

LOGISTIC GROWTH CURVE PARAMETER ESTIMATES FOR SCROTAL
CIRCUMFERENCE AND RELATIONSHIPS WITH FEMALE REPRODUCTION
IN CROSSBRED SHEEP

by

Stewart Lee Fossceco

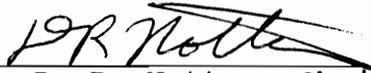
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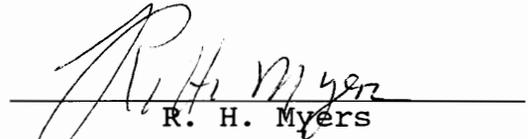
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(ABSTRACT)

Data from two groups of lambs were analyzed. In group one, seasonal patterns of testis growth through 16 mo of age were assessed on 40 spring-born ram lambs (eight Barbados Blackbelly, 10 Suffolk and 22 1/2-Dorset, 1/4-Finnish Landrace, 1/4-Rambouillet). Scrotal circumference (sc) and body weight (wt) were measured at mean ages of 30, 62, 96, 124, 153, 180, 212, 243, 290, 333, 364, 398, 427, 454, 488 and 517 d. A multivariate repeated measures analysis indicated that there were breed differences in ram sc and wt measurements at each age. When logistic growth curves were fit to ram sc data, breed differences were associated with parameters of the logistic curve that defined mature testis size and the period of rapid testis growth.

For group two, data were collected on 1,044 lambs from 727 spring lambings over 5 years; 67 sires and 525 dams were represented. Sc and wt were measured in rams at 5 times (mean ages of 44, 63, 97, 129 and 156 d); ewes were weighed at these times and at three additional times (187, 230 and 271 d). All ewe lambs were kept for fall breeding. Fertility, prolificacy and postweaning spring mating behavior of ewes that had lambed were measured. After ewes lambed, they were exposed to vasectomized rams and checked for postweaning spring mating behavior.

Restricted maximum likelihood (REML) was used to estimate variance components for additive genetic, ewe, and litter effects in group two lambs. Heritability estimates for wt at birth to 150 d ranged from .14 to .42. Heritabilities for sc and sc scaled to the 1/3 power of body weight

(rsc) ranged from .09 to .57 and from .13 to .55, respectively, and were largest at approximately 90 d. Logistic sc growth curves were fitted to data from individual ram lambs. Heritabilities of the estimated logistic parameters mature sc (A), sc maturing rate (k), age at inflection of the sc growth curve (t_i) and initial 14-d sc (SC_{14}), were estimated at $.09 \pm .15$, $.17 \pm .18$, $.37 \pm .29$ and $.40 \pm .14$, respectively. Heritability estimates for fertility and spring mating behavior (spbrd) were $.04 \pm .13$ and $.41 \pm .19$, respectively. The heritability estimate for prolificacy was zero.

Longitudinal additive genetic covariances among wt, sc and rsc at the second, third and fourth measurements were estimated from approximate multivariate REML analysis treating variances as known. Estimated genetic correlations among wts were largest, and ranged from .77 to .93. Estimated genetic correlations for rsc traits were between .48 and .90. Estimated genetic correlations for sc ranged only from .10 to .67. Pairwise genetic correlations among sc or rsc with fertility or spbrd were estimated to be moderate and positive (.20 and .34, respectively); t_i had correlations of -.32 and -.48 with fertility and spbrd, respectively.

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Introduction

Although rams and ewes have different reproductive characteristics, genes controlling these characters are common to both sexes, as is the environment they must share (Land, 1978). Many characters have been identified as contributing to control of reproduction (Turner, 1969), but thus far three stand out as being most important (Shelton and Menzies, 1970): fertility (which is binomial because a ewe either conceives, a success, or fails to conceive, a failure), prolificacy (the number of lambs born at a given lambing) and lamb survival to weaning.

Dickerson (1970) stated that the cost of animal products depends primarily upon the efficiency of three basic functions: (1) female production, (2) reproduction, and (3) growth of the young. Consequently, one mechanism for increasing profitability in sheep is to increase the rate of reproduction. One possible route to achieve this goal is to enhance the fertility and prolificacy of ewes, thereby increasing profitability under intensive ewe management. Since domestic sheep breeds have a mean gestation length of 148 d, and, in fall at least, can generally resume estrous 30 to 60 d after lambing (Notter, 1986), it is possible for a ewe to lamb twice a year. Several accelerated lambing systems have been designed to capture at least part of this reproductive potential. Unfortunately, most breeds of sheep exhibit a period of anestrus somewhere between March and July (Notter, 1986; Jeffcoate et al., 1984). Reducing this period of anestrus would enable the use of one or more accelerated lambing systems.

An improvement in reproductive performance can be achieved in several ways (Land, 1978). The environment could be changed by improving feeding, but this approach is not expected to override the seasonal anestrus (Land, 1978). Use of exogenous hormones and photoperiodic control as discussed by (Thimonier, 1981) could be used to improve reproductive performance of ewes when exposed to rams in spring. However, these changes do not yield permanently enhanced reproductive performance. Instead, the use of genetic differences between

breeds and individuals within a breed could provide a long-term solution to the problem of poor spring breeding (Carr and Land, 1975; Walkley and Smith, 1980; Notter, 1986).

Because traits such as conception and prolificacy are sex limited (expressed only in the female), a lack of selection criteria for the ram has limited the rate of genetic improvement in such traits. However, Land (1973) found that testis weight and diameter were greater in lines or breeds of both sheep and mice with higher ovulation rates, which indicated that the quantitative expression of certain reproductive characteristics in male and female mammals was genetically correlated (Land 1973). Notter et al. (1981) monitored testicular growth by measurement of scrotal circumference (sc) and found that this measurement was relatively easy to obtain and accurate. Thus sc measures may assist to identify males in the first year of their life (Land 1978; Walkley and Smith, 1980; Notter et. al., 1985) that are expected to produce daughters of superior fertility, prolificacy and reduced seasonality.

In this dissertation, changes in sc of spring-born ram lambs were modeled to evaluate seasonal effects and possible breed differences in testis growth patterns. Relationships among scrotal circumference (sc), sc growth patterns of young ram lambs and female reproductive traits (fertility, prolificacy and spring mating behavior) were investigated. A restricted maximum likelihood (REML) procedure was used to estimate (when possible) additive direct, additive genetic maternal, permanent environment and litter variance components, and heritabilities. Approximate multitrait REML was used to estimate genotypic and environmental covariances among the traits that were considered most important.

Literature Review

Environmental Effects on Reproduction and Growth

Growth of lambs will vary systematically depending upon their age, sex, season of birth, type of birth and rearing, and dam's age (Martin et al., 1980; Shelton and Campbell, 1962). Reproductive performance can likewise be affected by age, type of birth and rearing, season and weight and condition at the start of breeding (Lucas et al., 1983; Land, 1978; Laster et al., 1972, Dickerson and Glimp, 1975). Only when variation due to such environmental factors has been accounted for, can superior individuals be selected based on their genetic potential and subsequently used for breeding. Prior to investigating the genetic relationship of male and female reproduction, a review of previous research in the area of environmental and potential genetic effects on sheep reproduction appears reasonable. For environmental effects on growth traits, the literature suggests that different forms of adjustments be used for various effects: multiplicative for lamb sex and birth-rearing type and additive for age of ewe (Lewis et al., 1989; Notter et al., 1975).

Ewe age. Laster et al. (1972) looked at factors affecting reproduction in ewes of 19 breed groups and found that a small increase in ewe age at first breeding significantly increased ($P < .01$) the number of ewes lambing and number of lambs born per ewe exposed. Also, number of lambs born per ewe lambing increased curvilinearly with age of ewe from 105% at 1 year to 160% at 6 years and back to 135% at 9 years of age (Dickerson and Glimp, 1975). Fertility also increased curvilinearly with age of ewe. Similarly, Notter and Copenhaver (1980) reported that conception rates among ewes 3 years old or older increased with age until ewes were 5 to 6 years old.

Notter et al. (1975) found that age of ewe effects for 90 d lamb weight were highly significant ($P < .005$). Ewe subclasses were defined as 1, 2, 3 to 6, and over 6 years of age. Lamb weight was heaviest for ewes between 3 and 6 years of age. Subsequently, lambs were adjusted to a 3 to 6 year old ewe basis; additive adjustment factors ranged over breeds from 3.62 to 6.29 kg

for 1 year old ewes, .15 to 3.04 kg for 2 year old ewes and 2.14 to 3.21 kg for ewes over 6 years old. Weaning weights at 120-d in Rambouillet range lambs were adjusted to a four-year-old ewe basis (Lewis et al., 1989); adjustment factors were 3.31, .46, 0.0 and .87 kg for 2, 3, 4, and 5 to 6 year old ewes, respectively.

Age of lamb. Females tend to first show oestrus and males to mount for the first time at 7 to 19 months of age (Land, 1978). Relationships between male scrotal measures and female reproductive traits have been found (Land, 1973; Purvis et al., 1988). However, the age at which testicular size is measured may influence the relationship between sc and female reproductive traits (Land, 1978). The scrotal circumference growth pattern in the young spring-born ram can be well described through 5 mo. of age by a logistic curve (Notter et al., 1985) and for rams that differ in body size, the pattern of testicular growth over time may be more informative than any single measure of testicular size (Notter et al., 1985). However, Land (1978) showed that the inherent seasonality of sheep breeding puts a "mask" effect over the age scale, and therefore makes it difficult to separate age and season effects because of the interaction between the age of the animal and the season.

Body weight. Body weights of ewe lambs at the beginning of the breeding season and weight at lambing did not affect number of ewes lambing or lambs born per ewe, respectively in one study (Laster et al., 1972). Conversely, Fletcher (1971) found a 1.3% increase in the incidence of twin ovulations for each 1.0 kg increase in weight at breeding. Furthermore, weight appeared strongly correlated with ovulation rate and litter size in studies of Ray and Smith (1966), Dyrmondsson (1973) and Hohenboken et al. (1976). Flushing, or a temporary increase in the level of nutrition prior to breeding, has been a common technique to improve ewe reproduction (Cumming, 1977). However, growth of ewe lambs to breeding maybe more important in stimulating sexual maturity and ovulation rate than flushing (Foote et al., 1959; Dyrmondsson, 1973).

Breed group means in sc were, on average, proportional to the .28 power of body weight (Notter et al., 1985), which was close to the proportionality constant of 1/3 for linear body measures suggested by Lyne and Verhagen (1957).

Birth and rearing type. Dun and Grewal (1963) found that fertility was considerably higher in twin versus single-born Australian Merino ewes. Vakil et al. (1968) indicated that ewes born as twins tended to produce more offspring than ewes born as singles. Conversely, Baharin and Beilharz (1977) reported that twin-born Corriedale ewes had reduced fertility at first mating and an earlier decline in reproductive rate as the ewes aged. Litter size explained a significant part of the variation ($P < .001$) in testis diameter at 5 and 8 mo of age in 14 strains of Australian Merino rams (Purvis et al., 1984).

Generally, type of birth and type of rearing are combined into a single adjustment based on the birth and rearing type (e.g., single born and reared as a single) (Thrift and Whiteman, 1969; Sidwell et al., 1964). Notter et al., (1975) reported that both type of birth and type of rearing were significant effects when considered separately for 90 d lamb weight; however, even with 7,166 purebred lambs of seven breeds in the study, the effects of triplet birth or rearing were still not estimable with reasonable accuracy. Notter et al. (1975) reported that the adjustment factor required to adjust twin lamb weights to a single lamb basis ranged from 3.7 to 6.4 kg for the various breeds. However, Lewis et al. (1989) found that multiplicative adjustments were more appropriate than additive adjustments for birth-rearing-type for 120-d weaning weights of Rambouillet range lambs, especially when those adjustments would possibly be applied to rams raised in different environments.

Sex. Generally, rams and wethers have proven to be about 11% and 3% heavier, respectively, than ewes at 90 days (Notter et al., 1975; Hazel and Terrill, 1945; Thrift and Whiteman, 1969). Furthermore, Cundiff et al. (1966) reported differences in scaling patterns in 205-d weights

between calf sex categories and suggested use of a multiplicative factor to adjust weaning weight for sex in cattle.

Season. Notter and Copenhaver (1980a) analyzed data from 1/2-Finn, 1/2-Rambouillet ewes; 1/4-Finn, 3/4 Rambouillet ewes, and 1/2-Suffolk, 1/2-Rambouillet ewes. Ewes were bred in August, November and April to lamb in January, April and September, respectively. Conception rate of ewes significantly decreased ($P < .005$) from 90% in August and 79% in November to 53% in April. Furthermore, litter size for January (2.21), April (2.46) and September (1.48) differed ($P < .001$).

Wiggins et al. (1970) found considerable variation in the cyclic patterns exhibited by Rambouillet ewes; some ewes cycled year round, others cycled once during the year, and yet a third group cycled twice a year. The lowest estrual activity was expressed in the spring months. Results of Ford (1979) indicated that poor reproductive performance before day 40 postpartum in Finn-crossbred ewes lambing in the fall was not due to impairment of gonadotropin secretion or ovulation. Rather, the main limitation appeared to be the absence of estrous behavior and possibly the inability to maintain pregnancy. Incidence of ovulation was 28 to 63% higher in April through August in Rambouillet ewes located in Texas than in rather comparable ewes located in Idaho (Hulet et al., 1974a); number of hours of darkness was suggested as the primary mechanism controlling the level of reproductive activity. Also, the percentage of Rambouillet ewes lambing and lambing rate were lowest in October, highest in April and July, and intermediate in January (Hulet et al., 1974b).

Testis weight and growth for summer-born Finn-Dorset ram lambs reared during a period of decreasing daylength was more rapid than that of winter-born lambs reared during a period of increasing daylength (Land et al., 1979). Photoperiodicity may further influence ram performance through sperm morphology. The incidence of morphologically normal sperm cells was highest in October, with a transient rise in morphologically normal sperm in April in Suffolk and Lincoln rams

(Mickelsen et al., 1981). The interaction of age of the ram lamb and season was evident in a figure presented by Courot et al. (1975) which depicted the sc growth of ram lambs born in September or February. September-born lambs had a sharp reduction in sc at approximately 155 days of age whereas the spring-born February ram lambs continued to increase sc beyond 200 d.

Measurement and analysis of estimated scrotal circumference in rams is further complicated by seasonal fluctuations in testicular size (Land and Sales, 1977; Land et al., 1979; Mickelsen et al., 1981; Dufuor et al., 1984).

Notter and Copenhaver (1980b) reported that the average 150-d wt of lambs born in April was 41.3 kg, which was 1.9 kg less than weights of January or September born lambs ($P < .05$). Conversely, Gould and Whiteman, (1971) found that spring-born lambs (out of Dorset, Rambouillet and Dorset x Rambouillet ewes) were 2.5 kg heavier than fall-born lambs at 70 d of age.

Genetic Effects on Reproduction and Growth

Generally, reproductive traits have low repeatabilities and heritabilities (Turner, 1969). Although reproductive traits are inherited in the same manner as continuous traits, many are phenotypically expressed binomially or categorically as a threshold is passed (Dempster and Lerner, 1950). As a result, assumptions of the linear model are violated when these traits are analyzed in the same fashion as traits having normally distributed errors (Gianola, 1982). Also, selection is restricted since reproductive traits are sex-limited; only the female expresses conception, prolificacy, rebreeding, etc, although the ram still has a role in the expression of these traits (Land, 1978; Mickelsen et al., 1981). It would be, therefore, helpful to identify continuous traits in the ram that are highly correlated with female reproductive traits (Walkley and Smith, 1980). If in conjunction with selection based on the female trait, selection was also implemented using a continuous male trait with a moderate to high heritability which also had a moderate to high correlation with a female reproduction, two obstacles could potentially be circumvented:

distributional inconsistencies present when analyzing binomial or multinomial data could be reduced, and overall accuracy of selection would be improved.

However, this assumes that accurate estimates of covariance components among the traits of interest are available. If this is not the case, then less genetic gain than was expected would result.

Breed

Reproduction. Breeds vary in time of initiation of their breeding season and in its length (Notter, 1986). Quirke et al. (1985) reported that the duration of the first breeding season of Finn, Finn x Dorset, Dorset, Suffolk and Rambouillet ewe lambs was 127, 131, 87, 77 and 34 d, respectively. However, results of Dickerson and Glimp (1975) indicated that breed differences in age-adjusted fertility were large within years but rather inconsistent among years.

Notter and Copenhaver (1980a) found that although conception rates did not differ for 1/2-Finn and 1/4-Finn ewes in August and November, the 1/2-Finn ewes exhibited an April conception rate of 60% vs 45% and 38% for 1/4-Finn and Suffolk x Rambouillet ewes respectively ($P < .05$). Furthermore, the 1/2-Finn ewes averaged .48 and .50 more lambs per litter than did 1/4-Finn or SR ewes, respectively. Rambouillet and Finn-cross ewes produced more lambs per ewe exposed and more lambs per ewe lambing than 17 other breed groups (Laster et al., 1972). Also, the Finn-cross ewes produced significantly more lambs per ewe exposed and per ewe lambing than the Rambouillet crosses ($P < .01$). Meyer and Bradford (1973) found that Finn x Targhee ewes gave birth to more lambs (2.22) than did Targhee ewes (1.50). When lambing at one year of age, the spring-lambing 1/4-Finn ewe effect in place of Rambouillet breeding resulted in an increase ($P < .10$) of 3.5 kg in weight of lamb weaned per ewe which was due primarily to the greater proportion of the 1/4-Finn ewes that lambed (Thomas and Whiteman, 1979a). Conversely, Thomas and Whiteman (1979b) found that fall-lambing 1/4-Finn ewes weaned fewer kilograms of lamb per ewe exposed than did Rambouillet crossbred ewes in the fall of both 1974 and 1975 (-2.5 kg and -6.4 kg, $P < .05$; respectively) due to the smaller proportion of the 1/4-Finn ewes that

lambled. However, the 1/4-Finn ewes produced litters that were .15 lambs larger than those of Dorset-Rambouillet ewes (Thomas and Whiteman, 1979a,b).

