A STUDY OF PHYSIOLOGICAL AND PRODUCTIVE DIFFERENCES BETWEEN FLEECE WEIGHT SELECTED AND CONTROL ROMNEY SHEEP

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in partial fulfilment of the requirements
for the degree of

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INTRODUCTION

Single trait fleece weight selection flocks, such as the Massey University PT (Progeny Tested) flock, provide excellent experimental material for the study of the biological basis for genetic differences in wool production. Similar Australian Merino flocks have formed the basis for studies on such diverse traits as: digestive ability; intake; body weight gain; wool growth efficiency; chemical composition of wool; wool follicle anatomy; amino acid metabolism and a range of other subjects. Equivalent studies have not been as fully initiated in coarse wool breeds such as the New Zealand Romney.

Merino studies have concluded that differences in wool production, both within and between flocks, are mainly due to differences in the efficiency of conversion of feed to wool. This topic is of considerable importance because unless gains in wool production per head are due, at least in part, to differences in efficiency then economic benefits from fleece weight selection may be limited.

Sheep which are genetically superior wool producers are also superior in their ability to utilize supplementary amino acids for wool growth. This is particularly true for the sulphur containing amino acids cyst(e)ine and methionine. Lower wool sulphur content, in fleece weight selected sheep, is maintained under periods of adverse nutrition. Selected Merinos appear to have increased physiological versatility with respect to wool growth. The ability to utilize nutrients effectively, when present, and to sustain production in the presence of limited essential substrates, would appear to be close to the biological ideal in fleece weight selection programmes. The examination of biological differences, brought about as correlated responses, could also lead to the discovery of additional traits which may be incorporated into the selection criteria of prime breeding stock.

Unlike the Merino, the New Zealand Romney is a highly seasonal animal with many aspects of its biology being influenced by photoperiod. The extent to which selection for fleece weight has removed or altered this seasonal dependence is an important concern for animal breeders. Seasonal responses are related to an animal's ability to reproduce as a hogget, to lamb as an adult out of season, and to produce wool of relative uniformity throughout the year.

Studying these productive differences in selected lines should involve intensive indoor trials in addition to field evaluations under conditions which resemble the environment under which these lines were selected.

The purpose of this project was to examine a variety of traits which are central to the biological basis of genetic differences in wool production of fleece weight selected (FW) and control (C) New Zealand Romney lines in the Massey University PT Romney flock.

The project involved a number of separate and concurrent trials designed to evaluate selection line differences in: digestive ability under controlled feeding; wool growth response to supplemental dietary protein; seasonality of wool growth under natural grazing; body weight changes from weaning to hogget shearing; intake and efficiency on pasture; reproductive traits as hoggets and their relationship to subsequent lambing performance; and, the relationship between seasonal wool growth and staple strength of hogget wool.

REVIEW OF LITERATURE

The examination of flocks selected for various measures of wool production including clean fleece weight (Turner et al., 1968; Dun and Eastoe, 1970; Turner et al., 1970; Pattie and Barlow, 1974; McGuirk and Atkins ,1976; Heydenrych et al., 1977; Turner and Jackson, 1978), greasy fleece weight (Blair et al., 1985), and crimp frequency (Robards and Pattie, 1967) have demonstrated a variety of correlated responses to selection. Excellent reviews of the genetic and physiological changes in these various flocks have been published (Williams, 1976;1979;1987; McGuirk, 1979;1983; Butler and Maxwell, 1984).

2.1 Live weight and intake

In the absence of large (Blair et al., 1985) or consistent (Williams, 1979; 1987) differences in mature size of fleece weight selected (F+) sheep, it may be concluded that fleece weight and live weight were relatively independent in most studies with F+ lines. While increased live weight could be a component of increased fleece weight, due to increased surface area and increased feed capacity, in most studies the increased intake of larger sheep was only in keeping with increased maintainance requirements and did not represent a large productive advantage (Williams, 1979).

