td>.14**</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Col₂</td>
<td></td>
<td>- .54**</td>
<td>- .73**</td>
<td>.03</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Tar₁</td>
<td></td>
<td>- .52**</td>
<td>- .64**</td>
<td>.05</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Col₂-Tar₁</td>
<td></td>
<td>- .53**</td>
<td>- .65a</td>
<td>.04</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Ram₂-Col₂-Tar₁</td>
<td></td>
<td>- .55**</td>
<td>- .66a</td>
<td>.09**</td>
<td></td>
</tr>
<tr>
<td>Body type</td>
<td>Ram₂</td>
<td></td>
<td>- .56**</td>
<td>- .11*</td>
<td>.11</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Col₂</td>
<td></td>
<td>- .47**</td>
<td>.05</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Tar₁</td>
<td></td>
<td>- .50**</td>
<td>.06</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Col₂-Tar₁</td>
<td></td>
<td>- .55**</td>
<td>.06</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Ram₂-Col₂-Tar₁</td>
<td></td>
<td>- .54**</td>
<td>- .02a</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Condition</td>
<td>Ram₂</td>
<td></td>
<td>- .12**</td>
<td>.01</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Col₂</td>
<td></td>
<td>- .01</td>
<td>.01</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Tar₁</td>
<td></td>
<td>- .04</td>
<td>.04</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Col₂-Tar₁</td>
<td></td>
<td>- .04</td>
<td>.04</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Ram₂-Col₂-Tar₁</td>
<td></td>
<td>- .03a</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*This estimate was obtained by combining individual estimates which differed significantly at either the 1 or 5 per cent levels of probability.

** and * distinguish estimates which differ significantly from zero at the 1 and 5 per cent levels of probability, respectively.
is a reflection of true differences between the correlations (involving face cover) in different populations, although sampling fluctuations could be partially responsible.

The most important correlations are those between staple length and body type and those among weaning weight, body type, and condition. One might logically expect correlations in the latter group to be high, but the relatively high correlations between staple length and body type suggest that staple length is really influencing the scoring of body type. It may be that lambs having longer staples are given superior scores in body type only because the fluffy appearance of the fleece in these individuals obscures poor body configuration, making such lambs appear to be better than they really are.

In general, corresponding correlations in each breeding group are reasonably comparable in size. However, all correlations involving folds are uniformly higher for the Ram₂ lambs than for the other lambs. Three of these correlations in the Ram₂ group differ significantly from the corresponding correlations in the other groups. Tables 4 and 5 show that the mean and standard deviation of folds were appreciably higher in the Ram₂ group than in the Col₂-Tar₁ group. Thus, it appears that correlations involving folds logically could be larger for Ram₂ lambs because of the higher incidence and greater individual variation in folds for that group.

2. Genetic correlations

It is evident from Table 9 that none of the genetic correlations are estimated with high accuracy. Yet, in those cases where the similarity
Table 9. Genetic Correlations among Ram₂, Col₂, and Tar₁ Weanling Traits

<table>
<thead>
<tr>
<th>Trait</th>
<th>Group</th>
<th>Staple length</th>
<th>Weaning weight</th>
<th>Body type</th>
<th>Condition</th>
<th>Folds</th>
</tr>
</thead>
<tbody>
<tr>
<td>Face cover</td>
<td>Ram₂</td>
<td>-.06 ± .18</td>
<td>-.21 ± .16</td>
<td>.28 ± .23</td>
<td>.34 ± .22</td>
<td>.18 ± .19</td>
</tr>
<tr>
<td></td>
<td>Col₂</td>
<td>.27 ± .29</td>
<td>-.11 ± .72</td>
<td>.31 ± .36</td>
<td>.47 ± .46</td>
<td>.40 ± .18</td>
</tr>
<tr>
<td></td>
<td>Tar₁</td>
<td>.04 ± .25</td>
<td>-.43 ± .24</td>
<td>.13 ± .42</td>
<td>.12 ± .26</td>
<td>.16 ± .27</td>
</tr>
<tr>
<td></td>
<td>Col₂-Tar₁</td>
<td>.13 ± .19</td>
<td>-.40 ± .24</td>
<td>.24 ± .29</td>
<td>.20 ± .24</td>
<td>.33 ± .16</td>
</tr>
<tr>
<td></td>
<td>Ram₂-Col₂-Tar₁</td>
<td>.03 ± .15</td>
<td>-.27 ± .15</td>
<td>.26 ± .18</td>
<td>.27 ± .16</td>
<td>.27 ± .12</td>
</tr>
<tr>
<td>Staple length</td>
<td>Ram₂</td>
<td>-.13 ± .30</td>
<td>-.64 ± .20</td>
<td>-.05 ± .26</td>
<td>-.63 ± .15</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Col₂</td>
<td>-.18 ± .32</td>
<td>-.14 ± .33</td>
<td>-.01 ± .38</td>
<td>-.47 ± .18</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Tar₁</td>
<td>-.14 ± .45</td>
<td>-.52 ± .42</td>
<td>.18 ± .29</td>
<td>-.46 ± .42</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Col₂-Tar₁</td>
<td>-.17 ± .27</td>
<td>-.28 ± .27</td>
<td>.11 ± .24</td>
<td>-.47 ± .18</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Ram₂-Col₂-Tar₁</td>
<td>-.15 ± .20</td>
<td>-.51 ± .16</td>
<td>.04 ± .18</td>
<td>-.56 ± .12</td>
<td></td>
</tr>
<tr>
<td>Weaning weight</td>
<td>Ram₂</td>
<td>-.29 ± .40</td>
<td>-.54 ± .18</td>
<td>.36 ± .22</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Col₂</td>
<td>-.28 ± .37</td>
<td>-.61 ± .33</td>
<td>.32 ± .23</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Tar₁</td>
<td>-.25 ± .42</td>
<td>-.43 ± .35</td>
<td>.14 ± .25</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Col₂-Tar₁</td>
<td>-.28 ± .29</td>
<td>-.47 ± .25</td>
<td>.23 ± .18</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Ram₂-Col₂-Tar₁</td>
<td>-.27 ± .23</td>
<td>-.51 ± .15</td>
<td>.28 ± .14</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Body type</td>
<td>Ram₂</td>
<td>.61 ± .21</td>
<td>.23 ± .25</td>
<td>.23 ± .25</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Col₂</td>
<td>.74 ± .42</td>
<td>.19 ± .26</td>
<td>.19 ± .26</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Tar₁</td>
<td>.59 ± .35</td>
<td>.54 ± .82</td>
<td>.54 ± .82</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Col₂-Tar₁</td>
<td>.66 ± .29</td>
<td>.22 ± .26</td>
<td>.22 ± .26</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Ram₂-Col₂-Tar₁</td>
<td>.62 ± .17</td>
<td>.25 ± .18</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Condition</td>
<td>Ram₂</td>
<td>-.03 ± .43</td>
<td>-</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Col₂</td>
<td>-.35 ± .33</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Tar₁</td>
<td>.07 ± .33</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Col₂-Tar₁</td>
<td>-.14 ± .24</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Ram₂-Col₂-Tar₁</td>
<td>-.11 ± .21</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
among estimates from group to group is close, perhaps the estimates are not greatly in error. Because signs of corresponding correlations in the various groups are, with a few exceptions, the same, one can feel reasonably confident that the signs, at least, are accurate. In most of the exceptions, the true correlations are probably near zero.

Except for correlations between staple length and weaning weight, weaning weight and folds, and condition and folds, genetic correlations among the Ram02 traits indicate that genetic merit in any one trait is positively associated with genetic merit in all other traits. With the exception of correlations between staple length and face cover, staple length and weaning weight, weaning weight and folds, probably staple length and condition, and possibly condition and folds, genetic correlations among Gen2 and Tar1 traits also indicate that the traits are positively correlated with regard to genetic merit.

It is not entirely clear why staple length is involved in so many of these exceptions. For the correlation between staple length and face cover and between staple length and condition, sampling errors could be the reason. Sampling errors also may be the cause of the negative association between staple length and weaning weight, although the close agreement among the estimates in all three breeding groups makes this rather implausible. The Western Sheep Breeding Laboratory (1946) similarly found this correlation to be negative (-0.26) for Rambouillet lambs, and Morley (1950) obtained evidence of a high negative association between genetic merit in staple length and body weight of Australian Merino sheep of approximately yearling age. It may be that staple length is negatively associated (from a merit point-of-view) with the above traits, all of which affect meat
production, for reasons similar to those which cause milk production and butterfat percentage or milk production and meat production to be negatively associated in cattle.

A comparison of Tables 9 and 2 (pages 88 and 9) revealed that estimates from the Western Sheep Breeding Laboratory are in general agreement with those from this investigation. However, the estimates in Table 2 are in several cases somewhat smaller than those in Table 9; and there are a few minor contradictions in sign, the most important of which involves the correlation between weaning weight and folds. Morley (1950) found a genetic correlation of 0.23 between body weight and folds and a correlation of -0.65 between staple length and folds. Rae (1950) estimated a genetic correlation of 0.21 ± 0.31 between staple length and body type in New Zealand Romney ewes. Rae's estimate is essentially in agreement with corresponding estimates (Table 9) in this investigation inasmuch as his scoring system was so arranged that a high score for body type indicated superior instead of inferior merit.

Finally, attention should be drawn to differences in sign between phenotypic and genetic correlations (Tables 8 and 9) involving staple length and weaning weight (all three groups), staple length and condition (Tar group), and body type and folds (Ram group). In view of the large sampling errors of the genetic correlations, it is difficult to know whether there is real significance to these differences. However, similar important differences in sign were noted by the Western Sheep Breeding Laboratory (Tables 1 and 2) for correlations between staple length and weaning weight and, in one instance, between body type and folds. Morley (1950) found phenotypic and genetic correlations between staple length and
body weight in yearling Merinos to have opposite signs. Such differences
in sign ordinarily can occur only when the product of the environmental
effects on the two traits, times the correlation between these effects, is
larger and opposite in sign to the product of the genetic effects on the
same two traits times the genetic correlation between these effects. If
heritability is sufficiently high for each trait that environmental effects
are small and if the genetic correlation is also high, the signs of the
phenotypic and genetic correlations should be the same.

C. Heritabilities of Weanling Traits

Estimates of heritabilities were obtained by doubling estimates of
regressions of daughter on dam and estimates of correlations between type
of birth of daughter and dam. The standard errors of the heritabilities
are twice the standard errors of the corresponding regressions and correla-
tions. The standard errors were based upon only the number of dams involved
in each estimate, even though some dams had more than one offspring. Con-
sequently, they are somewhat too large. As was true of certain phenotypic
correlations, certain corresponding heritabilities appear to differ
significantly among breeding groups. In these cases a combined estimate
does not constitute an improved estimate. It is simply an average of
estimates of different heritabilities and may not apply exactly to a
particular random breeding population.
1. Heritabilities of traits which could be evaluated quantitatively

Estimates of heritabilities of all traits except type of birth are summarized in Table 10. In general, body type and condition seem to be least heritable among these traits; whereas face cover, folds, and staple length appear to be most heritable. The only heritabilities which differ significantly from group to group are those involving face cover and folds.