Mean testis diameter of 20 to 25-wk-old Scottish Blackface, Finn and Merino rams ranked in the same order as the ovulation rates of females of those breeds (Land and Carr, 1975). Breed differences in sc were greatest from 70 to 100 d in Finn, Rambouillet, and Dorset ram lambs (Lucas et al., 1983). Differences in testicular growth patterns between blackfaced and whitefaced (WF) rams involved scaling effects due to differences in body size and the more rapid maturing rate of WF rams (Notter et. al., 1985). Furthermore, Notter et. al. (1985) found that the primary breed difference in sc among three groups of rams was associated with age differences during the period of rapid testicular growth.

Growth. Notter and Copenhaver (1980b) observed that lambs from SR and 1/4-Finn ewes grew faster, both preweaning and postweaning, than did lambs from 1/2-Finn ewes. Substitution of 1/4 Rambouillet in place of 1/4 Dorset breeding in the ewe resulted in a significant ($P < .01$) increase of 1.6, 3.0 and 4.3 kg body weight at breeding at 7, 18 and 29 months of age, respectively in spring lambing ewes (Thomas and Whiteman, 1979a). When ewes lambled in late winter-early spring (Thomas and Whiteman, 1979a), the 1/4-Finn effect resulted in little change in breeding weight, relative to the 1/4 Rambouillet, and the 1/4 Dorset effect resulted in a significant ($P < .01$) decrease in ewe breeding weight of -5.3 and -4.4 kg for 1974 and 1975, respectively, relative to the Rambouillet. Among Dorset, Blackbelly x Dorset, Finn x Dorset and Dorset x Finn rams, Finn x Dorset rams were heaviest at all ages and had the largest sc; however, among Hampshire and Suffolk rams there were no differences (Notter et al., 1985) in body wt.

Repeatability

Reproduction. Repeatability estimates of reproductive traits are, in general, low (Turner, 1969). However, most of these estimates have been obtained from ewes of less prolific breeds managed under an annual lambing scheme. Thus the estimates may be inappropriate for ewes

from more prolific breeds (i.e., Finn) managed under an accelerated lambing system (Speedy and FitzSimons, 1977). Overall estimates of repeatability for litter size for ewes in an accelerated lambing system that were allowed to lamb three times every two years in September, January and April ranged from $.166 \pm .031$ to $.156 \pm .080$ (Notter, 1981). Within-season repeatabilities for litter size were $.162 \pm .066$ in January, $.375 \pm .080$ in April and $.318 \pm .072$ in September.

Repeatabilities for litter size at birth were found to be .12, .17 and .09 for Targhee, Columbia and Suffolk breeds, respectively (Adbulkhaliq et al., 1989). These estimates agreed well with those of Mechling and Carter (1969), Notter (1981), Dzakuma et al. (1982), Clark and Hohenboken (1983) and Fogarty et al., (1985). Also, Notter (1981) reported estimates of repeatabilities for conception rate (fertility) that varied from $.076 \pm .022$ to $.127 \pm .024$. Gabina (1989) obtained repeatability estimates for fertility of zero and for litter size ranging from .02 to .41 for ewes that were mated in March - April, July - August and November - December. However, Fogarty et al., (1985) obtained a repeatability for fertility of .06, which was in agreement with those of Notter (1981). Purser (1965) estimated repeatabilities of .09 and .08 for conception rate of Blackface and Welsh ewes, respectively. Similarly, Shelton and Menzies (1970) estimated a repeatability for conception rate of .094 for Rambouillet ewes under moderately intensive management. However, Shelton and Menzies (1970) obtained a repeatability of -.006 for Rambouillet ewes under more strict management. Bunge et al. (1990) obtained estimates for fertility and prolificacy of .03 and .19, respectively, from a population of Rambouillet ewes. In general, estimates of repeatability for fertility and prolificacy reported in the literature ranged from 0 to .40, with prolificacy having the higher estimates.

Growth. Repeatability estimates among ewes across years for weight of lambs at birth, 4, 8, 12, and 16 weeks of age in a synthetic dam line of sheep were .36, .35, .27, .27, .25 ($\pm .03$), respectively; the line was composed of 49% Finn, 22% East Friesian, 16% Border Leicester and

13% Dorset Horn breeding (Martin et al., 1980). These values generally agreed with previous estimates (.12 to .37) of Harrington and Whiteman (1967).

Heritability and Genetic Correlations

Reproduction. Heritabilities for litter size at birth were found to be .23, .35 and .18 for Targhee, Columbia and Suffolk breeds, respectively (Adbulkhaliq et al., 1989). Similarly, Shelton and Menzies (1968) obtained an estimate of .26 for litter size at birth and .07 for fertility in Rambouillet ewes. Bunge et al. (1990) estimated heritabilities for fertility and prolificacy of .03 and .34, respectively. However, Purser (1965) and Fogarty et al. (1985) reported lower heritability estimates for prolificacy of .14 and .10, respectively. Also, Purser (1965) estimated heritability of fertility to be .03 in Welsh Mountain ewes, which agreed well with the estimate obtained by Shelton and Menzies (1968). Piper et al. (1980) reported a heritability of $.05 \pm .07$ for ovulation rate and determined that there was little advantage to using ovulation rate over litter size as a selection criterion for increasing numbers of lambs born in Merino sheep.

Land (1973) estimated the genetic correlation between ovulation rate and testis weight to be 0.97 before and 0.82 after data were adjusted to a constant body weight, which indicated that the removal of variation in body weight had only a small effect on the magnitude of the correlation between ovulation rate and testis weight. Also, the age at which testis size is measured may influence the correlated responses that can be expected in female reproductive traits (Land, 1978).

Scrotal circumference is more closely associated with the reproductive performance of a ram than are typical growth traits, and although body weight and sc measures have some inherent relationship, it cannot be assumed that sc and wt have similar heritabilities (Land, 1973; Land and Carr, 1975). Scrotal circumference heritability and correlations may, in fact, be similar to those found in beef cattle. Kriese et al. (1991) obtained heritability (in the narrow sense) estimates for yearling sc of .53 and .16 for Hereford and Brangus bulls, respectively. Genetic correlations between yearling sc and other growth traits were moderate and positive, indicating that selection

for yearling sc would not adversely affect other growth traits in cattle. These heritabilities and genetic correlation estimates for cattle agree well with those of Bourdon and Brinks (1986), but were slightly lower than the genetic correlation between sc and yearling weight of .68 reported by Knights et al., (1984). Scrotal circumference has been found to be correlated negatively with age of puberty in female cattle (Brinks et al., 1978) and correlated positively with pregnancy rates, age at first breeding and age at first calving (Toelle and Robinson, 1985).

Purvis et al. (1988) estimated the genetic relationship between ovulation rate at 4 ages (18, 30, 42 and 54 months) and testicular diameter at 3 ages (5, 8 and 12 months) in a random-breeding Merino flock. Generally, Purvis et al. (1988) found that the genetic correlations between male and female traits at different ages did not differ significantly; as a result, the pooled estimate between ovulation rate and testicular diameter was $.35_{\pm}.08$ from a dam-son covariance method, and $.16_{\pm}.11$ from a half-sib covariance method. The size of these estimates suggested that a useful genetic response in ovulation rate would result from selection on testicular size, at least in the Merino breed.

Growth. A wide range of heritability estimates for weights were reported in the literature. Shelton and Campbell (1962) obtained estimates of .14 to .25 for heritability of 160 d weight in range Rambouillet rams. Vogt et al. (1967) found heritability estimates for 120 day weights to be .31 to .59 and .03 to .12 for single and twin lambs respectively. Thrift et al. (1973) reported values of .1 and .09 for birth and 10 week weights, respectively. An intensively managed flock had higher heritability estimates for body weights than did a less intensively managed flock (Osman and Bradford, 1965). Martin et al. (1980) reported estimates of heritabilities for body weights in a synthetic line of sheep at birth, 4, 8, 12 and 16 weeks of age of .17, .24, .22, .23 and .23 (\pm .09), respectively. Mavrogenis et al. (1980) reported relatively high body weight heritability estimates at birth, 5, 10, 15 and 20 weeks of age of .13, .34, .63, .73 and .66, respectively.

Several studies found birth weight to have a low correlation with weights at other ages (Mavrogenis et al., 1980; Ercanbrack and Price, 1972). However, other studies indicate substantial correlation of birth weight and weights taken at later ages (Martin et al., 1980; Thrift et al., 1973; Vogt et al., 1967). In general, estimates of genetic correlations for body weights at various ages have been high, and have indicated that selection for one weight would result in considerable positive change in all weights (Martin et al., 1980; Thrift et al., 1973; Vogt et al., 1967; Osman and Bradford, 1965).

Analytical Procedures

All-or-None Traits

Even though phenotypes for many female reproductive traits are expressed in a binomial or multinomial fashion (i.e., fertility, rebreeding and prolificacy), their inheritance appears to be multifactorial/polygenic (Dempster and Lerner, 1950). Furthermore, Dempster and Lerner (1950) proposed that characters with an all-or-none phenotypic expression be treated as dependent on one or several continuous underlying variates. The value of each individual's underlying variate(s) would be dependent on both genetic and non-genetic factors. Expression of the all-or-none trait would require that some threshold on the continuous underlying scale be exceeded. Traits such as litter size which are categorical can be thought of as traits with several thresholds (Gianola, 1982), each resulting in a different outcome (i.e., an increase in number of offspring born for prolificacy)

Dempster and Lerner's (1950) viewpoint allowed heritability of a character to be measured in terms of its probability of appearance, with values of 1 and 0 assigned depending on a success or failure, respectively; they defined this binomial character as the "p scale". The use of the p scale might, however, produce inaccuracies as a result of three potential pitfalls in its use. Since the limiting genotypic values, when only one phenotypic class is present in the data, defined as

probability of "1", are 0 and 1, it is unlikely that a given gene substitution would have the same effect near these limits as in the middle of the range (Dempster and Lerner, 1950). When at the extreme ranges of the p scale (i.e., 0 to .1 and .9 to 1), the environmental variation becomes almost directly proportional to the product of the probability that the event occurs, p, and the probability that the event does not occur, q. However, when p is near .5, the environmental variance is reasonably constant (Dempster and Lerner, 1950). Because the p scale is a crude approximation to the underlying continuous scale, finer degrees of measurable variation may be obscured, as well as genetic differences associated with those finer degrees of variation (Dempster and Lerner, 1950). Heritability, genotypic and phenotypic correlation estimates on the p scale are much smaller than on the underlying scale when p is near 0 or 1 (Gianola, 1982).

Reproductive traits in females such as fertility and prolificacy are limited in the degree of genetic gain that can be achieved because, in most production scenarios, a substantial proportion of females must be kept to serve as replacements. Thus the amount of selection pressure that can be applied to them is minimal. As a result, there would be considerable value in an indirect selection criterion which does not suffer from the limitation and the distributional related problems stated above. Traits in the male closely associated with the female reproductive potential would allow direct selection of males at 4 to 5 mo of age to improve the correlated female trait.

Although sc measurements have proven to be correlated with female reproductive traits, Notter et al. (1985) suggested that in rams that differ in body size, the pattern of testicular growth over time may be more informative than any single measure of testicular size. Analysis of parameters of a growth function which adequately fits the data could be performed similarly to that of Eisen et al. (1969). The result would be a set of sc growth curve parameter estimates for each ram lamb which described the sc growth pattern of the ram lamb and could then be correlated with female reproductive traits. Walkley and Smith (1980) demonstrated that if there was a moderate to high genetic correlation between the physiological trait, sc, with a moderate heritability, and litter

size, which has a low heritability, substantial gains over direct selection on litter size would be realized. Note, however, that Walkley and Smith (1980) stressed that good estimates of variance components be obtained, and that the most important parameter to estimate was the genetic correlation of the male trait with litter size.

Mixed Models

Variance component estimation using general mixed linear models began with the paper of Henderson (1953), which discussed the use of mixed model analyses to estimate variance components based on the use of mixed model equations (MME) for best linear unbiased estimation (BLUE) and prediction (BLUP) of fixed and random effects, respectively. The MME equations allowed the incorporation of relationships among animals via the numerator relationship matrix (NRM) (Henderson, 1973), and became the basis for all subsequent specialized methods of variance component estimation. Generally, this method of estimating variance components was used on reasonably large data sets such as those derived from national dairy sire evaluations (Meyer, 1986). However, Lawlor et al. (1984) found that only small gains in accuracy were achieved in estimates of between and within sire progeny group variances for sire models when the NRM was used unless its inclusion removed selection bias because the sires had lots of progeny, but the NRM made a difference when an animal model was used. However, for smaller designed experiments, such as selection experiments, more detailed models were desirable. In order to obtain reasonable variance component estimates in these smaller designed experiments, all the information available needed to be used. These more detailed models initially took the form of the individual animal model (IAM) and the computationally less demanding equivalent reduced animal model (RAM) of Quaas and Pollak (1980). Unfortunately, the computational methodology needed to utilize more detailed models lagged behind their theoretical development until recently.

REML

The currently preferred method for variance component estimation is restricted maximum likelihood (REML) which was described for unbalanced data by Patterson and Thompson (1971). REML estimates by definition are always in the statistical parameter space, consistent, asymptotically normal and efficient (Harville, 1977). Consider the simple univariate model with one random factor,

$$y = Xb + Zu + e ,$$

where y is a vector of observations, b is a vector of fixed effects, u is a vector of random effects, e is a vector of random residual errors, X is the design matrix associated with b and Z is the incidence matrix pertaining to u . Also, assume: $E(y) = Xb$, $E(u)=0$, $E(e)=0$; $V(u)=A\sigma_u^2$, where A is the NRM between levels of the random effect; $V(e)=\sigma_e^2$, and $Cov(u,e')=0$, such that $V(y) = ZAZ'\sigma_b^2 + \sigma_w^2$. Variance components estimated by REML are characteristic only of u , which suggests estimating σ_b^2 and σ_w^2 from functions of y , say $K'y$, that do not involve b . In order to accomplish this, K' must be chosen such that $K'X=0$ resulting in what have been called error contrasts (Harville, 1974). The method of maximum likelihood is then applied to $K'y$, as first suggested by Patterson and Thompson (1971). REML operates on the likelihood of these error contrasts that have expectation zero, or equivalently, on the part of the likelihood that is independent of fixed effects (Harville, 1974). The result is to take account of a loss in degrees of freedom due to fitting fixed effects in the model (Patterson and Thompson, 1971). For $y \sim N(Xb, V)$, the log likelihood for the univariate model given above is (Harville, 1977):

$$\log L = -1/2[\text{const} + \log |V| + \log |X^*{}'V^{-1}X^*| + (y-X\hat{b})'V^{-1}(y-X\hat{b})],$$

where $\hat{b} = \text{BLUE}(b)$, X^* is a full rank submatrix of X . REML estimates can be found in two-way: use of analytical derivatives, i.e., the EM algorithm, or algorithms not requiring analytical derivatives,

referred to as derivative-free algorithms. Meyer (1989) examined the utility of, and implemented Simplex, Quasi-Newton and Quadratic approximation computational strategies suggested by Nelder and Mead (1965), Gill et al. (1981) and Graser et al. (1987), respectively, to develop a REML program to estimate variance components for animal models with several random effects using a derivative-free algorithm.

Standard software for variance component estimation include Harvey's (1978) mixed model least-squares and maximum likelihood computer program (LSML76) and various procedures in SAS (1985).

The animal model relates the data directly to the breeding values of the animals producing the records. Breeding value estimates of animals without records are obtained through genetic relationships with animals having records. Thus, unlike a sire model which usually has much fewer unknowns than observations, the animal model may have more unknowns than there are animals with records and fixed effects in the model. The simplest of these models fits only one fixed effect, the overall mean, plus additive genetic and error effects; additive genetic and error variance components must be estimated for this model. However, this model is seldom sufficient, thus other effects must be added and their variance components estimated.

Although REML has been successfully used to accommodate the complex MME to produce accurate estimates of genetic parameters (i.e., variance components), the correct model for each situation must be used. Several factors have been sources of concern when analyzing data. Of particular concern were data where litters were involved and where full sibs were treated as half sibs in estimating heritability from half sib covariances. Jackson (1983) demonstrated that when dams were ignored, heritability estimates from sire family variance components were biased upward. Furthermore, Jackson (1983) determined that if dominance, epistatic, or maternal components were insignificant and only additive genetic variance components were significant, the

bias may be removed by use of a computed average genetic relationship (r) for sire families in place of a nominal $r = 0.25$. The advantage of this method was that dam identity was not required.

However, national evaluations and designed experiments generally have dam identities available for analyses. Animal models exploit this added information by way of the NRM and through fitting additional genetic effects maternal effects. Several REML programs have been designed to accommodate fixed additive genetic group effects as well as several random effects. It is important that the way in which these fixed additive genetic groups have been defined reflect the population being analyzed. Van der Werf and de Boer (1989a) simulated populations of Dutch Friesian (DF) x Holstein Friesian (HF) cows with the amount of HF genes ranging from 0 to 100% in 12.5% increments and varied the amount of heterosis and recombination loss from -10% to 10% to determine the influence of nonadditive effects on estimation of genetic parameters in dairy cattle. Additive models gave biased estimates for breed differences, group effects, and breeding values when heterosis and recombination were present; however, estimates were unbiased with a nonadditive model (Van der Werf and de Boer, 1989a). Furthermore, Van der Werf and de Boer (1989b) reported estimates for heterosis and recombination loss which ranged from 0% to 2.5% and -1.9% to 1.5% in a population of DF and HF cows. Even though the effects of heterosis and recombination loss were small, differences between a nonadditive model and additive models were substantial for estimates of breed differences, genetic parameters and breeding values across breeds (Van der Werf and de Boer, 1989b). Additive models with progeny (groups defined according to breed composition of the progeny making the record) and sire groups (additive sire group model) overestimated genetic variance by 6 and 33%, respectively.

