



Genetic analysis of growth and its relationship with lifetime production in Rambouillet Targhee and Columbia ewes under range conditions of Montana
by Juan Francisco Chavez

A thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Biological Sciences
Montana State University
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Abstract:

Growth characteristics of sheep from birth to maturity and the evaluation of the genetic and phenotypic relationships between growth traits with lifetime lamb and wool production were studied using data from 302 Rambouillet, 338 Targhee and 175 Columbia ewes born between 1960 and 1976. The Brody (1945) growth model was used for the derivation of growth parameters mature weight (A) and maturing rate (k). The Fitzhugh and Taylor (1971) equation-free model was used for the estimation of growth statistics; Absolute Growth Rate (AGR), Relative Growth Rate (RGR) and Absolute Maturing rate (AMR) for five intervals from birth to 18 mo. Genetic and phenotypic parameters were estimated by half-sib intraclass correlation using Harvey (1977) least-squares method for each breed and for the pooled data. Targhees were superior to Rambouillet and Columbias for weight of lamb at weaning (ATWW) and efficiency index (EI). ATWW was the lifetime yearly average of kg of lamb weaned and EI was ATWW per unit of ewes mature weight (A). Columbias were superior for yearly average grease wool produced (ATFP). Age at maturity was estimated on 39 mo, 38 mo and 41 mo for Rambouillets, Targhees and Columbias, respectively. Columbias had the highest A and the smallest k, Targhees matured the fastest. Ewes born twins had the highest EI. From the pooled data, heritability estimates of average total of lambs born (ATLB), average total of lambs weaned (ATLW), average total weight of lambs weaned (ATWW), average total grease fleece produced (ATFP) and EI were $.43 \pm .15$, $.33 \pm .15$, $.11 \pm .15$, $.68 \pm .16$ and $.15 \pm .15$, respectively. Genetic correlation, between ATWW and A, indicated that ewes with high additive genetic potential for ATWW will have high genetic potential for larger A. The genetic correlation between ATWW and k was zero. For the three Fitzhugh and Taylor (1971) growth statistics, highest heritabilities were obtained for the weaning-12 mo interval: AGR2 ($.80 \pm .16$), RGR2 ($.76 \pm .16$) and AMR2 ($.81 \pm .16$). RGR2 had the highest positive genetic correlations with ATWW ($.95 \pm .81$), EI ($.77 \pm .52$) and ATFP ($.39 \pm .19$) among growth statistics. Inclusion of AGR2 and RGR2 in the construction of selection indexes would improve accuracy of selection for ATWW, ATFP and EI. However, the contributions of A and k were inferior to AGR2 and RGR2. The use of any of the growth traits studied in selection indexes for improvement of ATFP and EI simultaneously gave no advantage in improving efficiency of selection.

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A thesis submitted in partial fulfillment
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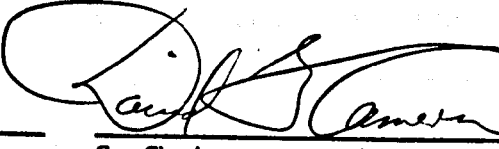
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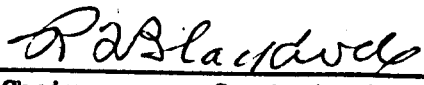
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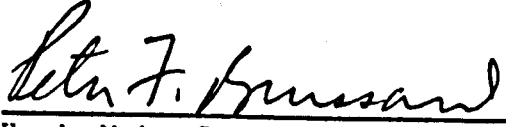
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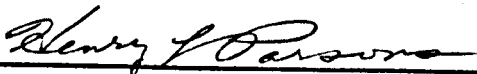
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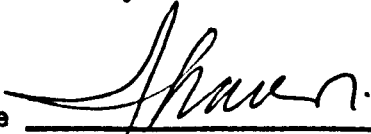
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To my wife, my parents,
my children and my
country.

To Martha, my sister.

VITA

Juan Francisco Chavez Cossio was born to Mrs. Martha Cossio and Mr. Gerardo Chavez in Lima, Peru, on October 8, 1948.

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ABSTRACT

Growth characteristics of sheep from birth to maturity and the evaluation of the genetic and phenotypic relationships between growth traits with lifetime lamb and wool production were studied using data from 302 Rambouillet, 338 Targhee and 175 Columbia ewes born between 1960 and 1976. The Brody (1945) growth model was used for the derivation of growth parameters mature weight (A) and maturing rate (k). The Fitzhugh and Taylor (1971) equation-free model was used for the estimation of growth statistics; Absolute Growth Rate (AGR), Relative Growth Rate (RGR) and Absolute Maturing rate (AMR) for five intervals from birth to 18 mo. Genetic and phenotypic parameters were estimated by half-sib intraclass correlation using Harvey (1977) least-squares method for each breed and for the pooled data. Targhees were superior to Rambouillet and Columbias for weight of lamb at weaning (ATWW) and efficiency index (EI). ATWW was the lifetime yearly average of kg of lamb weaned and EI was ATWW per unit of ewes mature weight (A). Columbias were superior for yearly average grease wool produced (ATFP). Age at maturity was estimated on 39 mo, 38 mo and 41 mo for Rambouillets, Targhees and Columbias, respectively. Columbias had the highest A and the smallest k. Targhees matured the fastest. Ewes born twins had the highest EI. From the pooled data, heritability estimates of average total of lambs born (ATLB), average total of lambs weaned (ATLW), average total weight of lambs weaned (ATWW), average total grease fleece produced (ATFP) and EI were $.43 \pm .15$, $.33 \pm .15$, $.11 \pm .15$, $.68 \pm .16$ and $.15 \pm .15$, respectively. Genetic correlation, between ATWW and A, indicated that ewes with high additive genetic potential for ATWW will have high genetic potential for larger A. The genetic correlation between ATWW and k was zero. For the three Fitzhugh and Taylor (1971) growth statistics, highest heritabilities were obtained for the weaning-12 mo interval: AGR2 ($.80 \pm .16$), RGR2 ($.76 \pm .16$) and AMR2 ($.81 \pm .16$). RGR2 had the highest positive genetic correlations with ATWW ($.95 \pm .81$), EI ($.77 \pm .52$) and ATFP ($.39 \pm .19$) among growth statistics. Inclusion of AGR2 and RGR2 in the construction of selection indexes would improve accuracy of selection for ATWW, ATFP and EI. However, the contributions of A and k were inferior to AGR2 and RGR2. The use of any of the growth traits studied in selection indexes for improvement of ATFP and EI simultaneously gave no advantage in improving efficiency of selection.

INTRODUCTION

The large numbers of sheep breeds and the individual characteristics of the wide range of environments to which they are adapted plays a fundamental role in their universal productive potential relative to other domestic species. Their ability to subsist and produce under different ecosystems attests to their broad adaptive capabilities. Reproductive performance or fitness has been used as an indicator of how well a population is adapted to a particular environment. Fitness has also been shown to be influenced importantly by genetic effects other than additive, the latter being the raw material by which selection accomplishes the goals of improvement.

Some advance has been achieved in the genetic improvement of strains or breeds of sheep for reproductive performance and a major gene for multiple births has been discovered in the Australian strain of Merinos called Booroola. Yet, in many of the well established breeds of sheep reproductive performance is the main limiting factor of productivity.

It has been observed that reproductive performance, evaluated in many different ways, does not respond readily to artificial selection. Reasons for limited response to artificial selection may be due to our lack of knowledge about the many possible biological variables and their interactions involved in the expressions of reproduction and (or) that we have not yet discovered the most practical way for evaluation and application of information in selection.

Growth has also been associated with fitness and it is possible that a genetic relationship exists between these two basic traits. If that is true, the use of growth as an indicator of future lifetime reproductive performance would be important in the development of breeding plans to improve reproductive performance and efficiency of production in sheep. Additional information is needed regarding the relationships between growth and lifetime production, giving consideration to the fact that growth and lifetime production, are cumulative processes in development.

The purpose of the present study was to estimate the genetic and phenotypic relationships among measures of early growth, rates of maturity, mature size, reproduction and production of range sheep, and to identify traits that can be measured early in life that will have value for predicting genetic merit of lifetime production.

REVIEW OF LITERATURE

Growth

Growth has always been linked to progressive development. In particular, when development is evaluated in terms of body weight gains, that development is considered to be a consequence of general body growth. Brody (1945) defined growth as "Constructive or assimilatory synthesis of one substance at the expense of another (nutrient) which undergoes dissimilation". Earlier Brody (1928) defined growth as the increase in the number of cells due to an unstable equilibrium between the organism and the environment surrounding it. The approach to a stable equilibrium is called growth.

Bonner (1958), indicated that accumulation of protoplasm by growth is a consequence of development. He wrote,

"The teleological purpose of development is to create an individual that is well adapted and successful in its environment". "Another implication in that there has been an increase in division of labour, for clearly this is vital for adaptive success. In terms of development this means differentiation. Increase in size and division of labour are the two primary goals of development..". "In large measure the success of organisms in nature depends upon their being well knit and closely co-ordinated. It is not enough to have a large organism which parcels out its activities; it must be a discrete, smoothly functioning unit, physiologically well balanced within, as well as adjusted to its environment. It must have systems of physiological regulation, correlation and control, so that it is stable even in adversity. This kind of stability by co-ordination plays an important role in the survival of the fittest and must be constantly improved by selection."

From the previous paragraph it might be inferred that growth is a reaction of the animal to its environment. Implicitly there is an ideal, a balanced successful size for a specific environment. That

ideal could be called the fittest size corresponding to the optimum proportionality and division of labor among all the constituent parts in the organism. Thus, the trends of differentiation could be analyzed in terms of growth patterns. An important variable within the system would be the time required for an individual to reach the point of balance itself, which would be related to fitness and, implicitly, strongly influenced by natural selection.

In sheep, Butterfield et al. (1983a,b) demonstrated that between a large and small strain of Merinos, there exists a wide range of proportions of muscle, bone, fat, alimentary tract and other internal organs relative to weight. However, when the proportions of these tissues and organs were compared in relation to maturity, a reduction of these differences was observed. McClelland et al. (1976) reached a similar conclusion in a study on the differences in body composition of four breeds of sheep at maturity. These studies suggest that weight at a specific age is only an indicative point within a whole biological process called growth. That process involves an important group of variables, and is meaningful in considering comparative responses about animal efficiency.

The patterns of growth are similar for each organ, however, they differ in earliness of maturity (complete development). The increase in body weight with time, as noted by Brody (1927a), produces a sigmoidal curve with two well differentiated stages: the "self-accelerating" phase, before an inflection point, and the following "self-inhibiting" phase. The shape of the growth curve for

each constituent body part will tend to have a similar pattern to that of the whole body (Hammond, 1932).

The self-accelerating phase, starting at conception, shows a broken pattern of at least three cycles called infantile, juvenile and adolescent (Robertson, 1908; cited by Brody, 1928). A phenomenon occurs that others have called "metamorphosis" (Davenport, 1926). At least four of these cycles were considered to be present by Brody (1928). These could be related to changes in proportion due to the different sizes of the components when differentiated in the embryo, as well as their different asymptotic weights and growth curves at different phases, as pointed out by Fowler (1980).

These cycles are evidently products of the development of the internal organs. They proceed toward their mature weights earlier than does the body as a whole (Butterfield et al, 1983b). Muscle and bone development are also included. The amount of fat, the tissue of latest development (Butterfield et al., 1983a), is an indication of maturity. Taylor (1982), suggests that mature weight can be defined as an equilibrium weight containing 15% of chemical fat.

Thus, growth is a gradual process of reaching a balanced equilibrium of an organism to a specific environment. It is possible that the faster growing animals which reach maturity earlier will probably be the fittest. It would be important to know, as regards the mature animal performance, whether there is any selective advantage for the fast maturing animals compared to the slow maturing ones. Two approaches can be taken to look for a possible answer; an analysis of

longevity and an analysis of productive performance, including especially reproductive performance.

Brody (1928) suggested the application of the equation $W_t = Ae^{kt}$ for representing any of the segments (cycles) of the self-accelerating phase of growth. (W_t), represents the weight of a given animal at age (t); (A) corresponds to the adult weight (mature weight); (e) is the base of the natural logarithm; and (k) is the relative rate of growth with respect to mature weight (A).

Growth and longevity

After the onset of puberty, the rate of growth decreases gradually until the maximum size in all the organs is reached and the maturity of the individual is attained. Along with developmental growth, a gradual change in the capability of the organism to overcome disease (vitality) occurs. The maximum vitality is reached at puberty (Brody, 1928). Senescence, theoretically, starts at puberty, when sexual activity begins.

According to Comfort (1961), aging or senescence means a decline in vigor or vitality with the passing of time, and is characterized by the increased probability of dying. He further states that longevity or the long duration of life has been found to be correlated with size in different animal species, but a closer relationship apparently exists between longevity and net reproductive rate. However, longevity's closest single correlate seems to be the "index of cephalization" which is measured by the excess of brain size over that expected from the general pattern of mammalian organic proportions (Comfort, 1961).

Normally growth and senescence are expressed as a consequence of time, but for growth and senescence, time is somewhat relative and can be considered as a conjugate effect of all the factors involved in a specific environment where the individual grows and reproduces. The more important environmental factors appear to be temperature, nutrition and ionizing radiation (Comfort, 1961). The effect of nutrition on growth and senescence has been demonstrated in rats (McCay et al., 1935; Berg and Sims, 1961).

Rats have a much shorter life span under optimum feeding for rapid growth than rats under a system of feeding which checks growth but avoids any vitamin deficiency. The restricted rats apparently remain juvenile, and are more active and disease free than rats having a normal diet. When the diet restricted rats receive additional food, they mature and develop normally. From these results (Comfort, 1961) it appears that rapid growth tends to shorten life span, and nutritional level seems to be the factor of greatest importance on growth rate. This idea was also maintained by Brody (1945).

Growth and efficiency

Efficiency in animal production can be evaluated in terms of energy utilization or in terms of net monetary income when other factors, in addition to the bioenergetic aspects of productivity, are involved. In some circumstances bioenergetic aspects are transformed to current monetary values. However, a better basis for comparing efficiencies among species, breeds or strains in particular environments would be in terms of energy utilization. Fluctuations in

economic factors are less stable for evaluating animal efficiency, and therefore of limited value except for short periods of time.

With respect to growth, energetic efficiency can be evaluated by the proportion of growth achieved (work performed) relative to the free energy expended (Brody, 1945). In general, animal efficiency can be expressed in terms of growth. However, two aspects must be considered: (1) the growth which is related to development (assuming a maximum is reached at adult age) which is cumulatively increased until adulthood and later maintained (meat production), and (2) other aspects of growth, not directly associated with development, which could be called cyclic growth, occurring at any period in the life cycle of an animal, and related to a certain productive component (i.e. milk, eggs, wool, etc). Reproductive traits would be a particular case because of their implicit dependence on other factors besides the animal itself (i.e. mating). In general, the synthesis of any product within the organism could be called growth.

Efficiency, according to Brody (1945) is the ratio of growth achieved over free energy expended. Some of the expended energy is normally dissipated as heat. Energetic efficiency is easier to measure and evaluate in organisms at embryological stages (during pre-natal growth). However, after birth, due to the influence of many variables, that task is more difficult (Brody, 1945).

Animals use food energy to meet survival requirements which include maintenance, developmental growth, reproduction and production after maturity. Holmes (1977) states that the estimation of feed

efficiency should be done in relation to the lifetime animal yield and the total inputs of feed resources.

Differences in animal efficiency are related in varying degrees to the genetic make-up of the animals. This is quantified in terms of genetic variation. For example, selection for clean wool weight per head results in a correlated increase in efficiency (Turner and Young, 1969). There are, however, few estimates of genetic parameters for efficiency. Terrill (1975) indicates that little is known of the genetic differences among sheep regarding requirements of specific nutrients, and that the available information comes from research with different objectives.

Most studies have used units of feed consumed per unit of weight gained as a measure of efficiency and heritability estimates cited by Terrill (1975) were obtained by Botkin (1955), Witt et al. (1967), Vesely and Robison (1968) and Ercanbrack (1974). Lasley (1978) gives .20 to .25 as the average heritability for this measure of efficiency in sheep.

In other studies, due to the difficulty of measuring daily food consumption per animal, the analyses of efficiency for weight gain have used body weights gains in specific periods of growth. The assumption has been made that the genetic and phenotypic correlations between average daily weight gains and feed efficiency in sheep are high ($-.73$ and $-.60$, respectively) according to Lasley (1978). Feed efficiency and digestibility are highly correlated (Price et al., 1965). Wool production efficiency has also been studied and the existence of genetic differences demonstrated. Even at low levels of feed intake

Terrill (1975) considers the possibilities of efficiency improvement by selection to be feasible.

Studies regarding the efficiency of reproductive performance are scarce. Yet the main limiting factor in the success of the sheep industry is the low reproductive rate (Blaxter, 1968; Turner, 1969). Holmes (1977) indicated that reproductive performance is a very important trait, which can be measured in terms of its constituent parts; age at first breeding, length of reproductive cycle, regularity of breeding, litter size and peri-natal mortality. He states that doubling the number of progeny in sheep would increase efficiency by 50%. A reproductive index (Holmes, 1977), annual mass of live offspring born divided by the mass of their dam in terms of metabolic weight ($W^{.75}$), suggests that sheep are among the species with the poorest performance (Table 1). However, Robinson (1974) presented the feasibility of an intensive indoor production system, utilizing a lambing interval of 205 days. The central emphasis was litter size and frequency of breeding, manipulated by controlling nutrition, lactation, and day length; with individual feeding according to the level of production of the ewes. Interest was also centered on reproductive efficiency in this intensive system.

From a practical point of view, the commercial producers' interest is to maximize net returns (efficiency in terms of income). At this point, balance must be found among the more important productive traits as to their relative importance (increase in net return per unit change in a specific trait). That balance usually involves reproductive rate, wool and meat (Rae, 1982). The ideal condition, in terms of growth

would be to produce faster growing animals with low mature size to reduce maternal costs (Robertson, 1982). A correlated advantage would be an earlier age at puberty and higher proportion of multiple ovulations in the ewe lambs that reached puberty earlier (Lang and Hight, 1967). Tierney (1969) also suggests that selection for ewes having first estrous at a young age can result in increased overall fertility. A similar result has also been reported in cattle (Lesmeister et al., 1973).

A negative relationship exists between size and wool production (Turner and Young, 1969) due to the positive relationship between size and surface area of skin. Therefore, small size results in a reduction in wool production. However, a greater number of small animals could be raised per unit of land (or feed available) which would compensate for the negative effect of individual size on wool production.

Models for growth evaluation

The representation of growth in terms of body weight was discussed by Brody (1927a). He indicated three ways that growth could be represented: (1) a velocity curve; (2) a cumulative curve representing the sums of all gains; and (3) a relative-rate curve (or percentage curve). He recommended the cumulative curve as the most useful of these three. The advantage that Brody saw for the use of the cumulative growth representation was mainly related to its biological interpretation: (1) for early comparison of the relative progress of growth of different animals; (2) representation of growth standards; and (3) for purposes of interpolation, because accidental variation and experimental errors can be minimized.

TABLE 1. REPRODUCTIVE INDEX^a

	Typical mass of dam kg	W ^{.75} kg	Progeny mass at birth kg	No. of progeny per year	Progeny mass per year kg	Reproductive index	
						kg	kg ^{.75}
Chicken	2.5	1.99	.05	100	5.0	2.0	2.51
				150	7.5	3.0	3.77
				250	12.5	5.0	6.28
Turkey	10.0	5.62	.10	50	5.0	.5	.89
				80	8.0	.8	1.42
Rabbit	4.5	3.09	.05	20	1.0	.22	.32
				40	2.0	.44	.65
Sow	170.0	47.1	1.5	12	18.0	.11	.38
			1.2	24	28.8	.17	.61
Ewe	70.0	24.2	4.5	1	4.5	.06	.19
			4.0	2	8.0	.12	.33
			3.0	3	9.0	.13	.37
Cow	500.0	105.7	42.0	1	42.0	.08	.40
			35.0	2	70.0	.14	.66

^aAfter Holmes, 1977.

The use of the cumulative curve gave rise to terminology which is basic to the understanding of the graphical representation and the analysis of growth. That terminology, applied to the model used by Brody (1927a,d) for the definition of the post-puberal phase of growth (self-inhibiting), involves three parameters. Two of them have important biological meaning: (1) mature size (A), which is also called asymptotic weight; and (2) the slope (k) which is the relative velocity of growth or the relative-rate of growth with respect to the growth yet to be made (A - W), represented by:

$$k = \frac{dW/dt}{A-W}, \quad \begin{array}{l} \text{Where; } W = \text{Weight at age } t \\ t = \text{Age in time units} \\ A = \text{Mature weight.} \end{array}$$

The third parameter (B), which has no biological significance, is an age-parameter representing the intercept of the curve (A-W) when $t=0$ (at birth).

Other models were proposed for the post inflection (self-inhibiting) phase of growth previous to Brody's model. After thorough study Brody concluded that the following non-linear three-parameter equation was the most appropriate model:

$$W_t = A - Be^{-kt}$$

Where:

W_t = Weight at time t

A = Mature weight

B = Constant of integration

e = Base of natural logarithm

k = Rate at which the curve approaches the asymptote.

This equation can be transformed to;

$$W_t - W_{t^*} = A - Ae^{-k(t-t^*)},$$

in which the growth curve has been forced to a specific point (W_{t^*} , t^*). A particular case occurs when the origin of the curve is set to the intersection of the ordinate and abscissa ($t^*=0$ $W_{t^*}=0$). In this special case (Figure 1), B equals A and the function is reduced to a two parameter equation: $W_t = A - Ae^{-kt}$. Nelsen et al. (1982) utilized this approach as an alternative for adjusting by B , facilitating the direct comparison of the k values among animals.

Models other than Brody's have also been discussed in the literature for fitting animal growth curves. Many have the capability of fitting the whole growth curve, including the pre-puberal self-accelerating phase (Eisen et al., 1969; Timon and Eisen, 1969; Brown et al., 1976; DeNise and Brinks, 1985). Other models have also been proposed and applied in the analysis of growth curves, but apparently have not been compared with others (Sprent, 1967; Warren et al., 1980; Fletcher, 1974). The initial theory about the mathematical representation of growth developed by Brody (1927a, 1927b, 1927c, and 1928) has also received new important contributions (Taylor, 1980a,b, 1965, 1968, 1982, 1985; Taylor and Fitzhugh, 1971; Fitzhugh and Taylor, 1971).