Table 10. Heritabilities of Ram₂, Col₂, and Tar₁ Weanling Traits

<table>
<thead>
<tr>
<th>Trait</th>
<th>Ram₂</th>
<th>Col₂</th>
<th>Tar₁</th>
<th>Col₂-Tar₁</th>
<th>Ram₂-Col₂-Tar₁</th>
</tr>
</thead>
<tbody>
<tr>
<td>Face cover</td>
<td>.78±.12</td>
<td>.41±.14</td>
<td>.44±.15</td>
<td>.42±.12</td>
<td>**.59±.12</td>
</tr>
<tr>
<td>Staple length</td>
<td>.48±.12</td>
<td>.48±.18</td>
<td>.36±.14</td>
<td>.41±.13</td>
<td>.44±.09</td>
</tr>
<tr>
<td>Weaning weight</td>
<td>.31±.15</td>
<td>.35±.18</td>
<td>.39±.16</td>
<td>.36±.14</td>
<td>.33±.09</td>
</tr>
<tr>
<td>Body type</td>
<td>.19±.10</td>
<td>.25±.20</td>
<td>.13±.15</td>
<td>.18±.15</td>
<td>.19±.08</td>
</tr>
<tr>
<td>Condition</td>
<td>.27±.12</td>
<td>.16±.16</td>
<td>.29±.15</td>
<td>.23±.13</td>
<td>.25±.09</td>
</tr>
</tbody>
</table>

** and * distinguish estimates obtained by combining individual estimates which differed significantly at the 1 and 5 per cent levels of probability, respectively.

Although most of the estimates in Table 10 are somewhat larger than comparable* estimates in Table 3, page 13, they seem, with a few exceptions, not to differ significantly from those in Table 3. In nearly all cases the estimates have standard errors large enough to suggest that differences could be simply the result of sampling fluctuations. Notable

*It should be emphasized here that estimates for the Col₂ and Tar₁ groups of Table 10 are for animals descended from recent breed crosses and may not be strictly comparable to the Columbia and Targhee estimates of Table 3.
exceptions are the estimates for folds in the Col₂ group and for weaning weight in the Tar₁ group. One might expect a significant difference in the case of folds, because the incidence and variability of folds in the Col₂ group, which descended from recent crosses involving Rambouillet ewes, probably was higher than in the Columbia group of Table 3. The large discrepancy between estimates for weaning weight in the Tar₁ group and in the Targhee group of Table 3 seems to be due primarily to sampling errors.

There is some interest in comparing the heritabilities of weanling traits with yearling traits for animals of Rambouillet breeding. Terrill and Hazel (1943) calculated estimates of heritabilities for face cover (0.32), staple length (0.36), body weight (0.40), body type (0.12), neck folds (0.26), and body folds (0.32) for range Rambouillet yearling ewes. Jones et al. (1946) estimated heritability to be 0.51 for neck and body folds in a Texas Rambouillet flock. The most outstanding difference between the weanling estimates (Tables 10 and 3) and the yearling estimates (above) is that for heritability of face cover. All other differences, except possibly those involving folds, seem to be no greater than one might expect to occur from sampling. A logical explanation for the difference in estimates of heritability of face cover may be that lambs permitted to remain in the herd after weaning age were selected rather intensively for open faces. Such selection among the offspring would cause estimates of heritability obtained by doubling the regression of daughter on dam to be biased downward, thus lowering the estimate for yearling face cover.
2. Heritability of type of birth

Several different investigators working on divers breeds have observed that the percentage of multiple births among sheep increases with the age of the ewes. The type of birth, then, of a particular lamb depends in part upon the age of its dam. Hence, the correlation between the type of birth of dam and offspring would depend not only upon the age of the dam when the offspring were born but also upon the age of the granddam when the dam was born.

An estimate of the heritability of type of birth can be most useful if it is calculated from a random sample. To have a random sample in this instance would necessitate, among other things, that the dams be of random ages themselves and at the same time be offspring of granddams having random ages. In this investigation only dams of ages two, three, and four years born to granddams of ages three and four years could be included. The estimates of heritability in Table II consequently have a rather limited applicability.

Table II. Heritability of Type of Birth, Classified by Age of Granddam When the Dam Was Born

<table>
<thead>
<tr>
<th>Group</th>
<th>Age of Granddam</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Three years</td>
</tr>
<tr>
<td>Ram₂</td>
<td>.05 ± .20</td>
</tr>
<tr>
<td>Col₂ - Tar₁</td>
<td>.21 ± .18</td>
</tr>
<tr>
<td>Ram₂ - Col₂ - Tar₁</td>
<td>**.17 ± .10</td>
</tr>
</tbody>
</table>

**This estimate is significantly different from zero (P < 0.01) when N is based upon the number of offspring involved. It is not significant when N is based upon the number of dams.
If a ewe can express her inherent prolificacy more accurately at older ages, one can expect the correlation between type of birth of offspring and dam to be higher for older dams born to older granddams. It is assumed here that the type of birth of the dam is an expression of the granddam's prolificacy, whereas the type of birth of the offspring is an expression of the dam's prolificacy. Table 11 shows that for both the Ram* and Col2-Tar1 groups, estimates are higher when the granddams were older. However, estimates corresponding to the two ages of granddam do not differ significantly; so the evidence, while apparently supporting the hypothesis of different heritabilities (or correlations) for different ages of granddam, is by no means conclusive.

If, in testing the significance of the heritabilities, chi-square is computed with N equal to the total number of observations involved, the starred estimates (Table 11) differ significantly from zero. If N is considered to be equivalent only to the number of individual dams included in the estimates, none of the estimates differ significantly from zero. Hence, the statistical significance of the starred estimates is somewhat in doubt; but the remaining estimates definitely are not significant.

The large sampling errors indicate that additional data will be required before more accurate inferences can be made. Still, the combined estimates (Table 11) are reasonably close to estimates calculated from Rietz' and Roberts' (1915) data for Shropshires (0.14) and Wentworth's and Sweet's (1917) data for Southdowns (0.18).* They are also comparable to an estimate of 0.14 calculated from Johansson's and Hansson's (1943) data

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*Estimates in these two investigations may have been biased upward by inter-flock differences.
for heritability of litter size and to a similar estimate of 0.10 obtained by Cockerham (1949). The estimates are probably slightly higher than those which would have been obtained had the sample been wholly random. It is assumed, of course, that heritabilities involving only dams born to two-year-old granddams would be smaller than those in Table 11, thus reducing the combined estimates. Naturally, the possibility remains that correlations involving animals older than four years would carry sufficient weight to nullify any such reduction.

D. Relative Economic Values

It was indicated in a previous section that two important characteristics of each trait, the indirect economic value per unit improvement and the genetic standard deviation, were required for estimating relative economic values of weanling traits. The indirect economic value is equivalent to the ultimate effect of a unit of genetic improvement (in the weanling trait) upon net income.* To determine this effect it is first necessary to estimate the average relative value of wool and lamb per pound.

1. Relative values of wool and lamb

The following information is based upon statistics published by the Bureau of Agricultural Economics, U. S. Department of Agriculture (cf. Crops and Markets). During the period 1910–49 the average annual income

*For traits affecting wool production, the ultimate effect upon income should be multiplied by the factor 1.25 to give credit for yearling fleece production (cf. p. 64).
to farmers in the U. S. per pound of wool (grease basis) was about 3.06 times the income per pound of lamb. Five-year averages of annual ratios of income per pound of wool and lamb throughout this period ranged from 2.5 to 3.5. During war periods annual ratios tended to be above average; during depression years they tended to be below average; but during other periods they hovered near the mean. During the period 1928-49 the average ratio (based on the June price of wool and the October price of lambs) in the mountain states (Montana, Idaho, Wyoming, Colorado, New Mexico, Arizona, Utah, and Nevada) was 2.99. The annual U. S. average for the same period was 2.95. In view of these findings, the value 3.0 was used as the ratio of incomes from wool and lamb.

To make comparisons of income more realistic, quantitative values per pound of lamb and wool were used. These values were obtained by finding the average price of lamb in the mountain states during the period 1928-49 and by multiplying this average price by 3.0 to obtain a comparable price for wool. Computations were based on the period 1928-49 because a complete business cycle, including war and depression, is covered by this period. The relative values per pound of wool and lamb were 31.2 cents and 10.4 cents, respectively.

A lamb's fleece as well as its carcass contributes to the value of the lamb. One might conclude, therefore, that the above relative values are slightly biased. However, it seems rather unlikely that a genetic improvement in fleece quality or quantity would be reflected to an appreciable extent in the price paid to the producer for lamb. This may not be true in periods when wool prices are high and sheep numbers are being expanded, but it is likely to be true under average conditions.
2. **Effect of improvement in traits upon production and income**

The ultimate effect upon income of a unit of genetic improvement in a weanling trait depends in part upon the partial regressions of the genetic expressions of traits having direct economic values on the genetic expression of the weanling trait. It also depends upon the average effect on income of a unit improvement in those traits having direct economic values. Unfortunately, there were not sufficient data in this investigation to permit estimation of the desired genetic partial regressions. However, other studies provide some information about phenotypic correlations and regressions among the traits involved. Thus, it was possible to calculate rough approximations of the indirect economic values by substituting, in appropriate cases, phenotypic regressions for the more suitable genetic regressions. The accuracy of the approximations may be relatively low for traits of low heritability. The effect upon income (of a unit improvement in each trait having a direct economic value) was estimated from market statistics compiled by the Bureau of Agricultural Economics and the Production and Marketing Administration.

(a) **Face cover.** Spencer *et al.* (1928) examined 990 Rambouillet fleeces from ewes of all ages and found that face covering was not significantly correlated with either grease fleece weight, clean fleece weight, or staple length. However, the Texas Agricultural Experiment Station (1945) reported that a higher percentage of open-faced than covered-faced Rambouillet ewes dropped lambs. Terrill (1941) studied the lifetime production of 393 registered Rambouillet ewes and found that open-faced ewes weaned 8.6 pounds more lamb annually, and partially covered-faced ewes
weaned 4.4 pounds more lamb annually, than covered-faced ewes. Terrill (1949b) repeated this study, using the life-time production of 798 additional Rambouillet ewes. The results in the second investigation indicated that open- and partially covered-faced ewes had 11.1 and 7.7 pounds advantage, respectively, over covered-faced ewes in pounds of lamb weaned annually. In neither investigation were differences in fleece weights and staple lengths large enough to be of economic importance.

The results of Terrill's (1949b) investigation were used to estimate the effect of face cover on net income because they are the most reliable results available and because herd environmental conditions at the U. S. Sheep Experiment station seem reasonably similar to those in southern Utah. Terrill (1951) found that the regression of pounds of lamb weaned on face cover score was near -7.50 for Rambouillet ewes. This figure was multiplied by the regression of yearling on weanling score (0.51), since the ewes had been classified into face cover groups on the basis of their yearling scores. The resulting estimate of the ultimate income per unit improvement in weanling face cover is 39.8 cents for the Ram₂ data. This estimate is undoubtedly too high for the combined Ram₂-Col₂-Tar₁ and combined Col₂-Tar₁ groups, since the average effect of a unit improvement in face cover is unlikely to be as large for the Columbia and Targhee crosses as for the Rambouillets. The Columbia and Targhee crosses tend to be more open-faced and therefore are less in need of improvement in face cover. The average face cover score in the Col₂-Tar₁ group was 3.07 as compared to 3.99 for the Ram₂ group. Estimates of 32 and 24 cents were accepted intuitively as being more accurate for the Ram₂-Col₂-Tar₁ and Col₂-Tar₁ groups, respectively.
(b) **Staple length.** The results of Spencer *et al.* (1928) show that although staple length was not significantly correlated with either unscoured fleece weight or fiber fineness, it was significantly correlated \((r = 0.29)\) with clean fleece weight in Rambouillet ewes. The correlations between staple length and fleece weight might have been higher in this investigation had the analysis been made on a within-age basis. Combining yearling ewes, which have longer staples and lighter fleeces, with older ewes, which have shorter staples and heavier fleeces, tends to reduce these correlations. Neal (1943) concluded that long-fibered, smooth Rambouillet rams produced offspring with more valuable fleeces than did short-stapled, wrinkled rams when both kinds of rams were mated to short-stapled, wrinkled ewes. Jones *et al.* (1944) observed highly significant correlations of 0.24, 0.56, and -0.48 between staple length and grease fleece weight, clean fleece weight and shrinkage, respectively, among Rambouillet ewes of all ages (except yearlings). They also found that staple length had relatively little effect on fiber fineness.