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Testis Growth in Ram Lambs

**TESTIS GROWTH PATTERNS THROUGH 17 MONTHS OF
AGE FOR THREE BREEDS OF SHEEP**

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Summary

Forty spring-born ram lambs (eight Barbados Blackbelly (BB), 10 Suffolk (S) and 22 1/2-Dorset, 1/4-Finnish Landrace, 1/4-Rambouillet (F₁)) were used to assess seasonal patterns of testis growth through 16 mo of age. Scrotal circumference (sc) and body weight (wt) were measured at mean ages of 30, 62, 96, 124, 153, 180, 212, 243, 290, 333, 364, 398, 427, 454, 488 and 517 d, and a multivariate repeated measures analysis was conducted to test breed effects and breed x age interaction. Suffolk rams were not measured at the first two ages. Breed differences in sc and wt increased in magnitude and significance as rams matured. Testes descended into the scrotum at approximately 14 d; however, little growth occurred before 30 d, followed by a sharp increase in testis growth. Testis growth plateaued in early winter (December) and this plateau was followed by a reduction in testis size ending in early spring. As day length subsequently increased, testis growth resumed, and attained a second plateau by the following September, when the study was terminated. Logistic growth curves were used to describe testis growth for each ram. Suffolk rams had the largest asymptotic sc with BB and F₁ being similar. F₁ rams had the fastest maturing rate, followed by S and BB rams, respectively. No differences existed in asymptotic sc when sc was scaled by body weight to the 1/3 power. Breed differences were associated primarily with

mean sc measures at each age and with parameters of the logistic curve defining the timing of rapid testis growth. (Key Words: Sheep, Testis, Breeds, Growth Curves, Scrotal Circumference.)

Introduction

Breed differences in seasonal breeding patterns of ewes are well documented (Hafez, 1952; Quirke et al., 1985; Notter, 1986) and generally correspond to seasonal fluctuations in testis growth in rams of the same breeds (Land and Sales, 1977; Land, 1978). Also, mean testis diameter of 20 to 25-wk-old Scottish Blackface, Finn and Merino rams ranked in the same order as the ovulation rates of females of those breeds (Land and Carr, 1975). Divergent selection among spring-born Finn x Dorset males for large and small testis diameter at 10 wk of age (Land, 1978) produced females in the line selected for large testis size that exhibited first estrus 3 wk earlier than ewes of the line selected for small testis size.

Although selection for testis size seems to have influenced reproductive characteristics of females, the measure of testis growth that would be most effective as a selection criterion is not clear (Land, 1973, 1978; Notter et al., 1985). Both age effects and seasonal fluctuations in testis size must be considered in choosing when to measure sc. The objectives of this study were to model sc of spring-born ram lambs through 16 mo of age, and to evaluate breed and seasonal differences in testis growth patterns .

Materials and Methods

Experimental Procedures. Forty ram lambs (eight Barbados Blackbelly (BB), 10 Suffolk (S), and 22 1/2-Dorset, 1/4-Finn, 1/4-Rambouillet (F₁)) were used for the study. Average birth dates were April 10, 1 and 6 for BB, S and F₁ lambs, respectively. Blackbelly rams were advanced backcross generation BB animals with 7/8 to 15/16 BB and 1/8 to 1/16 Dorset breeding. Rams were born at the Virginia Tech Sheep Center, Blacksburg, and transferred to the Southwest Virginia

Agricultural Experiment Station, Glade Spring, at about 90 d of age. Rams remained at Glade Spring for the rest of the study. BB and F₁ rams were maintained with their dams on expanded metal feeding facilities until weaning at an average age of 62 d. After weaning lambs remained on expanded metal until transferred to Glade Spring. Suffolk rams were weaned at about 90 d of age and immediately transferred to Glade Spring. Rams in all three groups were fed the same creep diet ad libitum until weaning and this diet was also fed ad libitum to the weaned BB and F₁ rams on expanded metal.

After transfer to Glade Spring, lambs were changed from a ground, concentrate diet to a grazed forage diet over a period of about 2 wk and were subsequently maintained on permanent bluegrass-white clover pastures and stockpiled fescue. Fescue hay was provided during late winter. Scrotal circumferences and body weights were measured at average ages of 30, 62, 96, 124, 153, 180, 212, 243, 290, 333, 364, 398, 427, 454, 488 and 517 d (\pm 8 d sd). However, S rams were not measured at 30 and 60 d. Early testis growth in S rams was thus not monitored; the S males were included in the study primarily to allow comparison of their testis response to changes in season to that of rams of the other two breeds. Scrotal circumferences were obtained by measuring the scrotum at the point of maximum circumference of the paired testes (Notter et al., 1981).

Statistical Procedures. Least squares (LS) means were obtained for sc and wt at each age using the repeated measures option of the general linear models procedure of the Statistical Analysis System (SAS, 1985). The model was:

$$Y_{ijk} = \mu + b_i + q_{ij} + t_k + (bt)_{ik} + e_{ijk}, \quad (1)$$

where Y_{ijk} is the sc or wt of the j^{th} ram (q) of the i^{th} breed type (b) at the k^{th} measurement age (t), μ is the overall mean, $(bt)_{ik}$ is the breed x age interaction, and e_{ijk} is residual error with all effects in

the model being fixed. Breed effects were tested with the among-ram mean square; all other effects were tested with residual error. The repeated-measure analysis accounted for the correlation structure present in the data when calculating significance levels for effects in the model, and as a result yielded the preferred set of hypothesis tests for these data (Morrison, 1976). The SAS algorithm could not accommodate missing observations. Therefore, to include S rams in the analysis, observations at 30 and 62 d were eliminated from the repeated measures analysis for all animals. Arithmetic means were computed for sc and wt at 30 and 62 d of age for F₁ and BB rams for use in subsequent growth curve calculations.

Nonlinear regression procedures (SAS, 1985) were used to describe growth in sc. Within the first year of the rams' life, sc had attained its maximum value by about 243 d of age. Means for sc for each breed group at each age through 243 d were thus used to fit logistic curves to the data using the model of Notter et al. (1985):

$$SC_{it} = A_i / (1 + B_i e^{-k_i t}) + r_{it}, \quad (2)$$

where SC_{it} is the mean sc of the *i*th breed at *t* days of age, *A* is the estimated maximum sc, *k* is a maturing rate parameter, *B* is a constant of integration, *e* is the base of the natural logarithm and r_{it} is the residual about the mean curve for each breed at age *t*. The iterative nonlinear regression procedure of SAS (SAS, 1985) was used to obtain logistic parameter estimates.

Notter et al. (1985) modified the age and sc scale to $t' = t - 14$ and $sc' = sc - 10$ before fitting the logistic model. By implementing the $t' = t - 14$ adjustment, the origin of the lamb age scale was shifted in order to appropriately corresponded with the descent of the testes into the scrotum. The sc' redefined a new origin on the ordinate axis roughly corresponding to the sc of the empty scrotum. For the current data, the same procedure was followed except that values chosen to transform *t* and *sc* were those that minimized the pooled within-breed mse for model 2.

Incremental adjustments in t' from 7 to 18 did not influence the mse so $t' = t-14$ was retained. However, adjustments in sc' affected the probability that the nonlinear algorithm of SAS (1985) converged to stable parameter estimates and the magnitude of the pooled within-breed mse. For these data, $sc' = sc-6$ minimized the pooled within-breed mse. Thus, to evaluate an estimated asymptote, A , of the logistic curve, 6 cm must be added to the estimate in order to return it to the original scale. Definition of sc' differs from that of Notter et al. (1985), but reflects the need to allow the data to determine the sc adjustment required in order to obtain best-fitting curves.

After determining general characteristics of the logistic curves through 243 d using mean sc measurements, logistic sc growth curves were fit for each ram. In addition to parameter estimates from equation 2, two composite parameters were estimated for each ram. These were $C_{14} = [A/(1+B)] + 6$, which is the estimated sc at 14 d and $t_l = [\ln(B)/k] + 14$, which is the estimated age at the point of inflection of the logistic curve, and which is equivalent to estimated age at which testis growth rate was maximum (Notter et al., 1985). Estimates of individual growth curve parameters for each lamb were then analyzed with the model:

$$X_{ij} = \mu + b_i + e_{ij}, \quad (3)$$

(Eisen et al., 1969) where X is the estimated parameter for the j th lamb of the i th breed (b), μ is the overall mean and e_{ij} is random residual error.

Scrotal circumference decreased after about 243 d of age (December) in all rams and returned to values achieved prior to the start of testis regression by about 398 d (April). Declines in sc for each ram during the winter period of testis regression and recrudescence were analyzed using model 3. Finally, data from 454 through 517 d were combined with those through 243 d and used to fit logistic curves describing growth in sc through 517 d of age, but excluding data from the period of testis regression and early recrudescence. These curves were again fitted to both

breed mean and individual data. This analysis considered sc growth after 398 d to be a continuation of that observed through 243 d, but with a period of interrupted growth. As an alternative to use of the absolute decline in sc, the minimum sc observed during winter was also expressed as a deviation from this combined logistic regression curve and reanalyzed with model 3.

Testis size is related to body weight. The quantitative relationship between them, however, has not yet been empirically determined. To account for body size, it has been proposed that linear measures be scaled relative to the one third power of body weight (Lyne and Verhagen, 1957; Taylor, 1968) such that $sc_a = sc/wt^{1/3}$. By scaling sc to the one third power of body weight, remaining differences should more closely represent differences in sc that are independent of body size. Thus for each individual, logistic growth curves were refitted using sc measurements scaled by the one third power body weight, and resulting parameter estimates from model 2 were analyzed with model 3.

Results and Discussion

Testis growth through 250 d of age was sigmoidal (figure 1). In BB and F₁, a rapid increase in testis size began after 30 d, and maximum growth rate in sc was achieved between 84 and 93 d. Testis size plateaued by 250 d for all breed types. A reduction in testis size occurred around 250 d in all breed types; sc was minimum at near 330 d. Following testicular regression, an increase in sc occurred, and a second asymptote was reached at about 490 d. In contrast, body weights tended to show an approximately linear increase through 350 d, with a reduced rate of growth after 400 d (figure 2).

There were significant differences among breeds in sc and wt at each age after 90 d (table 1). Breed differences in sc were smallest at 96 d ($P < .03$) and increased through 517 d ($P < .0001$). Suffolk rams had the largest sc at each age followed by F₁ and BB. However, unlike results of Lucas et al. (1983) and Notter et al. (1985), there was no significant breed x age interaction for sc

from the repeated measures analysis. This was probably because the large S rams were not measured at 30 and 60 d. Notter et al. (1985) observed that S rams were significantly older at the point of maximum testis growth than whitefaced types including Dorset, Finnsheep and BB breeding. There were, however, significant breed x age interaction effects for weight.

The choice of data to fit the initial logistic curve was necessarily somewhat arbitrary. Mean sc increased through 243 d in all breeds and means for sc at 212 and 290 d were approximately symmetrical about the 243 d maximum. When sc means through 212, 243 or 290 d were used to fit the initial logistic curve, the data through 243 d yielded the maximum estimate of A and the smallest mean square for deviations about the regression line. Thus the first eight sc observations were used to fit the initial curves.

Parameter estimates for logistic curves describing mean growth in sc through 243 d of age (table 2) were similar to those reported by Notter et al (1985). Suffolk rams had the largest asymptotic sc whereas F1 and BB rams were similar. Furthermore, when tested against the pooled deviations from regression, curves fitted separately by breeds (figure 2) produced a significantly better fit ($P \leq .0001$) than the overall curve ignoring breed differences.

When logistic curves were fitted separately for each ram using data through 243 d of age, convergence of parameter estimates to reasonable values was obtained for 33 of 40 rams. One BB, one F1 and five S rams did not yield reasonable logistic parameter estimates. Failure to converge was associated with inability to project logistic curves due to missing data in S rams at 30 and 60 d and to essentially linear growth in sc in a few rams. The analysis of individual growth curve parameter estimates was thus based only on the 33 rams that yielded reasonable logistic parameters.

Analysis of parameters estimated from individual logistic curves revealed significant differences among breeds in A and k ($P \leq .0002$ and $P \leq .05$, respectively), but not in B, t_1 and C_{14} (table 3). Although differences in t_1 were not statistically significant, they followed those in k, but

were of lesser magnitude, in part due to a positive correlation within breeds ($r = .52$ to $.98$) with, and greater variation in, B which tended to reduce differences in calculated t_1 . Growth in sc was most rapid at an average of 87 d for F_1 , 93 d for S , and 84 d in BB rams; these estimates were consistent with the mean t_1 values of 95 and 88 d found for Suffolk and Finn x Dorset reciprocal cross rams, respectively, by Notter et. al. (1985).

When sc was scaled by body weight to the $1/3$ power, the only significant breed differences were in B and k ($p = .0007$ and $.005$ respectively; table 3). However, differences in B and k tended to act in different directions in calculation of t_1 , and t_1 again did not differ among breeds. These results indicate that observed differences in asymptotic scrotal sizes at 243 d of age occurred primarily because of scaling effects due to differences in body size among the breeds. Also, breed differences in the maturing rate parameter, k were not consistent across the scaled vs. unscaled sc data analyses. F_1 ram lambs tended to reach the point of maximum growth rate sooner than S rams regardless of whether or not sc was scaled by body wt (table 3). In contrast to results of Notter et. al. (1985), however, estimates of k based on sc adjusted for body weight were largest for Suffolk rams but were also associated with larger values of B (table 3). Thus, maximum growth in sc occurred at the youngest ages in F_1 rams. The purebred S and advanced backcross generation BB rams were similar in age at maximum sc growth after scaling of sc for body weight. This may be an indication that heterosis expressed in the F_1 rams allowed them to mature most quickly.

The period of testis regression and recrudescence was marked by a decrease in testis size that began in December shortly after 243 d of age. Mean sc measures decreased from their 243 d circumference by 1.6, 1.2 and 1.8 cm for BB , F_1 and S , respectively, by 333 d of age. Breed differences in sc remained relatively constant during the period of sc reduction (table 1, figure 1) and there were no significant differences among breeds in the magnitude of decrease in sc . Scrotal circumferences returned to their 243 d values by about 398 d of age.

For the overall logistic curve, using data through 243 d and after testes recrudescence, only the second asymptote, A_2 , was of biological interest because the curve fit to the first eight observations underestimated the older ram's asymptote. To estimate A_2 , a decision of when rams were under minimal negative seasonal influence was required (figure 3.) Due to the lack of power in testing differences in parameter estimates when including various subsets of observations, the decision of which observations should be allowed to contribute to the estimation of the second plateau was performed empirically and graphically. When scrotal circumferences at 454, 488 and 517 d of age were included for analysis with the first eight sc measurements, the largest estimates of A_2 were obtained. Estimates of A_2 differed among breeds ($P = .0001$; means of $31.45 \pm .47$, $32.45 \pm .82$ and $35.90 \pm .47$ cm for BB, F_1 and S respectively). These differences were removed by scaling for body weight to the $1/3$ power; means for scaled A_2 were 6.7, 6.4 and 6.5 $\text{cm/kg}^{1/3}$ for BB, F_1 and S respectively.

When scrotal circumference growth curves were fit for each individual, differences in A_2 among breeds were significant. As expected, estimates of A_2 were larger for S rams than for F_1 and BB rams. When sc was scaled for body weight to the $1/3$ power, differences in A_2 were no longer significant.

Thus, it appears from this study that differences in testicular growth patterns among these breeds were due primarily to differences in body weight, with a possible additional difference associated with differences in their maturing rate, k . However, k is difficult to interpret because of its high correlation with B when estimating individual sc logistic growth curves.

General Discussion. Although the logistic curves fit to these data described scrotal circumference growth in this set of rams, few statistically significant differences among breeds were identified. In particular, no differences were found in age at maximum testis growth, t_1 . Keeping in mind that t_1 is a function of other estimated logistic curve parameters, it becomes apparent that precise estimates of B and k are required to allow precise estimates of t_1 . In

retrospect, better logistic parameter estimates may have been obtained by taking measures at increased frequencies during early growth of the animal, thus reducing the error of estimation of logistic parameters. In order to obtain more accurate logistic growth curve estimation, it also appears critical to obtain measures at an increased frequency at each asymptote. As seen from the S curve (figure 3), the effect on parameter estimation of not having data around 30 and 60 days caused some difficulty, but was not so profound as to completely prohibit curve estimation. However, it must be noted that S sc estimates for less than 96 d of age extrapolate beyond the data. The small numbers of ram lambs per breed likely further contributed to the lack of significant breed differences in A, B, k, t_1 and C_{14} .

Extended scrotal circumference growth curve estimation is complicated by seasonal variations that occur in sc for each breed (Land, 1978). Although no significant differences among breeds were found in the magnitude of sc reduction, further investigation may yield valuable information into any correspondence with the period of seasonal anestrus in females. Thus, scrotal circumference measurements obtained more frequently at later ages may further facilitate the ability to discern when these fluctuations occur, their duration and implications with regard to their female relatives reproductive potential (Mickelsen et al., 1981; Dufour et al., 1984).

All three breeds in this study had two plateaus in their sc growth curves, the first occurring in December at approximately 8 mo of age, and the second occurring the following September at 16 mo of age. These growth patterns agree well with those reported by Land and Sales (1977), who illustrated a seasonal depression in testis size that began in late winter and ended in early spring, with a second plateau in scrotal size attained early in the second fall of the ram's life. Recall that figure 2 used parameter estimates obtained from the first year's data. Curves for figure 3 used parameter estimates obtained from the use of the first eight observations plus a selected subset of the observations from the second year. It is obvious from figures 2 and 3 that if the objective was to obtain the best fitting model for data of the first year, then subsequent

prediction of the second year's growth with that model would be poor. Conversely, if the objective was to obtain the best estimate of the final asymptotic sc, then prediction in general would be poor for the first year of ram's life. The most desirable model would be one that could accommodate both the early growth and cyclic (seasonal) growth patterns in sc. To this end, the A parameter in the logistic function might be replaced with a sine or sine-cosine structure to accommodate cyclic sc growth, as well as the initial logistic sc growth pattern (Stroup et al., 1987). Unfortunately, the amount of data in this experiment was not sufficient enough to fit this type of model.