Eisen et al. (1969) made a comparison among the growth functions (Logistic, Gompertz and Bertalanffy) in mice from birth to 54 d of age. These growth models correspond to the group of three parameter equations with fixed inflection points. Based on the differences in residual variances, they found that the Logistic function gave the best fit. Also, the coefficients of variation of A , t' (age at point of

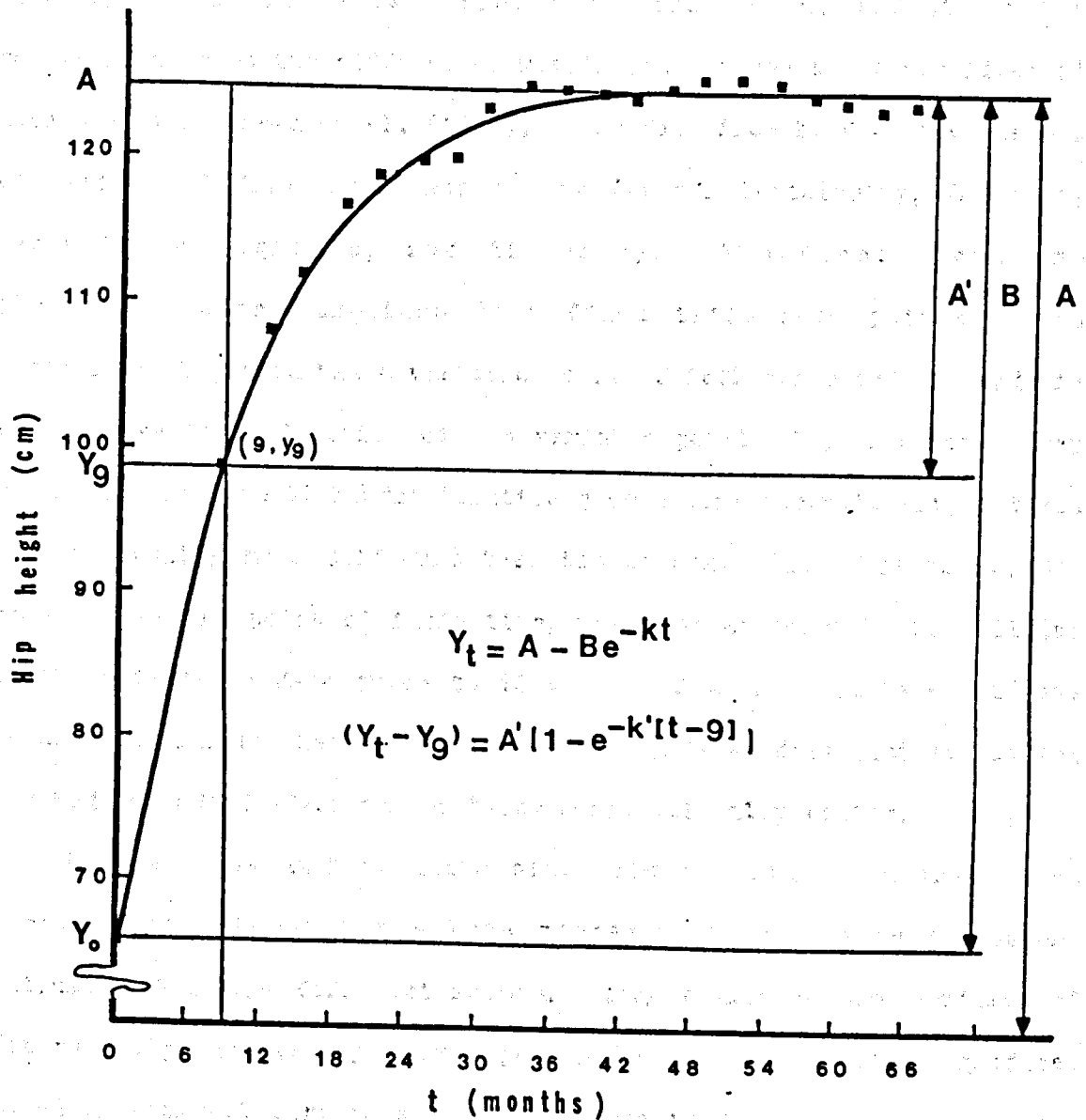


FIGURE 1. A REPRESENTATIVE OF BRODY'S EQUATION (AND A MODIFICATION) FITTED TO AN ANGUS HEIGHT-AGE CURVE (After Nelsen et al., 1982).

inflection) and k , estimated from the Logistic function were smaller than those calculated from the other two functions. However, the accuracy of fit for these three functions had no effect on the conclusions about the differences within and between the three lines of mice studied. Brown et al. (1976), using data from beef cattle, made a comparison of five non-linear models (Brody, Bertalanffy, Gompertz, Generalized Logistic, and Richards). The first three are three-parameter functions with fixed inflection points. The Generalized Logistic has a variable point of inflection and Richards is a four parameters function with a variable point of inflection. They concluded that the Richards' function gave a more accurate fit, but was computationally more difficult than the others. Richards' model, due to its variable point of inflection, was most appropriate for fitting cattle weight-age data prior to 10 months of age. Brody's model gave results similar to that of Richards for weight-age data past six months and had the added advantage of being computationally easier.

However, the authors cited above did not find a near-perfect correlation between the values representing the same parameters estimated from the different models. They evaluated the goodness of fit visually, preferring this approach to the usual test of goodness based on residual variances. This was due to the implicit inaccuracy expected from the correlated errors (dependency) among the longitudinal growth data. The same limitation was also indicated by Fitzhugh (1976). These authors concluded that the selection of any one of the models would depend upon the nature of the study to be performed, as well as, the intended application of the results.

Timon and Eisen (1969) observed in mice data that the fit of the Richards and the Logistic functions were very similar. However, the asymptotic weight was underestimated, mainly by the Logistic function. Both functions gave a mean point of inflection at nearly half the asymptotic weight ($A/2$), which is contradictory to the views of Brody (1945) and Taylor (1965). Great differences were observed between the k values obtained from each of these functions. The genetic correlation was zero which suggested that the two estimates of k represented different traits by the two functions. That observation contrasted markedly with the very high genetic correlations between the other derived growth parameters. Another important finding was the very close relationship between the Richards' k and m parameters ($r_g=.91$ and $r_p=.95$). The m parameter is called the shape parameter, representing a point in the curve where inflection takes place which is expressed as a relative measure to the limit of the curve.

DeNise and Brinks (1985) compared the goodness of fit of Brody's and Richards' functions using data from beef cattle. They concluded that Richards' function had smaller residual variance and a better fit to the actual data points, however, Brody's curve was faster and less costly to compute.

Fitzhugh and Taylor (1971) developed a general method for the analysis of genetic relationships involving maturity rate, size, and growth rate with other traits involving degree of maturity. They used a simple two-component, equation-free model where the two components are: (1) mature size (A), and (2) proportion of mature size reached at a specific stage of growth (u). The Fitzhugh and Taylor model, used

for analyzing genetic relationships among maturing rate, size and growth rate, is:

$$Y_t = u_t A,$$

where,

Y_t = size at age t (expressed as a function of degree of maturity u and mature size A),

u = proportion of mature size A attained at a given stage or age t ,

and,

$$u_t = Y_t/A.$$

The growth statistics derived or approximated by Fitzhugh and Taylor (1971) are: (1) Absolute Maturing Rate (AMR), defined as the proportional change in the degree of maturity per unit of time expressed as percentage in a given interval: $AMR = du/dt$. AMR is a consequence of the maturing rate or change in u over time for the trait, and can also be expressed as:

$$AMR = 1/A (dY/dt) = 1/A (Y_{t2} - Y_{t1})/(t_2 - t_1).$$

(2) Absolute Growth Rate (AGR) is the change per unit of time, expressed in kilograms and commonly referred as average daily gain:

$$AGR = dY/dt = (Y_{t2} - Y_{t1})/(t_2 - t_1),$$

(3) Relative Growth Rate (RGR) refers to the change in the proportion of size per unit of time in a given interval, or percentage of size attained per unit of time in a given interval : $RGR = 1/Y dY/dt$. May also be regarded as Absolute Growth Rate (AGR) relative to size over the period of interest:

$$RGR = [(Y_{t2} - Y_{t1})/(t_2 - t_1)] (1/Y_{t2}).$$

Stobart (1983) makes a clear interpretation of three biologically important growth statistics derived from that model, and their application in the analysis of growth and correlated responses on ewe productivity. He states that, "The major advantages of Fitzhugh and Taylor (1971) method over the fitting of growth curves is that the rate of maturing is not forced to remain constant over time; but rather both genetic and environmental variability in maturing rate can be assessed for any age interval, and degree of maturity can be estimated from fewer and less uniformly spaced measurements than required for fitting of growth curves."

Genetics of growth parameters and their relationship to productive traits.

There are no published studies for sheep assessing the relation between estimated values of the growth parameters; A and k , and subsequent productive performances. There are, however, studies regarding the application of the growth statistics derived from the equation free model of Fitzhugh and Taylor (1971) and productive performance in ewes (Stobart, 1983; Stobart, 1985). Stobart's data included a portion of that used in the present study. He found that animals more mature at any stage of growth were more mature at later stages of growth, and also lighter at maturity. The faster maturing animals weighed more than the others up to 12 mo of age. There was no general constancy in the growth rates up to maturity. Animals growing faster in a given time interval tended to grow slower in the interval immediately following.

Several heritability estimates reported in the literature are presented for the growth parameters k , m , A and t' (the age at the

inflection point) (Table 2) and the growth statistics derived from the application of the free-equation model of Fitzhugh and Taylor (1971) (Table 3).

TABLE 2. HERITABILITY ESTIMATES FOR GROWTH CURVE PARAMETERS

Source	Model ^a	Method ^b	Species	Age	Estimates			
					k	A	t'	m
Eisen et al. (1969)	L	FS	Mice	B-54d	.50	.47	.80	
	G			B-54d	.74	.40	.75	
	Be			B-54d	.81	.51	.85	
Timon & Eisen (1969)	R	FS	Mice	5-98d	.30 \pm .1	.66 \pm .2	1.17 \pm .1	.53 \pm .2
	L			5-98d	.76 \pm .2	.76 \pm .2	1.32 \pm .2	
Brown et al. (1972)	B	PHS	Cattle	B-109mo	.33 \pm .2	.34 \pm .2		
				B-109mo	.75 \pm .3	.21 \pm .2		
DeNise & Brinks (1985)	B	PHS	Cattle	B-4yr	.20 \pm .3	.44 \pm .3		
	R			B-4yr	.32 \pm .3	.44 \pm .3		.21 \pm .3

^a B=Brody, L=Logistic, G=Gompertz, Be=Bertalanffy, R=Richards.

^b Estimation method: FS=Full-sibs, PHS=Paternal half-sibs.

Great variation existed among the heritability estimates. Differences due to species, breed and environmental conditions could be reasons for that variability. The different methodologies applied in the estimation of the heritabilities are also possible factors. The estimated heritabilities for all the curve parameters, as well as the growth statistics range from intermediate to high values, suggests that these traits are susceptible to change by selection.

Stobart (1983) found the highest heritability estimates for Absolute Maturing Rate in the intervals birth-12 mo, birth-18 mo, and weaning-12 mo, (.66 \pm .12, .59 \pm .12 and .64 \pm .12, respectively). His heritability estimate for AMR in the interval 12 - 18 mo was .32.

TABLE 3. HERITABILITY ESTIMATES FOR GROWTH STATISTICS^a

Source	Method ^b	Species	Age	Estimates		
				AGR	RGR	AMR
Fitzhugh & Taylor (1971)	PHS	Cattle	Prenatal	.38		.22
			B-6 mo	.40	.27	.42
			6-12mo	.45	.47	.46
			12-18mo	.35	.24	.24
			18-mature	.48	.42	.42
Smith et al. (1976b)	PHS	Cattle	B-200d	.57±.30	.67±.31	.62±.31
			200-396d	.42±.30	-.07±.25	.31±.29
			396-550d	.69±.31	.69±.31	.44±.30
			550d-3.33yr	.19±.28	.19±.28	.09±.27
Stobart (1983)	PHS	Sheep	B-W	.21±.11	.28±.11	.19±.11
			B-12mo	.29±.11	.50±.12	.66±.12
			B-18mo	.35±.12	.44±.12	.59±.12
			W-12mo	.52±.12	.48±.12	.64±.12
			12-18mo	.43±.12	.39±.12	.32±.11

^aAll papers used Fitzhugh and Taylor (1971) methodology.

^bEstimation method: PHS=Paternal half-sibs.

In addition to the application of this information through selection to directly change maturing rate, mature size and growth, it is desirable to have knowledge of the expected correlated response of such selection in other traits of biological and economical importance, particularly reproductive performance. Tables 4 and 5 summarizes published estimates of genetic correlations among these parameters and growth statistics, respectively, and their correlations with productive traits.

The results in Tables 4 and 5 indicate a negative genetic relationship between mature size (A) and rate of maturing (k). This relationship has been highlighted in other studies. Taylor and

TABLE 4. GENETIC CORRELATIONS BETWEEN GROWTH PARAMETERS AND PRODUCTIVE TRAITS

Source	Model ^a	Method ^b	Species	Trait	Age	Estimates			
						k	A	B	m
Eisen et al. (1969)	L	FS	Mice	k	B-54d				
				AGR	B-54d	.55±.5	-.50±.5	.54±.5	
Timon & Eisen (1969)	R	FS	Mice	k	5-98d		-.29±.3	.91±.0	
				A	5-98d			-.11±.2	
	L			k	5-98d		-.34±.2		
Brown et al. (1972)	B	PHS	Cattle	k	B-109mo		-.62±.3	.98±.2	
				A	B-109mo			-.50±.4	
DeNise et al. (1983)	B	PHS	Cattle	MPPA ^c	B-78mo	.68±.7	-.28±.5		
					B-78mo	1.32±1.	-.52±.6		
DeNise & Brinks (1985)	B	PHS	Cattle	k	B-4yr		-1.16±2.	.82±1.	
				A	B-4yr			-.84±.5	
				k	B-4yr		-.84±1.	-.97±2.	1.10±.3
				A	B-4yr			.31±.6	-.50±1.
				B	B-4yr				-.98±2.

^aGrowth Functions: B=Brody, R=Richards, L=Logistic.^bEstimation method: FS= Full-sibs, PHS= Paternal half-sibs.^cMost Probable Producing Ability for weight of calf at weaning.

TABLE 5. GENETIC CORRELATIONS BETWEEN GROWTH STATISTICS AND PRODUCTIVE TRAITS^a

Source	Method ^b	Species	Trait	Age	Estimates		
					AGR	RGR	AMR
Smith et al. (1976)	PHS	Cattle	Growth ^c rate	B-200d	-.59±.5	-.34±.4	-.35±.4
				200-396d	.80±.594±.6
				396-550d	-.11±.4	-.02±.4	-.06±.5
				550d-3.33yr	.36±.7	.63±.7	.80±1.
Stobart (1985)	PHS	Sheep	Average ^d fleece weight	B-W	-.89±.4	-.78±.4	-.74±.5
				W-12mo	.63±.2	.68±.3	.64±.2
				12-18mo	.36±.3	-.31±.3	-.38±.3
				B-12mo	.09±.3	-.18±.3	.24±.2
				B-18mo	.27±.3	.38±.3	-.02±.2
			Average number of lambs born	B-W	.19±.3	-.37±.3	-.11±.3
				W-12mo	-.06±.2	-.01±.2	-.02±.2
				12-18mo	.36±.2	-.32±.2	.40±.3
				B-12mo	-.22±.3	-.26±.2	-.07±.2
				B-18mo	.10±.2	-.18±.2	.16±.2
			Average number of lambs weaned	B-W	-.30±.7	-1.05±.9	-.11±.7
				W-12mo	.00±.4	.06±.5	.02±.4
				12-18mo	.17±.5	.04±.5	.08±.5
				B-12mo	-.20±.6	-.68±.6	-.02±.4
				B-18mo	.00±.5	-.77±.7	.04±.4
			Average weight lambs weaned	B-W	1.11±2.	-.97±2.	1.07±2.
				W-12mo	-.05±.7	-.17±.7	.01±.6
				12-18mo	.98±2.	.47±1.	.93±2.
				B-12mo	.59±1.	-.83±1.	.44±.9
				B-18mo	1.32±2.	-.77±1.	1.77±2.

^aFrom application of Fitzhugh and Taylor (1971) method.^bEstimation method: PHS=Paternal half-sibs.^cCorrelations are between growth rate at different age-intervals and the growth statistics at puberty.^dCorrelations between productive traits with growth statistics at different age-intervals.

Fitzhugh (1971) refers to this characteristic relationship as the basic determinant in the shape of the growth curve, indicating that the genetic change in the shape of the growth curve will depend on its flexibility which is based on the degree of independence among size, rate of maturing and inflection parameters. For example, they found that in Hereford females 78% of the additive variance for the time taken to mature was independent of mature weight.

There are two basically different patterns of growth according to Brown et al. (1972): (1) the animals have similar mature weights but different k values, and (2) the animals have similar k values but different mature weights. In both cases, the variable which accounted for the differences in k or A is the length of time required to attain mature weight. The k value is indicative of differences in growth rate only when two animals reach similar mature weights. When the mature weights are different, the k value measures the differences in growth rate relative to mature size.

When the Richards model was used, the curve shape parameter (m) showed a very high positive genetic correlation ($>.90$) with the rate parameter (k) (Timon and Eisen, 1969; DeNise and Brinks, 1985). This suggests that many of the genes which influence the maturing rate (k) also influence the shape or inflection parameter (m). These two parameters may refer to the same underlying genetic trait. Similarly, a high correlation exists between k and t' (age at inflection point) when the Logistic model was applied (Eisen et al., 1969).

Assuming that k and m are influenced primarily by the same genes, for practical application in animal breeding, the use of a simpler model (i.e. Brody) would be advantageous. Its use would permit a faster, more economical derivation information that is easier to interpret.

There are cases in which the correspondence between the growth parameters was not as close as expected when two different models were applied to the same data. The genetic correlations between the A , B and k growth parameters estimated from Brody and those estimated from Richards by DeNise and Brinks (1985) are a typical example. However, in another publication, (Timon and Eisen, 1969), the genetic correspondence between the growth parameters A and k estimated from Richards and those estimated from the Logistic model were similar.

All the productive characters analyzed by Stobart (1985), except the average number of lambs born, were positively correlated genetically with the growth statistics AGR, RGR and AMR for the 12 - 18 mo interval. Growth performance in the interval 12 to 18 mo was indicative of the ewe's genetic potential for lamb production, including weight of lamb weaned. Growth performance between weaning to 12 mo was more highly related to the genetic potential for wool production.

MATERIALS AND METHODS

Animals and Environmental Conditions.

The data for this study came from the lifetime records of 815 purebred Rambouillet, Columbia and Targhee ewes. The sheep were raised by the Montana Agricultural Experimental Station, Red Bluff Research Ranch, Norris, Montana, between 1960 and 1981.

The Red Bluff Research Ranch, located along the West side of the Madison river, contains approximately 5,000 ha, which are mostly range with some meadows. The elevations extend from 1,402 to 1,890 m. The annual average precipitation is 47 cm, and the average temperature is around 8 C with maximum average of approximately 21 C (July) and minimum of -5 C (December). The upland zone is composed of bunchgrass type vegetation and with bluebunch wheatgrass (Agropyrum spicatum) as the dominant species. The north slopes are characterized by some areas of brush and trees.

The animals were managed and herded on the range areas of the experimental station and on the high mountain national Forest Service allotments. They were gathered and brought to the station headquarters only during breeding, lambing, shearing and data collection times. The ewes were pen-mated in single-sire groups of 20 to 40 each for approximately 20 d in November and December and then returned to the range and mass mated to blackface rams for 15 d. Their lambs were born in April and May.

During the breeding season, mixed grass and alfalfa hay were supplied free choice and at other times during the winter only when the

snow cover was too deep for grazing. At the end of the breeding season, the ewes were herded together on the range until the start of the lambing season. Shortly after parturition, ewes and lambs were placed in 1.3 m^2 lambing pens for 24 h or more. All the lambs were ear-tagged and their weights recorded within that interval. Then, the ewe and her offspring were moved to small pens, with capacity for approximately 8 dams and their lambs, and maintained there for 2 to 3 days.

The lambs were weaned in the fall at an average age of 128 d, wintered on the ranch, and feed .23 kg of protein supplement per day.

Data.

Table 6 presents the number and distribution of the ewes that provided data for the study.

TABLE 6. DISTRIBUTION OF THE EWES BY BREED, AGE PRODUCTION GROUP AND YEAR OF BIRTH

Breed	Group number of records	Year of birth															Total
		60	61	62	63	64	65	66	67	68	69	70	72	73	75	76	
Rambouillet	3	9	4	11	1	3		6	11	2	16	3	3	2	3		74
	4	7	7	1	1	6	1	8	3	4	4	21				1	64
	5	12	12	5	13	12	20	13	17	15	13		10	15	7		164
Targhee	3	4	1	3	6	2	10	6	6	6	6	3	12	5	2	2	74
	4	6	3	3	6	4	4	4	3	5	2	3	1	1		2	47
	5	17	10	15	15	27	30	21	16	10	14	19	12	3	8		217
Columbia	3		5	4	2	4	7	6	6		5	5	5	3	2		54
	4		1	3	5	1	2	2	2			2	3				21
	5		13	7	13	14	9	4	9		8	10	5	1	7		100
Total		55	56	52	62	73	83	70	73	42	68	66	51	30	29	5	815

Only ewes having at least three consecutive years of lamb production, four years in the case of wool production, were included in the study. The normal culling age for ewes was done after the 5 yr of production, thus the maximum age for ewes in this study was 6 yr.

Ewes that provided data for the study were classified according to whether they had a total of three, four or five cumulated reproductive records in order to study the level of performance of ewes that remained in the flock for these different periods of time. This classification is referred to as "group" in the thesis. Only data from the ewes which left the flock were considered for study. For example, for Rambouillet ewes born in 1960, 9 left the flock after 3 records, 7 after 4 records and 12 after 5 records.

Variables were calculated to evaluate the cumulative lifetime producing ability of each ewe. These new variables were; Average total number of lambs born (ATLB), Average total number of lambs weaned (ATLW), Average total weight of lambs weaned (ATWW) and Average total weight of grease fleece produced (ATFP).

A minimum of seven body weights were required for ewes with three cumulative production records. The other ewes with four and five cumulative production records had eight and nine weights, respectively. The weights were recorded at birth, weaning and 12 mo during the first year, then in the fall for the subsequent years. The corresponding ages were recorded in months.