Direct comparisons of voluntary feed intake of F+ versus C lines have been conducted both in and out of doors. The conclusion has generally been that differences in intake (when adjusted for live weight) do not represent significant contributions to differences in wool production (Ahmed et al., 1963; Williams and Miller, 1965; Dolling and Piper, 1968; Hamilton and Langlands, 1969; Robards et al., 1974). Similar work comparing breeds and strains (Daly and Carter, 1955; Weston, 1959) also concluded that voluntary intake was not a reliable predictor of wool production in the presence of substantially larger variation in wool growth efficiency. Although Schinkel (1960) showed significant contributions of voluntary intake to between sheep differences in wool production, subsequent studies (Hutchinson, 1961; Williams, 1966; Wodzicka-Tomaszewska, 1966; Dolling and Piper, 1968; Saville and Robards, 1972) have contested the strength of this relationship.

2.2 Wool growth efficiency

Selection for fleece weight appears to have resulted in improved fleece weight and a correlated response in efficiency. Relative levels of wool production per unit of feed intake have been summarized by Butler and Maxwell (1984) and range from a 9% advantage (Ahmed et al., 1963), to a 71% advantage (Hamilton and Langlands, 1969) over a range of feeding levels. Most estimates are between 9% and 38% (Dolling and Moore, 1960; Williams and Winston, 1965; Williams, 1966; Dolling and Piper , 1968; Hamilton and Langlands, 1969).

Studies comparing between breed or between strain differences in wool growth efficiency have reported similar variation with values ranging between 0% and 54% relative advantage of one breed/strain over another (Daly and Carter, 1955; Weston, 1959; Dunlop et al., 1960; Dunlop et al., 1966; Langlands and Hamilton, 1969; Saville and Robards, 1972; Sumner, 1979).

Correlated responses in wool growth efficiency have not been found in Crimps minus selection flocks (Robards et al., 1974), in skin fold plus flocks (Robards et al., 1976) or in fertility plus or body weight plus flocks (Pattie and Williams, 1967; Atkins and Robards, 1976). High body weight selection flocks did produce more wool, but without accompanying changes in efficiency.

Many of the reported studies have found that the relative advantage of various groups is dependent on the level of nutrient intake. The most dramatic example is that of Hamilton and Langlands (1969) in which F+ and F- rams grazed three pastures differing in herbage availability. The relative advantage of F+ over F- rams increased from 138% to 242% as herbage quality and availability increased. Similar results have been reported in other selection line and breed/strain comparisons (Weston, 1959; Schinckel, 1960; Williams and Winston, 1965; Williams, 1966; McManus et al., 1966; Piper and Dolling, 1969; Saville and Robards, 1972).

The efficiency of conversion of feed into wool appears to be a major factor contributing to variation in wool production when comparisons are made between genotypes. Much of the within flock variation appears to be under similar control. What remains to be determined is the physiological routes through which efficiency has been increased. These paths may involve the quality of forage consumed under free choice grazing; the ability of the digestive tract to absorb a larger quantity of nutrients from ingested forage; or differences may be due, primarily, to changes in the post-absorptive utilization of nutrients.

2.2.1 Diet selection

Evidence on the selectivity of intake by lines, breeds or strains appears to be ambiguous. Using the nitrogen and crude-fibre content of faeces as a guide, Weston (1959) concluded that strong-wool Merinos selected feed of slightly higher quality than fine-wool Merinos. Moore and Dolling (1961) found a 10% coefficient of variation, in nutritive value of feed consumed, that was related to feed selection by the sheep. Ahmed et al. (1963) were unable to demonstrate, in a pen feeding trial, any preference of F+ for diets with higher protein content. Variability in diet selection does not appear to be a major factor influencing the variation in efficiency of wool production between genotypes.