The repeated measures analysis was capable of elucidating when and by what degree breed differences existed for given sc measures. However, a more complete data structure would be needed to delineate differences in the actual timing of maximum growth, initiation and duration of seasonal fluctuations in sc and the differences among breeds. Results of this study indicate that breed differences do exist in the rate of scrotal development as well as in scrotal circumferences measured at each age.

Implications

Walkley and Smith (1980) proposed sc as a potentially useful selection criterion to improve reproductive ability in both sexes, provided the measure used had at least a moderate heritability and a moderate genetic correlation with female reproductive traits. Although breed group differences in growth curves were limited and dependent on scaling effects, inherent breed differences observed among mean breed sc growth curves and measurements at each age did exist. Also indicated was the potential for sufficient variation among individual rams in their sc measurements and growth patterns to warrant further investigation into heritabilities and correlations with female reproductive traits. In fact, rate of testis growth and (or) degree of seasonal variation in testis size may be a better predictor of reproductive characteristics in females than any single sc measure (Land, 1973; Notter et al., 1985). Breed differences among young

rams in sc growth tended to be the greatest in the interval between 60 and 90 d of age since differences at later ages were reduced when scaled to the one-third power body weight. Further evaluation of testis size as a selection criteria should focus on 60 and 90 d sc and t_j .

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TABLE 1. MEANS FOR SCROTAL CIRCUMFERENCE AND BODY WEIGHT OF BARBADOS BLACKBELLY(BB), CROSSBRED(F1) AND SUFFOLK(S) RAMS.

Age(d)	SC(cm)			Body wt(kg)		
	BB	F1	S	BB	F1	S
30	9.4 ^a	9.9 ^a	e	10.89 ^a	13.25 ^a	e
62	12.7 ^a	13.2 ^a	e	17.11 ^a	21.51 ^a	e
96	15.2 ^b	19.6 ^c	21.9 ^d	20.41 ^b	28.21 ^c	37.83 ^d
124	18.9 ^b	23.3 ^c	27.1 ^d	22.41 ^b	31.25 ^c	44.59 ^d
153	22.4 ^b	25.4 ^b	29.8 ^c	27.58 ^b	35.52 ^c	53.07 ^d
180	23.2 ^b	26.9 ^c	31.0 ^d	27.76 ^b	38.19 ^c	57.43 ^d
212	25.4 ^b	28.2 ^c	31.9 ^d	33.20 ^b	45.99 ^c	68.18 ^d
243	26.9 ^b	28.9 ^b	32.4 ^c	36.65 ^b	50.80 ^c	74.66 ^d
290	25.5 ^b	28.1 ^b	31.3 ^c	38.92 ^b	59.42 ^c	83.96 ^d
333	25.3 ^b	27.7 ^c	30.6 ^d	44.00 ^b	65.09 ^c	92.40 ^d
364	26.5 ^b	28.0 ^b	31.0 ^c	48.26 ^b	67.86 ^c	95.66 ^d
398	27.0 ^b	29.1 ^b	32.3 ^c	47.54 ^b	69.49 ^c	93.58 ^d
427	29.3 ^b	32.1 ^c	35.5 ^d	48.63 ^b	70.53 ^c	94.17 ^d
454	30.5 ^b	32.1 ^b	34.9 ^c	53.16 ^b	73.12 ^c	101.20 ^d
488	32.1 ^b	33.6 ^b	36.6 ^c	56.61 ^b	75.16 ^c	104.19 ^d
517	31.3 ^b	33.3 ^c	36.4 ^d	58.06 ^b	75.52 ^c	99.66 ^d

^a arithmetic means.

^{b,c,d} sc or wt within a row that do not have a common superscript differ at $p < .05$.

^e Data not available

TABLE 2. BREED SC GROWTH CURVE PARAMETER ESTIMATES FROM ANALYSIS OF MEANS FOR THE FIRST EIGHT MEASUREMENTS^a

Parameter	Breed type		
	BB	F ₁	S
A+6 ^b	27.86 ± .82	28.71 ± .38	32.33 ± .21
B	6.78 ± .87	7.80 ± .95	9.10 ± 1.67
k	.0205 ± .0019	.0288 ± .0018	.0322 ± .0021
MSE	.323	.226	.059

^a Using model 2 on mean observations for each breed.

^b Estimated uncoded final scrotal circumference.

TABLE 3. BREED LEAST-SQUARES MEANS FOR SC GROWTH CURVE PARAMETER ESTIMATES USING DATA THROUGH 243 D OF AGE^a

Breed	Parameter				
	A(cm)	B	k	t _l (d)	C ₁₄ (cm)
-----unscaled-----					
BB	21.8 ^b ±1.0	18.5±4.1	.029 ^{b,c} ±.004	83.9±7.7	8.1±.6
F ₁	22.9 ^b ±0.5	12.8±1.9	.034 ^b ±.002	86.6±2.8	8.0±.2
S	27.3 ^c ±0.9	8.7±3.4	.026 ^c ±.003	93.4±5.5	8.1±.4
-----scaled by (body wt) ^{1/3} -----					
BB	6.7±.2	12.4 ^b ±10.4	.029 ^b ±.005	79.9±6.7	e
F ₁	6.3±.1	10.1 ^b ± 5.0	.039 ^b ±.002	71.5±2.9	e
S	6.5±.2	56.2 ^c ± 9.5	.052 ^c ±.004	78.6±5.1	e

^a least square means using model 3.

^{b,c,d} means within a column and analysis (scaled vs unscaled) that do not have a common superscript differ at p < .05.

^e Data not available

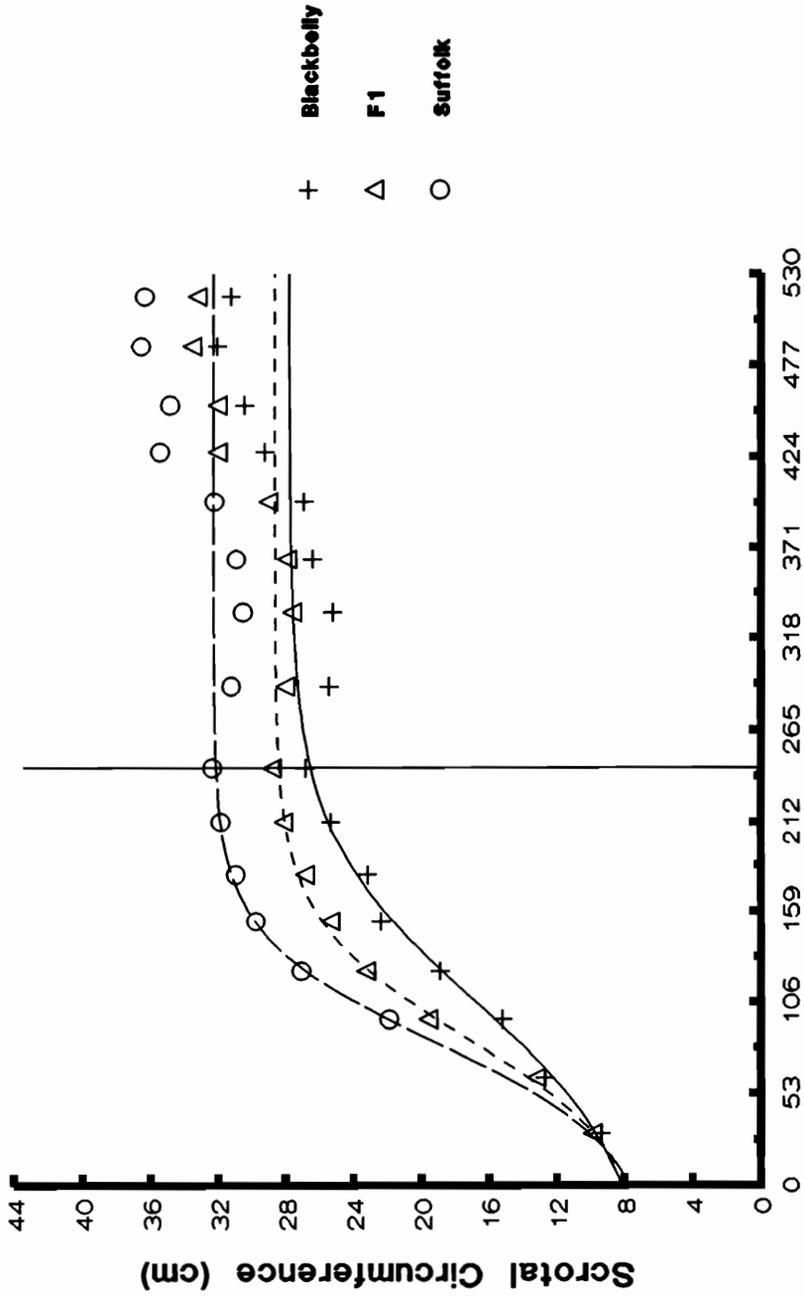
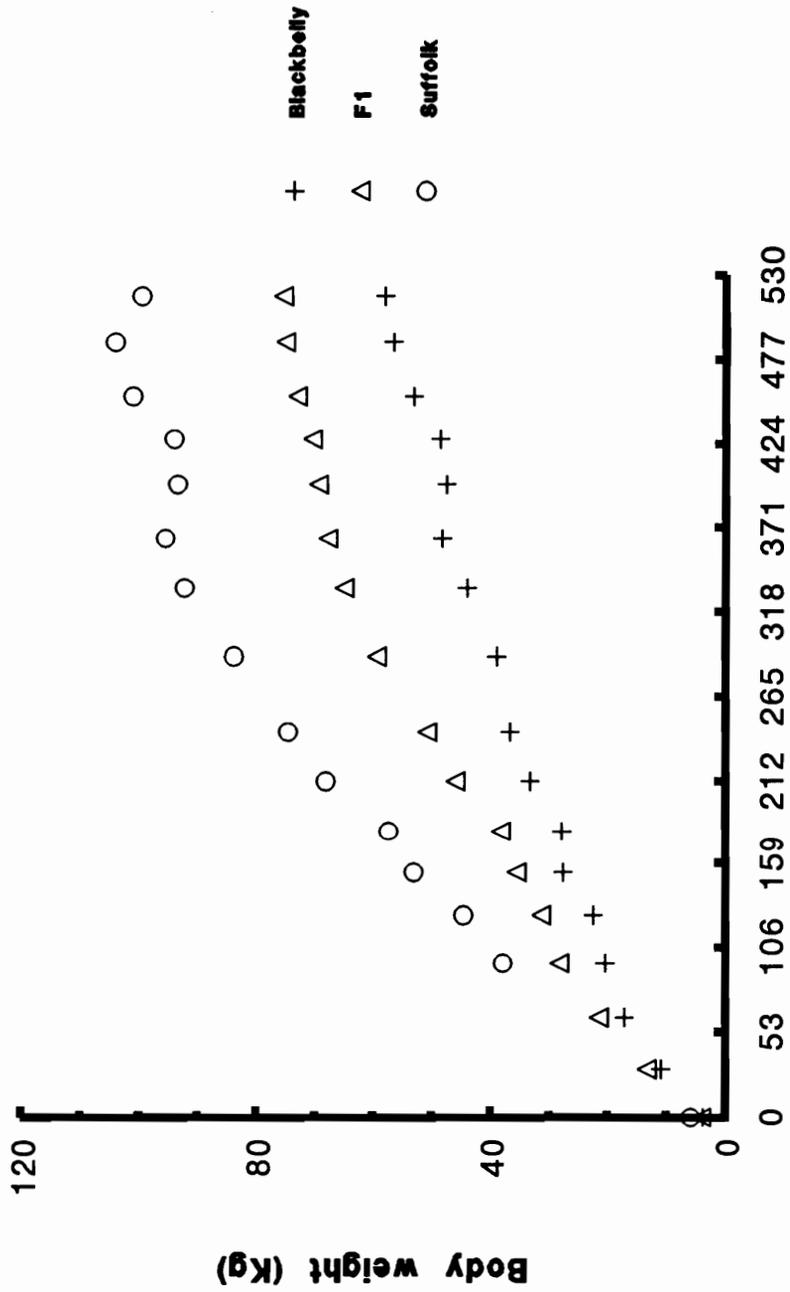


Figure 1. Means for sc of Blackbelly, Suffolk and F1 rams through 530 days of age and logistic curves using data through 243 d of age. The vertical line denotes the 243 d age limit used to fit logistic curves.



Age (d)
 Figure 2. Least-square means for body weight for Blackbelly, Suffolk and 1/2 Dorset x 1/4 Finn x 1/4 Rambouillet rams through 530 days of age.

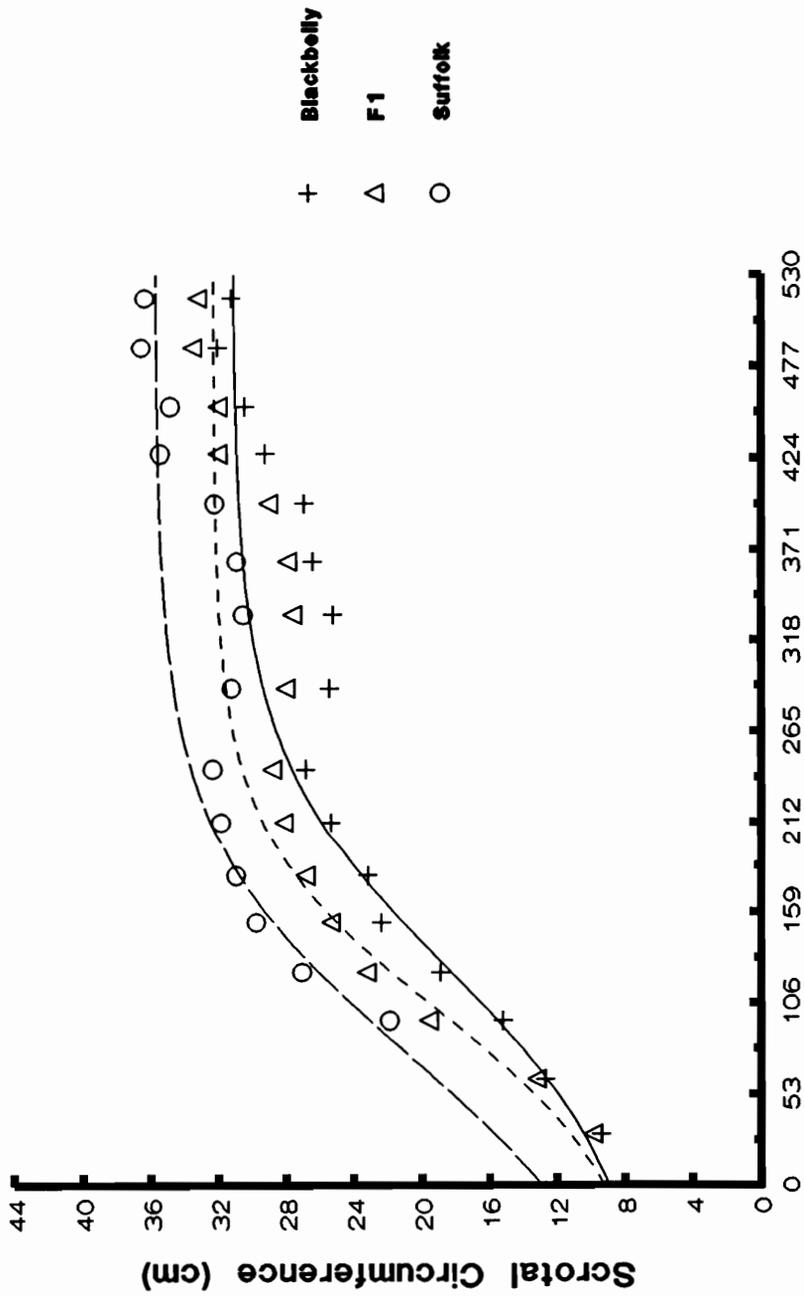


Figure 3. Means for sc of Blackbelly, Suffolk and F1 rams through 530 days of age and logistic curves using data through 243 d of age plus observations at 454, 488 and 517 d.

HERITABILITIES OF AND GENETIC CORRELATIONS AMONG SCROTAL GROWTH AND FEMALE REPRODUCTION IN CROSSBRED SHEEP

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Summary

Data were collected on 1,044 lambs from 727 spring lambings over 5 years. Sixty-seven sires and 525 dams were represented. Fifty-one sires had progeny in only one yr. For dams, 323 lambed in only one year. Scrotal circumference (sc) and body weight (wt) were measured at five times (mean ages of 44, 63, 97, 129 and 156 d) on ram lambs. Weights were collected at eight times (mean ages of 42, 62, 96, 128, 156, 187, 230 and 271 d) for ewe lambs. Ewe lambs were kept for fall breeding, and fertility, prolificacy and subsequent postweaning spring mating behavior when exposed to vasectomized rams were measured. Several mixed models were fitted to these data and Restricted Maximum Likelihood (REML) estimates of heritabilities and genetic correlations were obtained. Measurements at younger ages required models that included maternal and litter, as well as additive direct genetic effects. By 90 d of age maternal genetic effects became unimportant, but a litter (within-year permanent environment) effect remained through 90 d. For measures at ages greater than 90 d, a model with only additive direct genetic effects appeared sufficient. Heritability estimates for weights at birth and average ages of 45, 60, 90, 120 and 150 d ranged from .14 to .42 and most were significantly different from zero. Heritabilities for sc and sc scaled to the 1/3 power of body weight (rsc) ranged from .09 to .57 and from .13 to .55, respectively, with estimates at later ages tending to be smaller and not significantly different from zero, especially for sc. Logistic growth curves were fitted to sc data for individual ram lambs. Estimates of heritabilities for sc logistic growth curve parameters were $.09 \pm .15$, $.17 \pm .18$, $.37 \pm .29$

and $.40 \pm .14$, for mature sc, sc maturing rate, age at maximum growth and initial (14-d) sc, respectively. Heritability estimates for fertility and spring mating frequency were $.04 \pm .13$ and $.41 \pm .19$, respectively, but the heritability estimate for prolificacy was zero. Longitudinal additive genetic correlations among second, third and fourth measures of wt, sc and rsc were estimated by approximate multi-trait REML. Genetic correlations among wt were large, ranging from .77 between 60-d and 120-d weight to .93 between 90-d and 120-d weight. Additive genetic correlations for rsc ranged from .48 between rsc2 and rsc3 to .90 between rsc3 and rsc4. Estimated genetic correlations for sc were smaller; .10 between sc2 and sc3 and .67 between sc3 and sc4. Correlations of sc and rsc with fertility and spring mating behavior were moderate and positive (.20 to .34); age at maximum sc growth had correlations of -.32 and -.48 with fertility and spring breeding, respectively.