These weight-age records for each ewe were analyzed to estimate the parameters of Brody's (1927a) non-linear growth model by using a microcomputer program written specifically for this study (S. Kachman,

personal communication). Those analyses provided estimates of A, k and B for each ewe from which growth curves for each breed and group were derived. The parameter values for A and k were added to the set of variables (traits). The B parameter which is a constant of integration, having no biological importance, was not included.

A new variable called Lamb Production Efficiency Index (EI) was calculated from the cumulative litter weight at weaning and the ewe's mature weight. This index expresses average annual lamb production as a proportion (%) of mature weight (A).

$$EI = \frac{\text{Ewe's average annual lifetime lamb production, kg}}{\text{Ewe's mature weight, kg}} \times 100$$

Growth statistics (traits) proposed by Fitzhugh and Taylor (1971) (AGR, RGR and AMR) were calculated for each ewe. Mature weight (A) obtained from Brody's model was used to derive AMR. These growth statistics (traits) were calculated for five age-intervals: (1) Birth to weaning (B-W), (2) Weaning to yearling age (W-12), (3) Yearling to 18 months (12-18), (4) Birth to yearling age (B-12), and (5) Birth to 18 months (B-18). These same intervals were studied by Stobart (1983). Table 7 shows the tabulation of all traits studied, their description and units of measurement.

Statistical Analyses.

Maximum, minimum, average, standard deviation and coefficient of variation were calculated for each trait by breed-group subclass. In addition, the cumulative annual average of ATLB, ATLW and ATWW, for first, first two, first three, first four and first five reproductive

TABLE 7. EWES' PRODUCTIVE AND GROWTH TRAITS ANALYZED IN THE STUDY

Trait symbol	Description of the trait	Units
ATLB	Average of the total number of lambs born to the ewe per year	n
ATLW	Average of the total number of lambs weaned by the ewe per year	n
ATWW	Average of the total weight of lambs weaned by the ewe per year	kg
ATFP	Average of the grease fleece weight produced by the ewe per year	kg
A	Asymptotic weight (mature) of the ewe derived from Brody's growth equation (model)	kg
k	Maturing rate coefficient, or rate of decline in growth as the asymptotic weight (A) is approached, derived from Brody's model	%/mo
EI	Lamb Production Efficiency Index, the ratio of ATWW divided by (A) expressed as kg/kg x 100	%
AGR ^a	Absolute Growth Rate, body weight gains for specified intervals from birth to 18 mo	kg/mo
RGR ^a	Relative Growth Rate, body weight gains for specified intervals from birth to 18 mo relative to final weight for the specified interval	%/mo
AMR ^a	Absolute Maturing Rate, body weight gains for a specified interval from birth to 18 mo relative to mature weight: AGR divided by (A)	%/mo

^aThe five intervals for AGR, RGR and AMR are: (1) birth to weaning (B-W); (2) weaning to yearling (W-12); (3) yearling to 18 mo (12-18); (4) birth to yearling (B-12); and (5) birth to 18 mo (B-18).

records as the ewes progressed through their lifetime production. In the case of wool production (ATFP), the corresponding number of records were first two, first three, first four, first five and first six records. The UNIVARIATE procedure from SAS (1986) was applied in these analyses.

Breeds and groups were compared on the basis of all traits listed in Table 7 and for their first, first two and first three cumulative reproductive records for ATLB, ATLW, ATWW and ATFP. Similarly, a final comparison was made of the groups with four and five cumulative reproductive records. Least squares method (Harvey, 1977) was used to perform these analyses using a model (model A) which included year of birth of the ewe, breed of the ewe (B), group of the ewe (G), B x G interaction, age of dam in years, type of birth-rearing of the ewe, day of birth (covariate) and residual as sources of variation. Also, the growth statistics (A, k, AGR, RGR, and AMR) derived from the complete information of recorded weights were analyzed using model A. Ewes born as triplets as well as the only one observation in 1976 for Columbias (total of 11) were not included. Also, the analyses involving the growth parameters and growth statistics, as well as EI, did not included a Columbia ewe which had a k value more than 3 standard deviations from the mean. That ewe was not involved in all the subsequent genetic and phenotypic analyses.

Estimation of genetic and phenotypic variance and covariance components. Least-squares analyses (Harvey, 1977), using a mixed model, were performed for all traits listed in Table 7. Analyses were made for each breed separately (model B) and for the combined data set

(model C). The elements of model B (sources of variation) were birth year of the ewe, sire of the ewe within birth year, type of birth-rearing of the ewe, day of birth, age of dam in years and an error term (residual). Model C included as sources of variation birth year-breed of the ewe, sire of the ewe within birth year-breed, type of birth-rearing of the ewe, day of birth, age of dam and an error term (residual). For both models, sires and the residual elements were considered random variables and all other elements fixed. Variance and covariance components among and within sires were derived from these analyses. The distribution of sires and their offspring per year is shown in Table 8.

Heritabilities of the traits studied, and the genetic, phenotypic and environmental correlations among them were provided directly by the Harvey (1977) analyses of models B and C. The formulas for calculating these estimates as well as the standard errors for heritabilities and genetic correlations are presented in appendix A of the Harvey (1977) User's guide for LSML76.

TABLE 8. DISTRIBUTION OF SIRES (S) AND OFFSPRING (O) PER BREED AND YEAR

Breed		Year																Total
		60	61	62	63	64	65	66	67	68	69	70	72	73	75	76		
Rambouillet	S	10	3	7	6	6	3	7	7	6	8	7	7	12	7	1	97	
	O	28	23	17	15	21	21	27	31	21	33	24	13	17	10	1	302	
Targhee	S	7	4	6	6	5	7	7	8	7	7	8	8	5	5	3	93	
	O	27	14	21	27	33	44	31	25	21	22	25	25	9	10	4	338	
Columbia	S		6	7	5	6	8	6	8		6	4	3	3	4		66	
	O		19	14	20	19	18	12	17		13	17	13	4	9		175	
Total	S	17	13	20	17	17	18	20	23	13	21	19	18	20	16	4	256	
	O	55	56	52	62	73	83	70	73	42	68	66	51	30	29	5	815	

Selection indexes. Selection indexes were derived from the genetic and phenotypic parameters estimated from the pooled analyses in this study using the methods presented by Falconer (1981). The traits for which selection indexes were computed were ATWW, EI, ATWW+EI, ATWW+ATFP, ATFP+EI and ATWW+ATFP+EI, using various growth trait combinations as predictive elements in the indexes.

Summary of the steps followed for handling and analysis of data.

Figure 2 shows the flow chart of all the steps followed in handling the data, calculation of the new variables and the types of analyses employed.

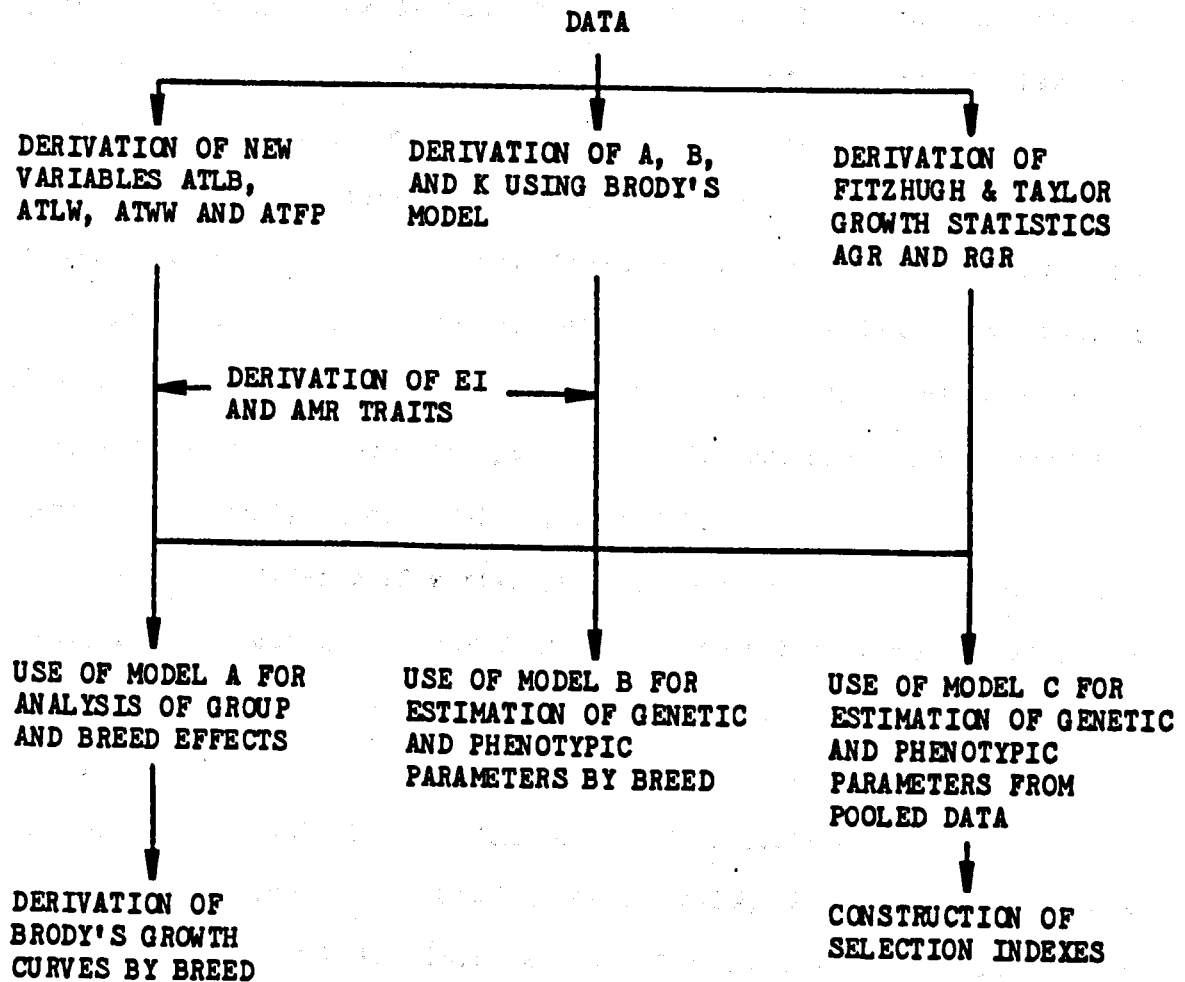


FIGURE 2. FLOW CHART INDICATING THE STEPS FOLLOWED IN HANDLING THE DATA AND STATISTICAL ANALYSES.

RESULTS AND DISCUSSION

Descriptive statistics for all traits by breed and group are presented in Appendix Tables 22 through 44. These tables show the number of records, average, standard deviation, coefficient of variation and range values for each trait within each breed-group subclass. These data are considered useful for obtaining an understanding of the general level of merit in each trait, the magnitude of the absolute variation and the relative variation (coefficients of variation) encountered in each data set. Specific comparisons among breeds, groups or other factors are obtained from the more complex analyses of models A, B, and C.

High coefficients of variability were observed in the reproductive traits. This was due to the fact that zero values were included as records for the ewes that failed to give birth to or wean offspring any year.

Breed and group differences for the productive traits

The four productive traits, ATLB, ATLW, ATWW and ATPF, were analyzed using model A. This was done for the average of all records (lifetime production), and the average of the cumulative production through the first, second, third and fourth records. These results are presented from Table 9 to 13, respectively.

Lifetime production. Table 9 presents the mean squares and least-squares means for the four productive traits. The effects of breed and groups were highly significant for all the traits with exception of breeds for ATLB ($P < .05$). The interaction between breed and group was generally unimportant except for ATLW and ATWW ($P < .05$).

Targhees were superior to Columbias for ATLB and ATW. For ATLB, Rambouillets did not differ from Targhees and Columbias, and for ATW, Targhees and Rambouillets had similar performances. The least squares means for ATLB were 1.38, 1.43 and 1.33, and for ATW 1.14, 1.22 and 1.05, for Rambouillets, Targhees and Columbias, respectively. Targhees were superior in ATW to Rambouillets and Columbias (48.69, 42.39 and 41.19 kg of lamb produced per year, respectively). Columbias had the highest ATP, with Targhees being superior to Rambouillets (4.91, 4.73 and 4.45 kg, respectively). The five-record group was superior to three- and four-record groups for ATLB, ATW and ATW, while the three- and four-record groups showed no difference. There was no difference between the four- and five-record groups for ATP, but the three-record group was inferior for this trait.

First record. Table 10 shows the mean squares and least squares means for the average production for the first record. Breeds were different for all the traits, but the differences were not so distinct as in the previous analysis of complete production for ATLB and ATW. For ATLB and ATW, Targhees were superior to Rambouillets, but similar to Columbias and Columbias were not different from Rambouillets. For ATW, Targhees were superior to the other breeds which were similar to each other. Columbias and Targhees showed similar performance for ATP and were superior to Rambouillets.

There was no group effect for ATLB, ATW and ATW. The five-record group was superior to the three-record group for ATP. The ewes having five records were intermediate. This result from early performance (first record) when compared to the results from lifetime

TABLE 9. MEAN SQUARES AND LEAST SQUARES MEANS FOR THE LIFETIME AVERAGES OF PRODUCTIVE TRAITS OF EWES (HARVEY LEAST SQUARES ANALYSES, MODEL A)

Source of variation	df	Mean Squares			
		ATLB	ATLW	ATWW	ATFP
Year of birth	14	.4607**	.6999**	1,786.1**	1.5411**
Breed (B)	2	.3588*	1.1132**	2,919.7**	8.4934**
Group (G)	2	3.0920**	5.5445**	8,408.2**	3.3332**
B x G	4	.1329	.2883*	414.0*	.2391
Age of dam	5	.0267	.0849	97,873.0	.6116
Type of birth-rearing	2	.5692**	.1762	335.4	2.4522**
Birth date	1	.0107	.2844	405.3	.3328
Residual	773	.1006	.0958	124.0	.2822
Least Squares Means					
Breed:	N	n	n	kg	kg
Rambouillet	295	1.38±.02ab	1.14±.03a	42.39±.95b	4.45±.04c
Targhee	335	1.43±.02a	1.22±.02a	48.69±.91a	4.73±.04b
Columbia	174	1.33±.03b	1.05±.03b	41.19±1.2b	4.91±.06a
Group:					
3 records	198	1.30±.03b	1.02±.03b	39.50±.97b	4.57±.05b
4 records	129	1.33±.03b	1.10±.03b	42.44±1.26b	4.72±.06a
5 records	477	1.50±.02a	1.30±.02a	50.34±.78a	4.80±.04a

a, b, c, are LSD comparisons ($P < .01$)
 * $P < .05$, ** $P < .01$

TABLE 10. MEAN SQUARES AND LEAST SQUARES MEANS FOR THE CUMULATIVE AVERAGE OF PRODUCTIVE TRAITS OF EWES THROUGH THEIR FIRST RECORD (HARVEY LEAST SQUARES ANALYSES, MODEL A)

Source of Variation	df	Mean Squares			
		ATLB	ATLW	ATW	ATFP ^a
Year of birth	14	.8134**	.7026**	1,627.3**	5.5370**
Breed (B)	2	1.0492**	1.2170**	3,530.4**	4.2920**
Group (G)	2	.1811	.1638	320.7	1.1413**
B x G	4	.0512	.3851	575.9	.5860
Age of dam	5	.1034	.1107	111.9	.7529**
Type of birth-rearing	2	.4219	.2489	472.5	5.4354**
Birth date	1	.0866	.0145	27.6	4.1140**
Residual	773	.1853	.1943	264.7	.2580

Least Squares Means					
Breed:	N	n	n	kg	kg
Rambouillet	295	1.14±.04b	.88±.04b	32.95±1.4b	4.22±.04b
Targhee	335	1.28±.03a	1.03±.04a	40.93±1.3a	4.43±.04a
Columbia	174	1.19±.05ab	.91±.05ab	34.89±1.8b	4.53±.05a
Group:					
3 records	198	1.22±.04a	.93±.04a	35.87±1.4a	4.34±.04b
4 records	129	1.17±.05a	.92±.05a	35.30±1.8a	4.38±.06ab
5 records	477	1.23±.03a	.97±.03a	37.59±1.2a	4.46±.03a

^asecond record

a, b, are LSD comparisons (P<.01)

** P<.01

records, suggests that grease fleece production is more indicative of lifetime production than the other traits. This suggestion is supported by the high repeatability reported for that trait in the literature (Turner and Young, 1969).

Second record. Table 11 shows the mean squares and least squares means for the average production for the first two records. Breed differences at this level were more marked than for the analysis at the second record. For ATLB, Targhees performed better than Rambouillets, but were not different from Columbias which were similar to Rambouillets. Targhees were superior to Rambouillets but similar to Columbias for ATLW. Rambouillets and Columbias were no different. The change in rank of Rambouillet from ATLB to ATLW could be taken as indication of a higher lamb loss from birth to weaning in Rambouillets which have a higher frequency of triplets at lambing. Subandriyo (1984) reported the lowest survivability for progeny of 3-yr-old Rambouillet dams. He also reported low survivability to be associated with small birth weights. Targhees were superior to Rambouillets and Columbias for ATWW, but no difference was observed between these last two breeds. For ATFP, Columbias were superior to Targhees and Rambouillets, and Targhees had greater ATFP than Rambouillets.

The three groups were not different when compared for ATLB, however, they were different for each of the other traits. Ewes with five records had the highest average performances. They were superior to those having three, but not different from the four-record ewes. The trend toward higher performance for the five-record ewes began to emerge more clearly after two records than after one record.

TABLE 11. MEAN SQUARES AND LEAST SQUARES MEANS FOR THE CUMULATIVE AVERAGE OF PRODUCTIVE TRAITS OF EWES THROUGH THEIR SECOND RECORD (HARVEY LEAST SQUARES ANALYSES, MODEL A)

Source of variation	df	Mean Squares			
		ATLB	ATLW	ATWW	ATFp ^a
Year birth	14	.5237**	.6930**	1,788.1**	5.4310**
Breed (B)	2	.4616*	.7510**	2,532.9**	6.0880**
Group (G)	2	.4153*	.9450**	1,243.9**	1.2550**
B x G	4	.2547	.1488	173.7	.3660
Age of dam	5	.0630	.0313	56.7	.5151
Type of birth-rearing	2	.5337*	.2440	381.4	3.7370**
Birth date	1	.0059	.0514	131.6	1.4420*
Residual	773	.1298	.1330	174.1	.2610

Least Squares Means					
Breed:	N	n	n	kg	kg
Rambouillet	295	1.23±.03b	.99±.03b	37.41±1.10b	4.32±.04c
Targhee	335	1.32±.03a	1.10±.03a	44.31±1.15a	4.56±.04b
Columbia	174	1.24±.03ab	1.02±.04ab	39.94±1.4b	4.70±.05a
Group:					
3 records	198	1.26±.03a	1.00±.03b	38.65±1.1b	4.46±.04b
4 records	129	1.23±.04a	1.02±.04ab	39.65±1.5ab	4.53±.06ab
5 records	477	1.31±.02a	1.10±.02a	43.03±.9a	4.60±.03a

^athird record

a, b, are LSD comparisons (P<.01)

* (P<.05), ** (P<.01)

Third record. Table 12 presents the mean squares and least squares means for cumulative performance of the first three records. Breed effect was very important for all the traits except for ATLB. The Rambouillets and Columbias had similar performances for ATLW and ATWW. Targhees showed the highest performance for these traits. Each breed differed for ATFP. Columbias had the highest ATFP followed by Targhees, with the Rambouillets having the lowest performance.

With respect to the group effect, the differences for the average of four records were clearer than for three. The five-record ewe group showed the highest performances for the four traits. Three- and four-record groups were not different. The five-record group was superior to the three-record group for ATFP, but was not different from the four-record group. Breed group interactions ($P < .05$) were observed for ATLW and ATWW.

Fourth record. The analysis of average performances of ewes at their fourth record is different than the analyses using the averages of one, two and three records. This comparison included the three breeds but only the four- and five- record groups. Table 13 displays the mean squares and least squares means from these analyses. No breed differences were found for ATLB. For ATLW, Targhees were superior to Columbias and Rambouillets. For ATWW, Targhees performed better than Rambouillets and Columbias, which were not different. The Columbias again had the highest performance for ATFP, with the Targhees second and Rambouillets third in rank. Ewes having five records were superior to ewes having four for all the traits except ATFP where no differences

TABLE 12. MEAN SQUARES AND LEAST SQUARES MEANS FOR THE CUMULATIVE AVERAGE OF PRODUCTIVE TRAITS OF EWES THROUGH THEIR THIRD RECORD (HARVEY LEAST SQUARES ANALYSES, MODEL A)

Source of variation	df	Mean Squares			
		ATLB	ATLW	ATWW	ATFP
Year of birth	14	.5365**	.7436**	1,878.8**	3.4430**
Breed (B)	2	.2837	.9830**	2,917.9**	6.8130**
Group (G)	2	.6948**	2.2330**	3,177.8**	1.1910**
B x G	4	.1069	.3314	431.2*	.2824
Age of dam	5	.0648	.0707	77.0	.5813
Type of birth-rearing	2	.6015**	.2930	450.3*	2.9930**
Date of birth	1	.0055	.2815	431.8	.7328
Residual	773	.1130	.1100	140.7	.2726

Least Squares Means					
Breed:	N	n	n	kg	kg
Rambouillet	295	1.32±.03a	1.09±.03b	40.85±1.0b	4.41±.04c
Targhee	335	1.38±.02a	1.19±.03a	47.53±.97a	4.67±.04b
Columbia	174	1.29±.04a	1.03±.03b	40.58±1.3b	4.85±.06a
Group:					
3 records	198	1.31±.03b	1.02±.03b	39.79±1.0b	4.58±.04b
4 records	129	1.28±.04b	1.09±.04b	42.52±1.3b	4.66±.06ab
5 records	477	1.39±.02a	1.20±.02a	46.63±.83a	4.71±.03a

^afourth record

a, b, c, are LSD comparisons (P<.01)

* (P<.05), ** (P<.01)

TABLE 13. MEAN SQUARES AND LEAST SQUARES MEANS FOR THE CUMULATIVE AVERAGE OF PRODUCTIVE TRAITS OF EWES THROUGH THEIR FOURTH RECORD (HARVEY LEAST SQUARES ANALYSES, MODEL A)

Source of variation	df	Mean Squares			
		ATLB	ATLW	ATWW	ATFP ^a
Year of birth	14	.3835**	.4710**	1,304.9**	1.6060**
Breed (B)	2	.1586	.5142**	1,716.6**	5.3390**
Group (G)	1	1.1512**	1.9944**	3,190.3**	.1444
B x G	2	.2047	.3967*	544.3**	.2668
Age of dam	5	.0674	.0638	52.9	1.0280**
Type of birth-rearing	2	.4589**	.1052	142.8	2.6980**
Date of birth	1	.0429	.1929	227.4	.1443
Residual	578	.0950	.0933	114.9	.2720
Least Squares Means					
Breed:	N	n	n	kg	kg
Rambouillet	223	1.39±.03a	1.16±.03b	43.58±1.13b	4.53±.05c
Targhee	262	1.42±.03a	1.24±.03a	49.74±1.08a	4.81±.05b
Columbia	121	1.34±.04a	1.10±.04b	43.06±1.5b	4.98±.07a
Group:					
4 records	129	1.33±.03b	1.09±.04b	43.27±1.3b	4.75±.06a
5 records	477	1.45±.02a	1.25±.02a	48.65±.85a	4.79±.04a

^a fifth record

a, b, c, are LSD comparisons (P<.01)

* (P<.05), ** (P<.01)

were detected. Interactions between breed and group were observed for ATLW ($P < .05$) and ATWW ($P < .01$).

