

THE SHEPHERD

A GUIDE FOR SHEEP AND FARM LIFE

Volume 39-Number 7

July, 1994

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Simplified Principles of Selection

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Selection is the force which has induced changes in all creatures from the beginning of creation until now. How present-day animals will evolve in the future depends on what kind of selection done by the breeder and by nature. If the breeders practice no selection, nature may do it for him, but they cannot predict the outcome. Natural selection, is responsible for many of the characteristics of the present-day animals. Even after breeders have selected for a specific objective, if their effort is not maintained, nature usually reverts the change achieved back to where they started.

Breeders practice a kind of selection based on the animal's appearance. When a breeder eliminates animals with under- or over-shot jaws, twisted legs, colored spots, and some other traits considered as faults in certain breeds, despite their merit as breeding animals, he is selecting against defects. These defects may be associated with recessive genes, and the breeder gradually eliminates these genes from the flock. Many breeders also practice selection based on visual assessment of easily measurable traits such as size and fibre quality.

Several factors determine the success and effectiveness of a selection program. The first is to know if the character to be selected for responds to selection or not and to what degree. Selection for a character controlled by one or a few genes (geneticists call them qualitative to distinguish them from those controlled by many genes and are called quantitative characters) is very effective. Continuous selection of rams without horns, noticeably reduces the number of horned animals and, if selection is also applied on females, the breeder may end up with a hornless flock. The same thing happens when selection is made for colour, or soundness of teeth.

However, most of the economically important traits in livestock are quantitative traits controlled by numerous genes, each contributing a small effect. Improvement as a result of selection is rather slow. In quantitative traits, the genetic component of the trait is important. To explain that, consider the trait a breeder can measure, as the result of

two components, its genetic make-up and the effect of environment. The genetic make-up, i.e., the genes inherited, is fixed at conception and is derived from the two parents. The environment affects the degree of expression of this genetic make-up. For example, if the genetic potential of weaning weight is 20 kg, the lamb that receives ample milk from the dam and enough creep feed to maximize growth would attain that or close to that limit. On the other hand, if that same animal receives less than adequate feeding, suffers from diseases or any other factor affects its growth, the weight would definitely be less than the 20 kg predetermined by genetics. So environment, whether in the form of nutrition (quantity and quality of feed), management (different types of stress or lack of it), or climate (extreme heat, cold dampness, or dryness), profoundly affects the degree of expression of the trait, and, accordingly, the ability to make the right selection decisions.

The environment plays such a great role that in some quantitative traits it may hide the potential predetermined by the genetic make-up of the individual. Traits of reproduction such as fertility, litter size, and lamb mortality are examples of such traits. On the other hand, performance in traits such as wool production, fibre characteristics, and carcass traits is almost equally determined by the genetic make-up and the environmental effects. Growth traits fall between these two categories.

A measurement for evaluating the genetic component of each trait is called "heritability." It measures the proportion of the genetic component of the total variation observed. If heritability is zero for a trait, the breeder will lose time and effort trying to select for it. The higher the heritability, the more effective and fast the response to selection would be. The general idea behind heritability estimates is to determine the amount of variation existing between relatives such as sibs, and parent-offspring as a ratio of the total variation existing between animals of that population. Therefore, heritability may change from breed to breed and even from flock to flock within the same breed. Ideally breeders should calculate the heritability of the traits of interest from the animals of their own flocks. But, since calculating heritability is complicated, and requires a large number of animals, use of average estimates from the literature of studies conducted in the past provides the second best alternative. The breeder can use the average estimates, presented in Table 1, for some of the economically important traits often considered in selection programs.

The other important factor is the "variation." If all lambs weigh 20 kg at weaning, it is impossible to choose parents that would increase weaning weight. So, before we can induce change, there must be variation, because selection simply means that breeders choose the best parents for specific traits to produce the next generations.

To illustrate the concept and measurements of variation, an example is presented in Table 2 for corrected weaning weight of lambs in three flocks. The use of the word "corrected" is intentional since the breeder should, before practicing selection, correct the records to a standard basis. For example, they should adjust for the influence of factors such as age of dam, type of birth, type of rearing, season of birth, and age at weaning, which, among others, have significant effects on weaning weight of

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a lamb. Procedures for correcting records vary in complexity. The simplest procedure is to get the averages for the different levels within the factors, for example, males and females or singles and twins; then calculate the difference and adjust female and twin records to male and single equivalent by adding the difference to each record. More complex methods consider several factors which are considered simultaneously, for example, sex and type of birth of lamb and age of dam all at the same time.