2.2.2 Digestive ability

The increased efficiency of feed conversion in F+ animals may also be related to differences in the ability to digest or absorb dietary nutrients. Hutchinson (1961) found considerable individual differences in apparent digestive ability but was unable to significantly relate these to measures of efficiency. Weston (1959) found small but significant increases in the ability to digest nitrogen in strong wool Merinos (2%). In a study by Brookes (1983,unpublished), subsequently reported by McClelland et al., (1986), C rams had higher apparent abilities to digest dry matter (62.9±.6% vs. 60.1±.9%) than FW rams. Other reports have demonstrated inconsistent small and non-significant differences between lines and strains (Dunlop et al., 1966; Piper and Dolling, 1969; Robards and Atkins, 1976). Williams (1979) quoted that the concentrations of ammonia in the rumen fluid were similar for F+ and F- sheep.

Given relatively large strain differences in efficiency and small and inconsistent differences in apparent digestive ability, it is unlikely that digestive ability or the total quantities of nutrients available to the sheep has been altered by selection for fleece weight. The possibility of differences in apparent digestive ability must be completely ruled out, however, before comparisons of dietary intake (based on faecal output) are used to compare selection lines.

Metabolic rate has not been shown to differ between F+ and C or F- flocks (Williams and Miller, 1965; Williams and Winston, 1965) although Graham (1968) showed some evidence of higher fasting heat production in F+ compared to F- rams.

2.3 Utilisation of amino acids for wool growth

2.3.1. Sulphur content of wool

Many of the ongoing studies into differences in wool growth efficiency are centered on the availability and utilisation of amino acids. These investigations have focused on the sulphur-containing amino acids (S-amino acids) cyst(e)ine and methionine and their relationship to the sulphur content (S-content) of wool. Most of the sulphur in wool is present as cystine with smaller amounts of cysteine and methionine.

These S-amino acids are not spread homogeneously throughout the wool fibre, rather, separate sub-fractions of the soluble proteins extracted from wool contain differing amino acid balances (Bradbury, 1973). Low sulphur proteins, concentrated mainly in the microfibrils of the cortical cells, account for over 60% of wool proteins and contain all of the methionine and most of the lysine found in wool. High sulphur proteins, concentrated primarily in the matrix proteins surrounding the microfibrils, contain large amounts of cystine, proline and serine. High tyrosine proteins, also in the cellular matrix, are rich in tyrosine and glycine but do not contain many other amino acids.

The balance of cortical cell types within a fibre is also related to the S-content of wool. The S-content of fibre cell types varies considerably, decreasing in order from para-, meso-, ortho-, and meta-cortex to medulla (Black, 1987). Fine fibres, with higher crimp frequency and high paracortex content, will have higher S-content than coarse fibres containing more orthocortex and (perhaps) medulla. Although the commitment of fibre cells to specific cortical types remains reasonably constant over a wide range of wool growth rates, it can be affected by both plane of nutrition and photoperiod (Orwin et al. 1984). In a similar but qualitative study, Woods and Orwin (1987) showed that the wool proteins of individual sheep remained constant and characteristic despite changes in season, age or nutritional status and did not vary between different body positions. Between-sheep differences in protein pattern were displayed most markedly in the high-sulphur group. Differences in protein pattern were presumed to reflect genetic differences between sheep (Woods and Orwin, 1987). The relationship between S-content, protein profiles, and the balance of cortical cell types has not been fully explored in Romney fleeceweight selection lines.

Phenotypic associations between the S-content of wool and wool growth have clearly been demonstrated (Reis, 1965; Reis and Williams, 1965, Reis and Tunks, 1968; Reis, 1979). In all cases, high wool production was associated with lower S-content of the wool.

Differences in the S-content of wool in selected Merino sheep have also been demonstrated and result from F- or C sheep having a greater proportion of the high sulphur proteins than F+ sheep. Within this group of proteins, there is also a change in the balance of high cystine proteins (Williams, 1987). These compositional changes related primarily to resistance to compression and super-contraction properties. These were higher, and lower, in high S-containing wools, respectively. No differences were found on stress/strain properties at 30% fibre extension. The lower concentration of S-amino acids in the wool of F+ sheep is not merely a consequence of dilution. F+ sheep have higher daily sulphur outputs than C or F- sheep (Williams, 1979;1987). F+ sheep are capable of increasing the S-content of wool when supplementary S-amino acids are supplied. To date, no differences in the S-content of the Massey University FW and C lines have been published, but investigations are underway.