(Key Words: Sheep, Testis Logistic Growth Curves, Heritabilities, Reproduction)

Introduction

Cost of animal products depended primarily upon the efficiency of three functions: (1) female production, (2) reproduction and (3) growth of the young (Dickerson, 1970). Subsequently, interest was generated in the potential to increase production by increasing rate of female reproduction. In sheep, breed differences in seasonal breeding patterns exist (Hafez, 1952; Quirke et al., 1985; Notter, 1986) and can have a major impact on reproductive efficiency in the relatively lowly fecund seasonally breeding sheep. Heritability and repeatability estimates for female reproductive rates are low (Purser, 1965; Shelton and Menzies, 1968; Notter and Copenhaver, 1980; Fogarty et al., 1985; Bunge et al., 1990). Positive relationships between female reproductive traits and male measures of testis size have been reported (Land, 1973; Land and Carr, 1975; Land and Sales, 1977; Land, 1978; Purvis et al., 1988). Walkley and Smith (1980) concluded that if a male measurement had at least a moderate heritability and a moderate genetic correlation with a

female reproductive trait, it could be a potentially useful selection criterion to improve reproductive ability in the female. Also, Land (1973) and Notter et al. (1985) proposed that the rate of testis growth in the young ram may be a better predictor of reproductive characteristics in females than any single sc measure. Thus the objectives of this study were to identify environmental and genetic sources of variation in testis growth in the young ram, to estimate heritabilities for weight (wt), scrotal circumference (sc), and sc logistic growth curve parameters through 150 d and to estimate genetic correlations among testis growth traits and between these traits and female fertility, prolificacy and spring mating behavior.

Materials and Methods

Experimental Procedures. Data were collected on 1,044 lambs from 727 lambings over 5 years beginning in 1984. Animals stemmed from matings required in the formation of a three-breed composite population containing 50% Dorset (D), 25% Rambouillet (R) and 25% Finnsheep (F) breeding. Foundation ewes (table 4) were primarily Dorset, but grade Rambouillet, Finnsheep and Finnsheep x Rambouillet ewes were also present. In the early years of the project, the majority of matings yielded first-generation three-breed-cross progeny, although a few two-breed-crosses were also produced for use in later matings. In later years of the project, matings primarily involved inter se matings among first and second generation three-breed-crosses (table 4).

Sixty-seven sires and 525 dams were represented in the data. For sires, 51 were represented in only one year; 16 had progeny in different years. For dams, 323 lambed in only one year, whereas 202 had records in more than one year. Scrotal circumference (sc) and body weight (wt) were measured at five times (mean ages of 44, 63, 97, 129 and 156 d) on ram lambs. Weights were collected at eight times (mean ages of 42, 62, 96, 128, 156, 187, 230 and 271 d) for ewe lambs. Of the ewe lambs that were kept for breeding, fertility, prolificacy and postweaning spring mating behavior were measured.

Ewes grazed permanent swards of grass (primarily orchard grass and fescue) and clover from about May 1 until November. Ewes were mated for 6 wk beginning about October 1 and lambled in an enclosed barn in spring. Lambs were weaned in two groups in early and late May of each year; subsequently, all ram lambs were raised to 150 d in an open-fronted barn on an elevated expanded metal floor. Ewe lambs were also raised on expanded metal until 90 to 120 d of age, but were moved to permanent pastures with limited supplemental feeding at this time to prepare them for breeding.

Minimal selection was placed on females and males; all females over 27 kg at the start of the fall breeding season were exposed to rams. Ram lambs were chosen at random from those that were considered capable of mating as ram lambs based on measures of wt and sc. Body weights in excess of about 45 kg and sc in excess of about 28 cm at 150 d were usually required, and generally required that replacement rams come from the largest one half of the available rams. Ewe lamb replacements were bred with the older ewes in October and lambled the following March and April. Yearling ewes that lambled were then checked for spring mating behavior after weaning their lambs by exposing them, after the final weaning in late May, to vasectomized rams fitted with marking harnesses. Over a 4-wk period, ewes were checked twice weekly for evidence of mating. Whenever an initial mark was observed, jugular blood samples were collected at that time and at the next two observation times to determine if a progesterone peak indicative of ovulation had occurred. A potentially fertile mating was assumed to have occurred (a success, 1, in terms of the binomial event) only when ewes were marked and an elevated progesterone level was observed. The ewe was presumed not to have successfully mated if she failed to achieve any of the criteria (a failure, 0, with respect to the binomial event).

Some form of adjustment of sc at each age for weight of the ram may be desirable to account for any inherent relationship between wt and sc. It has been proposed that linear measures be scaled relative to the one third power of body weight (Lyne and Verhagen, 1957;

Taylor, 1968) to account for body size. Thus, relative scrotal circumference (rsc) was calculated as $sc/wt^{1/3}$ in the hope that differences in rsc would more closely represent differences in sc that were independent of body weight.

Means for sc at each age were used to fit logistic curves within each year using the model of Notter et al. (1985):

$$SC_{it} = A_i / (1 + B_i e^{-k_i t}) + r_{it}, \quad (1)$$

where SC_{it} is the mean sc in the i th year at t days of age, A is the estimated maximum sc, k is a maturing rate parameter, B is a constant of integration, e is the base of the natural logarithm and r_{it} is the residual about the mean curve for each year at age t . The iterative nonlinear regression procedure of SAS (1985) was used to estimate logistic parameters.

The age and sc scales were each modified by subtraction of a constant in order to obtain convergence of logistic parameter estimates. The lamb age scale was modified as $t' = t - 14$ to adjust the origin to approximately correspond with the descent of the testis into the scrotum. The choice of t' had little effect on the goodness of fit of equation 1 (i.e., on the mean squared error(mse)). The constant used to scale sc did affect the probability that the nonlinear procedure of SAS (1985) converged to reasonable parameter estimates and the magnitude of the residual mse. For these data, $sc' = sc - 9$, which was close to the scaling constant of 10 cm used by Notter et al. (1985), minimized the residual mse (table 25, appendix B), and defined the point on the sc axis which roughly corresponded to the sc of an empty scrotum. Logistic growth curves were estimated for each ram after scalings. Additionally, two composite parameters were estimated for each ram. These were $t_1 = [\ln(B)/k] + 14$, which was the estimated age at which testis growth rate was maximum and $C_{14} = [A/(1+B)] + 9$, which was the estimated sc (cm) at 14 d (Notter et al., 1985).

Preadjustments to Data. Prior to variance component estimation, data were preadjusted for a variety of additive environmental effects. Birth type effects (single, twin or \geq triplet) were

calculated for birth weight. Combined effects of birth and rearing type (single birth - raised as a single, single or twin birth - raised as twin, twin birth - raised as single, multiple birth - raised as single, multiple birth - raised as twin and a multiple birth - raised as triplet) were calculated for wt, sc, rsc and sc growth curve parameter estimates. However, the classes for multiple birth, raised as a single and for multiple birth, raised as a twin were combined for traits measured only on males (sc, rsc and sc growth curve parameter estimates) due to the reduced subclass numbers when data were restricted to male lambs. Ewe age at lambing was categorized as 1, 2, 3 or ≥ 4 yr and ewe age effects were calculated for all traits. Sex effects on the first five weights were also considered, as was the regression of each wt, sc and rsc measurement on age at measurement.

In order to determine which environmental effects were important, linear models were fitted using the general linear models (GLM) procedure of the Statistical Analysis System (SAS, 1985). Models to determine the adjustment factors were of the form:

$$y = X_1 \underline{b}_1 + X_2 \underline{b}_2 + e \quad ,$$

where \underline{b}_1 and \underline{b}_2 are fixed, y is a $n \times 1$ vector of observations; \underline{b}_1 is a $k \times 1$ vector of effects to be absorbed, \underline{b}_2 is the $p \times 1$ vector of fixed effect coefficients used to calculate adjustment factors, e is a vector of errors $N(0, \sigma^2_e)$, and X_1 and X_2 are incidence matrices. Models were fitted separately to estimate effects of type of birth or birth-rearing and of ewe age. Thus, if constants for ewe age were being estimated, then effects in \underline{b}_1 were the overall mean (μ), sex, lamb birth year (byr), breed code which was determined by the breed of the parents of the lamb (phbrco), birth-rearing-type of the lamb (brtyre) and sire of the lamb (sire), leaving effects of ewe age and regression on lamb age in \underline{b}_2 . Similarly, if constants for brtyre were estimated, then the absorbed effects in \underline{b}_1 were μ , sex, byr, phbrco, ewe age and sire. The GLM procedure of SAS assumed the absorbed effects to be nested, thus they were absorbed sequentially as they entered the model.

Sex effects on wt1 through wt5 were obtained from performing a GLM with no absorbed effects, and the resulting parameter estimates were used as adjustment factors. Parameter estimates used in calculating adjustment factors were the result of using the solution option of the GLM procedure (SAS, 1985). Interactions of sex with byr were also tested for wt1 through wt5.

The class within an effect with the largest number of observations was chosen as reference class. Each observation was adjusted by subtracting the mean estimated reference group effect from the estimated effect of the group an observation came from; the resulting adjustment factor was then added to observations to obtain adjusted measurements. This procedure was followed for each fixed effect for which a trait was adjusted. Two estimated regression coefficients for age were obtained, one for the model that estimated brtyre effects and one for the model that estimated ewe age effects. These were averaged, and each observation was then regressed back to 45, 60, 90, 120 or 150 d, respectively, for each age classification. The last three female weights were not adjusted for age.

Mixed Model Analysis

REML variance component estimation. Patterson and Thompson (1971) first described use of Restricted Maximum Likelihood (REML) to estimate variance components from unbalanced data. In REML, estimates of variance components maximize the likelihood of a set of error contrasts (Harville, 1977) which have expectation zero and are independent of fixed effects; the result is to account for a loss in degrees of freedom due to fitting fixed effects in the model. A derivative-free algorithm was suggested by Graser et al (1987) to estimate the additive and error variance under an animal model for univariate analyses. Meyer (1989) described a derivative-free approach to estimate variance components by REML for animal models which included not only additive genetic and error components, but also additional random effects, as well as the calculation of their standard errors, thus covering a wider range of models suitable for the analysis of animal breeding data.

Usually the random effects considered include at least the additive genetic and error variances. However, additional random effects such as maternal genetic, permanent maternal environmental and full-sibs common environmental (litter) effects also may be present in the data. These additional random effects generate additional resemblances among individuals, and, for at least some of the traits investigated in this study, these effects were suspected to exist. These additional resemblances may bias estimates of additive genetic and residual variance if not accounted for in the analytical model. Thus, data structures and models were used which attempted to either eliminate or account for these additional random effects, respectively.

All REML models included fixed effects of year (1984 through 1988) and lamb breed group. A total of 953 lambs from 55 rams and 413 ewes were used to obtain REML estimates. Animals were assigned to one of 10 breed groups representing F2, combined F3 and F4, D x FR, FR x D, FD x DR, R(DF) x D(DF), DR x FD, F x R, F x RX and R x F lambs. F2 lambs are those produced by inter se mating of first-generation three-breed crosses. F3 and F4 lambs represent progeny of additional generations of inter se matings. For specific crosses, the sire breed type is listed first. The F x RX lambs were out of 7/8 R, 1/8 F ewes of a different origin and a considerably different body type than the ewes used to produce the F x R lambs and were actually 9/16 F and 7/16 R.

The following animal models were fitted to these data (table 5):

1. Model a - additive variance. This animal model used all relationships in the data (including full-sib correlations which also involve maternal and common environmental effects) to estimate the additive and error variances and would be expected to overestimate additive variance in the presence of any sort of ewe or litter effects.

2. Model ae - This model estimated additive genetic (a) and total ewe (e) variances ignoring relationships among ewes in estimating ewe variances. It did not discriminate between maternal genetic, permanent environmental ewe and litter effects, but was roughly the animal model equivalent of the sire-cow models often used on dairy data before animal model

implementations (I. Hoeschele, personal communication). The difference was that the ewe effect here was a maternal effect instead of the direct cow effect in dairy cattle evaluation.

3. Model ael - This model estimated additive, ewe and litter (l) variances. The litter variance represented the additional resemblance among lambs born to the same ewe in the same year. It would be equivalent to fitting ewe and ewe x year effects. Relationships among ewes were again ignored in estimating ewe variances. Ewe effects now include primarily maternal genetic and across-year permanent environmental effects. However, K. Meyer (personal communication) has shown that the ewe effect in such a model is not simply the sum of the maternal genetic and permanent environmental effects, and that the exact partitioning of these two components among the estimated components depends on the relationships in the data.

4. Model ae1 - This model was fitted in response to concern about the partitioning of variance in model 3. Data were restricted to one random lamb/ewe/yr to avoid resemblances among littermates. This reduced the animals with records used to estimate variance components by about 1/3.

5. Model aml - This model estimated additive direct and additive maternal (m) variance plus the litter (full-sibs born in same year, or ewe x year interaction) variance as an uncorrelated random effect. Relationships among ewes were included in estimating the additive maternal component. The additional magnitude of the likelihood function was used to test this model against model a to give a test of overall maternal and common environmental effects. On this basis a decision was made as to whether or not maternal and(or) common environmental effects were important.

If maternal effects in model 5 were not significant, the heritability estimate from model 1 was accepted as satisfactory. However if maternal effects in model 5 were significant, complete partitioning of maternal effects had not yet been achieved. Litter maternal effects had been largely removed from the additive genetic variance, but permanent environmental effects common to

progeny of a ewe in different years had not been separated from additive maternal ewe effects. Permanent environmental ewe effects are highly confounded with maternal genetic effects in models which fit only one of the two effects, but are not perfectly correlated, and when both effects are present, but only one is fitted, the additive heritability estimate can be biased. Hence, an unbiased estimate of heritability was still needed.

6. Model a1M - In order to obtain the least biased estimate of heritability when both additive maternal and permanent environmental effects are present, pedigrees were edited so that only sire relationships remained. Dam relationships were ignored, and all but one lamb/ewe/yr was removed at random from the data, so that there were no full sibs born to the same ewe in the same year. When ewe relationships were ignored and no full-sibs were present in the same year, the maternal effects no longer appeared in the additive variance estimate. Instead, they were assigned to error, just as they would be in a sire model. Thus, the result was a less biased estimate of heritability, except that it did not use all the data. The model which utilized this data structure was denoted as Model 6-a1M to designate additive variance with 1 record/ewe/yr and using only male (M) pedigrees.

7. Model amp1 - In an effort to estimate remaining maternal effects, the same data structure was used as that in Model a1M, but with all relationships to estimate the additive direct, additive maternal, and across-year permanent environmental (ewe) variances. Models which utilized this data arrangement were specified as Model 7-amp1 to indicate fitting of additive, maternal genetic and permanent environmental variances with 1 record/ewe/year. A comparison of this model with Model 5-aml allowed an approximate partition of across-year and within-year (litter) common environmental effects. The covariance between the additive and maternal components was not estimated because the data were not substantial enough to yield reasonable estimates.

8. Model 8a - For sc data (male lambs only), sample size was considered insufficient to attempt such a detailed partitioning of maternal effects. Nonetheless, such a partitioning was attempted and as expected, it did not produce reasonable estimates. Few ewes had male lambs in more than one year. For 90 d sc, 336 lambs from 277 litters were present, so there were not more than about 59 full-sib sets of males. Only about 13 ewes had males in more than one year. Thus most of the maternal sibs were born in the same year, and it was not realistic to think that an across-year ewe component could be estimated from these data. Therefore, the best that could be done was to fit model 1-a to the data on sc, rsc and sc growth curve parameter estimates and to compare it to a new model, model 8-a, that fitted additive and litter components to attempt to remove at least a major part of the maternal and environmental resemblance of full-sibs. Model 8 was applied only to sc and rsc measures through 90 d of age because preliminary results suggested that maternal effects on wt were not important after 90 d and that maternal effects on sc were less important than maternal effects on wt. Models 1 and 8 were also applied to sc data with concomitant inclusion of the linear effect of body weight in the REML model in order to compare results with those observed for rsc.

Maternal and litter effects were assumed unimportant for ewe lamb reproduction traits. Model 1 was thus fitted to data on ewe fertility (n=336), prolificacy (n=260) and spring rebreeding (n=247). Fertility and prolificacy analyses were conducted with or without wt at the start of breeding as a covariate.

REML covariance component estimation. Covariance components and genetic and environmental correlations were estimated for selected sets of traits from the data by approximate multitrait REML. The sets of traits investigated included:

1. Longitudinal correlations among 60- 90- and 120-d sc, wt and rsc. No across-trait correlations (e.g., of 60-d wt with 120-d rsc) were considered in these analyses. Longitudinal correlations involving wt at 60, 90 and 120 d used 840, 826 and 780 animals, respectively, of both

sexes. The sc and rsc analyses utilized 345, 336 and 322 males measured at 60, 90 and 120 d, respectively. These were the same animals that were used for the single-trait sc analyses, but a few more were deleted for rsc to keep numbers consistent with sc since in general, more outliers were found for sc than rsc measures.

2. Intercorrelations among 90-d male traits (wt, sc and rsc) and correlations of these traits with age at inflection (t_i) from the sc growth curve. Data used for these runs were 336 males with 90-d wt, sc and rsc. Of these, 285 had t_i values. Correlations were estimated by analyzing pairs of traits, two traits at a time.