Brody equation parameters A, B, and k and the Efficiency index (EI).

Table 14 shows the mean squares and least squares means for the growth parameters A, B and k and the efficiency index. Rambouillets had the lowest mature weight (70.04 kg) while the Targhees and Columbias were similar (72.42 and 73.11 kg, respectively). The groups of ewes did not show differences in mature sizes and no interaction was detected between breed and group for this growth parameter.

The three breeds had different maturing rates. Columbias had the slowest (.1105) while Targhees had the fastest (.1200) and Rambouillets had an intermediate value (.1159). Ewes in the group of three records matured faster than the group of five records, but were no different than those in the group of four. Ewes in the four- and five-record groups had similar maturing rates.

The similarity in mature weights among the groups, but difference in maturing rates suggests that within breed, whatever the productive longevity of the ewes, mature weights would tend to be similar, but differences would exist among them with respect to maturing rates.

Targhees had the highest efficiency index, followed by Rambouillets which were superior to Columbias. The least squares means for these three breeds were .6781, .6099 and .5671, respectively. Ewes with five records were superior, those with four records were intermediate and the poorest performance was shown by ewes in the three-record group. Least squares means were .6983, .5941 and .5629

TABLE 14. MEAN SQUARES AND LEAST SQUARES MEANS FOR BRODY'S GROWTH CURVE PARAMETERS (A, B, k) AND THE EWE EFFICIENCY INDEX (HARVEY LEAST SQUARES ANALYSES, MODEL A)

Source of variation	df	Mean Squares			
		A	B	k	EI
Year of birth	14	424.34**	335.01**	.011054**	.1955**
Breed (B)	2	450.17**	385.40**	.003381**	.5051**
Group (G)	2	53.97	15.35	.003037**	1.3374**
B x G	4	32.75	23.86	.000301	.1036*
Age of dam	5	60.96	30.64	.000437	.0314
Type of birth-rearing	2	414.11**	57.39	.010965**	.1828**
Birth date	1	27.44	5.84	.006441**	.0520
Residual	772	33.58	30.99	.000605	.0276
Least Squares Means					
Breed:	N	kg	kg	%/mo ^a	% of A ^a
Rambouillet	295	70.04±.53 ^b	62.69±.48 ^b	11.59±.2 ^b	60.99±1.4 ^b
Targhee	335	72.42±.53 ^a	64.95±.45 ^a	12.00±.2 ^a	67.81±1.3 ^a
Columbia	173	73.11±.67 ^a	65.47±.60 ^a	11.05±.3 ^c	56.71±1.8 ^c
Group:					
3 records	198	71.23±.54 ^a	64.03±.48 ^a	11.97±.2 ^a	56.29±1.4 ^c
4 records	129	72.29±.70 ^a	64.66±.63 ^a	11.39±.3 ^{ab}	59.41±1.9 ^b
5 records	476	72.06±.43 ^a	64.41±.39 ^a	11.28±.1 ^b	69.83±1.1 ^a

^a Values are expressed as percentage
a, b, c, are LSD comparisons (P<.01)
*(P<.05), **(P<.01)

for the groups of five, four and three records, respectively. The breed by group interaction was significant ($P < .05$).

Brody's growth equations and age at maturity. Brody's growth curves and equations for each breed and group are shown in Figure 3. From these equations, the time at which each breed or group attained mature weight was determined. Appendix Table 45 shows the estimated weights generated from 6 to 84 mo for each growth equation.

For the purpose of defining the point at which mature weight was achieved, an arbitrary criterion was used. The asymptotic nature of Brody's equation does not give a definite point on the age scale when maximum weight is reached. Age at mature size was therefore defined as the age at which 99 % of A was attained. Using this criterion, the ages at maturity were approximately 39 mo, 38 mo and 41 mo for Rambouillets, Targhees and Columbias, respectively.

Comparisons of AGR, RGR and AMR for varying time intervals between birth and 18 months of age.

AGR comparisons. Table 15 presents the mean squares and least squares means for the effects of breed, group and their interaction for AGR in the five growth intervals studied. Differences in AGR among breeds were observed for all intervals. For AGR1 and AGR3, Targhees and Columbias were similar but superior to Rambouillets. Targhees were superior to Rambouillets and Columbias for AGR4, and Rambouillets were superior to Targhees and Columbias for AGR2. For AGR5, Targhees had faster growth rates than either Rambouillets or Columbias and Rambouillets had slower growth rates than Columbias. Targhees showed more stable performances across the different intervals. There was

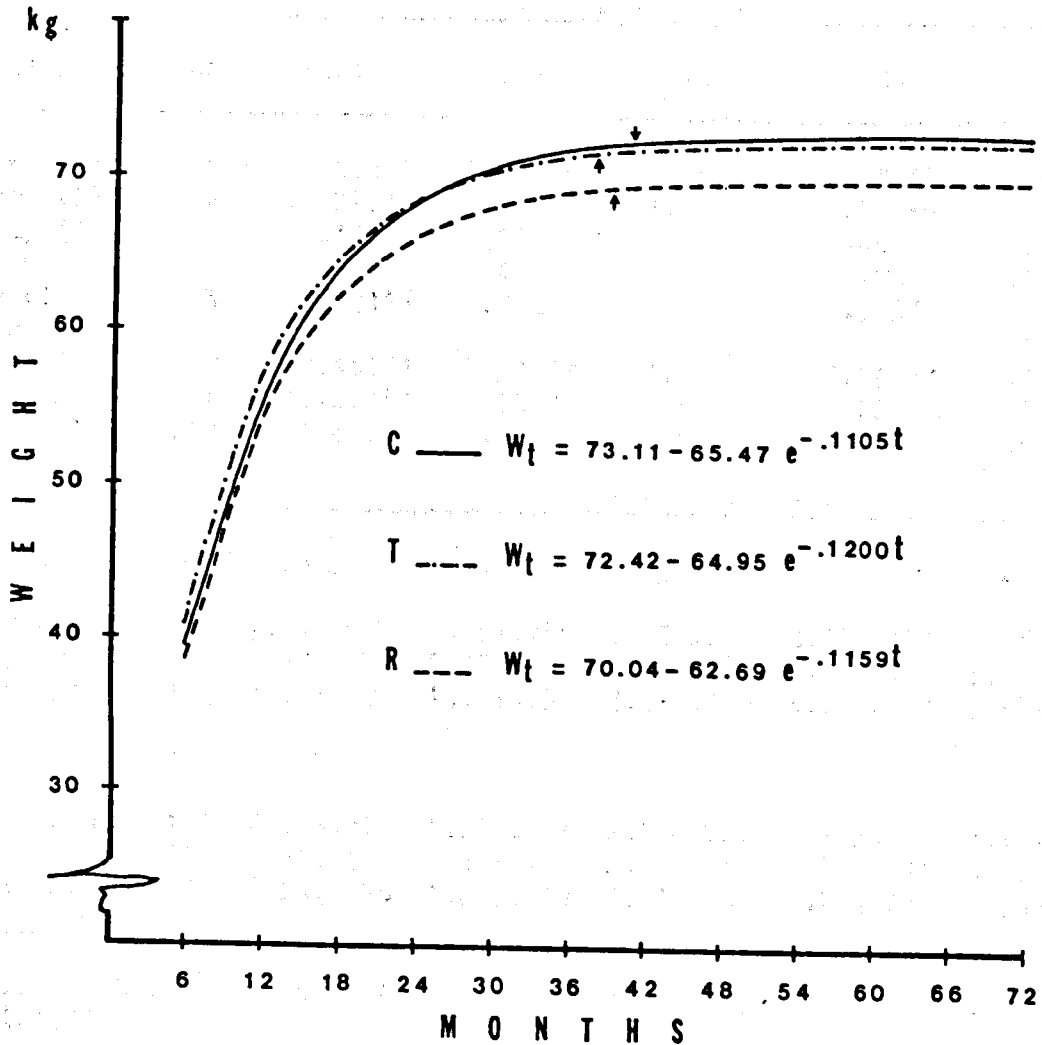


FIGURE 3. BRODY'S GROWTH CURVES AND EQUATIONS FOR RAMBOUILLETS (R), TARGHEES (T) AND COLUMBIAS (C) DERIVED FROM THE LEASE SQUARES MEANS FROM TABLE 14 (Arrows show ages at maturity).

TABLE 15. MEAN SQUARES AND LEAST SQUARES MEANS FOR ABSOLUTE GROWTH RATE (AGR) FROM BIRTH-WEANING (AGR1), WEANING-12 MONTHS (AGR2), 12-18 MONTHS (AGR3), BIRTH-12 MONTHS (AGR 4) AND BIRTH-18 MONTHS (AGR5) (HARVEY LEAST SQUARES ANALYSES, MODEL A)

Sources of variation	df	Means Squares				
		AGR1	AGR2	AGR3	AGR4	AGR5
Year of birth	14	24.284**	6.438**	107.718**	7.482**	4.069**
Breed (B)	2	18.247**	4.015**	14.191**	.706**	2.199**
Group (G)	2	.137*	.008	.912	.093	.024
B x G	4	.179	.496	.479	.158	.053
Age of dam	5	3.591**	.402	.399	.315*	.089
Type of birth-rearing	2	89.481**	6.336**	1.863*	2.972**	.513**
Birth rate	1	10.261**	.998*	.722	.035	.186
Residual	772	.830	.228	.544	.128	.075

Least Squares Means						
Breed:	N	kg/mo	kg/mo	kg/mo	kg/mo	kg/mo
Rambouillet	295	7.94±.08b	1.45±.04a	2.59±.06b	3.73±.03b	3.28±.02c
Targhee	335	8.54±.07a	1.23±.04b	3.03±.06a	3.81±.03a	3.49±.02a
Columbia	173	8.27±.09a	1.15±.05b	3.10±.08a	3.68±.04b	3.40±.03b
Group:						
3 records	198	8.22±.08a	1.28±.04a	2.99±.06a	3.72±.03a	3.41±.02a
4 records	129	8.29±.10a	1.27±.05a	2.86±.08a	3.76±.04a	3.37±.03a
5 records	476	8.24±.06a	1.29±.03a	2.87±.05a	3.76±.02a	3.39±.02a

a, b, are LSD comparisons ($P < .01$)

** ($P < .01$)

and Columbias were similar but superior to Rambouillets. Targhees were superior to Rambouillets and Columbias for AGR4, and Rambouillets were superior to Targhees and Columbias for AGR2. For AGR5, Targhees had faster growth rates than either Rambouillets or Columbias and Rambouillets had slower growth rates than Columbias. Targhees showed more stable performances across the different intervals. There was evidence of compensatory growth in adjacent intervals from birth to weaning (AGR1), from weaning to 12 mo (AGR2) and from 12 to 18 mo (AGR3); however, the three breeds did not respond the same. Rambouillets had high gains in AGR2 and low in AGR1 and AGR3; while the opposite was generally true for the other two breeds. In no case were differences detected among groups nor was there a breed by group interaction.

RGR comparisons. Table 16 presents the mean squares and least squares means for RGR in the five growth intervals. In all intervals, except from birth to weaning (RGR1) and birth to 12 mo (RGR4), breed effects were significant. For RGR2, Rambouillets had superior performance and Targhees and Columbias had lower but similar growth. However, Targhees and Columbias were superior to Rambouillets, and Columbias superior to Targhees for RGR3. Group differences were not detected for any interval. For RGR5, Targhees and Columbias had similar growth rates and both were superior to Rambouillets. No breed by group interactions were observed.

AMR comparisons. Table 17 displays the mean squares and least squares means for AMR in each of the intervals studied. Breed differences were detected for all the intervals. For AMR1, Targhees

TABLE 16. MEAN SQUARES AND LEAST SQUARES MEANS FOR RELATIVE GROWTH RATE (RGR) FROM BIRTH-WEANING (RGR1), WEANING-12 MONTHS (RGR2), 12-18 MONTHS (RGR3), BIRTH-12 MONTHS (RGR4) AND BIRTH-18 MONTHS (RGR5) (HARVEY LEAST SQUARES ANALYSES, MODEL A)

Source of variation	df	Mean Squares				
		RGR1	RGR2	RGR3	RGR4	RGR5
Year of birth	14	.004851**	.002114**	.020499**	.001836**	.000059**
Breed (B)	2	.000223	.001867**	.001958**	.000006**	.000005**
Group (G)	2	.000381	.000002	.000173	.000001**	.000000
B x G	4	.000213	.000166	.000113	.000002	.000001
Age of ram	5	.000071	.000222*	.000169	.000010**	.000002**
Type of birth-rearing	2	.000432*	.004537**	.001135**	.000088**	.000035**
Birth date	1	.065677**	.001047**	.000618*	.000497**	.000184**
Residual	772	.000140	.000080	.000104	.000003	.000001
Least Squares Means ^a						
Breed:	N	%/mo	%/mo	%/mo	%/mo	%/mo
Rambouillet	295	21.6 ±.1a	3.01±.1a	4.18±.1c	7.86±.0a	5.42±.0b
Targhee	335	21.78±.1a	2.52±.1b	4.64±.1b	7.89±.0a	5.45±.0a
Columbia	173	21.65±.1a	2.39±.1b	4.86±.1a	7.87±.0a	5.45±.0a
Groups:						
3 records	198	21.80±.1a	2.66±.1a	4.67±.1a	7.87±.0a	5.44±.0a
4 records	129	21.63±.1a	2.63±.1a	4.51±.1a	7.88±.0a	5.44±.0a
5 records	476	21.56±.1a	2.64±.1a	4.51±.1a	7.86±.0a	5.44±.0a

a RGR expressed as percentage relative to Y_{t_2}

a, b, c, are LSD comparisons

**($P < .01$)

TABLE 17. MEAN SQUARES AND LEAST SQUARES MEANS FOR ABSOLUTE MATURING RATE (AMR) FROM BIRTH-WEANING (AMR1), WEANING-12 MONTHS (AMR2), 12-18 MONTHS (AMR3), BIRTH-12 MONTHS (AMR4), BIRTH-18 MONTHS (AMR5) (HARVEY LEAST SQUARES ANALYSES, MODEL A)

Source of variation	df	Mean Squares				
		AMR1	AMR2	AMR3	AMR4	AMR5
Year of birth	14	.00363**	.001550**	.01838**	.001980**	.000417**
Breed (B)	2	.00122**	.001053**	.00152**	.000242**	.000117**
Group (G)	2	.00013	.000004	.00031*	.000006	.000060**
B x G	4	.00007	.000089	.00013	.000024	.000029
Age of dam	5	.00026	.000098*	.00015	.000015	.000010
Type of birth rearing	2	.01080**	.001575**	.00084**	.000217**	.000026
Birth date	1	.00132**	.000141	.00014	.000048	.000007
Residual	772	.00017	.000044	.00009	.000025	.000011

Least Squares Means						
Breed:	N	%/mo	%/mo	%/mo	%/mo	%/mo
Rambouillet	295	11.39±.1c	2.09±.05a	3.66±.08b	5.36±.04a	4.71±.03b
Targhee	335	11.84±.1a	1.73±.05b	4.14±.08a	5.30±.04a	4.83±.03a
Columbia	173	11.41±.1b	1.61±.07c	4.16±.10a	5.11±.05b	4.68±.04b
Group:						
3 records	198	11.63±.1a	1.83±.05a	4.14±.08a	5.28±.04a	4.81±.03a
4 records	129	11.53±.1a	1.80±.07a	3.88±.10a	5.25±.06a	4.68±.04b
5 records	476	11.48±.1a	1.81±.05a	3.94±.07a	5.25±.03a	4.72±.02ab

^a AMR are expressed as percentage relative to A
a, b, are LSD comparisons (P<.01)
*(P<.05), **(P<.01)

were superior to Rambouillets and Columbias, but Columbias matured faster than Rambouillets. However, for AMR2, Rambouillets were superior to Targhees and Columbias. Targhees were faster maturing than Columbias in the interval (W-12 mo). The AMR3 performances of Targhees and Columbias were similar and higher than Rambouillets. AMR4 values were similar for Rambouillets and Targhees; both were superior to Columbias. Finally, for AMR5 Targhees were superior; the Rambouillets and Columbias showed no difference.

Groups were different only for AMR5. The three-record group had faster maturing rate than the four-record group, but was not different from the five-record group.

Growth statistics reported by Stobart (1983) for each of these breeds were similar. The main differences were observed for RGR estimates for the birth to weaning and 12 to 18 months intervals. Apparently, that difference was caused in part by the different formula used. Stobart used as reference the mean weight for the interval ($\text{initial weight} + \text{final weight} \div \text{two}$). In this study, instead, the final weight was used as reference. The final weight in the interval was used as reference in order to minimize the residual effects of the previous interval. Also, in the case of AMR values, differences were observed in the 12 to 18 mo interval, which would be caused by the different method used by Stobart (1983) for estimating mature size.

Effect of type of birth and rearing on growth and productive performance of ewes.

The effects of the type of birth and rearing of the ewes on their subsequent growth and productive traits were obtained for each breed from the Model B analyses using the least squares method of Harvey (1977). The least squares means for all traits are listed for each breed in Appendix Table 46 for reference. The analyses using Model C, for the combined data sets, provided the estimates of the least squares means presented in Table 18.

The general results of these analyses indicate that ewes born twin and raised as twins or as singles had the highest reproductive rate, weaned the greatest weight of lamb in absolute terms (ATWW) and in relative terms (EI). They produced slightly less wool and attained smaller mature weights (A). Ewes born and raised as twins approached mature weight at slower rate (smaller k) than either twins raised as singles or singles raised as singles. Evidence of cyclical growth from birth to 18 mo indicates some compensatory growth (Olson et al., 1976) following weaning (AGR2). This appears to be related to the environmental condition associated with type of birth and rearing. Twins raised as twins grew slower prior to weaning but faster following weaning. The opposite was generally true for twins raised as singles and singles raised as singles. After 12 mo of age, the absolute growth rates (AGR) for the three birth and rearing groups were essentially the same. The growth rates during the longer periods (AGR4 and AGR5) combined the influences of the differential growth rates during the earlier growth segments. The effects of type of birth and rearing were

TABLE 18. LEAST SQUARES MEANS FOR BIRTH-REARING EFFECTS ON ALL THE STUDIED LIFETIME TRAITS OF THE EWES USING THE BREEDS POOLED INFORMATION (HARVEY LEAST SQUARES ANALYSES, MODEL C)

Traits	Significance	Type of Birth-rearing		
		S/S	T/S	T/T
No of observations		411	65	327
ATLB (n)	**	1.38±.03	1.46±.04	1.47±.03
ATLW (n)		1.17±.03	1.23±.04	1.21±.03
ATWW (kg)		45.72±.90	48.17±1.7	47.63±.92
ATFP (kg)	*	4.81±.04	4.73±.07	4.68±.05
A (kg)	**	73.79±.50	69.80±.86	71.37±.51
k (%/mo)	**	11.66±.20	11.70±.30	10.52±.20
EI (%)	**	62.33±1.0	69.25±2.0	67.02±1.0
AGR1 (kg/mo)	**	8.81±.07	8.38±.13	7.71±.07
AGR2 (kg/mo)	**	1.09±.04	1.22±.07	1.39±.04
AGR3 (kg/mo)		2.94±.06	2.84±.10	3.02±.06
AGR4 (kg/mo)	**	3.79±.03	3.72±.05	3.59±.03
AGR5 (kg/mo)	**	3.44±.02	3.36±.04	3.38±.02
RGR1 (%/mo)	**	21.57±.10	22.15±.20	21.67±.10
RGR2 (%/mo)	**	2.17±.07	2.52±.10	2.97±.08
RGR3 (%/mo)	**	4.49±.08	4.55±.10	4.81±.08
RGR4 (%/mo)	**	7.75±.01	7.87±.02	7.83±.01
RGR5 (%/mo)	**	5.39±.00	5.47±.01	5.44±.00
AMR1 (%/mo)	**	11.99±.10	12.03±.20	10.85±.10
AMR2 (%/mo)	**	1.49±.06	1.76±.09	1.96±.06
AMR3 (%/mo)	**	3.93±.08	4.04±.10	4.20±.08
AMR4 (%/mo)	**	5.19±.04	5.34±.07	5.07±.04
AMR5 (%/mo)	*	4.68±.02	4.82±.05	4.69±.03

* (P<.05), ** (P<.01).

considerably dampened, but differences continued to be significant, with the twin born ewes having an apparent environmental disadvantage.

The effects of type of birth and rearing on RGR and AMR were significant. Twins raised as twins or singles had faster growth in the weaning to 12 mo interval. The cyclic effect which had been observed when growth was evaluated in terms of AGR almost disappeared between these two intervals when evaluated in terms of RGR and AMR. The need to adjust growth and reproduction records for type of birth and rearing for most traits studied is clearly evident. The effects of type of birth and rearing on reproductive performance include, in addition to environmental factors involved in that particular response, the effects of genotype of twins compared to singles. Evidence for this can be drawn from Basuthakur et al. (1973) in which the type of birth of the sires influenced the lifetime reproductive performance of their daughters.

Estimates of heritabilities, genetic and phenotypic correlations

Least squares mixed-model analyses were used to obtain estimates of the genetic and phenotypic parameters for each breed (model B). In the analyses of the pooled data, which included breed as one of the sources of variation, model C was employed. Genetic parameters for each breed are presented in Appendix Tables 47, 48 and 49 for Rambouillets, Targhees, and Columbias, respectively.