Pohle and Keller (1945) found the regression of unscoured fleece weight (in pounds) on staple length (in centimeters) to be 0.74, 0.60, and 0.40 pounds for Rambouillet, Targhee, and Columbia yearlings, respectively. The regression of clean yield on staple length was 2.5, 1.9, and 1.6 per cent, respectively, for each breed. Since these results, also, were obtained at the U. S. Sheep Experiment station, they were used to estimate the net income from improving staple length. Inasmuch as the increase in unscoured (grease) fleece weight associated with longer staple length is accompanied apparently by only a slight change in yield,
the income from the improved staple length will be approximately proportional to the increase in unsecured weight.

After converting the above regressions to units appropriate for this investigation, the ultimate income from a unit improvement in weanling staple length was estimated to be near 3.6, 3.0 and 2.5 cents for the Ram₂, Ram₂-Col₂-Tar₁, and Col₂-Tar₁ groups, respectively. As an example, the Ram₂ estimate (3.6) was obtained by multiplying the converted regression (0.118) of fleece weight (in pounds) on staple length (in sixteenths of an inch) by the value of a pound of wool (31.2 cents).* Multiplying each estimate by the factor 1.25 gives the following estimates, now adjusted for yearling wool production: 4.5 (Ram₂), 3.8 (Ram₂-Col₂-Tar₁), and 3.1 (Col₂-Tar₁).

Watkins (1940) gives actual prices received at Boston for fleeces of different staple lengths. From his data it may be shown that the additional income from one-sixteenth of an inch increase in staple length of fine combing fleeces valued at 60 cents per grease pound was approximately 6 cents. This figure agrees closely with the above estimates which were based on wool valued at 31.2 cents.

Increased staple length may increase quality as well as quantity of wool. Statistics from U. S. Department of Agriculture bulletin CS-37, 1949, show that clean fleeces of combing and French combing lengths had approximately 12 and 6 per cent greater average values per pound, respectively, than those of clothing length during the period 1924-47. This was true of fleeces in both fine and half-blood grades of wool. During

*Since Terrill (1951) found that the regression of yearling on weanling staple length for Rambouillet sheep was about 0.98, no adjustments of the yearling regression coefficients of Pohle and Keller (1943) were made.
the same period, three-eighths blood combing fleeces were valued at 9 per cent more per pound than clothing fleeces of the same grade. Although the price differentials between clothing and longer wools were somewhat smaller during war years, in general they remained relatively stable throughout the above period. No pronounced trends were apparent.

Data showing the distribution of combing, French combing, and clothing wools in the Utah station herd were not available. It is known, however, that nearly all of the wool is of half-blood and fine grade. The average staple lengths for the Rambouillet and Columbia crosses (omitting yearling fleeces) during the period 1947-49 were near 2.35 and 2.70 inches, respectively. Upon comparing these lengths with commonly accepted standards for combing fleeces described by Kammlade (1947) and Bergen and Mauersberger (1948), it appeared that a large number of the fleeces must already be of combing length. Probably no serious error in the relative economic value of staple length will result (in this instance) from ignoring the contribution to net income which would occur from increasing the proportion of combing wool. Nevertheless, the above estimates of income per unit improvement in staple length are slightly too low. If staple lengths were generally below accepted length standards, it would seem advisable to increase the estimates a small amount.

(c) Weaning weight. Although there seems to be little direct evidence of the effect of weaning weight upon production throughout maturity, several investigators have observed that yearling and mature body weights have
important effects.* Spencer et al. (1928) found that range Rambouillet ewes which were heavier as yearlings had somewhat heavier unsecured fleeces (but little, if any, heavier clean fleeces) slightly shorter staples, and slightly finer fibers at maturity than those lighter as yearlings. Brody and Campbell (1938) calculated that a 100 per cent increase in body weight was associated with a 32 to 45 per cent increase in (unsecured) fleece weight. Pohle and Keller (1943) calculated regressions of unsecured fleece weight on body weight to be 0.09, 0.07, and 0.08 pound respectively, for range Rambouillet, Targhee, and Columbia yearling ewes. The corresponding regressions of clean fleece weight on body weight were 0.03, 0.03, and 0.04 pound. Jones et al. (1944) observed a highly significant correlation of 0.41 between body weight and unsecured fleece weight and the same correlation (0.41) between body weight and clean fleece weight of Rambouillet ewes of all ages. Body weight was insignificantly associated with staple length.

Hunt (1935) found that during a four-year period under farm flock conditions, heavier ewes (of several breeds) annually produced more pounds of lamb and slightly heavier unsecured fleeces than lighter ewes. He considered the smaller ewes to be more efficient producers, however, when feed consumption and production per 100 pounds of ewe were considered. Under similar conditions, Winters et al. (1946) also found that although total production was proportional to size of ewe, the smaller ewes were more efficient producers. Yet, they concluded in this regard that it was

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*Terrill (1951, 1939) found that weaning and yearling weights of Rambouillet ewes were closely correlated (r = 0.69) and that each of these weights was rather closely correlated with average mature weight (r = 0.46 and 0.68, respectively).
questionable whether differences (in economy of production) associated with size of ewe were of major importance.

Joseph (1931) observed that the lifetime lamb production of heavy range Rambouillet ewes was higher than that of light ewes. The pounds of lamb weaned annually averaged about 5 pounds more for each 10 pounds more body weight. Differences in lamb production were due partly to higher percentages of twins and partly to heavier weaning weights of lambs from the heavier ewes. The heavier ewes also produced heavier fleeces. Ewes which were approximately 45 pounds heavier in body weight had 0.9 pound advantage in unscoured fleece weight. Besse (1937) reported that large Rambouillet ewes produced nearly 100 per cent more twin lambs and 1.1 pounds more grease wool per ewe than small ewes. Nozdračev (1939) observed that production of twins was 2.5 times greater in a heavier than in a lighter group of Merino ewes.

Terrill and Stoehr (1942) found that among range Columbia, Corriedale, and Rambouillet ewes grouped according to their fall yearling weights, the average increase in pounds of lamb weaned per ewe (based on average annual production for the first 4 lambing years) per pound of increase in yearling weight was 0.49, 0.48, and 0.63 pound, respectively. In general, a greater proportion of the difference in production was due to differences in per cent of lambs weaned than to differences in weaning weight. The mean difference between life-time average (unscoured) fleece weights of the lightest and heaviest group within each breed was 0.7, 0.4, and 0.2 pound, respectively, corresponding to average body weight differences of 30, 27, and 22 pounds. No appreciable differences in staple length were noted.
In arriving at the economic value of body weight, the question of efficiency of production (here defined to be pounds of production per unit of feed consumed) should receive some consideration. Although efficiency of production could be important under farm-flock conditions, it is usually of minor importance under range conditions. This is especially true when ranchers do not feed livestock for extended periods. Naturally, the carrying capacity of the range must be considered. Terrill and Stoehr (1942) found a little evidence that for maximum lamb production, there may be an optimum balance between body size and available range feed. Thus, larger sheep may be suitable for the better ranges whereas smaller sheep are possibly more adaptable to sparsely vegetated desert ranges.

On the other hand, to the extent that size is an indication of health and soundness, it is of considerable importance on the range where each animal must secure its own food and water. It is possible, therefore, that any advantages of more efficient production by smaller animals may be completely nullified by the occurrence of reduced viability. An additional factor of importance is that one actually selects, to some extent, for rate of gain and possibly for efficiency of gain by emphasizing higher weaning weights. In conclusion, it seems that little will really be sacrificed and much may be achieved under range conditions by selecting for heavier body weight.

The results of Terrill and Stoehr (1942) seem most suitable for estimating economic values of weaning weight appropriate for these data. Terrill (1951) found that the regression of yearling weight on weaning weight among Rambouillet ewes was near 0.76 pound. After taking this into consideration, the ultimate value of a pound increase in weaning weight
(adjusted for yearling fleece production) for the Ram$_2$, Ram$_2$-Col$_2$-Tar$_1$, and Col$_2$-Tar$_1$ groups was estimated to be near 5.3, 4.9, and 4.7 cents, respectively. The Ram$_2$ estimate, for example, was obtained as follows: the regression of yearling on weaning weight (0.76) times the approximate regression of fleece weight on yearling body weight (0.2/22) times the value of a pound of wool (31.2 cents) times the adjustment for yearling fleece production (1.25) plus the regression of yearling on weaning weight (0.76) times the regression of pounds of lamb weaned on yearling weight (0.65) times the value of a pound of lamb (10.4 cents) equals 5.3 cents.

(d) **Body type and condition.** It is convenient to discuss jointly the effects of improving body type and condition since the discussion, for the most part, applies to either trait. Little precise information regarding possible effects of weanling type and condition upon production throughout maturity was available. However, one can expect the weanling type and condition of a selected animal to reflect approximately the weanling type and condition of its offspring. Hence, evaluation of the effects of improving these traits in the selected animal was based on the effect of changes likely to occur in the value of the offspring.

The most apparent effect of an improvement in the weanling body type or condition of the offspring is to change that offspring's market grade. Exactly how large an improvement, in terms of scoring units, would be necessary to cause a change of one market grade is not known. However, it seems unlikely that one would be seriously wrong in assuming a change in market grade for each unit change in score, since the scoring system used should discriminate among lambs in a manner reasonably comparable to market (slaughter) grades.
It is difficult to determine accurately just how much credit should be given for an improvement in market grade. Production and Marketing Administration statistics (cf. The Livestock Market News) for the period 1932-50 revealed that the average effect of an improvement of one slaughter grade was to increase the value of the live lamb about 9 per cent. The effect was not linear and appeared to be more important for the inferior than for the superior grades of lambs. The average effect was estimated from prices on the Omaha market during the height of the lamb marketing season (September-October). Exactly what the average effect would be in the Utah herd is unknown. The above estimate is admittedly a rough approximation; but after weighing the importance of the effect, it seemed that less error would result from using the estimate than from ignoring it.

In the absence of appropriate data, it is also difficult to determine what fraction of an improvement in market grade is caused by improved condition and what fraction is caused by improved type. Ordinarily, both type and condition must improve before market grade improves. Because no precise information was available, it seemed best to credit each trait with an equal share of the responsibility.

The indirect value of a unit improvement in either body type or condition was estimated to be approximately 20.1 cents for the Ram₂ group, 21.2 cents for the Ram₂-Col₂-Tar₁ group, and 22.3 cents for the Col₂-Tar₁ group. These estimates were obtained by considering the genetic correlation (0.5) between offspring and dam, the increase in the value of lamb (4.5 per cent attributable to each trait) accompanying a unit improvement in either trait, the average weaning weights of appropriate groups of lambs, and the average per cent of lambs weaned by appropriate groups of dams. The
estimates may be too low because no consideration could be given to the possibility that ewes with superior weanling type and condition scores actually may produce more lambs* during their lifetimes than those with inferior scores.