3. Correlations of female traits (fert, spbrd and prolificacy) with body weight (both males and females), 90-d male traits (sc, rsc) and t_i . Correlations between male and female traits were performed using 336 and 247 records for female fertility and spring rebreeding, respectively. The 90-d traits correlated to these were 90-d wt (both sexes included; $n=826$), 90-d sc ($n=336$), 90-d rsc ($n=336$) and t_i ($n=285$). As before, these were pairwise correlations.

K. Meyer (personal communication) suggested estimating only covariances in all multi-trait analyses. Thus, the additive and error variances for each trait were estimated in preliminary, single-trait analyses for wt and rsc using only the 336 males with complete sc data.

Breed Effects. Although estimates of the means for each lamb breed group for a given trait in different models were the same, models did have different standard errors. The greatest reduction in standard errors occurred when weight was used as a covariate for scrotal circumferences. Conclusions remained the same for each model, so only the results from the additive model were reported here. Breed groups were combined into those animals that had 1/4 (groups 1-7, $\mu_{1/4}$) and 1/2 (groups 8-10, $\mu_{1/2}$) Finn breeding. Tests were performed using pooled standard errors and means. The test statistic was:

$$t = \frac{\delta}{s_p \cdot \sqrt{\sum (1/n_i)}} ,$$

where $\delta = \mu_{1/4} - \mu_{1/2}$, s_p was the pooled standard error, and n_i is the number of observations within a breed class.

Results and Discussion

Environmental Effects.

Mean wt, sc, and rsc for these data (table 6) were similar to those of Notter and Copenhaver (1980) and Notter et al. (1985).

Birth rearing type (brtyre). Brtyre was highly significant ($P < .001$) for wt1 through wt6; sc1 through sc3; rsc1 and rsc2; B, C_{14} and t_l . Also, brtyre was significant enough for rsc3 and k ($P < .20$ and $.07$, respectively) to warrant adjustment. However, for sc4 and sc5, rsc4 and rsc5, A and female reproductive traits, brtyre effects were not significant ($P > .20$). Thus these data were not adjusted for brtyre. Subsequently, adjustment to a single or twin born, twin reared basis was performed only on wt1-wt6, sc1- sc3, rsc1-rsc3, B, C_{14} , t_l and k (table 7, 8 and 9). Birth type effects were significant for bwt ($P < .0001$). Thus, bwt was adjusted to a twin birth (table 10). The 90-d wt adjustments were in general agreement with 90 d wt adjustments reported by Notter et al. (1975).

Ewe age. Ewe age had a strong effect on all weights ($P < .0001$); adjustments generally were in agreement with those of Notter et al (1975). Therefore, wts were adjusted to a mature ewe of 4 yr of age or older (tables 6 and 9). Although the ewe age effect was generally less for 45, 60 and 90 d scrotal measures ($P < .10$), as well as for the composite traits of C_{14} and t_l ($P < .30$), it was still strong enough to warrant adjustment of these traits to a mature ewe basis (tables 8 and 9). By the time ram lambs were 120 d of age, ewe age had little effect on sc; as a result, sc4, sc5, rsc4 and rsc5 were not adjusted for ewe age. All other sc measurements and growth curve parameter estimates appeared not to be affected by ewe age ($P > .56$).

Lamb age at time of measurement. The regression of wt, sc and rsc measurements on age were significant ($P < .0001$). Hence, wt, sc and rsc measurements were adjusted for the age of the lamb when the measurement was taken (tables 7 and 8). Female reproductive traits and sc growth curve estimates were not affected by lamb age.

Sex. The difference between ram and ewe lambs was significant for all weights ($P < .0001$); therefore weights were adjusted for sex of the lamb (table 7 and 10). Sex x byr interaction was also significant ($P < .005$) for 90, 120 and 150 d wts, probably due to removal of female lambs from the expanded metal floor environment at 90 vs. 120 d in different years, and which required adjustment to a 1985 ram basis (table 6).

Mixed Model Analysis.

REML breed group effects. The potential for a difference in 90d sc, rsc and wt measurements, A, t_1 , C₁₄, fert and spbrd between groups having 1/4 vs. 1/2 Finn breeding was investigated. Breed group means for additive models were used for comparisons (table 11). Breed differences were greatest for 90d-wt and sc, as well as for the estimated asymptotic sc, A (table 12). Smaller breed differences were found for fert and 90d-rsc, with no breed differences detected in t_1 and spbrd (table 12).

REML variance component estimates. Model a is expected to overestimate the additive direct variance relative to models including maternal effects; therefore, it gave an upper bound on heritability. A test for overall maternal and common environmental effects was conducted by comparing the log likelihood of model 1 (a) with model 5 (aml). If the difference between log likelihoods of the two models was significant, then maternal and(or) common environmental effects were considered important. For wts from birth through 90 d there was a slight difference between models a and aml in the log likelihood suggesting that maternal resemblance existed for these traits (table 13). Model aml variance component estimates indicated that overall maternal effect on weight was approximately equivalent to the additive direct genetic effect at birth and diminished to

nearly zero by 60 d (table 13). Similarly, the common environmental (litter) component decreased from twice to slightly less than 1/3 of the additive genetic effect from birth to 90 d, respectively. In an attempt to obtain an unbiased estimate of heritability for these data, model a1M was applied and produced heritability estimates that were between and less biased those of models a and aml.

Model amp1 was compared to model aml to attempt to partition maternal effects into across-year permanent and within-year (litter) common environmental effects. Across-year permanent environment was larger than the within-yr (litter) common environmental effect for wt at 45 d. However, for 60 and 90d-wt, the across-yr effect was reduced to approximately 1/4 and 1/2, respectively, of its value at 45 d. Conversely, the within-yr (litter) effect more than doubled by 90 d (table 13). Also, model amp1 gave the smallest heritability estimates (table 13). However, all heritability estimates from model a, aml, a1M or amp1 were in general agreement with those of Shelton and Campbell (1962) and Martin et al. (1980).

Results of Van der Werf and de Boer (1989b) indicated that additive models with progeny groups overestimated additive genetic variance by 6% when heterosis and recombination loss effects reached levels of around 2.5 to -2.0%, respectively in dairy cattle. This bias was greater than that predicted based on an earlier simulation by Van der Werf and de Boer (1989a), and was the result of breeding young sires to many F1 females. Since young crossbred rams were mated to crossbred ewes, biased heritability estimates were expected for an additive model. For these reasons and the fact that maternal, litter, or permanent environment were present for weight measurements \leq 90 d, it would be more conservative and perhaps more appropriate if heritability estimates of model aml or amp1 were used. Model aml estimates were best for bwt and for wts \leq 90 d, since a greater amount of the common environmental effect was accounted for and all the data were used with this model. However, for 45 and 60 d wt, model amp1, with the data restricted to 1 lamb/ewe/yr, may have produced the least biased heritability estimates, but with huge standard errors.

Since out of 59 sib sets of males, only 13 ewes had males in more than one year, an across-year maternal component could not be estimated for male traits. Thus, only additive and litter effects (with and without regression on body wt) were fit to sc, rsc and logistic growth curve parameter estimates with the assumption that maternal effects did not affect later sc measures (table 14). Differences in log likelihoods indicated that the only significant litter effect was for 60 d sc and rsc. In fact, for most sc measurements, comparison of log likelihoods of model a and al indicated that including the litter component did not result in a significant reduction in the log likelihood (table 13). The litter effect appeared to have no effect on 45 or 90 d sc, 45 d rsc and C_{14} heritability estimates. However, inclusion of the litter effect did decrease the heritability estimates for all other sc and rsc and for logistic growth curve parameter estimates.

When wt was included as a covariate in the a or al model, heritability estimates increased; standard errors and log likelihoods were reduced (table 14). Also, it appeared inclusion of a wt covariate increased the accuracy of heritability estimates due to having sequestered that effect away from each variance component estimate, as well as yielding a smaller log likelihood.

Even though the log likelihood was not, in general, higher when the litter effect was included in the model, the amount of bias in the heritability estimates that resulted when it was excluded suggested it should remain in the model. Also, more precise heritability estimates were produced by models that included wt as a covariate given the reduction in standard errors of heritability estimates. Furthermore, Hoeschele (1991) estimated additive x additive (a x a) and nonadditive (dominance and inbreeding) effects for female fertility of Holstein cows and found them to be as important as additive genetic effects. Again, given these results, the more conservative approach which used estimates from models that contained a litter and(or) wt covariate are probably preferable. Although variance and covariance estimates from models having maternal, litter, or permanent environmental effects did not account for dominance or

epistatic effects, they did probably provide less biased estimates than the additive direct model alone.

Heritability estimates of .09 and .04 were obtained for fertility using an additive model with and without wt as a covariate, respectively (table 14), but neither estimate was significantly different from zero in agreement with the literature (Purser, 1965; Shelton and Menzies, 1968; Bunge et al., 1990). Heritability of prolificacy was not estimable; however, low to moderate estimates of .10 to .35 have been reported by Fogarty et al., (1985), Abdulkhalik et al. (1989) and Bunge et al. (1990). A moderately large heritability estimate of $.41 \pm .19$ was obtained for sprbrd using an additive model (table 14).

REML covariance component estimates. As expected, longitudinal correlations for wt, sc and rsc were generally positive and larger for adjacent observations. Body weights had the highest genetic and environmental correlations. Genetic correlations ranged from .77 between wt2 and wt4 to .93 between wt3 and wt4 (table 15). Genetic correlation estimates for sc (.10 between sc2 and sc3 to .67 between sc3 and sc4) were smaller than those for rsc (.22 between rsc2 and rsc4 to .90 between rsc3 and rsc4, table 15). However, environmental correlation estimates were larger among sc than among of rsc measurements. Thus, prediction of a measurement based on earlier observations could be relatively good, particularly if the earlier observation was wt3, sc3 or rsc3 and wt4, sc4 or rsc4 was of interest.

The genetic correlation between 90d-sc and 90d-rsc was high at .96; positive moderate genetic correlations existed between 90d-wt and 90d sc and rsc (table 16). Thus, selection for any one of these traits should result in an increase in any of the other traits. The genetic correlation of fert with 90d sc and rsc was similar at .20 and .25, respectively (table 16). Thus selection of ram lambs with larger sc or rsc should result in ewe offspring that were more fertile. However, 90d-wt had a negative genetic correlation with fertility of -.25, indicating that selection of rams based on weight would have a negative impact on ewe fertility. Conversely, genetic correlations of sprbrd

with 90d sc, rsc and wt all were positive (.34, .26 and .34, respectively, table 16). The positive genetic correlation of wt with sprbrd is in contrast to the genetic correlations of weight with fertility. This was probably because larger ewe lambs were in better physical condition; thus, they were able to cycle in the spring more effectively than smaller ewes. These correlations among male and female traits are similar in magnitude to those reported by Purvis et al. (1988) for sc and ovulation rate in a random-breeding Merino flock.

All genetic correlations of 90d sc, rsc, wt, fert and sprbrd with t_1 were negative (-.43, -.91, -.74, -.32 and -.48, respectively, table 16). Thus, young ram lambs selected for smaller t_1 values should enhance all the above traits. Of particular interest was the noticeable negative and moderate correlations with the female reproductive measures fert and sprbrd, which indicated that a moderate increase in fert and sprbrd would result if selection were at least partially based on young ram lambs with smaller t_1 values rather than on fert or sprbrd alone.

Implications

Heritability estimates for sc, rsc and t_1 and their genetic correlations with ewe fertility and spring mating behavior indicated that any indirect selection for fertility or sprbrd in ewes through ram traits should be at least partially based on 90-d sc, 90-d rsc or t_1 . Selection of young rams and their relatives would favor those animals having larger 90d sc and rsc and(or) smaller t_1 values. Results of Walkley and Smith (1980) indicated that a greater response in selection for a ewe reproductive measure with a low heritability could be obtained if direct selection for the ewe reproductive trait was complemented with indirect selection based on a male trait with an approximate heritability of .35 and correlation of $\geq .3$ with the female reproductive trait. If the genetic correlation between the two traits was larger, say .7, the estimated response was greater than twice the response than when the genetic correlation was .3. Thus best responses in fert and sprbrd would occur when direct selection was supplemented with indirect selection based on the

male trait, t_1 . However, because ewe fertility had such a low heritability estimate, the absolute gain when indirect selection based on t_1 was used concomitantly with direct selection would be modest. Because $spbrd$ had a reasonably high heritability and moderate genetic correlation with t_1 , the response to combined selection might be almost as high as four times that of direct selection for $spbrd$ alone. Unfortunately, neither a heritability estimate for prolificacy, nor correlations with male traits were obtainable from these data. However, the literature suggests that prolificacy has a heritability ranging between .1 and .35 (Fogarty et al., 1985; Bunge et al., 1990). Thus, if the correlation of prolificacy with sc , rsc and t_1 was near that shown for $fert$ and $spbrd$, then at least some additional increase in prolificacy would occur if combined selection was used in place of simple direct selection for prolificacy.

Many of the heritabilities and correlations estimated for ram sc measurements and ewe reproductive traits were close to those reported by Walkely and Smith (1980) as needed to confer a possible advantage to selection which used both male and female traits. To determine how much, if any, selection advantage would be gained in the female reproductive trait of interest by the use of one or a combination of ram sc , rsc , and(or) t_1 parameter measurements in conjunction with the female trait, simple selection indices were calculated for a few scenarios which seemed potentially useful (table 17).

Suppose that interest was on maximizing ewe fertility, z_1 . Thus the genotype of interest would be H , where H = genotype for ewe lamb fertility (z_1). Now suppose the selection index, l , was based on the 90-d rsc of the sire, x_1 , where $l = b_1 x_1$. From these data the estimated phenotypic variance, $var_P[x_1]$ was .533060. The normal equations become:

$$var_P(x_1)b_1 = cov[x_1, z_1].$$

The relationship between a daughter and her sire is 1/2, thus the $cov[x_1, z_1] = 1/2 * (\text{the genetic covariance between } x_1 \text{ and } z_1, (1/2) * cov_G[x_1, z_1] = (1/2) * (.017680)$. Solving for b_1 yields $b_1 = .016583$. Subsequently, $var(l) = (.016583)^2 * (.53306) = .000147$; $stdev(l) = .01212$.

Therefore, genetic change, $dG = (.016583)(.017680)/.01212 = .02419i$, where i = selection intensity. Thus, a positive genetic increase would occur in ewe lamb fertility of $.02419 * \text{selection intensity}$ for a population of ewes based on their sire's 90-d rsc. This is a significant result in light of the fact that it is often difficult to practice direct selection for ewe fertility. For those producers who would measure ram wt and sc at 90d, then subsequently select daughters accordingly, an increase in ewe fertility of the flock should occur.

Again, interest is on ewe fertility. However, now $I = b_1x_1 + b_2x_2$, where x_1 = sire 90-d rsc and x_2 = 90-d rsc of one full-sib. The normal equations become:

$$\begin{aligned} \text{var}_P(x_1)b_1 + t \cdot \text{cov}[x_1, x_2]b_2 &= \text{cov}[x_1, H] \\ t \cdot \text{cov}[x_1, x_2]b_1 + \{\text{var}_P(x_2)/n\} \cdot (1 + (n-1)t)b_2 &= \text{cov}[x_2, H] \end{aligned}$$

where t is the relationship between relatives which is $1/2$ between a sire and son or sire and daughter; the $\text{cov}[x_1, x_2]$ is the phenotypic covariance between rsc of a sire and rsc of his son, but simplifies to $\text{var}_P(x_1)$ since the same trait was measured on both sire and son; only one full-sib was measured so $n=1$. The $\text{cov}[x_1, H] = \text{cov}[x_2, H] = (1/2) \cdot \text{cov}_G[x_1, z_1] = (1/2) \cdot (.017680)$. Solving for b_1 and b_2 yields $b_1 = .011056$ and $b_2 = .011053$. $\text{var}(I) = (.011056)^2 \cdot (.533060) + (.011053)^2 \cdot (.533060) + 2 \cdot (.011053) \cdot (.533060) \cdot (1/2) \cdot (.533060) = .000195$; $\text{stdev}(I) = .013979$. Thus, $dG = [(.011056) \cdot (.01768) + (.011053) \cdot (.01768)]/i \cdot .013797 = .027962i$. The difference between dG for I based on a sire 90-d rsc and I based on a sire 90-d rsc and one full-sib 90-d rsc was only $.004$.

However, now let $I = b_1x_1 + b_2x_2$, where x_1 = t_1 -sire and x_2 = one full-sib rsc. Recall the normal equation from above. The estimated phenotypic variance of x_1 , $\text{var}_P(x_1) = 174.9551$, phenotypic covariance between x_1 and x_2 , $\text{cov}[x_1, x_2] = -6.74250$, genetic covariance between x_1 and z_1 , $\text{cov}[x_1, z_1] = -.378401$. Inserting these variance component estimates into the normal equations and solving yielded estimated b_1 and b_2 of $-.0008678$ and $.011086$, respectively. The

$\text{var}(I) = .0002621$, with $\text{stdev} = .01619$. Now, $dG = .03239i$, which was $.008i$ above dG using sire 90-d sc alone.

For female spring breeding, H = the genotype for spring breeding behavior of a ewe lamb (z_2). Assume only information on a ewe lamb's dam was available; therefore, $I = b_1x_1$, where x_1 is the spring breeding of the ewe lamb's dam. This is a potentially important scenario since the estimated h^2 for this trait from this study was $.4144$ (high for a reproductive trait), thus data on a dam should be a good indicator as to which ewe lambs to retain for spring breeding purposes. The $\text{var}_G(z_2) = .092760$, $\text{var}_P(z_2) = .22363$, and the relationship between a dam and her daughter is $1/2$. Therefore, $b_1 = .207396$ and the $\text{var}(I) = .009619$ which resulted in a $dG = .19615i$. Thus it appeared significant progress in spring breeding could be obtained by selecting ewe lambs whose dam's tended to breed in the spring.