Low heritabilities for productive traits and some non-estimable heritabilities (ATLW, ATWW, EI, RGR1, RGR5 and AMR3) were obtained from the analysis of the Targhee data. This resulted in non-estimable genetic correlations involving these traits. Negative sire components

of variance were the direct cause of these results. Very low additive genetic variance for these traits in Targhees and poor precision in the parameter estimates could be a reason for that particular response. However, sample size was not considered as a specific factor because the Targhee sample size was larger than either the Rambouillets or Columbias. In each breed, the estimates of heritabilities and genetic correlations had relatively large standard errors.

In general, the Columbia heritability estimates were higher than Rambouillets except for some intervals of growth evaluated in terms of RGR and AMR. Genetic correlations showed more marked differences between Columbias and Rambouillets than their heritabilities. Genetic correlations involving ATWW with ATPF and k in Columbias were low, but positive in contrast to Rambouillets which were high and negative. Also, the genetic correlation between ATWW and EI was high and positive (.79) for Columbias compared to Rambouillets which was low and negative (-.03).

Genetic correlation involving growth statistics were similar for Columbias and Rambouillets. The growth statistics for the weaning to 12 mo interval showed high and positive genetic relationship with the most important reproductive traits (ATWW and EI) in both breeds. The constancy of that association in both breeds suggests a general relationship probably exists that is not particular to a specific breed.

The genetic correlation between ATPF and A in Columbias was positive; in the Rambouillets, the association was negative. The genetic association of ATPF with the growth statistics was quite

different in these two breeds. Almost all were negative in Rambouillet, even for the intervals weaning-12 mo and Birth-12 mo, while in Columbias these associations were positive. This suggests that the correlated response in ATFP from selection for growth statistics in the interval indicated would be different for the two breeds.

Differences were also observed for the genetic correlations between A and EI. This correlation was negative in Columbias which means that selection of animals for larger mature sizes will result in progeny with lower efficiency. The opposite would be expected in Rambouillets where the genetic correlation was positive.

Genetic parameters from the pooled data (Rambouillets, Targhees and Columbias). Table 19 shows the heritabilities, and genetic and phenotypic correlations among the traits studied from the pooled data using model C. These analyses were performed in order to obtain more general estimates of the genetic parameters with the advantages related to the greater sample size. The sample size consideration primarily affected the estimation of the sires components of variance.

Heritability estimates. The heritability estimates for the productive traits ATLB, ATLW, ATNW and ATFP were .43, .33, .11 and .68, respectively. Stobart (1983) found values of .42, .08, .03 and .31 for similar to those found in this study. Timon and Eisen (1969) reported estimates of heritabilities for A, estimated from Richards and Logistic models in mice, that were larger. The heritability estimates for k were smaller when k was derived from Richards equation, but greater when derived from the Logistic equation.

TABLE 19. ESTIMATES^a OF HERITABILITIES, GENETIC AND PHENOTYPIC CORRELATIONS FOR LIFETIME PRODUCTION AND GROWTH TRAITS (POOLED DATA FROM RAMBOUILLET, TARGHEE AND COLUMBIA EWES)

	ATLB	ATLW	ATW	ATFP	A	k
ATLB	<u>.43±.15</u>	.72	.65	.02	.02	.12
ATLW	.91±.12	<u>.33±.15</u>	.95	.01	-.11	.17
ATW	1.13±.54	1.13±.30	<u>.11±.15</u>	.04	-.07	.17
ATFP	.20±.24	.20±.28	.27±.50	<u>.68±.16</u>	.27	-.09
A	.23±.30	.17±.35	.51±.73	.04±.25	<u>.42±.15</u>	-.53
k	.13±.26	.09±.29	.004±.51	-.20±.22	-.68±.44	<u>.56±.16</u>
EI	.82±.30	.92±.10	.75±.32	.09±.40	-.29±.62	.46±.38
AGR1	.37±.43	-.27±.49	-.54±.91	-.81±.43	.07±.44	.06±.38
AGR2	.09±.23	.45±.27	.86±.74	.38±.18	.15±.22	.32±.19
AGR3	.31±.28	-.14±.33	-.16±.56	-.09±.24	.49±.26	-.38±.30
AGR4	.23±.28	.38±.32	.75±.72	.05±.23	.29±.26	.36±.22
AGR5	.49±.29	.30±.33	.62±.65	-.12±.24	.55±.21	-.02±.27
RGR1	.03±.25	-.24±.29	-.42±.59	-.42±.22	-.24±.25	.29±.21
RGR2	.08±.23	.51±.28	.95±.81	.39±.19	.07±.23	.36±.20
RGR3	.15±.30	-.28±.34	-.43±.65	-.14±.26	.38±.31	-.43±.34
RGR4	.01±.30	.26±.34	.64±.73	-.28±.27	-.21±.31	.64±.24
RGR5	.04±.24	.05±.27	-.11±.46	-.43±.22	-.09±.24	.46±.20
AMR1	.04±.29	-.35±.33	-.80±.77	-.58±.28	-.74±.47	.62±.15
AMR2	.09±.22	.46±.27	.82±.71	.34±.18	-.03±.23	.44±.17
AMR3	.30±.33	-.23±.36	-.39±.66	-.17±.29	.25±.36	-.19±.30
AMR4	.05±.25	.23±.27	.33±.49	-.04±.20	-.57±.37	.89±.05
AMR5	.26±.25	.14±.29	.12±.49	-.24±.23	-.56±.41	.78±.09

^aHeritability estimates are underlined, phenotypic correlations above the heritabilities, and genetic correlations below heritabilities.

TABLE 19. (Continued)

Traits	RGR1	RGR2	RGR3	RGR4	RGR5	AMR1
ATLB	-.002	.02	.06	.03	.06	.06
ATLW	-.05	.01	.06	.04	.06	.09
ATWW	-.04	.04	.05	.05	.06	.08
ATFP	-.09	.05	-.08	-.11	-.14	-.10
A	.006	.02	.06	.01	.01	-.40
k	.14	.13	-.28	.23	.15	.67
EI	-.04	.05	.02	.05	.05	.19
AGR1	.58	-.43	-.18	.18	.05	.70
AGR2	-.09	.97	-.50	.32	.12	-.34
AGR3	-.18	-.34	.93	-.24	.26	-.21
AGR4	.16	.48	-.55	.46	.19	.18
AGR5	.05	.14	.20	.22	.36	.01
RGR1	<u>.65±.15</u>	-.13	-.21	.34	.11	.57
RGR2	-.23±.20	<u>.76±.16</u>	-.43	.31	.12	-.43
RGR3	-.02±.26	-.72±.38	<u>.40±.15</u>	-.33	.23	-.23
RGR4	.31±.23	.53±.20	-.17±.36	<u>.40±.15</u>	.52	.17
RGR5	.18±.20	.24±.18	.13±.24	.70±.16	<u>.70±.16</u>	.04
AMR1	.80±.14	-.36±.30	.04±.31	.27±.29	.21±.24	<u>.44±.15</u>
AMR2	-.17±.20	.99±.01	-.73±.39	.61±.19	.30±.18	-.28±.26
AMR3	.02±.28	-.67±.40	.95±.03	-.02±.36	.25±.25	.22±.34
AMR4	.20±.20	.76±.13	-.65±.44	.77±.18	.50±.19	.30±.21
AMR5	.08±.22	.30±.20	.11±.27	.54±.25	.64±.16	.38±.21

TABLE 19. (Continued)

Traits	EI	AGR1	AGR2	AGR3	AGR4	AGR5
ATLB	.60	.09	.04	.11	.10	.17
ATLW	.92	.02	.01	.09	.05	.11
ATWW	.95	.04	.05	.09	.10	.15
ATFP	-.06	.11	.11	-.004	.20	.18
A	-.37	.36	.12	.27	.41	.61
k	.32	.26	.19	-.21	.38	.15
EI	<u>.15±.15</u>	-.08	.17	-.002	-.04	-.05
AGR1	-.57±.83	<u>.19±.15</u>	-.25	-.003	.51	.48
AGR2	.63±.48	-.45±.44	<u>.80±.16</u>	-.36	.65	.28
AGR3	-.44±.52	.51±.48	-.47±.30	<u>.44±.15</u>	-.27	.50
AGR4	.42±.52	-.18±.39	.96±.10	-.24±.32	<u>.48±.15</u>	.67
AGR5	.13±.50	-.03±.47	.43±.21	.72±.20	.55±.19	<u>.40±.15</u>
RG R1	-.20±.42	.90±.25	-.20±.20	-.09±.25	.04±.24	-.20±.25
RG R2	.77±.52	-.48±.51	.99±.01	-.52±.31	.94±.14	.39±.23
RG R3	-.60±.57	.59±.59	-.67±.38	.95±.04	-.44±.43	.56±.29
RG R4	.71±.59	.17±.43	.52±.20	-.10±.32	.67±.20	.28±.29
RG R5	.18±.39	.25±.35	.27±.20	.15±.23	.50±.21	.53±.20
AMR1	-.20±.45	.61±.24	-.40±.29	-.10±.31	-.31±.26	-.48±.32
AMR2	.73±.47	-.48±.47	.98±.01	-.54±.32	.90±.12	.34±.22
AMR3	-.45±.53	.73±.66	-.61±.39	.96±.04	-.32±.42	.72±.30
AMR4	.66±.41	-.27±.34	.70±.12	-.58±.38	.62±.15	.02±.26
AMR5	.49±.36	-.06±.38	.25±.19	.13±.25	.25±.23	.37±.23

TABLE 19. (Continued)

Traits	AMR2	AMR3	AMR4	AMR5
ATLB	.04	.11	.08	.16
ATLW	.04	.14	.13	.24
ATWW	.07	.12	.14	.24
ATFP	.04	-.11	-.05	-.14
A	-.08	-.09	-.44	-.50
k	.31	-.03	.85	.81
EI	.10	.14	.27	.38
AGR1	-.33	-.13	.20	.11
AGR2	.97	-.43	.53	.15
AGR3	-.41	.92	-.50	.22
AGR4	-.56	-.45	.62	.24
AGR5	.14	.28	.13	.37
RGR1	-.09	-.18	.16	.06
RGR2	.97	-.37	.46	.12
RGR3	-.51	.95	-.61	.14
RGR4	.33	-.27	.45	.22
RGR5	.12	.25	.18	.39
AMR1	-.26	-.07	.52	.48
AMR2	<u>.81+.16</u>	-.41	.63	.25
AMR3	-.65+.40	<u>.33+.15</u>	-.38	.41
AMR4	.81+.09	-.45+.38	<u>.64+.16</u>	.66
AMR5	.36+.18	.40+.25	.67+.12	<u>.56+.16</u>

each of these traits, respectively. The estimates were similar for ATLB and for ATWW. However, the differences were large for estimates of ATLW and ATPP.

Heritability estimates for A and k were .42 and .56, respectively, indicating that A and k each would respond readily to selection. Heritabilities reported for A and k in mice (Eisen et al., 1969), when estimated from the growth parameters derived from the Logistic growth equation, were very similar to the values found in this study. However, heritabilities for the k parameter derived from Gompertz and Bertalanffy models gave higher estimates. Heritability estimates for A, for all the growth models used by these authors, gave values very

These two studies derived growth parameters from different growth equation models and used the full-sib method for estimating heritabilities. This could be a cause of some of the difference in the estimates obtained. There is also a species and method of rearing effect involved.

The heritability estimates for A and k were higher than these found by Brown et al. (1972) using Brody's model in cattle. However, the average of the heritabilities found by these authors for k was very similar. DeNise and Brinks (1985) reported estimates of heritabilities for A, using Brody's and Richards' models, in cattle that were very similar to the values found in this study, but their estimate for the heritability of k was smaller.

The heritability estimate for EI was .15. This low value suggests that the direct selection by EI would not produce a rapid response. No other reports in the literature for this type of index could be found.

Heritabilities of the estimated growth statistics were in general larger than the growth statistics found in sheep (Stobart, 1983) and in cattle (Fitzhugh and Taylor, 1971; Smith et al., 1976). The heritability estimates found by Stobart (1983) that were in close agreement to those found in this study were for the 12-18 mo interval. For AGR, RGR and AMR, the author reported .43, .39, and .32 which are almost identical to .44, .40 and .33 found in the present study for these traits, respectively. The heritability estimates for the statistics in other intervals were different and did not follow the same patterns.

The lack of close agreement of Stobart's AMR heritability estimates with the AMR values found in this study might be due to computational difference used in each case as noted earlier. The A values used in calculating AMR values for the present study were obtained by applying Brody's equation independently to each animal's set of age-weight data. Stobart's approach was based on the determination of mature size, which corresponds roughly to Brody's A value, using the mean of weight data from 42 and 54 mo. These data represented 94.9 and 97.6% of mature mean weight, respectively. This result is in disagreement with the findings in this study where 97% of mature size was found at 30 mo and 98% at 36 mo of age. Mature size was reached in Rambouillets, Targhees and Columbias approximately at 39 mo, 38 mo and 41 mo, respectively.

With respect to the heritability estimates of RGR, the different formula used by Stobart (1983) could be the reason for part of the difference. For AGR, there might be the other causes; the sample itself

and the different model used for the estimation of the genetic and phenotypic parameters.

Genetic correlations. Genetic correlations between the most important productive traits, ATWW, ATFP, and EI, and the growth parameter A were .51, .04, and -.29, respectively. The corresponding genetic correlations with k were .004, -.20 and .46, respectively. The genetic correlation between A and k was -.68, a value very similar to those previously reported in other species: mice (Eisen et al., 1969) and cattle (Brown et al., 1972; DeNise and Brinks, 1985).

The genetic correlations found between the productive traits and the growth parameters A and k indicate that ewes with a higher additive genetic potential for production of lamb at weaning (ATWW) will have an additive genetic potential for larger mature size. However, ewes selected for lamb production (ATWW) would have neither a correlated advantage nor disadvantage in their genetic potential for maturing rate. The small but positive genetic correlation between ATFP and A is in agreement with Turner and Young (1969), but is contrary to the finding of Stobart (1983). The correlated effect of selection for rapid maturing rate, k, would be a reduction in mature size, higher lamb production efficiency (EI), reduction in grease fleece weight, but no effect on absolute weight of lambs weaned.

The disadvantage of using either A or k as a mass selection criteria rests on when it can be estimated. It would require keeping the animals until they reach adult or mature sizes which is too late for effective selection. However, selection on the basis of AGR2 or RGR2 would permit early selection at 12 mo. Both AGR2 and RGR2 have

high genetic correlations with ATWW (.86 and .95) and EI (.63 and .77). AGR2 and RGR2 also have relatively high genetic correlations with ATFP (.38 and .39). The correlated responses from selection on the basis of AGR2 or RGR2 would be positive for these traits but would show little effect on A.

Genetic correlations among productive traits were all positive. ATFP had low genetic correlations with ATLB, ATW and ATWW (.20, .20 and .27, respectively). ATLB was highly correlated with ATW and ATWW (.91 and 1.13, respectively). The correlation between ATW and ATWW was high (1.13). There was poor agreement with the genetic correlations reported by Stobart (1983), particularly for ATFP-ATW, ATFP-ATWW and ATW-ATWW which were -.44, -.01 and .84, respectively.

The very low positive genetic relationship obtained between ATFP with ATLB and ATW contradicts the finding of a lifetime productivity study in Rambouillet by Shelton and Menzies (1968) who found correlations of -.13 and -.25 between these traits, respectively. However, these correlations were very similar to those obtained in the present study for Rambouillets. Perhaps the effect of the pooled breed analysis contributed to this result since Rambouillets were different from Targhees and Columbias in this study.

Very high genetic correlations between AGR, RGR and AMR in the same intervals suggests that RGR and(or) AGR values could be used advantageously for early selection instead of AMR when selection for rapid maturity is desired. The genetic correlations between AGR, RGR and AMR within the same intervals reported by Stobart (1983) were

generally lower. This was especially true for birth to weaning and birth to 18 months intervals, where negative estimates were obtained.

Genetic correlations reported by Stobart (1985) between growth statistics and productive traits were generally different with the estimated values in this study. Good agreement was found for the correlations of ATFP with AGR2, RGR2 and AMR2 where the highest positive values were found in both studies. However, the correlations between the growth statistics with the reproductive traits ATLB, ATW and ATWW were different both in values and patterns. The difference in this case could be due to the fact that Stobart used data from ewes, some of which did not completed their lifetime production.

The genetic correlations of ATWW and EI with the Fitzhugh and Taylor (1971) growth statistics suggest that a positive additive genetic relationship exists between growth in the weaning to 12 mo period and productive performance. The genetic correlations between these growth statistics and ATFP were also positive but lower. From a practical point of view, RGR in the weaning to 12 mo interval age should be useful in selection.

The positive correlation found between the growth statistics for weaning-12 mo interval with ATWW and EI appears to be based in part on the animal's genetic capacity for overcoming stress after weaning and during the fall-winter growth period and its association with a more efficient lifetime production. However, the genetic correlations of EI with the growth during the birth-weaning interval were negative. This latter observation supports the idea that early growth from birth to weaning should not be used as selection criteria for subsequent

productivity. Shelton and Menzies (1968) indicated a preference for using yearling weight as a measure of the productive potential of the ewes instead of weaning weight.

Phenotypic correlations. The phenotypic correlations obtained from the pooled data (model C analyses) indicate relationships among traits due to a variety of factors that affect the individual animal. The correlations between ATLW-ATFP (.01) and ATWW-ATFP (.04) indicate that lamb production, under the range conditions in which these ewes produced their lambs, did not affect their ATFP. This response agrees with Basuthakur et al. (1973), but does not agree with Shelton and Menzies (1968).

Stobart (1983) reported phenotypic correlations that were somewhat higher, but had the same pattern. There were substantial differences between the correlations ATLB-ATFP and ATWW-ATFP. Stobart's values were .13 and .17, compared .02 and .04, respectively, found in this study. Also, the correlation between EI and ATFP (-.06) indicates that lamb production relative to mature size did not affect the ewe's performance for ATFP.

On the other hand, the correlation of -.37 found between EI and A indicates that the most efficient ewes tend to be smaller. The estimated genetic correlation and the estimated phenotypic correlation between EI and A were similar (-.29 and -.37, respectively) suggests that part of the relationship between them may be due to the effect of reproduction itself. Part of the reason smaller size ewes produced more lamb at weaning per unit of weight may be because their production contributes to smaller mature sizes. This suggestion is reinforced by

the environmental correlation ($r_e = -.42$) found between these two traits which indicates that the environment conducive to a high EI tends to have a negative effect on A.

Phenotypic correlations between growth statistics and productive traits tended to have low negative and positive values, from $-.14$ to $.24$. The lowest value corresponded to the correlation between ATRP and RGR5, and the highest to the correlation between AMR5 with ATWW and AMR5 with ATLW. Very low positive values were observed for the phenotypic correlations between AGR, RGR and AMR in the interval weaning-12 mo with all the productive traits. Stobart (1983) reported estimates with similar patterns, with differences mainly involving the AMR relationships.

Phenotypically, the relationship between growth statistics before 18 mo of age and the productive traits had low values. Correlations involving AMR tended to be slightly higher, but AGR5 appears to have greater practical application for early selection of animals with a phenotypic potential for subsequent production. However, the phenotypic correlation of AGR5 with EI indicates that animals selected on the basis of that criteria would not be necessarily the most efficient and also would tend to be of larger mature sizes. The most practical growth statistic in phenotypic terms appears to be AGR2 which has no negative correlations with the productive traits and also its correlation with EI is positive ($.17$).

Selection indexes.

Selection indexes were derived utilizing the growth parameters A and k or the growth statistics that showed the highest genetic

correlations with either ATWW or EI. In some indexes, ATPF was also included. The among sires and within sires variance and covariance components from which the genetic and phenotypic variances and covariances used in the development of the indexes are shown in the Appendix Tables 50 and 51.

Table 20 presents the 22 indexes, their respective standard deviation and expected responses to selection relative to selection for the single traits ATWW or EI. The inclusion of A and k, in index two, increased the accuracy of selection for ATWW 174%. From the other indexes, for ATWW that included A and(or) k, it was observed that the most influential positive effect was due to A. The influence of ATPF when included gave more advantage than the inclusion of k. When AGR2 and RGR2 were incorporated, index nine, a very significant, 380% response was observed compared to the use of mass selection for ATWW alone. The most influential effect in that response was due to RGR2.

The inclusion of A and k in the indexes derived for EI gave limited advantage, only 21% for index 13. Thus, there appears to be no practical use for A and (or) k as components for an index of selection for efficiency. The effects of AGR2 and RGR2 on the accuracy of selection for EI was more beneficial than A and k. Index 20 shows an advantage of 117%, which represents a substantial increase in expected response of EI.

When ATPF was included in the indexes for ATWW and EI, there was a very slight positive effect. This finding shows that the influential effects of ATPF on reproductive performance are at least not antagonistic.

TABLE 20. DERIVED SELECTION INDEXES FOR THE ANALYSIS OF THE EFFECT OF A, k, AGR2 AND RGR2 ON THE IMPROVEMENT OF AVERAGE TOTAL OF WEIGHT OF LAMBS WEANED (ATWW) AND EFFICIENCY INDEX (EI) BY SELECTION

N	Trait	Index	Index ^a standard deviation	Single ^b trait response	relative ^c response
ATWW				22.72	
1		.102ATWW+.292ATFP+.278A+30.01k	62.56		2.75
2		.105ATWW+.286A+30.15k	62.32		2.74
3		.113ATWW+.222A	59.12		2.60
4		.107ATWW-.3.22k	40.12		1.76
5		.093ATWW+1.09ATFP	43.80		1.93
6		.076ATWW+1.76ATFP-6.33AGR2+676RGR2	111.48		4.90
7		.088ATWW+.512TFP+6.03AGR2	101.24		4.45
8		.085ATWW+.831ATFP+350RGR2	108.72		4.75
9		.096ATWW-4.43AGR2+582RGR2	109.16		4.80
10		.093ATWW+6.09AGR2	100.88		4.44
11		.094ATWW+352RGR2	107.80		4.71
EI				.826	
12		.129EI+.014ATFP+.0006A+.764k	1.02		1.23
13		.131EI+.001A+.785k	1.00		1.21
14		.147EI-.0005A	.85		1.03
15		.123EI+.670k	.98		1.19
16		.157EI+.013ATFP	.88		1.06
17		.131EI+.019ATFP-.196AGR2+15.13RGR2	1.82		2.20
18		.151EI+.005ATFP+.079AGR2	1.48		1.79
19		.144EI+.008ATFP+4.99RGR2	1.66		2.01
20		.129EI-.175AGR2+14.11RGR2	1.79		2.17
21		.150EI+.080AGR2	1.48		1.79
22		.142EI+5.02RGR2	1.66		2.01

^aIndex standard deviation: σ_I

^bTrait response: $1h^2\sigma_p$

^cRelative response of index use: $1\sigma_I/1h^2\sigma_p$ (Falconer, 1981)

Additional indexes were estimated for the simultaneous improvement of ATWW, ATPF and EI. These indexes are presented in Table 21. In this set of indexes (1 to 8, except 4), AGR2 was found to have a high positive influence on the simultaneous improvement of the three traits. AGR2 explained approximately 60% of the variance of the aggregate genotypes that included these traits. Inclusion of AGR2, with RGR2, resulted in an additional 10% in accuracy.