Although in the three flocks mean weaning weight of the lambs is 20 kg, the flocks show great differences in variation (see range in Table 2). The simplest way to measure variation is to calculate the difference between the smallest and largest measurements. Although the method is simple, its disadvantage is that any extreme value increases the range tremendously. Better measurements which take into account all the observations are called "mean deviation" and "standard deviation." Mean deviation is simply calculated by adding the difference between each observation and the mean (ignoring the sign or otherwise the result would be 0), then dividing by the number of observations. For flock 1, this would be $1 + \frac{1}{2} + 0 + 0 + \frac{1}{2} + 1 = 3$ divided by $6 = \frac{1}{2}$, similarly for flock 2 it would be 2.33 and for flock 3, 4. Standard deviation is similar to mean deviation but, instead of ignoring the sign, each deviation is squared, all squared deviations added and averaged by dividing the total by the number of animals less one. The next step is to calculate the square root of the average obtained. For our first flock the standard deviation is $1 + \frac{1}{4} + 0 + 0 + \frac{1}{4} + 1 = 2\frac{1}{2}$, $2\frac{1}{2} \div 5 = 0.5$, $\sqrt{0.5} = 0.71$. All these methods, regardless of their complexity, show flock 3 to be more variable than flock 2 which, in turn, is more variable than flock 1.

If the objective is to improve weaning weight in the three flocks by selecting only one male to mate all the females, the obvious choice is to select the male with the heaviest weight at weaning, those weighing 21, 24, and 26 in flocks 1, 2, and 3, respectively. Needless to say, the ram in flock 3 will give his progeny more potential for heavier weights than rams chosen in flocks 1 and 2. The difference between the value of the selected ram and the average of all those available for selection is called "selection differential." In the above cited example these differentials are 1, 4, and 6 kg, respectively.

Table 1. Estimates of heritability from the literature (percent genetic to total variation)

Trait	Heritability estimates	Trait	Heritability estimates
Fertility	3	Lamb survival	10
Prolificacy	14	Grease fleece weight	58
Date of first heat	42	Clean fleece weight	56
Date of lambing	18	Staple length	53
Age at first lambing	31	Resistance to cold	70
Birth weight	28	Total milk yield	53
Weaning weight	20	Ewe productivity	27
Yearling weight	46	Kidney fat percent	53
Mature weight	53	Dressing percentage	25
Lambing interval	6	Carcass lean percent	35

Table 2. Weaning weight of lambs in three hypothetical flocks

Flock	Weaning weight of six lambs for selection						Mean	Range
1	19	19½	20	20	20½	21	20	2
2	16	18	19	20	23	24	20	8
3	13	16	19	21	25	26	20	13

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In the example, only the best male was selected; in practice the breeder usually needs to select more than one male to avoid inbreeding and in large flocks to service a large number of females. If selection differential is recalculated selecting two males, the selection differential will be lower than when selection was for only one male (because the second best male is inferior). Thus, by increasing the number of selected, the selection differential decreases which decreases the selection pressure applied. One important point to remember when calculating selection differential—only consider the animals actually available for selection, because if the best male is already dead, or infertile, there is no point in considering him in the calculations.

To calculate the theoretical outcome of selection, assuming again that the average of the flocks is 20 kg, first, divide selection differential by 2 because sires contribute only half the genetic make-up of the progeny (the other half comes from the dam). This calculation gives us selection differential of 1/2, 2, and 3 kg, respectively. Because the selection applied was based on the phenotype value, which as mentioned earlier is part genetic and part environmental, selection differential should be multiplied by the genetic portion, i.e., by the heritability. Assuming that heritability of weaning weight is 40%, the genetic gain in weaning weight of the progeny to be expected from selection is 0.2, 0.8, and 1.2 kg, in the three flocks, respectively.

If selection is also applied on the females using the same principles, the selection pressure and, accordingly, selection response may be increased. For example, if Table 2 also represents the weaning weights of females and only the heaviest half is selected for replacement. The selection differential for the females would be, 1/2, 2.3, and 4 kg in the three flocks, respectively. Divide each selection differential by 2 and multiplying it by 0.4 (as for the males) to arrive at 0.1, 0.46, and 0.8 kg, for the three flocks, respectively. So, if selection for weaning weight were applied on both males and females, the genetic improvement expected in progeny of the next generation would be 0.3, 1.25, and 2.0 kg more than the average of their parental generation, assumed in this example to be 20 kg. As a result of many factors, such as inability to obtain accurate measurements or use representative heritability estimates, the observed and expected gain seldom correspond.

In choosing weaning weight as an example, the simplest and easiest scenario was presented, the trait is manifested in both sexes and the animals are weaned only once in their life. The situation is more complicated when the trait appears in only one sex (such as in selecting for litter size), or the trait requires killing the animals (such as in selecting for carcass traits), or many records exist for each animal (such as in selecting for wool production).