(e) **Folds.** Considerable emphasis has been given to studying differences in wool production between wrinkled- and smooth-hided ewes. Several investigators, Spencer *et al.* (1928), Jones *et al.* (1936), Belschner *et al.* (1937), and Jones *et al.* (1944) found almost unanimously that although wrinkled ewes produced distinctly heavier unsheared fleeces than smooth ewes, they produced only slightly, if any, heavier clean fleeces. The wrinkled ewes also had fleeces with somewhat shorter (0.1-0.3 inch) staples and, according to three studies, slightly coarser (up to 1.5 microns) fibers. Bell *et al.* (1936), Belschner *et al.* (1937), Bosman (1937), and Jones *et al.* (1944) all observed that fleeces from wrinkled ewes exhibited greater variability of fiber fineness than those from smooth-bodied ewes, fibers on the crests of the folds generally being less fine than those between folds. Neale (1943) studied the lamb and wool production of 1,200 "smooth" and "tight" range Rambouillet ewes. The tight ewes were described as having smaller bodies, more folds, tighter (more dense) fleeces, shorter staples, and heavier pelts than the smooth ewes. Neale's findings are in general agreement with those mentioned above, although he observed that tight ewes had slightly lighter (0.12 pound) clean fleeces and slightly finer (0.7 micron) fibers.

*Terrill (1949b) and Terrill and Stoehr (1942) observed that the most important reason for the increased production associated with both improved face covering and body weight was that animals superior in these traits simply produced and weaned more lambs. Increased weaning weights were of minor importance. These findings may also be true for body type and condition.
Carter (1943) reviewed some of the advantages and disadvantages of skin folds in the Australian Merino and suggested, among other things, that the greater amount of yolk in fleeces from wrinkled ewes may give better protection to the wool fibers. On the other hand, he pointed out that folds increase the susceptibility of ewes to fly strike, increase the proportion of shearing wounds and "second-cuts" (with resulting staple length irregularities) at shearing time, cause occasional "mechanical blindness" by encroaching over the eyes, and cause pelts to be inferior for leather.

Little information seems to be available concerning the uncomplicated effect of folds upon lamb production. Neale (1943) observed that during a two-year period, smooth ewes weaned 8.24 per cent more lambs and 5.06 pounds more lamb annually than tight ewes. The average difference in weaning weight of lambs was 0.27 pound in favor of the smooth ewes. However, some and possibly all the advantage of the smooth ewes could be accredited to their superior sizes in place of their lack of folds. Consequently, the effects (upon production) of body weight and folds are confounded; and one cannot justifiably say without further investigation that folds alone had any significant effect. In this regard, Jones et al. (1936, 1944) observed that smooth ewes were not necessarily heavier than wrinkled ewes. Therefore, one might expect tight and smooth ewes of equal weight to be equally good producers.

The evidence so far presented seems to indicate that a unit improvement in fold score would affect income primarily just to the extent that resulting changes in staple length, fiber fineness, and fiber variability would influence wool quality. However, the possible influence upon wool
quality seems, in this instance, to be of doubtful economic importance. In
the southermost range areas, particularly in Texas, a reduced susceptibility
to fly strike could be important. It is likely to be relatively unimpor­tant in most other areas. The nature of any uncomplicated effect of folds
upon pounds of lamb weaned remains somewhat obscure. It seems desirable,
therefore, to examine (as in the case of body type and condition) the
effect of the trait upon the value of the offspring of the selected animal,
keeping in mind that the genetic correlation between offspring and dam is
one-half.

Carter (1943) indicated that wrinkled lambs were often considered to
fatten less readily and to have less desirable carcasses than smooth lambs.
Neale and Bell (1943) found that lambs sired by smooth Rambouillet rams
gained an average 0.015 pound more per day during feeding trials in two
successive years than lambs sired by tight (shorter stapled, more wrinkled)
rams. Average carcass grades were choice and choice-minus for the two
groups in the single year in which grades were obtained. In two other
trials smooth Merino lambs gained an average 0.033 pound more per day than
wrinkled Merino lambs. Average carcass grades for the year in which they
were obtained were good-plus and good, respectively. Nearly 5 per cent
more per pound was paid for the smooth lambs in this instance.

Inquiries to Iowa meat packers and to prominent lamb feeders and
buyers in Colorado, Iowa, Kansas, Nebraska, Missouri, and Texas revealed
that they commonly discriminate against wrinkled lambs for three principal
reasons. First, carcass yields are lower for wrinkled lambs because such
lambs have heavier hides. Second, some lamb feeders feel that wrinkled
lambs are slow and uneconomical to fatten, with inferior carcass grades
being the result. Third, wrinkled hides make inferior leather since they contain distinct ribs or lines coinciding with the location of the folds. Sentiment appears to be somewhat divided on the second point. Some feeders said wrinkled lambs made unsatisfactory gains, some took the opposite view, and some implied that gains were often but not invariably unsatisfactory.

Apparently, the size of any discount levied against wrinkled lambs depends upon the degree of wrinkling and the supply and value of lambs. Buyers indicated that, in general, they overlook slight neck wrinkles but discount heavy neck folds and body wrinkles roughly in accordance with the amount of wrinkling. They naturally tend to be more lenient when lambs are difficult to obtain. Many lamb contracts contain specific clauses pertaining to "wrinkled-bodied" lambs. From all indications, a discount of approximately 10 per cent would normally be levied against heavily wrinkled lambs. This amount would be scaled downward with reduced wrinkling.

In view of the results obtained in various investigations and in the absence of further evidence concerning the effect of folds upon pounds of lamb weaned, the most suitable criterion upon which to base evaluation of income from a unit reduction in folds seems to be the buyer's discount against wrinkled lambs. The evaluation presumably will be somewhat low if less wrinkled ewes generally do wean more pounds of lamb annually than the more wrinkled animals. After considering the genetic correlation between offspring and dam, the probable regression of discount on fold score (2.5 per cent), average annual weaning weights, and average weaning percentages, the indirect value of a unit reduction in folds was estimated to be near
11.2, 11.8, and 12.4 cents for the Ram$_2$, Ram$_2$-Col$_2$-Tar$_1$, and Col$_2$-Tar$_1$ groups, respectively.

(f) Type of birth. It is particularly noteworthy that investigations by Rietz and Roberts (1915), Williams and Cunningham (1916), Wentworth and Sweet (1917), Marshall and Potts (1921), Wriedt (1925), Nozdračev (1939), and Terrill (1949a) are in complete accord in revealing that ewes born in larger litters had slightly higher average numbers of offspring during their lifetimes. Although any one of these investigations may not be significant by itself, the collective evidence in this regard is highly convincing. In general, the average number of offspring per litter was proportional to the type of birth (single, twin, triplet) of the dam. The average number frequently was still higher if one or more of the grandparents came from large litters. Three of these investigations were based upon several thousand observations each (in two of the three, however, inter-flock differences may have biased the results), and a fourth contained over a thousand observations.

A cursory examination of the average lamb production of 216 single and 123 twin ewes (born to three- and four-year-old dams) was included in this study. The average annual production per ewe for single and twin ewes was 1.36 and 1.52 lambs, respectively, during the first three years each ewe was in the breeding herd. Twin ewes gave birth to 11.8 per cent more lambs than single ewes.

A single dissenting investigation was made by Dry (1936) who observed no relationship between litter size of daughter and dam.* He pointed out,

*At least three lambings of 183 dams, and one or more lambings from 308 daughters were included in this investigation.
however, that the particular flock investigated (Underley Wensleydales, New Zealand) probably stood at a uniformly high level of inborn fertility. During a 25-year period, the average number of lambs born annually per ewe bred was 1.71. Sixty-nine per cent of all lambings were multiple births.

The above findings do not present the most accurate picture of the importance of type of birth, however, since a more suitable measure of lamb production is the pounds of lamb weaned. Terrill (1948a) investigated the average difference in lifetime production between Rambouillet ewes born as singles and those born as twins. He found from extensive data that twin ewes weaned an average of 2.9 pounds more lamb per ewe annually than single ewes. The production from twins having either young (two-year-old) or old (seven-year-old and above) dams, however, actually was less than that of singles, possibly because such twins have an initially greater environmental handicap than twin lambs born to ewes in the prime of life. Consequently, their initial production may be relatively low. Several investigators have found that twin lambs, in general, have largely overcome their pre-weaning environmental handicaps by the time they reach 12 to 18 months of age. At maturity, twins seem equal to single lambs in practically all respects.

Using Terrill's results, the value of a unit improvement in type of birth (i.e., from single to twin) is estimated to be near 30.2 cents for Rambouillet sheep. It may be even more important for more prolific breeds.

3. Relative values of weanling traits

Estimates of the various indirect economic values (i.e., the ultimate income from a unit improvement in each weanling trait), the respective standard deviations, and the resulting relative economic values are
summarized in Table 12. Estimates of economic values for staple length are probably too low, especially for herds having many animals with staple lengths shorter than those required for combing wools. Estimates for body type, condition, and folds also may be too low. The natures of errors in the remaining estimates are not apparent. None of the estimates are precise; but within the limits of the information now available, they seem to be reasonable approximations. According to these approximations, weaning weight, face cover, and staple length are of predominant economic importance. Body type appears to be least important. The relative position of type of birth remains somewhat obscure because of the rather incomparable nature of its standard deviation.

Undoubtedly, it would be worth while to investigate in more detail the effects of improving the traits under the particular circumstances in which the estimates are to be applied. The average effect of an improvement, especially in the case of traits having non-linear effects on production and income, is likely to vary widely under diverse circumstances. More precise estimates of relative values could be obtained if the effects of all traits were determined conjointly and if effects were based on genetic instead of phenotypic relationships between traits having direct and indirect economic values. In this way concomitant effects could be discounted properly, and credit would be given only for the "direct" genetic effect of each trait. This is important for obtaining unbiased estimates of $r_{XW,H}$ to be used in computing the $b$ values of the selection index.

In conclusion, one should be aware that any decision to ignore an economically unimportant trait should not be made in disregard of informa-
Table 12. Indirect Economic Values, Genetic Standard Deviations, and Relative Economic Values of Weanling Traits