If information is available on the spring breeding of the ewe lamb's dam and sire's 90-d sc then using both results in an index $I = b_1x_1 + b_2x_2$, where x_1 = dam's spring breeding, x_2 = sire's 90-d sc. The $\text{var}_P(x_1) = .22372$, $\text{var}_P(x_2) = 8.3668$, genetic covariance between x_2 and z_2 , $\text{cov}_G[x_2, z_2] = .217797$ and the relationship between a nonrelated sire and dam is 0. Solving the normal equations gives $b_1 = .2073$ and $b_2 = .01302$, which results in $\text{var}(I) = [(.2073)^2 * (.22732) + (.01302)^2 * (8.3668) + 2 * (.2073) * (.01302) * (0) * (.217797)] / .105035 = .21007i$, which is only $.014i$ above dG which resulted from an index which used a dam's spring breeding. The apparent conclusion from this result was that since the estimated heritability of spring breeding was large ($.4144$), the advantage of including information on the sire's 90-d sc was negligible.

To investigate the utility of using sc as a selection criterion by itself, let $I = b_1x_1$, where x_1 = sire 90-d sc. The result was a dG of $.075297i$ for spring breeding behavior. The relationship between sc and spring breeding evidently was not high enough to confer as much selection advantage for spring breeding, when using sire 90-d sc as the selection criterion, as was hoped it

would be. Alternatively, let $I = b_1x_1$, where $x_1 = \text{sire } t_1$. The $\text{cov}[x_1, z_2] = -1.371242$ which resulted in a $dG = .10367i$. Thus, with a correlation between t_1 and spring breeding behavior of $-.4845$, the dG using t_1 was just slightly over $1/2$ the dG when selection was based on a ewe's dam spring breeding. However, when t_1 and dam spring breeding were combined into a single index, $dG = .22187$.

Of those scenarios examined, genetic gain in ewe lamb fertility would be greatest for the index which used a sire's t_1 + one full-sib's 90-d rsc; it gave a 34% increase over an index which used a sire's 90-d rsc. However, for most producers t_1 is not easily attainable. An index which used a sire's 90-d rsc and one full-sib's 90-d rsc would give a 15% advantage over the sire index. Since fertility has such a low estimated heritability, any of the selection indices investigated here would likely prove useful, with preference given to the index which utilized rsc(one full-sib) and t_1 (sire).

The greatest genetic gain in ewe spring breeding behavior would be achieved by an index which used dam spring breeding behavior and sire's t_1 ; it was 13% better than an index using only dam spring breeding behavior. However, the index which used a sire's sc + dam spring breeding behavior gave only a 7% advantage over the dam spring breeding behavior index. Thus, since the estimated heritability of spring breeding behavior was so high, information added by a ram's sc was of little value, but a sire's t_1 might prove useful when combined in an index with the dam's spring breeding behavior.

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TABLE 4. BREED GROUP BY YEAR FREQUENCIES

BREED GROUP ^a	YEAR					total
	84	85	86	87	88	
F2,F3,F4 ^{bc}	0	35	178	176	52	441
D x FR ^C	13	43	63	0	0	119
FR x D ^C	62	76	25	0	0	163
FD x D ^C	0	0	17	0	0	17
FD x DR ^C	0	27	0	0	0	27
R(DF) x D(DF) ^C	0	30	0	0	0	30
DR x FD ^C	0	46	0	0	0	46
F x R ^C	8	40	0	0	0	48
F x RX ^C	24	0	0	0	0	24
R x F ^C	22	12	4	0	0	38
FD X FR	13	0	0	0	0	13
D x R	6	0	0	0	0	6
R x D	8	0	0	0	0	8
DF x R	7	0	0	0	0	7
DR x D	5	0	0	0	0	5
DDF x D	20	0	0	0	0	20
DF x FR	7	0	0	0	0	7
DF x D	8	0	0	0	0	8
FD x D	13	0	0	0	0	13
DR x FR	2	0	0	0	0	2
F x F	0	0	2	0	0	2
total	213	309	289	176	52	1044

^a D = Dorset, F = Finnsheep, RX = 7/8 Rambouillet, 1/8 Finnsheep

^b F2, F3, F4 are inter-se matings of 1/2 Dorset, 1/4 Finnsheep, 1/4 Rambouillet sheep

^c Animals used in obtaining REML variance and covariance components.

TABLE 5. REML MODELS USED FOR WT, SC AND FEMALE REPRODUCTIVE TRAIT VARIANCE COMPONENT ESTIMATION^a.

model number	model components a e l m p	comments
1	x x	wt-covariate for sc data only
2	x x	
3	x x x	
4	x x	with 1 lamb/ewe/yr
5	x x x	
6	x	with 1 lamb/ewe/yr; male pedigrees only
7	x x x	with 1 record/ewe/yr
8	x x	wt-covariate for sc data only

^a a = additive direct genetic with all relationships, e = ewe with no relationships, l = litter with no relationships, m = additive maternal genetic with relationships, p = permanent environment with identity matrix.

TABLE 6. NUMBER OF OBSERVATIONS AND MEANS FOR WT, SC, AGE AND REPRODUCTIVE MEASURES OF RAM AND EWE LAMBS.

trait ^a	ram lambs		ewe lambs	
	N	mean	N	mean
bwt	410	3.93	543	3.57
wt1	380	15.97	512	14.41
wt2	399	21.50	543	19.23
wt3	389	31.34	533	25.49
wt4	342	41.00	504	30.91
wt5	292	46.91	461	35.74
wt6	—	—	440	40.06
wt7	—	—	343	41.59
wt8	—	—	140	41.47
age1	380	43.74	512	41.72
age2	399	63.04	543	62.17
age3	389	97.35	533	96.23
age4	342	129.15	504	128.32
age5	292	155.83	461	156.27
age6	—	—	440	187.22
age7	—	—	343	230.12
age8	—	—	140	271.38
sc1	327	10.95	—	—
sc2	386	12.90	—	—
sc3	380	19.32	—	—
sc4	337	25.07	—	—
sc5	287	27.30	—	—
fertility	—	—	306	.79
spbrd	—	—	247	.57
prolificacy	—	—	260	1.41

^a wt in kg, age in d, sc in cm and spbrd = spring mating behavior.

TABLE 7. ADJUSTMENT FACTORS FOR BODY WEIGHTS, KG.

variable	class	wt1	wt2	wt3	wt4	wt5	wt6
Birth-rearing-type	1	-3.61	-4.12	-4.39	-2.98	-2.24	-1.80
	2	0.0	0.0	0.0	0.0	0.0	0.0
	3	-2.0	-2.64	-1.92	-1.40	-1.35	-1.75
	4	0.76	0.27	1.41	2.18	2.50	2.91
	5	1.32	1.63	1.90	2.51	-1.84	1.47
	6	1.99	2.80	3.02	2.44	1.09	-0.57
Ewe age	1	3.30	3.86	4.71	3.55	2.68	2.94
	2	1.16	1.80	1.59	1.45	0.49	1.34
	3	0.53	0.77	0.26	1.02	0.32	0.66
	4	0.0	0.0	0.0	0.0	0.0	0.0
Sex ^a	R	0.0	0.0	0.0	0.0	0.0	0.0
	E	1.07	1.98	5.45	6.86	12.11	0.0
b(age)		0.482	0.484	0.461	0.367	0.438	0.271
sex x byr ^b							
	R-84			-3.45	0.57	4.78	
	R-85			0.0	0.0	0.0	
	R-86			0.63	-0.30	-0.27	
	R-87			-2.92	-3.46	-1.10	
	R-88			-1.45	1.58	0.0 ^c	
	E-84			-1.45	1.58	-1.10	
	E-85			-1.45	1.58	-1.10	
	E-86			-1.45	1.58	-1.10	
	E-87			-1.45	1.58	-1.10	
	E-88			-1.45	1.58	0.0 ^c	

^a R = ram, E = ewe.

^b sex x birth year interaction.

^c Measurements were not yet taken at time of analysis.

TABLE 8. ADJUSTMENT FACTORS FOR SCROTAL CIRCUMFERENCE (SC; CM) AND SCALED SCROTAL CIRCUMFERENCE (RSC; CM/KG^{1/3}).

		sc			rsc		
		1	2	3	1	2	3
adjustment factor							
birth-rearing-type	1	-1.22	-1.48	-1.68	-0.11	-0.18	-0.17
	2	0.0	0.0	0.0	0.0	0.0	0.0
	3	-0.92	-0.97	-0.59	-0.98	-1.76	-0.100
	4	-0.08	0.07	0.68	0.12	-0.03	0.08
	5	1.08	1.38	1.73	0.10	0.19	0.23
ewe age	1	0.77	1.16	2.75	-0.11	0.02	0.30
	2	0.67	0.40	1.23	0.07	-0.02	-0.19
	3	0.56	0.32	0.78	0.07	0.07	0.09
	4	0.0	0.0	0.0	0.0	0.0	0.0
b(age) ^{ab}		0.0879	0.12392	0.22298	0.01121	0.02025	0.0396

^a Regression of sc and rsc measurement on age.

^b Regression coefficients at 4 and 5 were .122 and .132 for sc and .015 and .016 for rsc.

TABLE 9. ADJUSTMENT FACTORS FOR SCROTAL GROWTH CURVE PARAMETER ESTIMATES.^a

		variable			
		B	k	C ₁₄	t _j
adjustment factor					
birth-rearing	1	58.48	0.0037	-0.381	9.76
	2	0.0	0.0	0.0	0.0
-type	3	-40.19	-0.0028	-0.146	8.81
	4	-25.05	0.0005	0.011	-4.72
	5	-44.12	-0.0035	0.296	-4.71
ewe age	1			0.128	-6.31
	2			0.054	-4.09
	3			-0.008	-4.28
	4			0.0	0.0

^a $SC_{it} = A_i / (1 + B_i e^{-k_i t}) + r_{it}$, $C_{14} = [A / (1 + B)] + 9$, $t_j = [\ln(B) / k] + 14$.

TABLE 10. ADJUSTMENT FACTORS FOR BIRTH WEIGHT.

class	number born	ewe age	sex
1	-0.93	1.13	(R) 0.0
2	0.0	0.63	(E) 0.28
3	0.93	0.53	
		(4) 0.0 ^a	

^a Birth weights were adjusted to a mature ewe \geq 4 yrs of age.

TABLE 11. FIXED EFFECTS ESTIMATES FOR LAMB BREED GROUPS FOR AN ADDITIVE ANIMAL MODEL.

Breed group	trait					
	90d-wt			90d-sc		
	n	s.e.	mean	n	s.e.	mean
F2	258	0.0	32.733	110		20.001
F3, F4	110	1.033	32.621	46	.840	20.034
DxFR	115	.893	32.853	46	.733	19.496
FRxD	133	.986	26.772	54	.777	18.547
FDxDR	27	1.617	32.768	5	1.661	19.960
R(DF)xD(DF)	30	1.487	31.749	15	1.157	19.905
DRxFD	46	1.351	28.352	15	1.173	17.283
FxR	46	1.517	29.819	26	1.178	17.674
FxRX	24	1.662	23.029	2	2.211	19.180
RxF	37	1.463	26.981	17	1.175	16.619
		90d-rsc ^a			C ₁₄ ^b	
F2	111	0.0	6.037	103	0.0	9.472
F3, F4	46	.222	6.045	23	.106	9.359
DxFR	46	.197	5.969	42	.089	9.557
FRxD	56	.205	5.948	51	.099	9.394
FDxDR	5	.449	5.995	5	.197	9.508
R(DF)xD(DF)	15	.309	6.159	14	.141	9.532
DRxFD	16	.312	5.627	14	.144	9.322
FxR	26	.320	5.688	23	.143	9.280
FxRX	2	.588	6.322	—	—	—
RxF	17	.320	5.455	11	.145	9.316
		t _l ^b			A ^b	
F2	102	0.0	90.585	103	0.0	29.381
F3, F4	23	4.110	94.987	23	.853	30.512
DxFR	42	3.506	91.595	42	.696	28.861
FRxD	51	3.818	90.553	51	.858	27.955
FDxDR	5	7.688	90.440	5	1.611	28.834
R(DF)xD(DF)	14	5.490	94.714	14	1.141	30.291
DRxFD	14	5.602	96.250	14	1.146	29.870
FxR	23	5.646	91.009	23	1.0400	26.884
FxRX	—	—	—	—	—	—
RxF	11	5.682	93.046	11	1.153	27.899

	fertility			spbrd ^c		
F2	75	0.0	.680	44	0.0	.614
F3, F4	9	.169	.889	3	.299	.000
DxFR	63	.086	.730	46	.138	.370
FRxD	86	.085	.779	67	.127	.672
FDxDR	18	.143	.889	16	.215	.500
R(DF)xD(DF)	11	.162	.727	8	.240	.750
DRxFD	27	.127	.815	22	.194	.900
FxR	16	.150	.875	13	.236	.692
FxRX	14	.162	.929	13	.231	.231
RxF	17	.148	.882	15	.225	.333

^a $r_{sc} = sc/wt^{1/3}$

^b $SC_{it} = A_i / (1 + B_i e^{-k_i t}) + r_{it}$, $C_{14} = [A / (1 + B)] + 9$, $t_i = [\ln(B) / k] + 14$.

^c spring mating behavior

TABLE 12. POOLED STANDARD ERRORS (s_p^2), DIFFERENCES BETWEEN 1/4 AND 1/2 FINN MEAN EFFECT (δ) AND TEST STATISTICS (t) FOR COMPARISONS .

trait	model	s_p^2	$\Sigma(1/n_i)$	δ	t
90d-wt	a	1.275	.212	3.998	7.696 ^a
90d-sc	a	.922	1.002	2.168	2.256 ^c
90d-rsc	a	.066	.997	.366	1.431 ^d
t _l	a	20.941	.574	.027	.008
A	a	.881	.574	1.963	2.761 ^b
C14	a	.014	.574	.164	1.845 ^c
fert	a	.021	.528	-.014	-1.334 ^d
spbrd	a	.026	.846	.181	1.226

^a significant at .001 level

^b significant at .01 level

^c significant at .05 level

^d significant at .1 level

TABLE 13. VARIANCE COMPONENT ESTIMATES FOR BW-150 d WEIGHTS ON COMBINED MALE AND FEMALE DATA FROM INDICATED UNIVARIATE REML MODELS.

BW						
model	a ^a	ae ^b	ae ^c	ae ^d	am ^e	a1M ^f
ln L ^g	-4606.910	-4592.181	-4585.156	-3171.668	-4584.442	-3175.553
σ^2_a	.2222	.1114	.1028	.0829	.0723	.0832
σ^2_m	—	.1402	.0771	.0888	.0765	—
σ^2_c	—	—	.1349	—	.1537	—
σ^2_e	.2980	.2516	.1923	.3567	.2062	.4449
σ^2_p	.5202	.5032	.5071	.5284	.5087	.5281
h ^{2l}	.427 \pm .087	.221 \pm .082	.203 \pm .130	.157 \pm .098	.142 \pm .083	.158 \pm .130

45 d Weight				
model	a	am1	a1M	amp1 ^m
ln L	-4751.851	-4748.791	-3245.240	-3242.971
σ^2_a	2.3167	1.6988	1.9306	1.5363
σ^2_m	—	.2180	—	39.E-06
σ^2_c	—	.8956	—	.9726
σ^2_e	4.9316	4.3401	5.1720	4.5801
σ^2_p	7.2483	7.1526	7.1025	7.0889
h ²	.320 \pm .089	.2385 \pm .092	.272 \pm .136	.217 \pm .106

60 d Weight				
model	a	am1	a1M	amp1
ln L	-5262.206	-5260.506	-3599.682	-3599.257
σ^2_a	3.4195	2.8568	3.2352	2.4702
σ^2_m	—	359.E-08	—	34095.E-08
σ^2_c	—	1.3356	—	.1691
σ^2_e	9.0505	8.1793	8.9474	9.4942
σ^2_p	12.4700	12.3717	12.1827	12.1339
h ²	.274 \pm .087	.231 \pm .101	.266 \pm .127	.204 \pm .093

90 d Weight				
model	a	am1	a1M	amp1
ln L	-1725.445	-1724.723	-1237.234	-1213.983
σ^2_a	6.3563	5.8188	6.6063	5.8133
σ^2_m	—	9344.E-09	—	5152.E-08
σ^2_c	—	1.8408	—	.4875
σ^2_e	19.0172	17.6671	20.3323	20.5162
σ^2_p	25.3735	25.3268	26.9386	26.8170
h ²	.251 \pm .085	.230 \pm .093	.245 \pm .149	217 \pm .n.a.