The poorest efficiencies were observed for the simultaneous improvement of ATPF and EI (indexes 4 and 9). In these cases, AGR2 alone (index 9) or combined with RGR2 (index 4) gave the highest efficiencies ($R^2=.18$). RGR2 when considered alone (indexes 10 to 13) had a very low or almost null effect (from $R^2=.003$ to .01) on the improvement of ATWW, ATPF and EI or their combination in pairs. Inclusion of ATPF as component in two of the indexes (5 and 18) for the improvement of ATWW and EI resulted in an increase of almost 5% in R^2 when associated with AGR2 and RGR2, and 20% when ATPF was involved along with A and k.

Depending on the objectives of selection, indexes for improving a single trait or the combination of simultaneous traits would require certain specific growth traits for maximizing the expected response to selection. In the case of single trait indexes, RGR2 proved to be the most useful; however, when more than one trait was the objective of improvement AGR2 was the most advantageous.

In general, the contribution of A and k was small in these two sets of indexes. Their late availability for selection purposes

TABLE 21. DERIVED SELECTION INDEXES FOR THE ANALYSIS OF THE EFFECT OF A, k, AGR2 AND RGR2 ON THE SIMULTANEOUS IMPROVEMENT OF AVERAGE TOTAL WEIGHT OF LAMBS WEANED (ATWW), EFFICIENCY INDEX (EI) AND AVERAGE TOTAL OF GREASE FLEECE PRODUCED (ATFP)

N	Traits to be improved	Index	Index variance	Aggregated genotype variance ^a	Accuracy r^2 ^a
1	ATWW, ATFP, EI	-4.08AGR2+591RGR2	11914	16622	.72
2	ATWW, ATFP	-3.89AGR2+576RGR2	11578	16216	.71
3	ATWW, EI	-4.32AGR2+587RGR2	10936	15480	.71
4	ATFP, EI	.044AGR2+19.6RGR2	38.83	209.1	.18
5	ATWW, EI ^b	-6.15AGR2+677RGR2+1.65ATFP	11677	15480	.75
6	ATWW, ATFP, EI	6.60AGR2	10123	16622	.61
7	ATWW, ATFP	6.52AGR2	9878	16216	.61
8	ATWW, EI	6.29AGR2	9172	15480	.59
9	ATFP, EI	.398AGR2	36.87	209.1	.18
10	ATWW, ATFP, EI	7.33RGR2	225.1	16622	.01
11	ATWW, ATFP	7.23RGR2	219.1	16216	.01
12	ATWW, EI	7.00RGR2	205.7	15480	.01
13	ATFP, EI	.422RGR2	.7459	209.1	.003
14	ATWW, ATFP, EI	.287A+36.9k	2271	16622	.14
15	ATWW, ATFP	.287A+36.0k	2273	16216	.14
16	ATWW, EI	.292A+40.3k	2356	15480	.15
17	ATFP, EI	-.005A-2.4k	2.571	209.1	.01
18	ATWW, EI ^b	.246A+37.5k+1.67ATFP	3103	15480	.20

^aMethod of estimation as presented by Falconer (1981).

^bFirst shearing grease fleece weight could be used instead of ATFP due to its high repeatability (Turner and Young, 1969).

further limit their use in programs of selection as predictors of genetic potential for productive efficiency.

Conceptual analysis of results.

From the genetic analysis of all the information in this study, some speculation could be made in terms of the possible biological basis of the relationship found between growth in the interval weaning to 12 mo and reproductive efficiency.

The particular response could be a selective effect of season favoring a specific genotype. The interval, weaning to 12 mo, is important from an adaptive point of view for the population. After weaning, the animals begin to depend on themselves and it is the interval when puberty occurs. As the animals are raised on the range, growth from weaning to 12 mo mostly occurs under the harsh effects of winter, capacity for efficient winter growth should be a very important characteristic.

An analogy between growth performance from weaning to 12 mo and subsequent annual reproductive efficiency could be made. Almost half of gestation occurs in winter. This presupposes that as natural selection has always selected the population towards the ideal fitness for this particular environment and that reproductive performance is the main trait affected by natural selection. It is possible that the effect of natural selection on achievement of gestation during an always repeated environmental event (winter), has developed a correlated response on growth specifically from weaning to 12 mo of age (source of genetic correlation).

Winter environmental conditions in Montana are harsh. Successful growth and reproductive performance could also be considered a capacity for overcoming stress. Stress and adaptability are two opposite terms that evaluate the same thing. It appears that lifetime performance is a conjugate of two genetic components; one related to the genetic potential capacity for production and the other related to the genetic capacity for overcoming the periodical stress produced by seasonal environmental changes. The reproductive requirements also have a seasonal onset. In this situation, the superiority of twinning ability, in terms of lifetime efficiency, could be associated with the capability for overcoming stress.

Price (1985) states that there exists an evolutionary, as well as ontogenic, determinant in the response to stress. In evolutionary terms, natural selection would tend to reduce the stressful effects of certain condition that affects a given population generation after generation. In the case of sheep under range conditions of Montana, the only alternative for their survival was to have gestation during winter. This capability already existed in domesticated sheep when introduced to United States from Europe. If we consider the biological needs of sheep for survival, it will be difficult to find other alternatives without substantial alteration of the environmental conditions. Undesirable effects of high temperatures during gestation in ewes (Thwaites, 1985) apparently has an evolutionary effect.

Perhaps the same genetic characteristic existing in twins for overcoming stress also exists in the group of singles. One way to observe it would be the evaluation of their relative growth rate from

weaning to 12 mo of age. Moberg (1985) states that in each event in which stressful conditions take place homeostasis is compromised. The active function of the central nervous system (CNS) dictates which of the physiological systems must respond to maintain homeostasis. Maybe the ability of certain animals for a fast and adequate response or efficient functioning of CNS under stress give them a cumulative superiority in their lifetime productive performances. This approach gives an apparent explanation to the association between the "index of Cephalization" and longevity suggested by Comfort (1961).

Genetic adaptability relies in large part on genetic effects other than additive. Dobzhansky (1951) indicated that heterozygotes have adaptive superiority over homozygotes, which is the essential condition for the establishment of balanced polymorphisms. Also, Lerner (1954) refers to the higher plasticity of heterozygotes. This means that if there exists additive genetic variability for dealing with stress, it would be at a very low level. The low additive variability found in the breed having the highest performances (Targhees) would give apparent support to this speculation.

SUMMARY AND CONCLUSIONS

Under the range conditions of Montana, Targhee ewes were more efficient in lifetime production (EI) than Rambouillet and Columbia ewes. Columbias were the poorest in productive efficiency, but had the highest grease wool production. Ewes remaining in the flock longer (6 yr) showed the highest average yearly performances for all productive traits. Apparently, this advantage was due to selection.

Ages at maturity were approximately 39 mo, 38 mo and 41 mo for Rambouillets, Targhees and Columbias, respectively. Rambouillets had the smallest mature size and Columbias the slowest maturing rate. Mature sizes were 70.04, 72.42 and 73.11 kg for the Rambouillet, Targhee and Columbia breeds, respectively. Targhees had the faster maturing rates (k) followed by Rambouillets. Columbia ewes were the slowest growing group.

Ewes remaining in the flock, until they had 4 and 5 reproductive records, were smaller at maturity, but differences were not significant. Maturing rate (k) in the five-record group of ewes was significantly slower. Phenotypically, the slower maturing rate could be explained by the higher rate of production in the five-record group.

There were breed differences in growth rates during all the intervals previous to 18 mo of age (birth-weaning, weaning-12 mo, 12-18 mo, birth-12 mo and birth-18 mo). Rambouillets had faster growth in the interval weaning-12 mo interval, but Targhees and Columbias excelled in the 12 to 18 mo interval.

Heritability estimates from the pooled data set were .43, .33, .11, .68, .42, .56 and .15 for the average number of lambs born, number of lambs weaned, weight of lamb weaned, fleece weight, mature size, maturing rate and efficiency index. The highest heritabilities for the growth statistics (AGR, RGR and AMR) were observed in weaning to 12 mo interval.

Genetic correlations between productive traits and Brody's growth parameters A and k derived from the pooled data set indicated that ewes with higher additive genetic potential for weaned lamb production will also have genetic potential for larger mature sizes. However, ewes selected for high additive genetic production potential for lambs at weaning would show no correlated effect for maturing rate. In terms of efficiency (EI), the opposite occurs. Ewes with genetic potential for larger mature sizes (A) tended to have lower efficiency, but faster maturing rates (k).

Genetic correlations of ATFP with A and k were low indicating that increased mature size will not affect ATFP and that faster maturing rate (k) will tend to slightly reduce ATFP. Growth statistics for weaning to 12 mo of age interval showed the highest genetic relationships with the subsequent productive traits in the ewes, as well as reproductive efficiency. The RGR growth statistic, in the weaning to 12 mo interval, appears to be the most efficient and practical for selective purposes.

Indexes of selection for ATWW which include RGR2 gave the highest relative response to selection compared to mass selection for ATWW. The advantage was 380% greater selection response per generation. When

EI was the trait of interest, growth parameters A and k showed no practical advantage in the indexes, however AGR2 and RGR2, especially RGR2, produced a significant improvement on the expected selection response of 117%. This indicates a possible practical use in selection for efficiency. ATRP showed a small positive effect when included in the indexes for improving the accuracy for selection for either ATWW or EI.

Twins raised as twins tended to grow slower up to weaning than did singles raised as singles and twin raised as singles, but they grew faster in the weaning to 12 mo interval. Twins had smaller mature sizes than singles and slower maturing rates. Ewes born twins produced 2.2 kg more lamb at weaning each year, on the average, than ewes born singles, and they had the highest productive efficiency indexes. However, they produced .1 kg less grease fleece weight yearly than ewes born singles.

The genetic relationships between growth during the interval from weaning to 12 mo and the productive traits and efficiency suggest that productive lifetime efficiency could be improved by selecting for growth during that period in the animal's life.

Some conceptual ideas were put forth regarding possible biological basis, in addition to linkage and pleiotropy which may contribute to the genetic correlations obtained between growth in the weaning to 12 mo interval and lifetime productive efficiency. This involved the effect of seasonal stress during the winter period following weaning to which each group of young ewes were subjected. It is in this period when the young ewes begin to depend on their own ability to forage for

food and it is the period when puberty normally occurs. Thus, it is an important developmental period, requiring the ability to adapt to a biologically stressful situation. The capacity to grow under these conditions was considered a good measure of adaptability. Twin born ewes may undergo an even greater stress than singles. The genotypes associated with this adaptive ability expressed as growth response, may also be the genotypes that affect reproductive fitness. The animals that are able to respond favorably to the early stress of the weaning to 12 mo period apparently are also able to produce well later in life.

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APPENDIX

TABLE 22. AVERAGES, VARIATION AND RANGES OF LIFETIME AVERAGE OF TOTAL NUMBER OF LAMBS BORN (ATLB) FOR EWE GROUPS WITHIN BREEDS

Breed	Number of records	N	Average	Standard deviation	Coef. of variation	Lowest	Highest
Rambouillet	3	74	1.28	.366	28.65	.33	2.00
	4	64	1.39	.284	20.40	.75	2.00
	5	164	1.46	.299	20.48	.60	2.20
Targhee	3	74	1.38	.388	28.12	.67	2.33
	4	47	1.34	.356	26.43	.25	2.00
	5	217	1.52	.312	20.50	.80	2.20
Columbia	3	54	1.23	.398	32.39	.67	2.00
	4	21	1.20	.444	36.97	.50	2.25
	5	100	1.47	.302	20.48	.80	2.40

TABLE 23. AVERAGES, VARIATION AND RANGES OF LIFETIME AVERAGE OF THE TOTAL NUMBER OF LAMBS WEANED (ATLW) FOR EWE GROUPS WITHIN BREEDS

Breed	Number of records	N	Average	Standard deviation	Coef. of variation	Lowest	Highest
Rambouillet	3	74	1.01	.407	40.14	.00	2.00
	4	64	1.16	.322	27.78	.50	1.75
	5	164	1.25	.300	24.00	.40	2.00
Targhee	3	74	1.12	.350	31.32	.33	2.00
	4	47	1.19	.332	27.96	.25	2.00
	5	217	1.33	.312	23.45	.60	2.00
Columbia	3	54	.90	.409	45.67	.00	2.00
	4	21	.93	.364	39.15	.50	1.75
	5	100	1.27	.271	21.24	.80	1.80

TABLE 24. AVERAGES, VARIATION AND RANGES OF LIFETIME AVERAGE OF THE TOTAL OF KILOGRAMS OF LAMBS WEANED (ATWW) FOR EWE GROUPS WITHIN BREEDS

Breed	Number of records	N	Average	Standard deviation	Coef. of variation	Lowest	Highest
Rambouillet	3	74	38.40	14.84	38.74	.00	71.40
	4	64	44.07	11.82	26.82	16.25	68.18
	5	164	47.90	11.20	23.39	17.54	80.48
Targhee	3	74	45.44	12.87	28.33	14.83	79.40
	4	47	48.32	13.37	27.68	9.10	68.98
	5	217	54.17	11.90	21.98	24.82	84.12
Columbia	3	54	36.65	16.63	45.37	.00	78.17
	4	21	37.58	13.21	35.14	18.08	70.35
	5	100	50.72	11.05	21.79	26.62	72.92

TABLE 25. AVERAGES, VARIATION AND RANGES OF LIFETIME AVERAGE OF KILOGRAMS OF GREASE FLEECE PRODUCED (ATFP) FOR EWE GROUPS WITHIN BREEDS

Breed	Number of records	N	Average	Standard deviation	Coef. of variation	Lowest	Highest
Rambouillet	3	74	4.32	.48	11.17	3.32	5.58
	4	64	4.52	.52	11.43	3.20	5.98
	5	164	4.54	.48	10.64	3.62	6.40
Targhee	3	74	4.65	.56	12.12	3.45	5.80
	4	47	4.82	.61	12.73	3.32	6.10
	5	217	4.86	.55	11.28	3.51	6.38
Columbia	3	54	4.82	.64	13.35	3.00	6.08
	4	21	4.97	.85	17.09	2.84	6.24
	5	100	5.19	.60	11.55	3.70	6.55

TABLE 26. AVERAGES, VARIATION AND RANGES OF MATURE SIZE (A) FOR EWE GROUPS WITHIN BREEDS

Breed	Number of records	N	Average	Standard deviation	Coef. of variation	Lowest	Highest
Rambouillet	3	74	69.55	6.64	9.55	53.62	84.81
	4	64	71.36	7.1	9.99	56.88	89.35
	5	164	71.56	5.49	7.67	58.15	85.79
Targhee	3	74	72.95	8.35	11.45	56.11	96.84
	4	47	72.96	7.30	10.01	58.85	94.45
	5	217	74.25	6.78	9.14	58.57	93.70
Columbia	3	54	74.53	9.70	13.01	54.24	98.76
	4	21	75.72	5.38	7.10	64.61	86.06
	5	100	73.56	6.31	8.58	59.12	93.38

TABLE 27. AVERAGES, VARIATION AND RANGES OF BRODY'S CONSTANT OF INTEGRATION (B) FOR EWE GROUPS WITHIN BREEDS

Breed	Number of records	N	Average	Standard deviation	Coef. of variation	Lowest	Highest
Rambouillet	3	74	62.52	5.84	9.35	47.92	76.50
	4	64	63.36	5.97	9.42	51.45	78.29
	5	164	63.90	4.84	7.58	53.22	77.87
Targhee	3	74	65.54	7.28	11.11	49.61	85.45
	4	47	65.45	6.74	10.29	52.71	86.63
	5	217	66.16	6.14	9.28	54.64	85.82
Columbia	3	54	66.45	8.50	12.81	51.17	86.85
	4	21	67.20	4.51	6.72	56.65	74.80
	5	100	65.46	5.55	8.48	52.58	82.15

TABLE 28. AVERAGES, VARIATION AND RANGES OF MATURING RATE (K) FOR EWE GROUPS WITHIN BREEDS

Breed	Number of records	N	Average	Standard deviation	Coef. of variation	Lowest	Highest
Rambouillet	3	74	.1160	.026	22.36	.0740	.1889
	4	64	.1104	.030	27.56	.0627	.1842
	5	164	.1072	.024	22.22	.0637	.2057
Targhee	3	74	.1216	.035	29.19	.0612	.2428
	4	47	.1154	.029	24.90	.0446	.1979
	5	217	.1101	.027	24.22	.0625	.2314
Columbia	3	54	.1060	.039	36.56	.0494	.2178
	4	21	.0947	.034	36.25	.0443	.1904
	5	100	.1042	.034	32.31	.0556	.3260

TABLE 29. AVERAGES, VARIATION AND RANGES OF EWE EFFICIENCY INDEX (EI) FOR EWE GROUPS WITHIN BREEDS

Breed	Number of records	N	Average	Standard deviation	Coef. of variation	Lowest	Highest
Rambouillet	3	74	.557	.218	39.20	.0000	1.007
	4	64	.623	.174	27.96	.2089	.986
	5	164	.673	.162	23.99	.2062	1.109
Targhee	3	74	.635	.200	31.58	.1531	1.216
	4	47	.671	.198	29.52	.1157	1.013
	5	217	.731	.152	20.80	.3381	1.172
Columbia	3	54	.498	.230	46.15	.0000	1.027
	4	21	.501	.185	37.00	.2370	.916
	6	100	.693	.151	21.80	.4010	1.062

TABLE 30. AVERAGES, VARIATION AND RANGES OF ABSOLUTE GROWTH RATE IN THE INTERVAL BIRTH-WEANING (AGR1) FOR EWE GROUPS WITHIN BREEDS

Breed	Number of records	N	Average	Standard deviation	Coef. of variation	Lowest	Highest
Rambouillet	3	74	7.736	1.114	14.41	5.080	9.925
	4	64	8.062	1.249	15.49	5.580	10.200
	5	164	7.896	1.165	14.75	5.150	10.825
Targhee	3	74	8.548	1.271	14.87	5.620	12.250
	4	47	8.351	1.107	13.16	5.620	11.225
	5	217	8.483	1.226	14.45	5.560	11.750
Columbia	3	54	8.461	1.115	13.55	6.280	10.900
	4	21	8.183	1.341	16.39	6.060	11.050
	5	100	8.257	1.329	16.09	5.140	11.450

TABLE 31. AVERAGES, VARIATION AND RANGES OF ABSOLUTE GROWTH RATE IN THE INTERVAL WEANING-12 MONTHS (AGR2) FOR EWE GROUPS WITHIN BREEDS

Breed	Number of records	N	Average	Standard deviation	Coef. of variation	Lowest	Highest
Rambouillet	3	74	1.437	.694	48.33	.244	3.413
	4	64	1.425	.470	32.98	.256	2.713
	5	164	1.504	.623	41.46	.000	3.817
Targhee	3	74	1.199	.514	42.92	.200	2.600
	4	47	1.193	.610	51.14	-.122	3.033
	5	217	1.090	.540	49.57	-.311	2.563
Columbia	3	54	.978	.720	73.62	-.514	2.438
	4	21	1.040	.534	51.26	.144	2.013
	5	100	1.044	.681	65.19	-.443	3.400

TABLE 32. AVERAGES, VARIATION AND RANGES OF ABSOLUTE GROWTH RATE IN THE INTERVAL 12-18 MONTHS (AGR3) FOR EWE GROUPS WITHIN BREEDS

Breed	Number of records	N	Average	Standard deviation	Coef. of variation	Lowest	Highest
Rambouillet	3	74	2.677	1.171	43.75	-.040	5.633
	4	64	2.451	1.276	52.03	.250	5.633
	5	164	2.918	1.579	54.13	.150	7.050
Targhee	3	74	3.326	1.613	48.49	.800	6.950
	4	47	3.349	1.577	47.07	.967	6.825
	5	217	3.565	1.722	48.31	.000	8.700
Columbia	3	54	3.510	1.955	55.70	.450	8.325
	4	21	3.388	1.857	54.82	.850	7.175
	5	100	3.396	1.552	45.68	.683	7.067

TABLE 33. AVERAGES, VARIATION AND RANGES OF ABSOLUTE GROWTH RATE IN THE INTERVAL BIRTH-12 MONTHS (AGR4) FOR EWE GROUPS WITHIN BREEDS

Breed	Number of records	N	Average	Standard deviation	Coef. of variation	Lowest	Highest
Rambouillet	3	74	3.715	.468	12.61	2.783	4.945
	4	64	3.744	.475	12.71	2.686	4.727
	5	164	3.664	.481	13.13	2.700	5.055
Targhee	3	74	3.765	.605	16.08	2.131	5.755
	4	47	3.707	.575	15.51	2.438	4.982
	5	217	3.667	.493	13.45	2.562	4.964
Columbia	3	54	3.530	.462	13.09	2.669	4.555
	4	21	3.492	.732	20.97	2.238	5.064
	5	100	3.548	.502	14.14	2.456	4.400

TABLE 34. AVERAGES, VARIATION AND RANGES OF ABSOLUTE GROWTH RATE IN THE INTERVAL BIRTH-18 MONTHS (AGR5) FOR EWE GROUPS WITHIN BREEDS

Breed	Number of records	N	Average	Standard deviation	Coef. of variation	Lowest	Highest
Rambouillet	3	74	3.335	.343	10.29	2.612	4.076
	4	64	3.260	.356	10.92	2.553	4.106
	5	164	3.358	.343	10.22	2.676	4.163
Targhee	3	74	3.544	.400	11.30	2.661	4.665
	4	47	3.517	.430	12.22	2.744	4.653
	5	217	3.544	.434	12.24	2.647	4.913
Columbia	3	54	3.437	.480	13.96	2.676	4.882
	4	21	3.347	.401	11.98	2.835	4.294
	5	100	3.413	.366	10.76	2.456	4.400