<table>
<thead>
<tr>
<th>Trait</th>
<th>Group</th>
<th>Indirect economic value&lt;sup&gt;a&lt;/sup&gt; (cents)</th>
<th>Genetic standard deviation</th>
<th>Relative economic value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Face cover</td>
<td>Ram&lt;sub&gt;2&lt;/sub&gt; Col&lt;sub&gt;2&lt;/sub&gt;-Tar&lt;sub&gt;1&lt;/sub&gt;</td>
<td>32.0 (?)</td>
<td>0.47</td>
<td>15.0</td>
</tr>
<tr>
<td></td>
<td>Col&lt;sub&gt;2&lt;/sub&gt;-Tar&lt;sub&gt;1&lt;/sub&gt;</td>
<td>24.0 (?)</td>
<td>0.56</td>
<td>8.8</td>
</tr>
<tr>
<td></td>
<td>Ram&lt;sub&gt;2&lt;/sub&gt;</td>
<td>4.5 +</td>
<td>2.60</td>
<td>11.7</td>
</tr>
<tr>
<td></td>
<td>Col&lt;sub&gt;2&lt;/sub&gt;-Tar&lt;sub&gt;1&lt;/sub&gt;</td>
<td>3.8 +</td>
<td>2.98</td>
<td>11.0</td>
</tr>
<tr>
<td>Staple length</td>
<td>Ram&lt;sub&gt;2&lt;/sub&gt; Col&lt;sub&gt;2&lt;/sub&gt;-Tar&lt;sub&gt;1&lt;/sub&gt;</td>
<td>3.1 +</td>
<td>3.10</td>
<td>9.6</td>
</tr>
<tr>
<td></td>
<td>Col&lt;sub&gt;2&lt;/sub&gt;-Tar&lt;sub&gt;1&lt;/sub&gt;</td>
<td>5.5</td>
<td>4.86</td>
<td>25.5</td>
</tr>
<tr>
<td>Weaning weight</td>
<td>Ram&lt;sub&gt;2&lt;/sub&gt; Col&lt;sub&gt;2&lt;/sub&gt;-Tar&lt;sub&gt;1&lt;/sub&gt;</td>
<td>4.9</td>
<td>5.51</td>
<td>27.0</td>
</tr>
<tr>
<td></td>
<td>Col&lt;sub&gt;2&lt;/sub&gt;-Tar&lt;sub&gt;1&lt;/sub&gt;</td>
<td>4.7</td>
<td>6.11</td>
<td>28.7</td>
</tr>
<tr>
<td>Body type</td>
<td>Ram&lt;sub&gt;2&lt;/sub&gt; Col&lt;sub&gt;2&lt;/sub&gt;-Tar&lt;sub&gt;1&lt;/sub&gt;</td>
<td>21.2</td>
<td>0.17</td>
<td>3.6</td>
</tr>
<tr>
<td></td>
<td>Col&lt;sub&gt;2&lt;/sub&gt;-Tar&lt;sub&gt;1&lt;/sub&gt;</td>
<td>22.3</td>
<td>0.15</td>
<td>4.0</td>
</tr>
<tr>
<td>Condition</td>
<td>Ram&lt;sub&gt;2&lt;/sub&gt; Col&lt;sub&gt;2&lt;/sub&gt;-Tar&lt;sub&gt;1&lt;/sub&gt;</td>
<td>21.2</td>
<td>0.28</td>
<td>5.9</td>
</tr>
<tr>
<td></td>
<td>Col&lt;sub&gt;2&lt;/sub&gt;-Tar&lt;sub&gt;1&lt;/sub&gt;</td>
<td>22.3</td>
<td>0.28</td>
<td>6.2</td>
</tr>
<tr>
<td>Folds</td>
<td>Ram&lt;sub&gt;2&lt;/sub&gt; Col&lt;sub&gt;2&lt;/sub&gt;-Tar&lt;sub&gt;1&lt;/sub&gt;</td>
<td>11.8</td>
<td>0.63</td>
<td>7.1</td>
</tr>
<tr>
<td></td>
<td>Col&lt;sub&gt;2&lt;/sub&gt;-Tar&lt;sub&gt;1&lt;/sub&gt;</td>
<td>12.4</td>
<td>0.24</td>
<td>3.0</td>
</tr>
<tr>
<td>Type of birth</td>
<td>Ram&lt;sub&gt;2&lt;/sub&gt; Col&lt;sub&gt;2&lt;/sub&gt;-Tar&lt;sub&gt;1&lt;/sub&gt;</td>
<td>30.2 (?)</td>
<td>0.15</td>
<td>4.6</td>
</tr>
<tr>
<td></td>
<td>Col&lt;sub&gt;2&lt;/sub&gt;-Tar&lt;sub&gt;1&lt;/sub&gt;</td>
<td>30.2 (?)</td>
<td>0.20</td>
<td>6.2</td>
</tr>
</tbody>
</table>

<sup>a</sup>Each value is for a unit improvement. The units are score (face cover), sixteenths of an inch (staple length), pounds (weaning weight), score (body type, condition, and folds), and litter size (type of birth). Traits that were scored were given negative values in calculating the indexes because superiority in those traits was indicated by low instead of high scores.
tion about heritability and correlations with other traits. It is possible that such a trait still may be useful in predicting over-all breeding value if its heritability and its genetic correlations with traits of greater economic importance are sufficiently high to cause it to be appreciably correlated with over-all breeding value.

E. The Indexes

Three sets of indexes were calculated from the basic statistics described thus far. An individual set was developed for the Ram_2 group because of the relatively greater accuracy of parameter estimates for this group and because of the distinct differences between the Ram_2 and the other groups. A second set was developed for the combined Col_2 and Tar_1 groups because of the similarity between animals from each of these groups. In addition, the smaller amount of data available for each of these groups would have made separate indexes less reliable than a joint Col_2-Tar_1 index. A third set of indexes suitable for all three groups was constructed to see whether or not it would differ appreciably from those sets developed for specific groups. This set will be useful only in the event that it should become impractical to maintain the distinction between the Ram_2 and the other groups.

1. **Indexes having maximum correlations with over-all breeding value**

The initial index (I_1) in each of the three sets includes the six primary traits previously discussed. Type of birth has been omitted only because reliable information concerning genetic and phenotypic correlations
between it and the other traits was unavailable. The probable importance of type of birth will be discussed later in this subsection.

The product of the standard deviation in over-all breeding value and the correlation between each trait and breeding value (the $r_{XW}$ values), the relative emphasis which should be placed on each trait (the $B_{X}$ values), and the $b$ values actually constituting indexes $I_1$ are included in Table 13. It is apparent that the two most important characters in each index are face cover and weaning weight, the latter being most important in the Col$_2$-Tar$_1$ index and the former being most important in the remaining indexes. Staple length ranks third in importance for both indexes involving the Ram$_2$ group, whereas condition is third in the Col$_2$-Tar$_1$ index. The least important trait for both the Ram$_2$ and Col$_2$-Tar$_1$ indexes is folds, whereas condition is least important for the Ram$_2$-Col$_2$-Tar$_1$ index. In all three indexes animals will be penalized slightly for superiority in body type. In the Col$_2$-Tar$_1$ index, animals will be penalized also for superiority in condition.

It is noteworthy that in the Ram$_2$-Col$_2$-Tar$_1$ index the emphasis upon any particular trait except body type and folds is a compromise between the emphasis upon that trait in the Ram$_2$ index and the emphasis upon that trait in the Col$_2$-Tar$_1$ index. This seems to be a logical consequence of constructing a single index suitable for all groups. The apparent discrepancy in the case of body type and folds possibly can be explained by the fact that the emphasis upon these traits is relatively unimportant in all indexes.

There are striking differences between the Ram$_2$ index of Table 13 and the Rambouillet lamb index developed by Hazel and Terrill (1946d; see also
Table 13. Products of the Standard Deviation in Breeding Value and the Correlation between Each Trait and Breeding Value (r_xWh H), the Relative Emphasis (Bo H) for Each Trait, and the b Values of Indexes I

<table>
<thead>
<tr>
<th>Trait</th>
<th>( r_{xWh} \sigma_H )</th>
<th>Bo_H</th>
<th>b</th>
<th>( r_{xWh} \sigma_H )</th>
<th>Bo_H</th>
<th>b</th>
<th>( r_{xWh} \sigma_H )</th>
<th>Bo_H</th>
<th>b</th>
</tr>
</thead>
<tbody>
<tr>
<td>Face cover</td>
<td>-30.25</td>
<td>-27.96</td>
<td>-40.76</td>
<td>-14.29</td>
<td>-9.36</td>
<td>-17.06</td>
<td>-20.02</td>
<td>-16.43</td>
<td>-26.73</td>
</tr>
<tr>
<td>Staple lgth.</td>
<td>11.44</td>
<td>6.40</td>
<td>1.70</td>
<td>3.47</td>
<td>2.69</td>
<td>0.55</td>
<td>7.17</td>
<td>4.16</td>
<td>0.95</td>
</tr>
<tr>
<td>Weaning wt.</td>
<td>16.95</td>
<td>10.81</td>
<td>1.24</td>
<td>20.24</td>
<td>22.90</td>
<td>2.25</td>
<td>18.48</td>
<td>15.82</td>
<td>1.66</td>
</tr>
<tr>
<td>Body type</td>
<td>-12.83</td>
<td>1.90</td>
<td>5.27</td>
<td>-8.95</td>
<td>2.95</td>
<td>6.95</td>
<td>-10.83</td>
<td>1.33</td>
<td>3.34</td>
</tr>
<tr>
<td>Condition</td>
<td>-15.29</td>
<td>-5.61</td>
<td>-10.91</td>
<td>-10.97</td>
<td>5.32</td>
<td>9.08</td>
<td>-12.59</td>
<td>-0.02</td>
<td>-0.02</td>
</tr>
<tr>
<td>Folds</td>
<td>-7.95</td>
<td>-0.03</td>
<td>-0.03</td>
<td>-2.41</td>
<td>-1.59</td>
<td>-4.51</td>
<td>-8.61</td>
<td>-2.18</td>
<td>-6.57</td>
</tr>
</tbody>
</table>

*The Bo_H values are for measurements in phenotypic standard deviation units. The b values (in order of listing) are for measurements in units of score, sixteenths of an inch, pounds, score, score, and score.

Table 14. Expected Selection Differentials and Expected Genetic Changes (for Individual Traits) Resulting from a Selection Differential of One Standard Deviation in Index (I) Values

<table>
<thead>
<tr>
<th>Trait</th>
<th>Selection differential</th>
<th>Genetic change</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Ram_2</td>
<td>Col_2-Tar_1</td>
</tr>
<tr>
<td>Face cover</td>
<td>-0.61</td>
<td>-0.34</td>
</tr>
<tr>
<td>Staple lgth.</td>
<td>1.26</td>
<td>0.73</td>
</tr>
<tr>
<td>Weaning wt.</td>
<td>4.35</td>
<td>8.99</td>
</tr>
<tr>
<td>Body type</td>
<td>-0.12</td>
<td>-0.17</td>
</tr>
<tr>
<td>Condition</td>
<td>-0.23</td>
<td>-0.28</td>
</tr>
<tr>
<td>Folds</td>
<td>-0.19</td>
<td>-0.04</td>
</tr>
</tbody>
</table>

*To attain a selection differential of one standard deviation in index values, only the upper 38 per cent of the population should be retained for breeding.
Phillips, 1947). The latter index places the following relative emphasis upon one standard deviation in each trait: face covering, -0.403; neck folds, -0.392; body (weaning) weight, 0.379; condition, 0.155; staple length, 0.142; and body type, 0.009. To facilitate comparing the indexes, the emphasis upon one standard deviation in each trait is indicated (below) relative to the emphasis for weaning weight.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Rambouillet</th>
<th>Ram₂</th>
</tr>
</thead>
<tbody>
<tr>
<td>Face cover</td>
<td>-1.063</td>
<td>-2.589</td>
</tr>
<tr>
<td>Neck folds</td>
<td>-1.034</td>
<td></td>
</tr>
<tr>
<td>Folds</td>
<td>-0.002</td>
<td></td>
</tr>
<tr>
<td>Weaning weight</td>
<td>1.000</td>
<td>1.000</td>
</tr>
<tr>
<td>Condition</td>
<td>0.409</td>
<td>-0.519</td>
</tr>
<tr>
<td>Staple length</td>
<td>0.375</td>
<td>0.592</td>
</tr>
<tr>
<td>Body type</td>
<td>0.024</td>
<td>0.176</td>
</tr>
</tbody>
</table>

The greatest differences occur in the relative emphasis upon folds and upon body type in each index. Probably, the most important difference is that involving face cover. Note that superiority in both condition and body type lowers the Rambouillet index as it does the Col₂-Tar₁ index of this investigation. Superiority in condition improves the Ram₂ index, however.

(a) Progress to be expected using indexes I₁. The results to be expected from using the indexes are not readily apparent from an examination of the indexes themselves. Neither do the standard partial regression coefficients indicate completely what one can expect from an index. A more accurate concept may be obtained by examining the expected selection
differential and expected genetic change per generation for each trait. These expected values are contained in Table 14 and are predicated upon the assumption that selection will be wholly on the basis of the index and that the index (I) values will be normally distributed. The expected values are unlikely to be distorted seriously, however, if any departures from normality (of the index values) are moderate.