As a rule, when a character can be measured repeatedly, the breeder can make a more accurate choice as the number of records increases, in most cases, averaging many records decreases environmental variation and may result in higher heritability estimates for the trait. To estimate the *breeding value* (g, the true hereditary value an animal can transmit to his progeny) of an animal with several records from the flock mean, multiply the deviation of the average of all the records from the flock mean (d) by the heritability (h^2) and then by [No. of records (n)] ÷ [1+(No. of records-1) x repeatability (r)].

$$\text{i.e., } g = d \times [(h^2 \times n) / [1 + (n-1) \times r]].$$

Repeatability (r) most simply defined, is the correlation between the different records. In case of wool production, for example, it is the correlation between first and second fleece weights. Given a third fleece weight, it is the average between the three possible correlations (1 and 2, 1 and 3, and 2 and 3). Repeatabilities are usually higher than heritability and preferably should be calculated for each specific flock. However, many estimates are available in the literature for most of the important traits.

To illustrate the impact of multiple records, assume heritability is 30% and repeatability is 0.6 in a flock with an average of 40. If the selected animal had three records averaging 43, its breeding value is $(3 \times 3) \times [3 \div (1 + 2 \times 0.6)] = 1.227$. This value is higher than 0.9 calculated if the animal had only one record of 43 (3×3). On the other hand, waiting for multiple records to accumulate has the adverse effect of increasing the *generation interval* and eventually reduce the genetic progress achieved per year.

To illustrate that, if we consider the generation interval to be 2.5 years, and assume the genetic gain made to be 0.8 kg, the genetic gain per year is $0.8 \div 2.5 = 0.32$ kg. If by using multiple records we increase the genetic progress to 1.0 kg, but also increase the generation interval to 3.5 years, the yearly progress is $1.0 \div 3.5 = 0.28$ kg lesser than in the first case. In the same context, by reducing the generation interval we can increase genetic progress per unit of time. For example, mating ewes at early age to lamb as yearlings results in faster gain per year than delay mating them until they reach one year of age. Also, using Record of Performance programs to predict the breeding value of animals has the same effect.

Selection based on relatives

How can a breeder select for a trait expressed only in one sex? For example, how can one select males for litter size or milk production? At one time or another, breeders selected their sires from those born twins and triplets and from those born to good mothers. This is exactly the principle, breeders should examine the performance of close relatives which show the trait and select accordingly. To select males for prolificacy, examine the performance of females over many reproductive cycles, take the average of these performances and select the sire from the mother that gave the highest performance. The same principle also applies when selecting for traits that require slaughtering the animal such as carcass quality. One method for selecting for carcass merit is to examine the performance of relatives. For example, the breeder can maintain half and full sibs and send some of them to slaughter, and keep the animals whose sibs demonstrate the highest performance.

Applying another procedure, breeders can obtain progeny from the sires considered for selection and test these progeny for the desired traits. This process, although lengthy and expen-

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sive, is considered the most accurate because breeders test what they would eventually get from their selection of particular sires. This *progeny testing* procedure now widely used in dairy cattle breeding is responsible for the great improvement obtained. When breeders select based on ancestors, they practice family or pedigree selection, and when they select based on the offspring, then they practice progeny testing. Both methods are effective in selecting for traits limited to one sex.

Multiple trait selection

Often sheep breeders have a wider objective for their animals, they should be prolific, fast growing, and produce heavy fleeces, and carcasses with more lean and less fat. Various procedures can help to achieve these objectives.

1-Tandem selection

In the first method, breeders select for each character one at a time in sequence, which may take a long time to achieve the objectives. However, there is no guarantee that by the time the breeders complete their selection for the last trait they have already lost the gain achieved in the early traits.

The alternative is to select for more than one character at the same time. The problem is that, by increasing the number of traits under selection, we decrease the amount of genetic improvement possible had we selected for each trait separately. Simply finding animals that excel in **all** selected traits is next to impossible. What can complicate the matter further is the possible genetic correlation between the traits in question.

Genetic and phenotypic correlations are measures of how closely the traits are related to each other. For example, the length of the wool and the weight of the fleece are positively correlated, an increase in one results in an increase in the other. Litter size and lamb birth weight is another example. The two traits are correlated but inversely, so an increase in litter size results in lighter lambs at birth. These two examples illustrate a positive and a negative correlation. As shown in the first section, the expression of each trait results partly from genetics and partly from environment; the combined effect, called phenotype, is what one can measure. Correlation, based on the direct phenotypic measurement taken, such as litter size or lamb weight is called phenotypic correlation.

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tant in selection. If it is positive, a strong correlation implies that the same genes are working in the breeder's favor improving both traits. However, if it is negative it implies that improving one trait causes the other one to deteriorate the other. Genetic correlations result from genes affecting more than one trait, from genes being so closely linked to each other that they mostly transmit as one block, or from different genes interacting together, or all three. Certain traits may not be correlated at all.