TABLE 35. AVERAGES, VARIATION AND RANGES OF RELATIVE GROWTH RATE IN THE INTERVAL BIRTH-WEANING (RGR1) FOR EWE GROUPS WITHIN BREEDS

Breed	Number of records	N	Average	Standard deviation	Coef. of variation	Lowest	Highest
Rambouillet	3	74	.2122	.018	8.31	.1722	.2805
	4	64	.2165	.022	10.28	.1685	.2908
	5	164	.2202	.025	11.45	.1706	.2847
Targhee	3	74	.2181	.011	4.92	.1751	.2274
	4	47	.2125	.017	8.37	.1726	.2272
	5	217	.2125	.017	7.95	.1722	.2317
Columbia	3	54	.2223	.014	6.13	.1730	.2828
	4	21	.2156	.014	6.32	.1736	.2272
	5	100	.2140	.016	7.40	.1739	.2312

TABLE 36. AVERAGES, VARIATION AND RANGES OF RELATIVE GROWTH RATE IN THE INTERVAL WEANING-12 MONTHS (RGR2) FOR EWE GROUPS WITHIN BREEDS

Breed	Number of records	N	Average	Standard deviation	Coef. of variation	Lowest	Highest
Rambouillet	3	74	.0302	.012	41.08	.0051	.0602
	4	64	.0298	.009	31.32	.0059	.0491
	5	164	.0314	.011	32.04	.0000	.0716
Targhee	3	74	.0247	.010	39.82	.0045	.0549
	4	47	.0242	.011	46.53	-.0033	.0602
	5	217	.0223	.010	46.91	-.0081	.0478
Columbia	3	54	.0206	.015	71.77	-.0129	.0488
	4	21	.0221	.010	46.27	.0042	.0429
	5	100	.0217	.013	59.73	-.0100	.0609

TABLE 37. AVERAGES, VARIATION AND RANGES OF RELATIVE GROWTH RATE IN THE INTERVAL 12-18 MONTHS (RGR3) FOR EWE GROUPS WITHIN BREEDS

Breeds	Number of records	N	Average	Standard deviation	Coef. of variation	Lowest	Highest
Rambouillet	3	74	.0433	.017	40.13	.0007	.0925
	4	64	.0399	.019	48.57	.0049	.0925
	5	164	.0461	.023	49.50	.0026	.0972
Targhee	3	74	.0501	.022	44.16	.0137	.0919
	4	47	.0507	.021	41.27	.0151	.0939
	5	217	.0533	.022	42.00	.0000	.1259
Columbia	3	54	.0534	.025	46.69	.0074	.1117
	4	21	.0539	.028	52.52	.0129	.1144
	5	100	.0530	.025	41.57	.0125	.0989

TABLE 38. AVERAGES, VARIATION AND RANGES OF RELATIVE GROWTH RATE IN THE INTERVAL BIRTH-12 MONTHS (RGR4) FOR EWE GROUPS WITHIN BREEDS

Breed	Number of records	N	Average	Standard deviation	Coef. of variation	Lowest	Highest
Rambouillet	3	74	.0797	.0047	5.85	.0677	.0850
	4	64	.0783	.0055	7.12	.0625	.0842
	5	164	.0774	.0057	7.40	.0635	.0844
Targhee	3	74	.0781	.0065	8.29	.0664	.0913
	4	47	.0769	.0068	8.85	.0651	.0916
	5	217	.0760	.0067	8.79	.0641	.0895
Columbia	3	54	.0770	.0060	7.72	.0629	.0847
	4	21	.0755	.0073	9.62	.0635	.0841
	5	100	.0758	.0064	8.51	.0638	.0850

TABLE 39. AVERAGES, VARIATION AND RANGES OF RELATIVE GROWTH RATE IN THE INTERVAL BIRTH-18 MONTHS (RGR5) FOR EWE GROUPS WITHIN BREEDS

Breed	Number of records	N	Average	Standard deviation	Coef. of variation	Lowest	Highest
Rambouillet	3	74	.0545	.0015	2.85	.0506	.0585
	4	64	.0541	.0015	2.74	.0501	.0585
	5	164	.0543	.0015	2.84	.0499	.0585
Targhee	3	74	.0544	.0012	2.31	.0508	.0592
	4	47	.0542	.0016	2.97	.0504	.0554
	5	217	.0543	.0013	2.48	.0503	.0583
Columbia	3	54	.0543	.0016	3.00	.0482	.0582
	4	21	.0539	.0014	2.51	.0509	.0556
	5	100	.0540	.0015	2.76	.0505	.0590

TABLE 40. AVERAGES, VARIATION AND RANGES OF ABSOLUTE MATURING RATE IN THE INTERVAL BIRTH-WEANING (AMR1) FOR EWE GROUPS WITHIN BREEDS

Breeds	Number of records	N	Average	Standard deviation	Coef. of variation	Lowest	Highest
Rambouillet	3	74	.1116	.014	12.89	.0826	.1402
	4	64	.1133	.016	13.87	.0780	.1509
	5	164	.1105	.015	13.89	.0720	.1428
Targhee	3	74	.1177	.016	13.37	.0886	.1617
	4	47	.1149	.013	11.67	.0809	.1403
	5	217	.1145	.015	13.08	.0813	.1476
Columbia	3	54	.1151	.017	17.45	.0772	.1557
	4	21	.1085	.019	17.21	.0822	.1448
	5	100	.1128	.019	16.84	.0756	.1755

TABLE 41. AVERAGES, VARIATION AND RANGES OF ABSOLUTE MATURING RATE IN THE INTERVAL WEANING-12 MONTHS (AMR2) FOR EWE GROUPS WITHIN BREEDS

Breed	Number of records	N	Average	Standard deviation	Coef. of variation	Lowest	Highest
Rambouillet	3	74	.0208	.010	48.84	.0035	.0503
	4	64	.0203	.007	36.54	.0041	.0395
	5	164	.0213	.009	42.71	.0000	.0519
Targhee	3	74	.0166	.007	44.98	.0022	.0410
	4	47	.0166	.009	54.09	-.0018	.0436
	5	217	.0149	.008	52.36	-.0045	.0408
Columbia	3	54	.0134	.011	79.27	-.0080	.0408
	4	21	.0140	.008	76.62	.0017	.0283
	5	100	.0143	.010	66.94	-.0058	.0497

TABLE 42. AVERAGES, VARIATION AND RANGES OF ABSOLUTE MATURING RATE IN THE INTERVAL 12-18 MONTHS (AMR3) FOR EWE GROUPS WITHIN BREEDS

Breed	Number of records	N	Average	Standard deviation	Coef. of variation	Lowest	Highest
Rambouillet	3	74	.0383	.016	41.35	-.0006	.0814
	4	64	.0342	.018	51.44	.0035	.0789
	5	164	.0405	.021	52.61	.0022	.0950
Targhee	3	74	.0456	.021	47.00	.0098	.0892
	4	47	.0455	.020	44.16	.0144	.0896
	5	217	.0475	.022	46.42	.0000	.1285
Columbia	3	54	.0466	.024	51.78	.0063	.1002
	4	21	.0442	.023	52.57	.0116	.0848
	5	100	.0459	.020	44.28	.0110	.0987

TABLE 43. AVERAGES, VARIATION AND RANGES OF ABSOLUTE MATURING RATE IN THE INTERVAL BIRTH-12 MONTHS (AMR4) FOR EWE GROUPS WITHIN BREEDS

Breeds	Number of records	N	Average	Standard deviation	Coef. of variation	Lowest	Highest
Rambouillet	3	74	.0537	.007	13.24	.0394	.0732
	4	64	.0529	.008	14.30	.0375	.0710
	5	164	.0515	.008	14.74	.0369	.0725
Targhee	3	74	.0520	.008	15.99	.0357	.0705
	4	47	.0512	.009	17.01	.0322	.0716
	5	217	.0497	.007	14.67	.0349	.0758
Columbia	3	54	.0482	.009	18.41	.0320	.0667
	4	21	.0465	.011	23.44	.0265	.0689
	5	100	.0486	.008	15.87	.0326	.0687

TABLE 44. AVERAGES, VARIATION AND RANGES OF ABSOLUTE MATURING RATE IN THE INTERVAL BIRTH-18 MONTHS (AMR5) FOR EWE GROUPS WITHIN BREEDS

Breeds	Number of records	N	Average	Standard deviation	Coef. of variation	Lowest	Highest
Rambouillet	3	74	.0481	.004	7.81	.0401	.0579
	4	64	.0459	.005	10.12	.0393	.0570
	5	164	.0470	.004	8.38	.0370	.0552
Targhee	3	74	.0480	.005	8.70	.0362	.0568
	4	47	.0483	.004	9.14	.0326	.0556
	5	217	.0478	.004	8.74	.0362	.0581
Columbia	3	54	.0465	.006	13.90	.0339	.0603
	4	21	.0443	.005	11.08	.0336	.0559
	5	100	.0465	.004	9.19	.0359	.0554

TABLE 45. PREDICTED BODY WEIGHTS AND PERCENT OF MATURE WEIGHT (A) FOR EACH BREED AND EWE GROUP USING BRODY'S GROWTH EQUATION DERIVED IN THIS STUDY IN SIX MONTH INTERVALS

Age	Breeds			Groups		
	Rambouillet	Targhee	Columbia	3 records	4 records	5 records
Birth	7.35	7.47	7.64	7.20	7.63	7.65
6 mo kg	38.76	40.80	39.37	40.00	39.64	39.32
% ^a	55.34	56.34	53.85	56.15	54.83	54.56
12 mo kg	54.44	57.03	55.72	56.00	55.80	55.42
%	77.72	78.75	76.21	78.61	77.18	76.90
18 mo kg	62.25	64.93	64.15	63.80	63.96	63.60
%	88.88	89.66	87.74	89.56	88.47	88.25
24 mo kg	66.15	68.77	68.49	67.60	68.08	67.76
%	94.44	94.96	93.68	94.90	94.17	94.03
30 mo kg	68.10	70.64	70.73	69.46	70.16	69.87
%	97.23	97.54	96.74	97.51	97.05	96.96
36 mo kg	69.07	71.55	71.88	70.36	71.21	70.94
%	98.61	98.80	98.31	98.77	98.50	98.44
42 mo kg	69.56	71.99	72.47	70.81	71.74	71.49
%	99.31	99.41	99.12	99.41	99.23	99.20
48 mo kg	69.80	72.21	72.78	71.02	72.01	71.77
%	99.66	99.71	99.54	99.70	99.61	99.59
54 mo kg	69.92	72.32	72.94	71.13	72.15	71.91
%	99.82	99.86	99.76	99.85	99.80	99.79
60 mo kg	69.98	72.37	73.02	71.18	72.22	71.98
%	99.91	99.93	99.87	99.92	99.90	99.88
66 mo kg	70.01	72.39	73.06	71.20	72.25	72.02
%	99.96	99.96	99.93	99.95	99.94	99.94
72 mo kg	70.02	72.40	73.08	71.21	72.27	72.04
%	99.97	99.97	99.95	99.97	99.97	99.97
78 mo kg	70.03	72.41	73.09	71.22	72.28	72.05
%	99.98	99.98	99.97	99.98	99.98	99.98
84 mo kg	70.04	72.42	73.10	71.23	72.28	72.05
%	100.00	100.00	99.98	100.00	99.98	99.98

^aPercentages represent the degree of maturity at each age.

TABLE 46. LEAST SQUARES MEANS OF BIRTH-REARING EFFECTS FOR EACH BREED (HARVEY ANALYSIS, MODEL B)

Trait	Rambouillet			Targhee			Columbia		
	S/S	T/S	T/T	S/S	T/S	T/T	S/S	T/S	T/T
ATLB	1.33	1.47	1.45	1.46	1.47	1.53	1.33	1.48	1.42
ATLW	1.19	1.18	1.21	1.24	1.32	1.28	1.08	1.20	1.13
ATWW	44.51	45.90	44.44	49.43	52.52	50.87	42.74	46.19	45.42
ATFP	4.50	4.37	4.44	* 4.84	4.72	4.65	5.12	5.16	4.97
A	71.55	69.73	69.64	**74.92	68.92	72.39	*75.12	71.84	72.09
k	**11.80	12.20	10.30	**12.30	12.00	11.20	10.60	10.90	10.20
EI	62.50	66.10	66.90	*66.20	76.00	70.60	57.00	65.00	63.00
AGR1	8.46	8.56	7.40	** 9.10	8.19	7.99	** 8.85	8.73	7.78
AGR2	* 1.34	1.44	1.55	** 1.10	1.20	1.39	** .81	.93	1.27
AGR3	2.61	2.62	2.68	2.99	2.86	3.13	3.27	3.13	3.19
AGR4	** 3.81	3.86	3.55	** 3.94	3.71	3.72	3.61	3.59	3.56
AGR5	** 3.35	3.39	3.21	** 3.57	3.38	3.46	3.42	3.34	3.36
RGR1	*21.70	22.60	21.90	21.40	21.70	21.50	21.60	22.30	21.70
RGR2	** 2.70	2.80	3.30	** 2.10	2.50	2.90	** 1.60	1.90	2.70
RGR3	4.10	4.10	4.40	4.44	4.60	4.80	5.00	5.10	5.00
RGR4	** 7.80	7.90	7.80	** 7.80	7.90	7.90	** 7.60	7.70	7.80
RGR5	** 5.40	5.50	5.40	** 5.40	5.50	5.40	** 5.40	5.40	5.50
AMR1	**11.80	12.30	10.70	**12.20	11.90	11.10	**11.90	12.20	10.90
AMR2	** 1.90	2.10	2.20	** 1.50	1.70	1.90	** 1.10	1.30	1.80
AMR3	3.60	3.70	3.80	* 3.90	4.20	4.30	4.30	4.30	4.30
AMR4	** 5.40	5.60	5.10	5.30	5.40	5.20	4.80	5.00	5.00
AMR5	** 4.70	4.90	4.60	4.80	4.90	4.80	4.60	4.70	4.70

Units of measure: A, ATWW and ATFP as kg; k as %/mo rate of growth decline; AGR as kg/mo; RGR as % of weight gain per month relative to Y_{t_2} ; AMR as % of weight gain per month relative to A; and EI as % of A.

**($P < .05$), *($P < .01$).

TABLE 47. ESTIMATES^a OF HERITABILITIES, GENETIC AND PHENOTYPIC CORRELATIONS FOR LIFETIME PRODUCTION AND GROWTH TRAITS OF RAMBOUILLET EWES

Traits	ATLB	ATLW	ATWW	ATFP	A	k
ATLB	<u>.38±.27</u>	.73	.66	-.002	.025	.07
ATLW	.94±.20	<u>.41±.27</u>	.96	-.06	-.11	.17
ATWW	1.80±6.4	1.97±6.7	<u>.03±.26</u>	-.06	-.11	.19
ATFP	-.14±.49	-.30±.50	-1.28±5.8	<u>.56±.27</u>	.32	-.09
A	.60±.53	.44±.54	1.86±8.3	-.11±.41	<u>.55±.27</u>	-.55
k	-.48±.48	-.23±.44	-.86±3.6	-.05±.40	-.69±.68	<u>.59±.27</u>
EI	.97±1.2	1.42±3.0	-.03±7.0	-.91±3.5	.22±1.9	.20±1.2
AGR1	-.24±.61	-.48±.64	-1.84±8.1	.20±.48	.11±.50	-.08±.49
AGR2	-.26±.37	.43±.37	1.68±7.1	-.20±.32	.17±.31	.47±.28
AGR3	-.05±.50	.28±.48	-.63±3.0	-.005±.42	-.01±.42	.55±.49
AGR4	.06±.44	.23±.42	.89±3.9	-.16±.36	.32±.32	.41±.30
AGR5	.38±1.3	.63±1.5	2.86±13.	-.60±1.3	.47±.81	-.18±.96
RGR1	-.07±.40	-.35±.42	-1.38±6.0	-.12±.34	-.20±.34	.26±.32
RGR2	.28±.38	.45±.38	1.74±7.4	-.27±.34	.12±.32	.47±.30
RGR3	-.05±.43	-.38±.42	-1.04±4.6	.08±.37	-.01±.36	-.44±.42
RGR4	-.19±.35	-.16±.34	-.62±2.8	-.51±.33	.01±.29	.25±.27
RGR5	-.20±.35	-.40±.37	-1.48±6.4	-.65±.37	-.30±.31	.61±.25
AMR1	-.61±.55	-.66±.51	-2.59±11.	.21±.41	-.63±.59	.43±.30
AMR2	.22±.36	.41±.35	1.49±6.3	-.24±.32	.01±.31	.58±.24
AMR3	-.21±.45	-.43±.44	-1.21±5.1	.18±.40	-.16±.41	-.35±.38
AMR4	-.28±.41	.01±.39	-.14±1.3	-.19±.35	-.48±.47	.91±.08
AMR5	-.45±.48	-.20±.45	-.76±3.2	-.10±.43	-.84±.75	.72±.17

^aHeritability estimates are underlined on diagonal, phenotypic correlations are above the diagonal, and genetic correlations are below the diagonal.

TABLE 47. (Continued)

Trait	EI	AGR1	AGR2	AGR3	AGR4	AGR5
ATLB	.60	-.01	.07	.12	.05	.13
ATLW	.92	-.03	.07	.06	.05	.08
ATWW	.96	-.01	.07	.07	.06	.10
ATFP	-.15	.22	-.004	-.02	.19	.17
A	-.38	.33	.15	.11	.43	.53
k	.33	.24	.20	-.13	.37	.23
EI	<u>.04±.26</u>	-.11	.03	.02	-.05	-.05
AGR1	-1.75±6.1	<u>.35±.27</u>	-.26	-.05	.46	.45
AGR2	1.24±4.0	-.35±.47	<u>1.05±.27</u>	-.43	.69	.28
AGR3	-.49±2.1	-.63±.61	-.41±.43	<u>.53±.27</u>	-.39	.44
AGR4	.38±1.8	.11±.45	.86±.12	-.74±.59	<u>.71±.27</u>	.63
AGR5	1.59±7.0	-1.55±2.3	1.35±2.2	.01±1.1	.79±.93	<u>.08±.26</u>
RGR1	-.98±3.4	.79±.22	-.13±.27	-.28±.39	.10±.30	-.61±1.3
RGR2	1.39±4.5	-.43±.56	.99±.01	-.33±.42	.81±.18	1.41±2.5
RGR3	-.86±2.9	-.30±.50	-.49±.40	1.05±.04	-.67±.54	.47±1.0
RGR4	-.35±1.5	.22±.34	.46±.18	-.31±.36	.59±.18	.47±.93
RGR5	-.79±2.7	.25±.35	.25±.22	.07±.30	.41±.24	1.04±1.6
AMR1	-1.39±4.4	.70±.24	-.40±.40	-.47±.48	-.15±.36	-1.65±3.0
AMR2	1.31±4.1	-.37±.48	.98±.01	-.41±.43	.82±.14	1.27±2.2
AMR3	-.82±2.7	.41±.55	-.46±.41	1.01±.03	-.69±.56	.31±.92
AMR4	.58±1.8	-.03±.42	.69±.16	-.66±.56	.67±.17	.24±.85
AMR5	.44±1.4	-.59±.52	.30±.31	.13±.41	-.003±.37	.11±1.0

TABLE 47. (Continued)

Traits	RGR1	RGR2	RGR3	RGR4	RGR5	AMR1
ATLB	-.005	.06	.09	.03	.04	-.02
ATLW	-.06	.07	.04	.01	-.03	.03
ATWW	-.05	.06	.04	.01	-.04	.06
ATFP	-.04	-.09	-.07	-.10	-.17	-.001
A	.01	.03	-.03	.06	-.04	-.37
k	.16	.13	-.19	.23	.25	.63
EI	-.05	.06	.03	.01	-.30	.15
AGR1	.65	-.44	-.17	.24	.13	.75
AGR2	-.09	.96	-.53	.41	.11	-.36
AGR3	-.20	-.39	.96	-.34	.24	-.13
AGR4	.20	.51	-.58	.53	.22	.16
AGR5	.07	.13	.21	.22	.38	.06
RGR1	<u>.87±.27</u>	-.13	-.22	.44	.16	.64
RGR2	-.17±.28	<u>.99±.27</u>	-.46	.39	.10	-.46
RGR3	-.15±.32	-.44±.39	<u>.75±.27</u>	-.40	.21	-.14
RGR4	.46±.19	.50±.18	-.27±.31	<u>1.28±.26</u>	.52	.20
RGR5	.34±.23	.25±.22	.07±.26	.66±.13	<u>1.26±.26</u>	.15
AMR1	.78±.17	-.42±.44	-.24±.38	.14±.28	.36±.28	<u>.57±.27</u>
AMR2	-.09±.26	.99±.01	-.50±.39	.50±.17	.31±.21	-.29±.35
AMR3	-.19±.34	-.41±.40	1.00±.02	-.30±.33	.15±.27	-.23±.39
AMR4	.24±.27	.70±.18	-.62±.48	.57±.17	.60±.21	.31±.29
AMR5	.01±.34	.37±.32	.22±.34	.19±.28	.76±.22	.11±.41

TABLE 47. (Continued)

Traits	AMR2	AMR3	AMR4	AMR5
ATLB	.07	.11	.04	.11
ATLW	.10	.09	.14	.20
ATWW	.10	.09	.15	.21
ATFP	-.09	-.10	-.08	-.17
A	-.07	-.17	-.41	-.54
k	.33	.02	.85	.83
EI	.12	.13	.27	.35
AGR1	-.34	-.13	.18	.09
AGR2	.97	-.48	.56	.10
AGR3	-.45	.95	-.48	.31
AGR4	.60	-.51	.64	.16
AGR5	.16	.28	.18	.42
RGR1	-.10	-.20	.19	.07
RGR2	.97	-.42	.48	.08
RGR3	-.53	.97	-.57	.25
RGR4	.42	-.37	.50	.16
RGR5	.13	.23	.26	.42
AMR1	-.29	-.02	.46	.47
AMR2	<u>1.15±.27</u>	-.45	.66	.22
AMR3	-.45±.39	<u>.64±.27</u>	-.38	.46
AMR4	.79±.12	-.53±.44	<u>.85±.27</u>	.62
AMR5	.44±.28	.33±.33	.62±.21	<u>.55±.27</u>

TABLE 48. ESTIMATES^a OF HERITABILITIES, GENETIC AND PHENOTYPIC CORRELATIONS FOR LIFETIME PRODUCTION AND GROWTH TRAITS OF TARGHEE EWES

Traits	ATLB	ATLW	ATWW	ATFP	A	k
ATLB	<u>.24±.22</u>	.72	.64	.03	.01	.10
ATLW		<u>-.03±.22</u>	.92	.005	-.13	.15
ATWW			<u>-.20±.23</u>	.04	-.08	.17
ATFP	1.24±3.6			<u>.04±.21</u>	.25	-.08
A	-.20±1.0			-4.46±13.	<u>.12±.21</u>	-.48
k	.44±.73			.87±3.0	-.19±1.3	<u>.23±.22</u>
EI						
AGR1	1.60±4.3			-6.12±23.	.24±2.1	.68±1.9
AGR2	-.99±1.1			-.52±2.1	-.29±1.1	1.14±.91
AGR3	.72±.86			.23±1.9	2.48±2.4	-1.24±1.5
AGR4	-.005±.62			-2.14±5.4	.07±.89	.90±.50
AGR5	.31±.52			1.72±4.4	1.06±.57	-.04±.54
RGR1						
RGR2	-.13±1.6			-.16±2.2	-.55±1.5	1.30±1.4
RGR3	3.45±4.4			5.29±70.	12.33±157.	-6.50±84.
RGR4	.50±1.2			-.47±2.9	-2.53±3.6	2.30±2.5
RGR5						
AMR1	1.01±1.2			-.24±2.4	-.97±2.4	.80±.47
AMR2	-1.02±1.2			.21±2.0	-.53±1.4	1.16±.87
AMR3						
AMR4	.02±.54			.15±1.3	-.67±1.3	1.00±.15
AMR5	.92±.99			.86±3.4	1.07±2.5	.28±.81

^aHeritability estimates are underlined on diagonal, phenotypic correlations are above the diagonal, and genetic correlations are below the diagonal.