A comparison of Tables 13 and 14 revealed that a trait receiving relatively little weight in the index may improve even though it does receive little weight. For example, note that folds in the Ram₂ index (Table 13) and condition in the Ram₂-Col₂-Tar₁ index receive almost no emphasis but that the expected selection differentials and genetic changes (Table 14) for these traits are, nevertheless, comparable to those for certain other traits receiving considerably greater emphasis. Also, one can expect an improvement in both body type and condition even though they receive negative emphasis in the indexes. Apparently, the genetic change in traits which receive little weight themselves is dependent to a considerable extent upon the emphasis placed upon other traits with which they are highly correlated genetically.

Table 14 shows that for none of the traits will the selection differential be unfavorable. The only trait in which one may expect a genetic decline is staple length in the Col₂-Tar₁ group. In view of the great emphasis placed upon weaning weight in the Col₂-Tar₁ index and the negative genetic correlation between weaning weight and staple length (cf. Table 9), this slight decline is not surprising.

Finally, it is apparent that the expected genetic gains are not necessarily proportional to the product of heritability and the selection
differential. Because one selects simultaneously for several traits, the expected genetic gain for any particular trait is conditioned by the emphasis placed upon other traits with which it is correlated genetically. Thus, a correlated response has increased the expected genetic gain of certain lowly heritable traits such as type and condition over that indicated possible by their respective heritabilities. On the other hand, the genetic gain in staple length in one instance is actually negative in spite of a positive selection differential. This probably occurs because of the great emphasis placed on weaning weight.

(b) **Probable importance of including type of birth.** It would be worthwhile to know whether any appreciable increase in the efficiency of the indexes would result from including type of birth. A rough approximation of the importance of this trait can be obtained by assuming that the phenotypic and genetic correlations involving the trait are of negligible magnitudes and that the relative emphasis on the trait (the $B_{GH}$ value) is proportional to the product of the square root of heritability and the relative economic value.

If the assumptions are reasonably accurate, little is to be gained from including type of birth in the indexes. The efficiency of the Ram$_2$ index will be increased only 0.1 per cent, that of the Col$_2$-Tar$_1$ index only 1.0 per cent, and that of the Ram$_2$-Col$_2$-Tar$_1$ index only 0.5 per cent. It seems unlikely that the efficiency would be increased more than two or three times these amounts even if precise information were available. If the increase in efficiency were actually three times larger than indicated above, it probably would be worth while to include type of birth in the Col$_2$-Tar$_1$ index and possibly in the Ram$_2$-Col$_2$-Tar$_1$ index. Inclusion of the
trait would still be unimportant for the Ram₂ index. The $b$ values (for
type of birth) appropriate under the assumptions described above are 2.89,
6.72, and 5.27 for the Ram₂, Col₂-Tar₁, and Ram₂-Col₂-Tar₁ indexes,
respectively.

2. Alternative indexes

In the interest of making each index as simple as possible without
seriously reducing its efficiency, it is important to know how much each
trait is contributing to that efficiency. Hence, several alternative
indexes were calculated, omitting those traits which were receiving the
least emphasis in the initial indexes in Table 13. The reduction in
efficiency caused by omitting a particular trait was determined by compar-
ing the respective alternative $R_{iH}^2$ values with those obtained for the
initial indexes. The alternative indexes and the relative efficiencies of
each are included in Table 15.

Apparently, omission of folds only from the Ram₂ index and condition
only from the Ram₂-Col₂-Tar₁ index made no visible reduction in the
efficiency of either index. Three traits may be omitted from each of the
three initial indexes without reducing efficiency appreciably more than 1
per cent in any case. Omitting folds, body type, and condition from the
Ram₂ index reduces the efficiency only 0.7 per cent. Omitting folds,
staple length, and body type from the Col₂-Tar₁ index reduces efficiency
only 1.1 per cent. Omitting condition, body type, and folds from the
Ram₂-Col₂-Tar₁ index reduces efficiency only 0.4 per cent.

From a practical standpoint, particularly under the more usual range
conditions, it would seem advisable to use indexes $I_4$ for all groups.
Table 15. Alternative Indexes (I's), the Relative Emphasis (BσH) for each Trait, Products of the Multiple Correlation Coefficient and the Standard Deviation in Breeding Value (R_{IH}σH), and the Relative Efficiency of each Index

<table>
<thead>
<tr>
<th>Group</th>
<th>Index</th>
<th>Face cover</th>
<th>Staple length</th>
<th>Mean weight</th>
<th>Body type</th>
<th>Condition</th>
<th>Folds</th>
<th>R_{IH}σH</th>
<th>Efficiencya</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ram2</td>
<td>I1</td>
<td>-40.77</td>
<td>1.10</td>
<td>1.24</td>
<td>5.23</td>
<td>-10.30</td>
<td></td>
<td>34.123</td>
<td>100.0</td>
</tr>
<tr>
<td></td>
<td>BσH</td>
<td>-27.99</td>
<td>5.41</td>
<td>10.81</td>
<td>1.91</td>
<td>-5.81</td>
<td></td>
<td>34.094</td>
<td>99.9</td>
</tr>
<tr>
<td></td>
<td>I3</td>
<td>-40.70</td>
<td>1.66</td>
<td>1.18</td>
<td>10.29</td>
<td>-4.95</td>
<td></td>
<td>33.872</td>
<td>99.5</td>
</tr>
<tr>
<td></td>
<td>BσH</td>
<td>-27.94</td>
<td>5.89</td>
<td>10.29</td>
<td>1.52</td>
<td>33.342</td>
<td></td>
<td>97.7</td>
<td></td>
</tr>
<tr>
<td></td>
<td>I4</td>
<td>-41.08</td>
<td>1.61</td>
<td>1.52</td>
<td>13.27</td>
<td>30.250</td>
<td></td>
<td>88.6</td>
<td></td>
</tr>
<tr>
<td></td>
<td>BσH</td>
<td>-28.20</td>
<td>6.07</td>
<td>1.81</td>
<td>14.09</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>I5</td>
<td>-42.08</td>
<td>1.81</td>
<td>1.81</td>
<td>14.09</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>BσH</td>
<td>-28.66</td>
<td>14.09</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Col2-Tar1</td>
<td>I4</td>
<td>-17.66</td>
<td>0.60</td>
<td>2.22</td>
<td>6.85</td>
<td>8.81</td>
<td></td>
<td>22.877</td>
<td>99.8</td>
</tr>
<tr>
<td></td>
<td>BσH</td>
<td>-9.68</td>
<td>2.90</td>
<td>22.60</td>
<td>2.91</td>
<td>5.16</td>
<td></td>
<td>22.717</td>
<td>99.1</td>
</tr>
<tr>
<td></td>
<td>I5</td>
<td>-17.70</td>
<td>1.70</td>
<td>3.95</td>
<td>8.74</td>
<td>5.12</td>
<td></td>
<td>22.517</td>
<td>97.3</td>
</tr>
<tr>
<td></td>
<td>BσH</td>
<td>-9.70</td>
<td>22.16</td>
<td>1.68</td>
<td>5.12</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>I6</td>
<td>-1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>BσH</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Col2-Tar1</td>
<td>I7</td>
<td>-17.64</td>
<td>2.12</td>
<td>9.56</td>
<td></td>
<td>22.676</td>
<td></td>
<td>98.9</td>
<td></td>
</tr>
<tr>
<td></td>
<td>BσH</td>
<td>-9.67</td>
<td>21.61</td>
<td>5.16</td>
<td></td>
<td>22.311</td>
<td></td>
<td>97.3</td>
<td></td>
</tr>
<tr>
<td></td>
<td>I8</td>
<td>-17.70</td>
<td>1.74</td>
<td></td>
<td></td>
<td>20.244</td>
<td></td>
<td>88.3</td>
<td></td>
</tr>
<tr>
<td></td>
<td>BσH</td>
<td>-9.71</td>
<td>17.74</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>I9</td>
<td>-1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>BσH</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ram2-Col2-Tar1</td>
<td>I1</td>
<td>-26.78</td>
<td>0.95</td>
<td>1.66</td>
<td>3.33</td>
<td>-3.57</td>
<td></td>
<td>25.476</td>
<td>100.0</td>
</tr>
<tr>
<td></td>
<td>BσH</td>
<td>-18.45</td>
<td>4.16</td>
<td>15.85</td>
<td>1.32</td>
<td>-2.18</td>
<td></td>
<td>25.455</td>
<td>99.9</td>
</tr>
<tr>
<td></td>
<td>I3</td>
<td>-26.64</td>
<td>0.86</td>
<td>1.59</td>
<td>14.84</td>
<td>-3.68</td>
<td></td>
<td>25.017</td>
<td>98.2</td>
</tr>
<tr>
<td></td>
<td>BσH</td>
<td>-16.38</td>
<td>3.75</td>
<td>15.19</td>
<td>1.60</td>
<td>-2.25</td>
<td></td>
<td>20.016</td>
<td>78.6</td>
</tr>
<tr>
<td></td>
<td>I6</td>
<td>-1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>BσH</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*Efficiency is expressed as a percentage of the efficiency obtained by including all six traits. R_{IH}σH values for indexes I1 are 34.123, 22.926, and 25.476 for the Ram2, Col2-Tar1, and Ram2-Col2-Tar1 groups, respectively.
Indexes $I_5$ also could be used with only a small additional decrease in efficiency. However, eliminating three traits to obtain indexes $I_4$ does not decrease efficiency as much as the further elimination of a single trait to obtain $I_6$. Either indexes $I_4$ or indexes $I_5$ could be used with considerably more facility in the field than indexes $I_1$. All would be relatively high in efficiency as compared to indexes $I_6$.

(a) Progress to be expected using indexes $I_4$. Inasmuch as indexes $I_4$ seem to be almost as effective as indexes $I_1$, it would be desirable to know the progress one might expect from selection on a basis of only the three traits in indexes $I_4$. In the case of the $R_{am_2}$ and $R_{am_2}-C_{ol_2}-T_{ar_1}$ indexes, selection would be based on face cover, staple length, and weaning weight. For the $C_{ol_2}-T_{ar_1}$ index, selection would be based on face cover, weaning weight, and condition. The expected selection differentials and genetic changes are listed in Table 16. As before, the expected values are subject to the conditions that selection is wholly on the basis of $I_4$ and that the $I_4$ values are distributed approximately normally.

A comparison of Tables 16 and 14 revealed that, in most instances, only insignificantly less progress can be expected from selecting on the basis of $I_4$. The most outstanding difference is in the genetic decline expected in staple length in the $C_{ol_2}-T_{ar_1}$ group. This decline will occur almost three times as rapidly using $I_4$ as it will using $I_1$. This probably occurs because selection for staple length, which opposes improvement in weaning weight, has been relaxed in index $I_4$. Note that there is a compensating increase in the expected genetic gain for weaning weight.

Finally, it is evident that with the exception of staple length in the $C_{ol_2}-T_{ar_1}$ index, improvement in the traits omitted from the indexes is
expected to be nearly as rapid when they are omitted as when they are included. This seems to be attributable primarily to the positive response of these traits to selection for the traits with which they are correlated. It serves to emphasize further that such traits contribute negligibly to the index.