The following methods are used to select for more than one trait simultaneously.

2-The independent culling levels

In this method the breeder sets a standard for each trait for selection and chooses animals that satisfy these levels. The breeder culls any animal below these levels for any one trait regardless of its performance in other selected traits. This simple method has its drawbacks. It does not take into account the relation between traits, and it fails to capitalize on animals superior in one trait but intermediate in others. Also, it gives no economic consideration to the different traits selected, even though a trait can be more important than another.

3-Selection indices

Constructing and using *selection indices* is the most efficient way of selecting for more than one trait, especially when correlation between traits is low or negative. This method takes into account all the drawbacks mentioned earlier. According to Dr. Hazel, who suggested this method, "give each animal a true value by adding into one figure the credits and penalties given each animal according to the degree of its superiority or inferiority in each trait." Although the idea is simple, the problem with this method is the complexity of calculating it. First, each trait is expressed as a deviation from the mean for all animals in the flock. The next step is to weigh each trait by its standard deviation in order to standardize traits measured in different units and combine them all later in one figure, to avoid adding lambs to kilograms to centimeters. Then weigh each trait by its economic value. Breeders selecting for litter size and wool production, for example, should find out how much a lamb and a kilogram of wool are worth, and the relative value of one to the other. Heritabilities, and phenotypic and genetic correlations among the traits are required to calculate selection indices. These calculations

are complicated and require the use of computers. The index is a set of figures for each trait. For example, the following index was calculated for live weight (LW), grease fleece weight (GFW) and fibre diameter (FD):

$$\text{Index} = 200 - 1.32 \text{ LW} + 30.73 \text{ GFW} - 7.197 \text{ FD}$$

Multiply the actual values for the performance with these figures and add them all together. The end result is a one figure for each animal. After ranking the animals in descending order the breeder selects the highest animal in the list.

Breeders who do not want such sophistication and who know that the traits they want to select for are positively correlated can construct a simple index themselves. All they need to know is the standard deviation of the traits in question which can be calculated from the records as outlined before, and their relative economic value.

Obtain the relative economic value by dividing the returns of the traits. For example, if a unit of wool production (1 kg of grease fleece weight) is worth 4 dollars, a unit of weaned lamb (1 kg of weaned lamb) is worth 2 dollars and the unit of prolificacy (1 extra lamb weaned) is worth 32 dollars, the relative value of the three traits is 1: 1/2: 8, respectively. Then divide the performance of each animal for trait one by its standard deviation and multiply the result by the relative economic value of that trait. Repeat that for each trait under consideration and, by adding all these figures, arrive at one estimate for each animal. Then rank the animals according to the calculated estimates and select those on top for reproduction.

How to choose effective selection plans?

Before determining which selection plan to choose, consider the following:

1—What is the overall objective of the improvement? What are the traits to consider, taking into account their relative importance and economic values.

2—How precisely will these traits be measured and recorded?

3—What are the variation, repeatabilities, and heritabilities of each trait, and the phenotypic and genetic correlations among these traits?

4—What procedure will be followed to correct for environmental differences such as sex, type of age, age of dam, etc.?

Based on this information, choose the appropriate selection procedure according to the following guidelines:

1—If heritability is near 0.3 or higher, select on the individual's own record; it indicates enough of the animal's breeding value.

2—If repeatability is high, then one record for each animal is sufficient, and there is no real advantage of waiting for more records, because this would increase the generation interval needlessly and reduce progress.

3—If heritability is low, i.e., between 0.1 and 0.25, examine ways of increasing the accuracy of selection. Consider progeny testing.

4—If the trait is expressed in one sex or can be measured only after slaughter, examine progeny testing and use of half sib families.

5—According to the number of traits to be considered in the selection program, decide the appropriate method.

The preceding section can be summarized in the following recommendations:

1—Select for heritable characters that respond to selection, identify these by the magnitude of their heritabilities.

2—Give animals the optimum feeding and management treatment to express their genetic potential fully; avoiding the risk of culling superior animals and selecting instead inferior ones simply because management prohibited the superior animals from showing their real potential.

3—Because selection depends on variation, try to increase variation in the flock before embarking on selection; continuous inbreeding and use of closely related rams reduce variability, while outbreeding increases it.

4—Whenever possible, select for both males and females, so as to increase response to selection.

5—Increase selection pressure by reducing the number of parents selected. In large flocks it may be preferable to consider dividing flocks into different strains, select within these strains and cross them from time to time to increase variability.

This article is extracted from a booklet published by Agriculture and Agri-Food Canada, entitled "Simplified Principles for Breeding Sheep," available free, in English (1903E) and French (1903F) from Communication Branch, Agriculture and Agri-Food Canada, Ottawa, Ontario, K1A 0C7.



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