TABLE 48. (Continued)

Traits	EI	AGR1	AGR2	AGR3	AGR4	AGR5
ATLB	.59	.11	-.55	.10	.06	.12
ATLW	.89	-.002	-.05	-.08	-.02	.03
ATWW	.90	.04	.02	.06	.07	.10
ATFP	-.06	.12	.07	-.005	.16	.15
A	-.42	.43	.10	.35	.47	.69
k	.32	.26	.19	-.26	.38	.10
EI	<u>-.09±.22</u>	-.11	-.01	-.06	-.01	-.15
AGR1		<u>.04±.21</u>	-.23	-.01	.58	.49
AGR2		<u>.54±2.8</u>	<u>.19±.21</u>	-.28	.59	.28
AGR3		<u>3.23±8.9</u>	<u>-.64±1.3</u>	<u>.18±.21</u>	-.20	.54
AGR4		<u>.31±1.1</u>	<u>1.26±.48</u>	<u>.32±.81</u>	<u>.33±.22</u>	.68
AGR5		<u>.87±1.8</u>	<u>.51±.52</u>	<u>1.15±.48</u>	<u>.64±.26</u>	<u>.48±.23</u>
RGR1						
RGR2		<u>.46±3.4</u>	<u>1.00±.07</u>	<u>-1.17±1.9</u>	<u>1.35±.96</u>	<u>.40±.70</u>
RGR3		<u>17.07±225.</u>	<u>-3.98±53.</u>	<u>2.57±29.</u>	<u>1.24±18.</u>	<u>4.66±58.</u>
RGR4		<u>-2.01±5.6</u>	<u>1.76±1.8</u>	<u>-.88±1.8</u>	<u>.75±.74</u>	<u>-.21±.73</u>
RGR5						
AMR1		<u>.16±2.3</u>	<u>.69±1.6</u>	<u>-.35±1.4</u>	<u>.16±.81</u>	<u>-.46±.84</u>
AMR2		<u>.24±2.5</u>	<u>.98±.05</u>	<u>1.14±1.8</u>	<u>1.19±.62</u>	<u>.25±.61</u>
AMR3						
AMR4		<u>-.18±1.2</u>	<u>1.16±.49</u>	<u>-.99±1.2</u>	<u>.73±.27</u>	<u>-.09±.39</u>
AMR5		<u>1.46±1.3</u>	<u>1.59±1.4</u>	<u>-.48±.92</u>	<u>1.40±1.0</u>	<u>.97±.66</u>

TABLE 48. (Continued)

Traits	RGR1	RGR2	RGR3	RGR4	RGR5	AMR1
ATLB	-.01	-.07	.06	-.03	-.003	.10
ATLW	-.05	-.04	.07	.00	-.004	.10
ATWW	-.04	.004	.03	.01	.01	.10
ATFP	-.06	.01	-.09	-.13	-.13	-.07
A	.02	-.02	.11	.04	.10	-.36
k	.14	.12	-.33	.18	.04	.69
EI	-.04	.02	-.01	.003	-.02	.22
AGR1	.56	-.42	-.22	.14	-.03	.68
AGR2	-.09	.97	-.44	.28	.18	-.32
AGR3	-.17	-.26	.92	.18	.24	-.31
AGR4	.16	.40	-.51	.42	.19	.22
AGR5	.03	.13	.22	.20	.35	-.05
RGR1	<u>-.04±.22</u>	-.13	-.21	.23	-.01	.57
RGR2		<u>.13±.21</u>	-.36	.27	.18	-.42
RGR3		6.83±89.	<u>.01±.20</u>	-.27	.20	-.33
RGR4		2.19±2.5	-4.33±57.	<u>.11±.21</u>	.48	.11
RGR5					<u>-.06±.22</u>	-.11
AMR1		.88±2.3	-.89±14.	.83±1.5		<u>.12±.21</u>
AMR2		1.04±.09	6.41±85.	2.31±2.5		.77±1.7
AMR3						
AMR4		1.40±.94	4.96±65.	1.84±1.6		.61±.51
AMR5		1.66±1.7	-4.63±58.	2.51±2.9		.11±1.2

TABLE 48. (Continued)

Traits	AMR2	AMR3	AMR4	AMR5
ATLB	-.06	.11	.04	.13
ATLW	-.02	.14	.08	.20
ATWW	.03	.10	.12	.21
ATFP	.002	-.11	-.07	-.15
A	-.12	-.05	-.42	-.46
k	.30	-.08	.85	.77
EI	.08	.11	.26	.36
AGR1	-.33	-.19	.20	.05
AGR2	.97	-.35	.51	.21
AGR3	-.35	.89	-.53	.19
AGR4	.47	-.41	.59	.23
AGR5	.12	.26	.07	.32
RGR1	-.10	-.18	.15	.03
RGR2	.97	-.28	.43	.18
RGR3	-.46	.93	-.63	.12
RGR4	.28	-.22	.42	.21
RGR5	.17	.20	.12	.32
AMR1	-.15	-.17	.56	.42
AMR2	<u>.17+.21</u>	-.34	.60	.30
AMR3		<u>-.12+.23</u>	-.40	.39
AMR4	1.27±.55		<u>.45+.23</u>	.64
AMR5	1.30±1.1		<u>.69±.38</u>	<u>.16+.21</u>

TABLE 49. ESTIMATES^a OF HERITABILITIES, GENETIC AND PHENOTYPIC CORRELATIONS FOR LIFETIME PRODUCTION AND GROWTH TRAITS OF COLUMBIA EWES

Traits	ATLB	ATLW	ATWW	ATFP	A	k
ATLB	<u>.65±.38</u>	.72	.63	.07	.06	.21
ATLW	.77±.26	<u>.48±.39</u>	.96	.10	-.04	.17
ATWW	.61±.42	.94±.08	<u>.35±.39</u>	.16	.03	.11
ATFP	.52±.38	.19±.42	.14±.48	<u>1.32±.36</u>	.29	-.11
A	.25±.49	.07±.56	.32±.67	.58±.31	<u>.70±.38</u>	-.60
k	.40±.37	.35±.44	.15±.53	-.36±.32	-.38±.82	<u>1.09±.37</u>
EI	.53±.46	.88±.14	.79±.27	-.21±.50	-.77±.71	.62±.50
AGR1	.44±.54	.03±.65	.01±.75	-.99±.59	.20±.52	.06±.45
AGR2	.40±.36	.56±.47	.64±.58	.97±.22	.31±.35	-.07±.30
AGR3	.29±.45	-.47±.51	-.60±.61	-.26±.34	.13±.43	.11±.38
AGR4	.72±.48	.69±.62	.83±.75	.70±.35	.58±.43	-.05±.44
AGR5	.82±.45	.16±.59	.15±.68	.25±.36	.51±.37	.04±.42
RGR1	-.03±.39	-.14±.47	-.07±.53	-.54±.35	.29±.40	-.16±.31
RGR2	.38±.36	.68±.49	.78±.62	.94±.23	.20±.35	.01±.30
RGR3	-.12±.52	-.71±.66	-.92±.85	-.57±.45	-.31±.49	.13±.45
RGR4	.22±.64	.70±.76	1.16±1.1	.04±.49	.84±.88	.46±.47
RGR5	.16±.35	.07±.41	.02±.48	-.30±.29	-.01±.35	.25±.28
AMR1	.10±.46	-.14±.52	-.34±.64	-1.14±.57	-.59±.71	.70±.19
AMR2	.42±.37	.64±.50	.69±.60	.93±.25	.10±.38	.10±.31
AMR3	.19±.45	-.48±.50	-.76±.65	-.60±.40	-.45±.50	.45±.37
AMR4	.47±.49	.57±.59	.48±.70	.05±.39	-.51±.78	.87±.10
AMR5	.45±.37	.09±.48	-.18±.53	.45±.34	-.74±.70	.92±.07

^aHeritability estimates are underlined on diagonal, phenotypic correlations are above the diagonal, and genetic correlations are below the diagonal.

TABLE 49. (Continued)

Traits	EI	AGR1	AGR2	AGR3	AGR4	AGR5
ATLB	.60	.14	.16	.09	.27	.31
ATLW	.93	.10	.05	.14	.17	.27
ATWW	.95	.08	.10	.16	.20	.30
ATFP	.05	-.03	.33	.03	.31	.27
A	-.26	.25	.15	.30	.34	.54
k	.29	.25	.18	-.19	.38	.17
EI	<u>.35±.39</u>	-.004	.06	.07	.09	.13
AGR1	-.12±.76	<u>.51±.39</u>	-.31	.03	.45	.47
AGR2	.43±.54	-.73±.65	<u>1.28±.36</u>	-.34	.67	.29
AGR3	.61±.68	.55±.55	-.43±.44	<u>.82±.38</u>	-.23	.52
AGR4	.43±.74	-.61±.44	1.01±.21	-.07±.51	<u>.55±.38</u>	.70
AGR5	-.19±.69	-.01±.64	.32±.36	.78±.30	.59±.34	<u>.58±.38</u>
RGR1	-.13±.54	1.04±.34	-.51±.35	-.01±.36	-.18±.42	-.16±.42
RGR2	.63±.58	-.72±.70	.99±.01	-.47±.44	1.02±.28	.31±.37
RGR3	-.70±.79	.42±.69	-.69±.65	.83±.12	-.52±.89	.29±.52
RGR4	.86±.93	.59±.70	.24±.47	.97±.98	.97±.57	1.49±.94
RGR5	.10±.47	-.14±.40	-.11±.27	.79±.25	-.05±.39	.56±.32
AMR1	.08±.61	.65±.28	-.75±.54	.28±.46	-.80±.52	-.36±.50
AMR2	.61±.57	-.78±.72	.98±.01	-.45±.48	.96±.24	.27±.39
AMR3	-.50±.58	.44±.57	-.59±.51	.83±.11	-.37±.65	.42±.42
AMR4	.82±.67	-.63±.56	.59±.28	-.14±.57	.39±.45	.12±.55
AMR5	.30±.49	-.17±.45	-.06±.31	.41±.35	.10±.44	.22±.41

TABLE 49. (Continued)

Traits	RGR1	RGR2	RGR3	RGR4	RGR5	AMR1
ATLB	-.05	.13	-.03	.18	.15	.07
ATLW	-.11	.05	.07	.19	.25	.09
ATWW	-.12	.10	.08	.16	.23	.01
ATFP	-.21	.28	-.08	-.08	-.12	-.26
A	-.04	.08	.08	-.06	-.09	-.52
k	.08	.13	-.28	.30	.18	.70
EI	-.10	.08	.05	.18	.25	.16
AGR1	.49	-.45	-.18	.22	.06	.69
AGR2	-.16	.97	-.51	.23	-.004	-.39
AGR3	-.23	-.34	.90	-.18	.36	-.19
AGR4	.05	.54	-.56	.43	.12	.14
AGR5	-.05	.18	.15	.28	.35	.002
RGR1	<u>1.14±.37</u>	-.18	-.22	.39	.13	.47
RGR2	-.55±.35	<u>1.31±.36</u>	-.46	.21	.01	-.46
RGR3	.04±.42	-.69±.62	<u>.61±.39</u>	-.28	.35	-.22
RGR4	-.10±.51	.15±.47	.73±.0	<u>.35±.39</u>	.60	.23
RGR5	-.15±.28	-.06±.27	.96±.33	.79±.32	<u>1.40±.36</u>	.10
AMR1	.62±.26	-.67±.53	.47±.59	-.08±.60	-.07±.33	<u>.79±.38</u>
AMR2	-.58±.37	.99±.01	-.65±.67	.19±.49	-.08±.28	-.63±.50
AMR3	-.10±.37	-.57±.49	.92±.07	.69±.85	.87±.23	.60±.45
AMR4	-.34±.41	.70±.29	-.18±.71	.29±.62	.02±.38	.01±.54
AMR5	-.32±.33	.04±.31	.47±.44	.50±.48	.50±.23	.45±.29

TABLE 49. (Continued)

Traits	AMR2	AMR3	AMR4	AMR5
ATLB	.16	.07	.20	.26
ATLW	.06	.18	.17	.31
ATWW	.10	.17	.13	.26
ATFP	.26	-.10	.02	-.07
A	-.04	-.11	-.50	-.54
k	.30	.04	.87	.86
EI	.11	.19	.27	.41
AGR1	.37	-.06	.20	.20
AGR2	.97	-.44	.50	.13
AGR3	-.40	.90	-.45	.18
AGR4	.60	-.39	.63	.32
AGR5	.18	.30	.18	.40
RGR1	-.16	-.21	.08	.005
RGR2	.97	-.40	.43	.09
RGR3	-.53	.92	-.59	.05
RGR4	.24	-.16	.43	.33
RGR5	.01	.43	.16	.43
AMR1	-.30	.02	.55	.58
AMR2	<u>1.16±.37</u>	-.43	.60	.22
AMR3	-.49±.50	<u>.81±.38</u>	-.29	.41
AMR4	.75±.24	.13±.53	<u>.58±.38</u>	.73
AMR5	.13±.32	.75±.27	.75±.20	<u>.99±.37</u>

TABLE 50. AMONG SIRES COMPONENTS OF VARIANCE AND COVARIANCE FOR LIFETIME PRODUCTION AND GROWTH TRAITS (POOLED DATA FROM RAMBOUILLET, TARGHEE AND COLUMBIA EWES)^a

Traits	ATLB	ATLW	ATWW	ATFP	A	k	EI	AGR1
ATLB	11.516	9.2949	235.49	4.8076	48.855	.12880	3.0265	7.9328
ATLW		8.9750	208.33	4.2046	32.487	.07598	2.9859	-4.9969
ATWW			3769.8	117.27	2004.8	.08170	49.497	-206.43
ATFP				49.654	17.659	-.40949	.72560	-35.689
A					4027.5	-12.850	-19.629	28.958
k						.08750	.14685	.11336
EI							1.1682	-3.8804
AGR1								39.097

^aValues are multiplied by 10^3
Covariances are on the diagonal

TABLE 50. (Continued)

Traits	AGR2	AGR3	AGR4	AGR5	RGR1	RGR2	RGR3
ATLB	2.1214	8.2745	3.0351	4.5570	.01419	.03252	.05189
ATLW	9.1915	-3.2437	4.4791	2.5148	-.10911	.18892	-.08805
ATWW	360.06	-77.667	181.31	103.99	-3.9388	7.2380	-2.7257
ATFP	18.451	-5.0981	1.4283	-2.3179	-.45044	.33943	-1.0005
A	66.471	241.21	71.344	96.774	-2.3261	.55004	2.4884
k	.64394	-.86869	.41368	-.01435	.01292	.01332	-.01298
EI	4.6735	-3.6649	1.7945	.38743	-.03278	.10400	-.06444
AGR1	-19.109	24.534	-4.3488	-.52669	.85067	-.37128	.38217
AGR2	46.448	-24.599	25.558	8.1354	-.21008	.84052	-.46912
AGR3		59.937	-7.1742	15.384	-10.709	-.50375	.75478
AGR4			15.364	5.9576	.02102	.45979	-.17647
AGR5				7.5630	-.08203	.13459	.15947
RGR1					.02275	-.00435	-.00034
RGR2						.01545	-.00929
RGR3							.01062

TABLE 50. (Continued)

Traits	RGR4	RGR5	AMR1	AMR2	AMR3	AMR4	AMR5
ATLB	.00039	.00162	.01643	.03070	.09036	.01137	.03528
ATLW	.01337	.00162	-.14273	.13161	-.06225	.04476	.01756
ATWW	.68342	.07545	-6.6246	4.8221	-2.1291	1.2846	.29344
ATFP	-.03466	-.03355	-.54901	.23071	-.10521	-.01969	-.06753
A	-.23014	-.06445	-6.2713	-.18861	1.4137	-2.3026	-1.4347
k	.00327	.00152	.02470	.01260	-.00509	.01678	.00935
EI	.01329	.00219	-.02886	.07602	-.04347	.04580	.02146
AGR1	.01823	.01753	.50942	-.29015	.40115	-.10656	-.01645
AGR2	.06187	.02028	-.36400	.63907	-.36732	.30396	.06976
AGR3	-.01337	.01264	-.10600	-.40028	.65433	-.27950	.04218
AGR4	.04550	.02183	-.16513	.33948	-.11022	.15435	.04033
AGR5	.01348	.01632	-.17625	.08922	.17584	.00283	.04143
RGR1	.00082	.00031	.01610	-.00244	.00033	.00195	.00050
RGR2	.00115	.00034	-.00597	.01179	-.00732	.00603	.00150
RGR3	-.00030	.00015	.00050	-.00718	.00865	-.00430	.00045
RGR4	.00030	.00014	.00064	.00101	-.00003	.00085	.00037
RGR5		.00013	.00032	.00032	.00025	.00036	.00029
AMR1			.01799	-.00358	.00256	.00259	.00208
AMR2				.00915	-.00548	.00495	.00139
AMR3					.00781	-.00252	.00143
AMR4						.00406	.00173
AMR5							.00162

TABLE 51. WITHIN SIRES COMPONENTS OF VARIANCE AND COVARIANCE FOR LIFETIME PRODUCTION AND GROWTH TRAITS (POOLED DATA FROM RAMBOUILLET, TARGHEE AND COLUMBIA EWES)^a

Traits	ATLB	ATLW	ATWW	ATFP	A	k	EI	AGR1
ATLB	95.252	68.749	2297.6	-.52157	1.0290	.86411	31.182	17.730
ATLW		99.758	3548.4	-2.4232	-248.83	1.3061	49.735	10.505
ATWW			138899	149.92	-6952.8	49.185	1916.3	654.76
ATFP				242.12	905.31	-.83799	-6.2037	89.373
A					34518.	-69.464	-379.05	1978.8
k						.53165	1.2521	5.6417
EI							29.122	-8.3204

^aValues are multiplied by 10^3
Covariances are on the diagonal

TABLE 51. (Continued)

Traits	AGR2	AGR3	AGR4	AGR5	RGR1	RGR2	RGR3
ATLB	3.5318	18.717	9.1839	11.026	-.02232	.02427	.13989
ATLW	-7.0139	25.847	1.2728	7.1302	-.08610	-.14612	.30654
ATWW	-70.252	892.41	236.19	396.50	-2.3511	-2.5530	8.5642
ATFP	11.059	3.5353	37.962	29.298	-.13964	-.08399	-.36436
A	308.48	1010.9	853.34	935.71	2.7604	.41043	1.5625
k	1.6711	-2.9422	2.9903	1.0629	.02710	.01551	-.05774
EI	-3.2579	3.4256	-4.0145	-2.5613	.05096	-.03226	.10383
AGR1	-90.472	-26.428	170.11	119.40	5.3657	-3.0859	-2.0931
AGR2	185.62	-102.50	86.874	28.411	-.29641	3.3528	-2.0156
AGR3		488.53	-65.624	86.495	-1.4680	-1.7464	6.3183
AGR4			113.38	59.462	.66334	1.0841	-1.8598
AGR5				67.407	.24062	.20676	.39454
RGR1					.11673	-.00917	-.02487
RGR2						.06544	-.03061
RGR3							.09533

TABLE 51. (Continued)

Traits	RGR4	RGR5	AMR1	AMR2	AMR3	AMR4	AMR5
ATLB	.01716	.01392	.23372	.04848	.26540	.11460	.14538
ATLW	.01232	.01482	.50711	-.03828	.51167	.16762	.24609
ATWW	.26475	.52503	18.542	.75560	16.268	7.1984	9.3086
ATFP	-.06708	-.03229	-.16022	-.08091	-.46539	-.11388	-.18479
A	.38715	.09341	-25.472	-3.3421	-7.1580	-11.334	-9.1314
k	.00657	.00157	.18929	.03901	-.00223	.09000	.05918
EI	.00085	.00593	.45617	.04158	.28071	.19118	.20197
AGR1	.26910	.02428	7.6238	-1.7225	-1.5860	.99451	.36015
AGR2	.20951	.02742	-1.7474	2.4953	-1.6439	.98341	.17451
AGR3	-.29498	.15299	-1.8855	-1.6329	5.9788	-1.5814	.51566
AGR4	.24161	.03693	1.0082	.99914	-1.4567	.97303	.25053
AGR5	.09051	.06836	.20357	.17618	.56334	.17999	.30653
RGR1	.00613	.00077	.07049	-.00511	-.02158	.00733	.00172
RGR2	.00370	.00054	-.04393	.04654	-.02514	.01465	.00229
RGR3	-.00559	.00186	.03112	-.02832	.08672	-.02706	.00449
RGR4	.00270	.00062	.00307	.00285	-.00457	.00310	.00093
RGR5		.00059	.00015	.00038	.00192	.00043	.00083
AMR1			.14548	-.01918	-.01099	.03111	.01899
AMR2				.03582	-.02161	.01628	.00436
AMR3					.08785	-.01601	.01226
AMR4						.02126	.00951
AMR5							.00990

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