Table 16. Expected Selection Differentials and Expected Genetic Changes for Individual Traits, Omitting from each Index the Three Traits Contributing Least to its Efficiencya

<table>
<thead>
<tr>
<th>Trait</th>
<th>Selection differential</th>
<th>Genetic change</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Ram₂ Col₂-Tar₁ Col₂-Tar₁</td>
<td>Ram₂ Col₂-Tar₁ Col₂-Tar₁</td>
</tr>
<tr>
<td>Face cover (score)</td>
<td>-0.61 -0.35 -0.49</td>
<td>-0.48 -0.17 -0.29</td>
</tr>
<tr>
<td>Staple length (16ths in.)</td>
<td>1.27 0.31 1.24</td>
<td>0.36 -0.37 0.12</td>
</tr>
<tr>
<td>Weaning wt. (pounds)</td>
<td>4.36 9.09 6.96</td>
<td>1.74 3.82 2.55</td>
</tr>
<tr>
<td>Body type (score)</td>
<td>-0.13 -0.19 -0.18</td>
<td>-0.05 -0.02 -0.05</td>
</tr>
<tr>
<td>Condition (score)</td>
<td>-0.19 -0.28 -0.28</td>
<td>-0.10 -0.06 -0.09</td>
</tr>
<tr>
<td>Folds (score)</td>
<td>-0.19 -0.01 -0.08</td>
<td>-0.08 0.01 -0.05</td>
</tr>
</tbody>
</table>

aResults are based on a selection differential of one standard deviation in index (I) values. Indexes I₄ (cf. Table 15) were used in each case.
VI. DISCUSSION

A. General Considerations

It seems appropriate to discuss briefly three pertinent considerations which confront the animal husbandman who is planning to select on the basis of a weanling index. First, he must decide upon which traits to include in the index. Second, he must decide how much of his total freedom to select is to be expended using the weanling index and how much, if any, is to be reserved until he can use a more efficient index, for example, a yearling or two-year-old index. Finally, he should be aware that selection which is effective in changing the population also will alter the biological parameters upon which the selection index is based.

1. Traits which should be included in an index

To make an effectual choice of traits for a selection index, one should have clearly in mind what characteristics of the breeding animal's production make that production economically important. The value of a sheep's fleece, for example, depends upon three principal and several subordinate characteristics. The principal characteristics (or attributes) are quantity of clean wool, average staple length, and average grade of wool (fiber fineness). Each of these contributes uniquely to the market value of the fleece. Other characteristics such as variability of fiber fineness, variability of staple length, unscourable paint content, burr content, and wool "character" also have distinct but less tangible and
less important influences upon fleece value. Paint and burr content, of course, are not biological attributes of the animals themselves and have no effect upon breeding value.

It is logical to include in an index as many as possible of these biological attributes (i.e., traits) which affect over-all breeding value directly. Naturally, some traits cannot be included because they are expensive, difficult, or impossible to evaluate at the time of selection. Frequently, however, one can evaluate at that time other traits which, although having no direct effect upon breeding value themselves, are correlated genetically with the unevaluated traits that do. Such traits can be substituted in the index in lieu of the more important ones which cannot be included. An example of this in sheep is face cover, which is correlated with pounds of lamb weaned. Such traits also may be included profitably even when the more important traits can be evaluated, if the evaluation (of the important traits) at the time of the selection is not very precise. The genetically correlated trait then serves, in effect, to improve or correct the evaluation of the trait having a direct value.

Of course, the ultimate decision to include or discard a trait depends upon its contribution to the efficiency of the index. Although properly considered traits can never decrease the efficiency, they may contribute little or nothing to it. The size of any contribution depends upon the trait's phenotypic correlation with over-all breeding value and with other traits which are in the index. If the correlation with over-all breeding value is low, the trait is likely to be of little use. If the phenotypic correlations with other traits are low, the trait may be more useful (other things being equal) than if the correlations are high. The
heritability of a trait will provide some indication of whether or not its correlation with over-all breeding value is likely to be low. This will by no means be conclusive, however. If a trait has a high relative economic value and is closely correlated genetically with other traits of high economic importance, it may have an appreciable correlation with over-all breeding value even when heritability is not high.

The most reliable and precise information about the usefulness of a trait can be obtained by actually including it in the index. Its unique contribution to the efficiency of the index may then be determined as described earlier in this dissertation. If it adds nothing to the efficiency, it is simply an encumbrance and should be discarded.

2. Latitude for subsequent selection

The economics of the range sheep industry requires that the initial selection of replacement stock be made at weaning age, when some of the traits are less closely correlated with over-all breeding value than they would be if the selected animals were older. It seems expedient, therefore, to reserve some latitude for additional selection to occur at a time when the traits are more highly correlated with breeding value. Selecting by index will accomplish this automatically to some extent (provided that extra replacements are retained at weaning time) by preventing intensive selection for any particular trait to the complete exclusion of other traits. Even the index, however, may emphasize some traits much more heavily than others.

One should not ignore the possibility that, as maturity approaches, changing phenotypic and genetic expressions may cause the optimum emphasis
upon the traits to change notably. If the initial selection exhausted one's total freedom to select, nothing can be done about culling animals whose inferior breeding values become more obvious at maturity. The question is, then, how much of the total freedom to select should be reserved for selection subsequent to weaning and when should that subsequent selection occur. The answer hinges upon the efficiencies of the indexes which could be developed for selection at later periods, for example, at eighteen months or at two years of age. It also depends upon the cost of maintaining surplus animals until that later selection occurs and upon any losses involved in marketing culled animals which are no longer lambs. Unfortunately, the question cannot be answered satisfactorily until indexes suitable for selection at later periods have been developed and their efficiencies determined.

Finally, the progressive breeder will be aware that opportunity for improvement does not end with the culling of those lambs not required for replacements. The opportunity still remains to select intensively (among the animals chosen as replacements) for those animals needed to renew what one might describe as the "replacement" flock.* This flock would be composed of the best ewes (randomly mated to the best rams) in the entire herd and likely would produce most of the lambs chosen as replacements. Selection would be unnecessary until the replacement animals entered the breeding herd at the age of eighteen months. Then, it could be based upon an index which would have the advantage of incorporating all the information

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*Somewhere between 30 and 45 per cent of all animals chosen as replacements would be required for this purpose in most range herds.
tion provided by the weaning index as well as unique and more accurate information of its own.

3. Effective selection changes parameters

It is noteworthy that effective selection can change biological parameters to the extent that selection indexes which have been in use for prolonged periods no longer have maximum efficiencies. This is likely to be of most concern when the indexes emphasize one or two traits much more heavily than others. If the expected genetic gain for a particular trait is large, some parameters involving that trait may change enough to justify recalculating the index after a relatively few animal generations.

In view of the prominent role that heritability plays in determining the correlation between each trait and over-all breeding value, perhaps changes in heritability are among the most important to detect. Changes in heritability probably would occur slowly (Lush, 1948) unless a threshold of expression was involved or unless most of the genetic variability was caused by only a few genes and selection was intense. Appreciable changes in the means would be important, also, for those traits having non-linear effects on production and income. Changes in the means would be among the most pronounced changes which would occur.

In this study, the changes most likely to be important are those involving the relative economic value of face cover. The expected genetic improvement in face cover is large enough in the Ram2 group that the mean can change rather rapidly under intense selection. Because face cover has a distinctly non-linear effect on production, an appreciable improvement in its mean will appreciably reduce its relative economic value.
B. Limitations

Certain limitations of a more specific nature than those already discussed in the section on analytical methods should be mentioned in connection with the indexes developed in this investigation. These are discussed in the following paragraphs.

1. Accuracy of the basic statistics

It is clear that the usefulness of the indexes will depend to a great extent upon the accuracy of the statistics from which they are constructed. It seems important, therefore, to know which of the basic elements are most likely to be in error and, if possible, how seriously the errors will affect the usefulness of the indexes.

The areas of greatest uncertainty surround the estimates of genetic correlations and relative economic values. Fortunately, there will be a tendency for random errors in these estimates to cancel one another because of their linear relationship in the phenotypic correlation between each trait and breeding value. Consequently, such errors seem less likely to be serious than those affecting estimates of heritabilities, provided the index contains enough traits to permit the cancelling to be effective.

The estimates of genetic correlations can be improved simply by obtaining a larger amount of data. Four times the present amount would reduce sampling errors approximately one-half, but even this reduction would leave many estimates with relatively large standard errors (cf. Table 9). The most serious weaknesses in the estimates of relative economic
values involve information about the genetic relationships between the weanling traits and the traits contributing directly to breeding value. Additional research must be completed before these estimates can be improved.

2. Adequacy of the indexes

Thus far, little has been said about the adequacy of the indexes as a whole. Unfortunately, little can be said, in this study, about the sampling errors of the various $b$ values constituting each index and about the efficiency of each index relative to a perfect knowledge of each animal's breeding value. This information is lacking because of the previously mentioned (page 71) inability to estimate the standard deviation in over-all breeding value. After considering information about the efficiencies of various other selection indexes and that the traits in the weanling indexes are not mature traits of the animals, the efficiencies of the weanling indexes are presumed to be somewhere between 25 and 40 per cent. Undoubtedly, there is considerable room for improvement.

Although fleece weight and grade (fineness) are important components of over-all breeding value, neither trait appears in the indexes. If included, these traits might make worthwhile contributions. Information on fleece weight is almost never available, for economic reasons, until several months after weanling selections have been made. Thus, it would be difficult to include information about the lamb's own fleece weight. However, information about the records of the dam (and, in some cases, the
sire) could easily be obtained. Including information about the dam's*
production would be at least one-half as effective as including the lamb's
own record. It could be even more than one-half as effective, since mature
fleece weight is likely to be more closely correlated with over-all breed-
ing value (particularly if several records are available) than weanling
fleece weight.

Unfortunately, fleece grade at weaning age is not highly correlated
with fleece grade at maturity (Pohle, 1942). Neither is fiber density
(which is closely correlated with grade) at weaning age highly correlated
with that at maturity. Including weanling information on these traits may
have little value. Hence, including the dam's record for such traits
might be especially useful.

The low heritabilities of body type, condition, and type of birth
indicate that mass selection for these traits is likely to be rather
ineffective. Lush (1947) has pointed out that family selection may be
used effectively to supplement mass selection provided that the average
coefficient of relationship (r) among members of the family is appreciably
higher than the average phenotypic correlation (t) among those members.
It would be difficult in sheep to obtain families of useful size with
relationships much higher than those of half-sibs (r = 0.25), unless con-
siderable inbreeding had occurred.

The phenotypic correlation among non-inbred half-sibs equals one-
fourth of heritability in the narrow sense plus other components caused by
environmental and non-additive genetic effects which are the same for

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*Including the dam's record would be more desirable than including
the sire's because dams would be less highly selected than sires and
selection differentials could be larger.
members of the same family but different for members of different families. These other components will contain none of the variance due to dominance and less than one-sixteenth of that due to epistasis. The component due to environmental effects probably will be negligible for paternal half-sibs and small for maternal half-sibs. Thus, the phenotypic correlations (t) is likely to be only slightly, if any, larger than one-fourth of heritability as it has been estimated in this study. For body type, t will be near 0.05 in each case; for type of birth, it will be as low as 0.025 in Ram₂ families.