120 d Weight

model	a
ln L	1674.455
σ^2_a	7.1501
σ^2_m	—
σ^2_c	—
σ^2_e	21.4357
σ^2_p	28.5857
h^2	.250±.095

150 d Weight

model	a
ln L	-1542.250
σ^2_a	10.8427
σ^2_m	—
σ^2_c	—
σ^2_e	23.3993
σ^2_p	34.2420
h^2	.317±.107

a additive genetic model

b additive genetic and total ewe (maternal genetic and permanent envir.)

c additive, ewe and litter variances

d additive and ewe with one random lamb/ewe/yr

e additive direct, maternal variance and litter effect (full sibs born in same year)

f additive with one record/ewe/yr and using only male (M) pedigrees

g log likelihood omitting constants

l heritability ± s.e.

m additive, maternal genetic and permanent environmental
with one record/ewe/yr

TABLE 14. VARIANCE COMPONENT ESTIMATES FOR 45–150 d SC MEASURES SCALED AND UNSCALED FOR BODY WEIGHT, SC LOGISTIC GROWTH CURVE PARAMETER ESTIMATES AND FEMALE REPRODUCTIVE TRAITS FROM INDICATED UNIVARIATE REML MODELS.

model	45 d rsc		45 d sc			
	a ^a	al ^b	a	a wt ^c	al	al wt
lnL	220.758	220.753	-158.068	-37.250	-510.060	-37.251
σ^2_a	2201.E-05	2188.E-05	3205.E-04	1356.E-04	3252.E-04	1393.E-04
σ^2_m	—	—	—	—	—	—
σ^2_c	—	9222.E-03	—	—	1174.E-08	1297.E-08
σ^2_e	4923.E-05	4956.E-05	7230.E-04	2951.E-04	7283.E-04	2921.E-04
σ^2_p	7124.E-05	7154.E-04	1.0436	4307.E-04	1.0535	4315.E-04
h^2_d	.309 \pm .147	.306 \pm .151	.307 \pm .155	.315 \pm .123	.307 \pm .163	.323 \pm .159

model	60 d rsc		60 d sc			
	a	al	a	a wt	al	al wt
lnL	149.063	-326.652	-326.782	-158.744	-326.652	-155.483
σ^2_a	3858.E-05	4798.E-04	5253.E-04	3886.E-04	4798.E-04	3039.E-04
σ^2_m	—	—	—	—	—	—
σ^2_c	—	2057.E-04	—	—	2057.E-04	3045.E-04
σ^2_e	9959.E-05	1.7437	1884.E-03	5102.E-04	1.7437	3039.E-04
σ^2_p	1382.E-04	2.4292	2410.E-03	8988.E-04	2.4292	9123.E-04
h^2	.279 \pm .151	.198 \pm .152	.218 \pm .159	.432 \pm .144	.198 \pm .152	.333 \pm .152

model	90 d rsc		90 d sc			
	a	al	a	a wt	al	al wt
lnL	-76.765	-76.680	-505.951	-395.701	-505.951	-394.378
σ^2_a	3730.E-04	3265.E-04	4.3871	2.4023	4.3911	1.9450
σ^2_m	—	—	—	—	—	—
σ^2_c	—	3440.E-05	—	—	1437.E-06	1.0592
σ^2_e	2256.E-04	2235.E-04	3.9797	1.7928	3.9889	1.2417
σ^2_p	5986.E-04	5844.E-04	8.3667	4.1952	8.3594	4.2459
h^2	.623 \pm .257	.559 \pm .297	.524 \pm .237	.573 \pm .217	.523 \pm .264	.458 \pm .211

model	120 d rsc		120 d sc	
	a	a wt	a	a wt
lnL	-48.371	-427.037	-509.824	-427.037
σ^2_a	82019.E-06	1.1037	77492.E-05	1.1037
σ^2_m	—	—	—	—
σ^2_c	—	—	—	—
σ^2_e	370674.E-06	3.9082	7.3667	3.9082
σ^2_p	452693.E-06	5.0119	8.1416	5.0119
h^2	.181 \pm .154	.220 \pm .150	.095 \pm .127	.220 \pm .150

	150 d rsc	150 d sc	
model	a	a	a wt
lnL	-34.160	-406.571	-376.956
σ^2_a	54139.E-06	64052.E-05	73199.E-05
σ^2_m	—	—	—
σ^2_c	—	—	—
σ^2_e	368360.E-06	6.7209	5.0197
σ^2_p	422490.E-06	7.3614	5.7517
h^2	.128±.119	.087±.134	.127±.117

TI SC Growth Curve

model	a	al
lnL	-846.297	-845.926
σ^2_a	86.4249	62.9614
σ^2_m	—	—
σ^2_c	—	23.8676
σ^2_e	88.5302	82.0731
σ^2_p	174.9551	168.9021
h^2	.494±.263	.373±.286

A SC Growth Curve

model	a	a wt ^B
lnL	-465.847	-413.003
σ^2_a	77959.E-05	78906.E-05
σ^2_m	—	—
σ^2_c	—	—
σ^2_e	8.9421	7.6545
σ^2_p	9.7217	8.4436
h^2	.080±.187	.094±.150

sc14 SC Growth Curve

model	a	al
lnL	147.381	147.381
σ^2_a	47584.E-06	47878.E-06
σ^2_m	—	—
σ^2_c	—	29192.E-10
σ^2_e	70569.E-06	70342.E-06
σ^2_p	11815.E-05	11822.E-05
h^2	.403±.133	.405±.144

B SC Growth Curve

model	a	al
lnL	-751.015	-748.538
σ^2_a	12.8805	6.8029
σ^2_m	—	—
σ^2_c	—	60.9136
σ^2_e	87.6109	39.8323
σ^2_p	100.4924	107.5487
h^2	.128±.243	.063±.130

k SC Growth Curve

model	a	al
lnL	-771.318	-767.511
σ^2_a	39.1607	17.6907
σ^2_m	—	—
σ^2_c	—	40.5678
σ^2_e	62.9488	41.9298
σ^2_p	102.1095	100.1883
h^2	.384±.189	.177±.181

fertility -(0,1)

model	a	a wt ^f
lnL	99.903	92.291
σ^2_a	16115.E-06	60051.E-07
σ^2_m	—	—
σ^2_c	—	—
σ^2_e	16312.E-05	16017.E-05
σ^2_p	17643.E-05	16618.E-05
h^2	.091±.125	.036±.127

Spring rebreeding

model	a
lnL	50.369
σ^2_a	92667.E-05
σ^2_m	—
σ^2_c	—
σ^2_e	13096.E-05
σ^2_p	22363.E-05
h^2	.414±.188

- a additive genetic
- b additive genetic and litter components
- c additive genetic, weight at measurement as a covariate
- d heritability ± standard errors
- e additive genetic with 150-d weight as a covariate
- f additive genetic with 180-d weight as a covariate

TABLE 15. LONGITUDINAL ENVIRONMENTAL AND GENETIC CORRELATIONS FOR WT, SC AND SCALED SC (RSC) AT 60, 90 AND 120 d AS OBTAINED FROM AN INDIVIDUAL ANIMAL MODEL MULTIVARIATE ANALYSIS.^a

TRAIT	wt2	wt3	wt4	sc2	sc3	sc4	rsc2	rsc3	rsc4
wt2	.32	.81	.77						
wt3	.69	.27	.93						
wt4	.60	.76	.25						
sc2				.22	.10	.13			
sc3				.85	.52	.67			
sc4				.37	.79	.10			
rsc2							.30	.49	.22
rsc3							.60	.59	.90
rsc4							.26	.52	.18

^a heritabilities on diagonals; genetic correlations above diagonal; environmental correlations below diagonal.

TABLE 16. ENVIRONMENTAL AND GENETIC CORRELATION ESTIMATES FOR MALE AND FEMALE TRAITS FROM AN INDIVIDUAL ANIMAL MODEL MULTIVARIATE ANALYSIS.^a

TRAIT	90d-wt	90d-sc	90d-rsc	t _l	fert	spbrd
90d-wt	.25	.67	.53	-.74	-.26	.34
90d-sc	.76	.52	.97	-.43	.20	.34
90d-rsc	.39	.91	.59	-.91	.25	.26
t _l	-.48	-.93	-.46	.49	-.32	-.48
fert	.2309	
spbrd	-.1641

^a heritabilities on diagonals; genetic correlations above diagonal; environmental correlations below diagonal.

TABLE 17. EXPECTED GENETIC GAIN (dG) FOR EWE FERTILITY AND SPRING REBREEDING FOR VARIOUS SELECTION INDEXES USING EWE REPRODUCTION AND VARIOUS COMBINATIONS OF MALE SC MEASURES.

Ewe trait	components in index	dG
fertility	rsc(sire)	.02419i
	rsc(sire) + rsc(one full-sib)	.02796i
	rsc(one full-sib) + t ₁ (sire)	.03239i
spring-rebreeding behavior	spring rebreeding of dam of ewe lamb	.19615i
	spring rebreeding of dam of ewe lamb + sc(sire)	.21007i
	spring rebreeding of dam of ewe lamb + t ₁ (sire)	.22187i
	sc(sire)	.07530i
	t ₁ (sire)	.10367i

APPENDIX A

TABLE 18. ABBREVIATIONS AND CORRESPONDING DEFINITIONS.

abbreviation	definition
F	Finnsheep breed code
R	Rambouillet breed code
D	Dorset breed code
RX	7/8 Rambouillet, 1/8 Finnsheep breed code
DX	crossbred Dorset breed code
FR	animal with a F sire and R dam
F1	50% D, 25% F, 25% R lamb
F2	first generation inter-se
F3	second generation inter-se
RDF	animal with R sire and DxF dam
DR	animal with D sire and R dam
DDF	animal with D sire and DxF dam
DFD	animal with D sire and FxD dam
DDR	animal with D sire and DxR dam
FDR	animal with F sire and DxR dam
DF	animal with D sire and F dam
FD	animal with F sire and D dam
byr	birth year
phbrco	breed code (see table 17 appendix A)
born	number of lambs that were in a lamb's litter
sire	sire of the lamb
eweage	age of ewe
brtyre	combined birth and rearing type of the lamb
age	regression on age of the lamb within a measurement time
ealam	ewe age at lambing
fert	fertility of the ewe (binomial [0,1])
spbrd	spring mating behavior
noff	number of ewe's offspring (i.e., prolificacy)
wt	weight
sc	scrotal circumference
rsc	sc adjusted to the 1/3 power body weight($rsc = sc/wt^{1/3}$)
wt1, sc1, rsc1	45 d measurements
wt2, sc2, rsc2	60 d measurements
wt3, sc3, rsc3	90 d measurements
wt4, sc4, rsc4	120 d measurements
wt5, sc5, rsc5	150 d measurements
wt6	180 d wt
A	estimated maximum sc
B	constant of intergration
k	maturing rate parameter
C ₁₄	estimated sc at 14 d of age
t _j	estimated age at which testis growth rate was maximum

TABLE 19. RAM AND EWE BREEDS THAT DEFINED THE BREED CODES (PHBRCO) FOR LAMBS DURING THE FIXED EFFECTS ADJUSTMENT ANALYSIS.

sire breed	ewe breed	phbrco
F	R,RX	1
R,RX	F	2
FR,FR	FD,DF	3
F1,F2	F1,F2	4 (F2,F3)
D	FR	5
RDF	DDF	5
DR	FD	5
R	DF	5
D	DF	5
DDF	FDR	5
D	FD	5
DDF	RDF	5
R	FD	5
FR	D	6
FD	DR	6
FR	DR	6
FR	DX	6
D	R	7
R	D	7
D	DR	7
D	DDR	7
D	DDF	8
D	DFD	8
DDF	D	8

TABLE 20. OBSERVATIONS, ABSORBED AND ESTIMATED FIXED EFFECTS ESTIMATING ADJUSTMENT FACTORS FOR VARIOUS VARIABLES.

variable	effects		significance
	absorbed	estimated	
bwt	sex, byr, phbrco, born, sire	eweage	p<.0001
bwt	sex, byr, phbrco, eweage, sire	# born	p<.0001
bwt ^a	sex, byr, sex*byr, phbrco, eweage, born	sex, sex*byr ^b	p<.0001, .0334
wt1	sex, byr, phbrco, brtyre, sire	eweage, age	p<.0001, .0001
wt1	sex, byr, phbrco, eweage, sire	brtyre, age	p<.0001, .0001
wt1 ^a	sex, byr, sex*byr, phbrco, eweage, brtyre	sex, sex*byr ^b	p<.0001, .1534
wt2	sex, byr, phbrco, brtyre, sire	eweage, age	p<.0001, .0001
wt2	sex, byr, phbrco, eweage, sire	brtyre, age	p<.0001, .0001
wt2 ^a	sex, byr, sex*byr, phbrco, eweage, brtyre	sex, sex*byr ^b	p<.0001, .1534
wt3	sex, byr, phbrco, brtyre, sire	eweage, age	p<.0007, .0001
wt3	sex, byr, phbrco, eweage, sire	brtyre, age	p<.0001, .0001
wt3 ^a	sex, byr, sex*byr, phbrco, eweage, brtyre	sex, sex*byr	p<.0001, .0001
wt4	sex, byr, phbrco, brtyre, sire	eweage, age	p<.0206, .0001
wt4	sex, byr, phbrco, eweage, sire	brtyre, age	p<.0001, .0001
wt4 ^a	sex, byr, sex*byr, phbrco, eweage, brtyre	sex, sex*byr	p<.0001, .0077
wt5	sex, byr, phbrco, brtyre, sire	eweage, age	p<.0216, .0001
wt5	sex, byr, phbrco, eweage, sire	brtyre, age	p<.0012, .0001
wt5 ^a	sex, byr, sex*byr, phbrco, eweage, brtyre	sex, sex*byr	p<.0001, .0042
wt6	byr, phbrco, brtyre, sire	eweage, age	p<.0241, .0001
wt6	byr, phbrco, eweage, sire	brtyre, age	p<.0188, .0001
sc1	byr, phbrco, brtyre, sire	eweage, age	p<.0114, .0001
sc1	byr, phbrco, eweage, sire	brtyre, age	p<.0001, .0001

rsc1	byr, phbrco, brtyre, sire	eweage, age	p<.0198, .0001
rsc1	byr, phbrco, eweage, sire	brtyre, age	p<.0019, .0001
sc2	byr, phbrco, brtyre, sire	eweage, age	p<.0257, .0001
sc2	byr, phbrco, eweage, sire	brtyre, age	p<.0001, .0001
rsc2	byr, phbrco, brtyre, sire	eweage, age	p<.5139, .0001
rsc2	byr, phbrco, eweage, sire	brtyre, age	p<.0005, .0001
sc3	byr, phbrco, brtyre, sire	eweage, age	p<.1271, .0001
sc3	byr, phbrco, eweage, sire	brtyre, age	p<.0515, .0001
rsc3	byr, phbrco, brtyre, sire	eweage, age	p<.3751, .0001
rsc3	byr, phbrco, eweage, sire	brtyre, age	p<.3940, .0001
sc4	byr, phbrco, brtyre, sire	eweage ^b , age	p<.6962, .0001
sc4	byr, phbrco, eweage, sire	brtyre ^b , age	p<.4584, .0001
rsc4	byr, phbrco, brtyre, sire	eweage ^b , age	p<.5432, .0001
rsc4	byr, phbrco, eweage, sire	brtyre ^b , age	p<.2150, .0001
sc5	byr, phbrco, brtyre, sire	eweage ^b , age	p<.9947, .0013
sc5	byr, phbrco, eweage, sire	brtyre ^b , age	p<.8865, .0001
rsc5	byr, phbrco, brtyre, sire	eweage ^b , age	p<.6797, .0712
rsc5	byr, phbrco, eweage, sire	brtyre ^b , age	p<.7996, .0001
A	byr, phbrco, brtyre	eweage ^b	p<.5878
B	byr, phbrco, brtyre	eweage ^b	p<.5737
k	byr, phbrco, brtyre	eweage ^b	p<.5545
C ₁₄	byr, phbrco, brtyre	eweage	p<.4248
t _l	byr, phbrco, brtyre	eweage	p<.3074
A	byr, phbrco, eweage	brtyre ^b	p<.5539
B	byr, phbrco, eweage	brtyre	p<.0001
k	byr, phbrco, eweage	brtyre	p<.0706
C ₁₄	byr, phbrco, eweage	brtyre	p<.0001
t _l	byr, phbrco, eweage	brtyre	p<.0001
noff	byr, phbrco, brtyre	eweage ^b , ealam ^b , wt6 ^b	p<.4242 p<.1281, .0013
noff	byr, phbrco, eweage	brtyre ^b , ealam ^b , wt6 ^b	p<.6449 p<.2444, .0002
spbrd	byr, phbrco,	eweage ^b ,	p<.0237

	brtyre	ealam ^b , wt6 ^b	p<.8726, .5100
spbrd	byr, phbrco, eweage	brtyre ^b , ealam ^b , wt6 ^b	p<.2205 p<.9983, .8959
fert	byr, phbrco, brtyre	eweage ^b , wt6 ^b	p<.6649, .1140
fert	byr, phbrco, eweage	brtyre ^b , wt6 ^b	p<.4001, .2269

^a no effects were absorbed in this model.

^b effects were insignificant or yielded unreasonable adjustment pattern for factor(s)

APPENDIX B

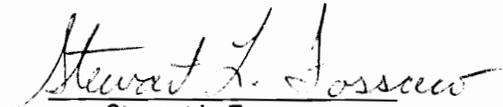
TABLE 21. PARAMETER ESTIMATES AND MSE FOR EACH YEAR ADJUSTED AS: $sc' = sc-i$.

i	parm	84	85	86	87	88
4	A	26.27	27.44	27.07	33.85	31.15
	B	6.47	7.00	8.03	8.53	6.29
	k	.026	.026	.029	.023	.024
	MSE	.514	.537	.142	.149	.
5	A	24.59	25.83	25.69	30.87	29.16
	B	7.98	8.49	9.76	10.13	7.26
	k	.028	.028	.031	.026	.025
	MSE	.400	.455	.111	.118	.
6	A	22.92	24.22	13.50	28.06	27.17
	B	10.36	10.713	N.C. ^a	12.32	8.62
	k	.032	.030	N.C.	.029	.027
	MSE	.274	.361	N.C.	.081	.
7	A	21.27	22.60	22.90	25.40	12.67
	B	14.41	14.27	16.15	16.08	N.C.
	k	.035	.033	.036	.033	N.C
	MSE	.142	.255	.062	.044	N.C.
8	A	19.65	20.99	21.48	22.90	23.17
	B	22.09	20.52	22.63	22.83	13.69
	k	.040	.037	.040	.037	.033
	MSE	.033	.144	.062	.013	.
9	A	18.10	19.38	20.05	20.59	21.16
	B	38.51	33.12	34.67	36.62	19.01
	k	.046	.043	.045	.044	.037
	MSE	.017	.044	.105	.011	.
10	A	16.65	17.80	18.61	18.49	19.13
	B	78.57	63.55	60.57	69.62	29.65
	k	.054	.050	.051	.051	.043
	MSE	.240	.006	.242	.101	.
11	A	15.28	16.26	17.17	16.66	17.08
	B	192.60	156.51	129.20	164.47	57.10
	k	.064	.060	.060	.061	.051
	MSE	.945	.167	.576	.437	.

^a program did not converge.

Vita

I was born in Fort Collins, Colorado on July 2, 1963. My Parents are Robert and Patricia Fosseco. I completed a Bachelor of Science in Animal Science with a minor in both Statistics and Mathematics from the University of Idaho in December, 1985. I earned a Master of Science in Statistics at Virginia Polytechnic Institute and State University in December 1988.


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