



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.

GENETIC ANALYSIS OF GROWTH AND ITS RELATIONSHIP WITH LIFETIME
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by

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A thesis submitted in partial fulfillment
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Doctor of Philosophy

in

Biological Sciences

MONTANA STATE UNIVERSITY
Bozeman, Montana

July 1986

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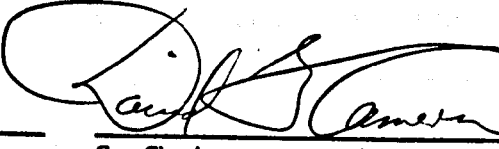
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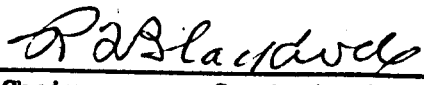
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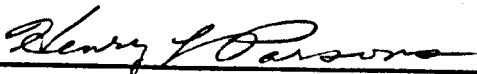
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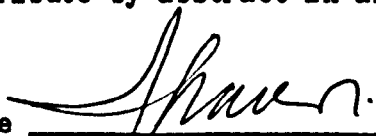
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To my wife, my parents,
my children and my
country.

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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ACKNOWLEDGEMENTS

I express my sincere thanks to Dr. D.G. Cameron and Dr. R.L. Blackwell for their patience, encouragement and guidance throughout my graduate program.

Appreciation is extended to the members of my graduate committee: Dr. D.D. Kress, Dr. R.E. Lund, Dr. H.J. Cameron and Dr. E.R. Vyse.

Special thanks are expressed to Dr. P.J. Burfening, Dr. M.J. Burris and Dr. J.G. Berardinelli, from whom I received all kinds of encouragement and friendship.

I am grateful to my friends Antonio Donado, Rodolfo Cantet, Darrell Nevins, Matthew Cronin and Shelly Waters, who made me feel at home.

I appreciate the data processing and computer programming assistance provided by K. Hanford and her husband S. Kachman, and to Joanne Jensen who assisted in editing the final copy of this thesis.

I appreciate the economical support provided by the Small Ruminant Collaborative Research Support Program, Breeding Project, through funds provided by the United States Agency for International Development.

I offer my sincere gratitude to all the members of Montana State University who helped me. The successful completion of my Graduate Program was due to the willingness of these people to give freely of their time.

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MEP..	la		Chavez, Juan Francisco.				
TIL.0	la		Genetic analysis of growth and its relationship with lifetime production in Rambouillet, Targhee and Columbia ewes under range conditions in Montana / by Juan Francisco Chavez.				
IMP.	la		Bozeman, MT., 1986.				
COL	la		xv, 116 leaves				
NOG	la		Thesis (PhD.)--Montana State U., Biological Sciences; David Cameron.				

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:

$$k = \frac{dW/dt}{A-W},$$

Where; W = Weight at age t
t = Age in time units
A = Mature weight.

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

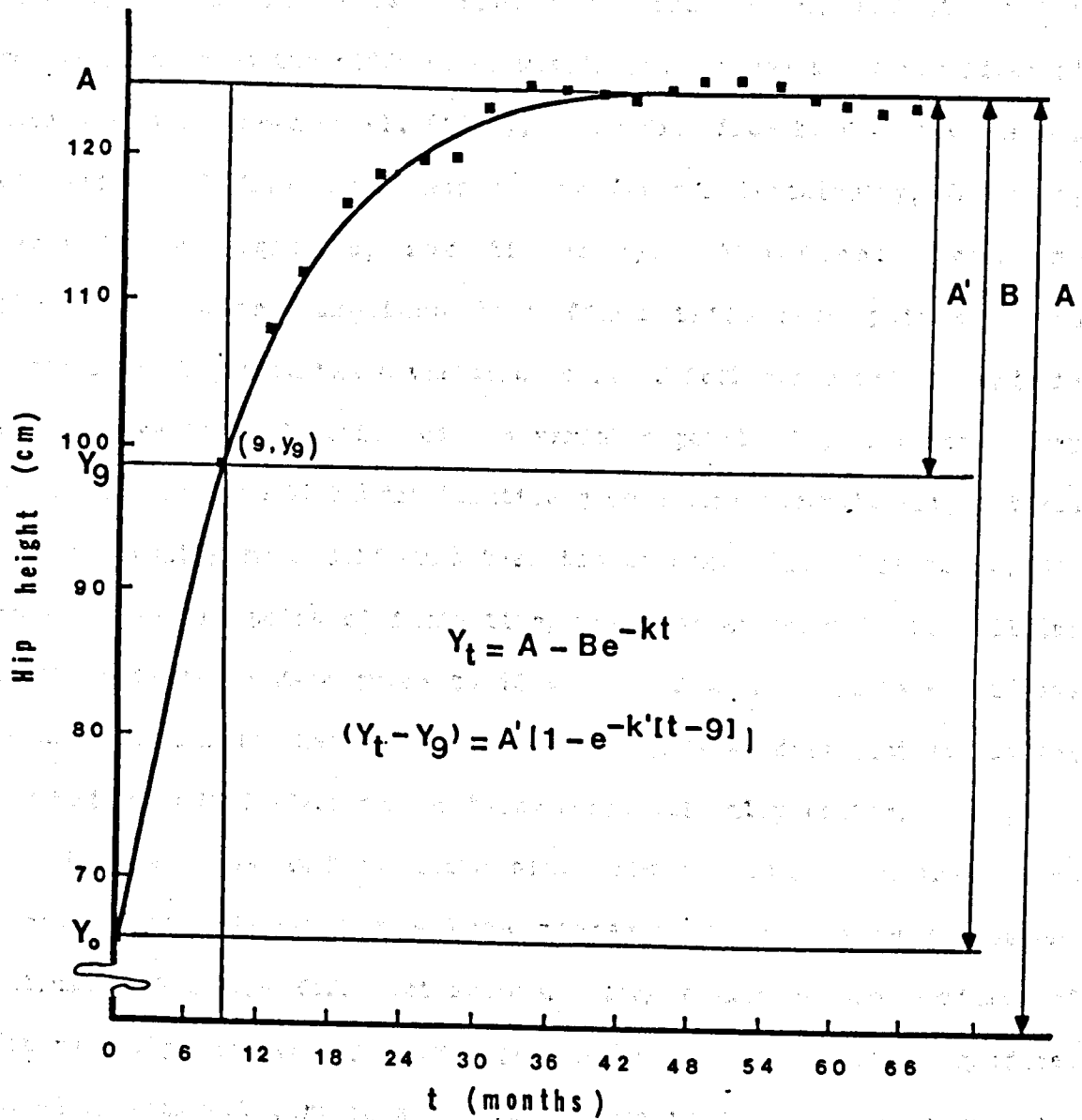


FIGURE 1. A REPRESENTATIVE OF BRODY'S EQUATION (AND A MODIFICATION) FITTED TO AN ANGUS HEIGHT-AGE CURVE (After Nelsen et al., 1982).

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:

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

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

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

(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:

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

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±.1	.66±.2	1.17±.1	.53±.2
	L			5-98d	.76±.2	.76±.2	1.32±.2	
Brown et al. (1972)	B	PHS	Cattle	B-109mo	.33±.2	.34±.2		
				B-109mo	.75±.3	.21±.2		
DeNise & Brinks (1985)	B	PHS	Cattle	B-4yr	.20±.3	.44±.3		
				R	B-4yr	.32±.3	.44±.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±.12, .59±.12 and .64±.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 summarize 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		-.50±.5		
				AGR	B-54d	.55±.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 m² 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,