By using the formula

\[ \sqrt{1 + \frac{(r-t)^2}{1-t}} \cdot \frac{n-1}{1 + (n-1)t} \] (Lush, 1947)

where n equals the size of the family, one can estimate the improvement which would result from supplementing individual with family selection. For body type, the improvement would be less than 8 per cent if only five half-sibs were included and about 27 per cent if fifty half-sibs were included in the family average. For type of birth in the Ram₂ group, the improvement would be less than 11 per cent if only five half-sibs were included and about 47 per cent if fifty were included. For condition, the improvement would be even less than that for body type inasmuch as t would be somewhat larger than 0.06 in this case. In view of the small contributions which these traits make to the index via mass selection, it is doubtful that including information about family averages would justify the extra labor and expense involved.
3. **Non-linear effects**

The indexes as presently constituted are aimed entirely at selection for additive genetic differences. The low heritabilities of the traits mentioned above indicate that non-linear genetic differences might be important for these traits. Of course, heritabilities could be low in these cases chiefly because of large environmental variations. In that event it would be important to exercise more effective control over environmental factors than was accomplished in this investigation, but selection would continue along the present pattern. If, however, heritabilities are low because epistasis or over-dominance is important, the present method of selection based entirely on additive genetic differences is inefficient for these traits. For example, the relative economic values, which at present are conditioned by the size of the (additive) genetic standard deviation of each trait, could be much larger for these traits thus leading to greater emphasis upon them.

It would still be desirable to include all traits in a selection index under any new plan of selection, since that would still be the most effective method of determining the optimum emphasis for each trait. The procedure for accomplishing this when selecting for non-additive differences (such as those causing specific combining abilities, for example) would have to be developed. Although the most expedient course of action is veiled by the uncertainty surrounding the cause of the low heritabilities, one significant fact is clear. Selection for traits influenced greatly by epistasis and overdominance will be relatively ineffective under
the present plan, and additional research is needed to determine a more effective arrangement.

C. Applications

At the conclusion of an investigation of this nature, two important questions arise. First, to what extent can the results be applied throughout the general area from which the data were obtained? Second, how can the results be applied most advantageously under the circumstances for which they are appropriate?

1. Extent of general applicability

In an attempt to determine how wisely one might safely generalize on the results, it seems advisable to consider how the conditions of this investigation typify or fail to typify those on other range sheep enterprises. Management methods in general were typical of those on many sheep ranches in Utah, Idaho, Wyoming, and Oregon where it is customary to graze the high mountain ranges in the summer and the lower desert ranges during the winter. A few unique features made them atypical in some respects, however.

Few range sheepmen provide the meticulous care and supervision which characterizes the lambing period at the Utah station. This occurs because some sheepmen choose not to do so and because others do not have the facilities to do so. Consequently, the indexes may give more emphasis to lamb production and less to wool production than would be desirable for enterprises on which the percentage of lambs weaned is much less than 100 per cent.
The accuracy and intensity of selection practiced on the Utah station herd is probably higher than that generally practiced on range herds in the Intermountain area. Presumably, this would reduce the general applicability of estimates of phenotypic and genetic parameters very little, inasmuch as the lambs on which the estimates were based were themselves unselected. The estimates, in most cases, are comparable to those obtained at the Western Sheep Breeding Laboratory (Dubois, Idaho). Management and environmental conditions there resemble those at the Utah station in most, although not all, respects. It seems reasonable to assume that estimates which might be obtained from many range herds in central and southern Utah, where sheepmen have been influenced greatly by practices at the Utah station, would be at least as comparable as those obtained at the Western Sheep Breeding Laboratory.

Still another point of departure from the more usual conditions occurs in summer range management. Because the summer range is fenced, it is unnecessary to herd the Utah station sheep during the summer months. This may have noticeable effects on the mean and phenotypic variability of such traits as weaning weight and condition but is unlikely to influence folds and face cover appreciably. A good herder can keep his sheep on fresh, succulent feed at all times; whereas ewes and lambs left undisturbed often remain in certain preferred areas even after the natural forage has been depleted in those areas. On the other hand, a herder can cause considerable distress among the lambs by habitually "bunching" his herd, thus separating lambs from their mothers. Such a procedure can be especially detrimental when the range is steep, rugged, and cut up into many small canyons. On ranges where water is scarce, a herder may inadvertently keep
his herd away from water too long; or he may trail weight and condition off the lambs by watering too often. It is evident that differences between effects caused by herding and those caused by non-herding would depend a great deal upon the herder, the nature of the range, and the proximity of water. The differences could be considerable under some circumstances and negligible under others.

After taking other pertinent factors such as relative economic values into consideration, it seems prudent to limit the applicability of the results, in the strictest sense, at least to herds in the following categories: (1) those in which the average per cent of lambs weaned annually is near or above 100 per cent; (2) those in which the breeding is predominantly Rambouillet or of Rambouillet origin; (3) those in which little or no inbreeding has occurred; and (4) those in which the mean and variation of each trait (particularly face cover and weaning weight) are reasonably comparable to the estimates obtained in this investigation.

Whether the findings actually are typical of any large number of range herds is unknown. The general similarity between estimates of biological parameters at the Utah station and at the Western Sheep Breeding Laboratory suggest that they might be.

2. Practical applications under range conditions

In order that the indexes might be used to the greatest advantage under practical conditions, the following applications are suggested:

The most progressive principles of animal husbandry require that lambs receive individual attention during and for a short period after the time of birth. In the light of the usual limitations characterizing the
majority of range operations, it seems most feasible to identify the lambs with regard to the particular environmental factors (such as type of birth, age of dam, etc.) which will affect them, at that time. Lambs can be identified with ear-tags containing (1) a code number for environmental effects and (2) an individual lamb number. The environmental code can easily be constructed so that lambs subjected to an identical group of environmental effects could be given the same code number.

At weaning time, lambs would be scored and measured for the three characteristics in the appropriate index $I_4$, and a separate index value would be computed for each lamb. The index values would then be sorted into various groups each of which would be characterized by animals having the same code number. An equivalent proportion of individuals having the highest index values would be selected from each code group. Selection would thus be unaffected by the various environmental factors encompassed by the code. In addition, the extent and complexity of the computations would be held to a minimum—an important consideration under practical conditions.

If it were not possible actually to compute the indexes for each animal, the lambs themselves could be segregated into groups on the basis of their code numbers. In this event ear-tags would be unnecessary, since code numbers easily could be paint-branded on each lamb. Such a procedure would have the advantage of expediting recognition and separation of lambs. Selection might then be made within each code group by visual inspection, choosing the same proportion of lambs from each group, as above. The person making the selections should keep in mind the relative importance of each trait as indicated by indexes $I_5$ or, if possible, by $I_4$. 
It is unlikely that visual selection under these circumstances could approach the accuracy of that based on actual computation of index values. Nevertheless, it would be distinctly superior to less well-defined selection under circumstances in which no adjustments for confusing environmental effects had been made.
A perplexing problem in selecting breeding stock is how much importance to attach to each of the several biological traits which contribute to an animal's breeding value. The present investigation was aimed at constructing selection indexes in which information about weaning traits could be used with maximum efficiency to predict the breeding values of range lambs.

Data were available on 1,080 unselected Rambouillet (Ram2), Columbia (Col2), and Targhee (Tar1) lambs of mixed ancestry reared near Cedar City, Utah, on mountain ranges owned by the Utah Agricultural Experiment Station. Among the seven traits observed on each lamb, staple length and weaning weight were measured, whereas type of birth was recorded as single or twin. Face cover, body type, condition (fatness), and skin folds were scored, using a scale ranging from 1 for most superior to 5 for most inferior lambs. Superior lambs had long staples, high weaning weights, open faces, good mutton conformation (body type), high condition, no skin folds, and were born as twins.

Environmental and physiological effects for which the traits were corrected were year, age of dam, type of rearing, sex, breeding, and age of lamb. The traits which appeared to be least influenced by these effects (Tables 4, 5, 6, and 7) were face cover and folds. The trait most influenced was weaning weight.
Phenotypic correlations (Table 8) between folds and weaning weight, folds and body type, and folds and condition in the Ram₂ lambs were the only phenotypic correlations which indicated impediments to improving all traits simultaneously.* The traits by far most highly correlated with one another phenotypically were weaning weight, body type, and condition.

Genetic correlations (Table 9) between weaning weight and staple length and between weaning weight and folds indicated that simultaneous genetic improvement in these traits would be obstructed to some extent. The largest genetic correlations (all positive with regard to merit) were those between body type and condition, weaning weight and condition, and staple length and folds.

Heritability of face cover, folds, staple length, and weaning weight in each group of lambs was sufficiently high to make mass selection for these traits reasonably effective (Table 10). Because of the low heritabilities of condition, body type, and type of birth (Tables 10 and 11), mass selection for these traits seemed likely to be only slightly effective.

Although the evidence was not entirely conclusive, weaning weight seemed to be the trait of greatest economic importance (Table 12). It was several (four to nine) times more important than body type, condition, folds, and type of birth, all of which seemed to be roughly equivalent in economic importance. Face cover was about equal in importance to weaning weight in the more wool-blind Ram₂ lambs but was of much less importance than weaning weight in the more open-faced Col₂ and Tar₁ lambs. Staple

*Estimates of phenotypic and genetic correlations involving type of birth were not obtained.
length was approximately twice as important economically as body type, condition, folds, and type of birth but less than half as important as weaning weight.

To achieve maximum efficiency in estimating over-all breeding value, using the six traits for which complete information was available, one should place the following relative emphasis upon one standard deviation in each trait (emphasis is relative to that for weaning weight):

1. For Ram₂ lambs—face cover, -2.589; staple length, 0.592; weaning weight, 1.000; body type, 0.176; condition, -0.519; folds, -0.002.

2. For Col₂ and Tar₁ lambs—face cover, -0.409; staple length, 0.117; weaning weight, 1.000; body type, 0.129; condition, 0.232; folds, -0.070.

The only trait in which a genetic decline was expected as a result of using the indexes was staple length in the Col₂ and Tar₁ lambs. This decline was expected to be so gradual, however, that the indexes would probably need to be recalculated for other reasons before it became important. Genetic improvement (Tables 14 and 16) was expected to be substantial for weaning weight and face cover in each group of lambs. It was expected to be relatively unimportant for the remaining traits.

Including information on type of birth seemed unlikely to increase the efficiencies of the indexes significantly. Omitting folds, body type, and condition from the Ram₂ index and folds, staple length, and body type from the Col₂-Tar₁ index did not reduce appreciably the efficiency of either index (Table 15). However, the genetic decline in staple length of Col₂ and Tar₁ lambs was expected to occur about three times more rapidly (for the same intensity of selection) under these circumstances.
The information most needed to improve the reliability of the indexes in their present form was (1) more accurate evidence concerning the magnitudes and signs of the genetic correlations and (2) more precise information about the relative economic importance of each trait. The additional information most needed to improve the efficiency of the indexes in predicting over-all breeding value was that concerning fleece weight and grade.

General applicability of the results seemed to be restricted to herds characterized as follows: (1) herds in which the annual weaning percentages are near or above 100 per cent; (2) herds in which the breeding is predominantly Rambouillet or of Rambouillet origin; (3) herds in which little or no inbreeding has occurred; and (4) herds in which the mean and variation of each trait (particularly face cover and weaning weight) are reasonably comparable to the corresponding estimates obtained in this investigation.

The indexes were expected to be most helpful under the more usual range conditions if lambs were segregated at weaning age into separate groups in each of which the important environmental and physiological effects (such as age of dam, type of rearing, etc.) were the same for all members. An equivalent proportion of individuals would then be selected from each group, emphasizing one standard deviation in each of the three most important traits (in each index) as follows:

(1) For Ram₂ lambs--face cover, -2.125; staple length, 0.457; and weaning weight, 1.000.

(2) For Col₂ and Tar₁ lambs--face cover, -0.447; condition, 0.259; and weaning weight, 1.000.

Selection might be accomplished with reasonable accuracy under these circumstances on a visual basis, although such selection is not likely to be as effective as that based on index values calculated arithmetically.
VIII. LITERATURE CITED


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