2.3.2 Metabolism of sulphur-containing amino acids

Many studies have documented the response in wool growth to supplementary supplies of S-amino acids (Reis, 1979). Supplementation of S-amino acids increases wool growth rate, and the S-content of wool. This relationship is more pronounced in F+ than F- or C sheep (Williams et al., 1972; Williams, 1973;1976).

S-amino acids in the form of L-cysteine, L-methionine or DL-methionine produced similar results whether given as abomasal supplements (Reis, 1967; Williams et al., 1972; Reis et al., 1973), intravenous infusion (Downes et al., 1970; Reis et al.,1973), or intraperitoneal or subcutaneous injection at one or two day intervals (Wickham, 1970; Barry et al., 1973).

Supplementary S-amino acids can also be supplied via abomasal supplies of casein. Reis (1979) summarized a number of studies with protein supplementation and concluded that amino acid imbalance in the supplement may yield poor wool growth response. This was true for gelatin and zein, while casein was fairly successful in stimulating wool growth. When a mixture of amino acids, including 10 essential amino acids, was infused into the abomasum, it stimulated wool growth to a similar extent as that of an equivalent amount of casein (Reis and Tunks, 1978).

The concentration of free cystine in the plasma has been found to be lower in F+ Merino lines (Williams et al., 1972; Williams, 1976). Although this difference is observable at very young ages (Williams, 1984) the mechanisms controlling this concentration difference have proved to be elusive.

Studies using radioactive cystine, have shown no differences in the entry rate of cystine into the plasma (Williams et al., 1972; Williams, 1976). Differences in plasma cystine concentration in these flocks were also independent of the level of wool growth. All results have demonstrated that superior wool growth is not due to higher availability of cystine in F+ sheep, or to the proportion of cardiac output supplying the skin (Williams, 1987). Ultimately, the cause/effect relationships need to be more clearly defined, and further understanding of the genes controlling wool protein synthesis is needed.

The importance of S-amino acid metabolism in the Massey FW and C lines is the subject of considerable recent study. Consistently lower blood urea concentration in FW rams has been related to lower rates of urea excretion (McCutcheon et al., 1987). Clark (1987) also reported that intravenous infusion of methionine reduced plasma urea concentration in C rams to a greater extent than that of FW rams. If, as in Merino lines, the wool of FW sheep has a lower S-content than that of C lines, this may indicate that high plasma urea concentrations of C rams reflect greater deamination of non-S-amino acids. The metabolism of S-amino acids appears to be related to plasma concentrations of urea. McCutcheon et al.,(1987) found a high ($r=-0.85$) correlation between corrected plasma urea concentration and nitrogen retention. The high blood urea concentration of some rams appears to reflect greater amino acid deamination consequent upon their inability to retain a high proportion of dietary nitrogen in wool/body tissues.

MATERIALS AND METHODS

3.1 Description of the experimental flocks and their management

The sheep used in these studies were from the fleece weight selected (FW) and control (C) subflocks of the Massey University PT (progeny tested) Romney flock. Both lines were established from the same base Romney flock, described by Rae (1958), in 1956 and have been closed since 1958. The management and selection methods used since that time have been described in detail by Blair et al. (1984) but are summarized here.

Each line has been maintained at 70-80 ewes and both lines are grazed together. Ewes were culled for age after their fourth lambing. Four 1.5 year old rams were replaced each year. Replacement 1.5 year old ewes and rams were selected at random in the C line while FW replacements were those with the heaviest greasy fleece weights as hoggets. Oestrus ewes from both lines were pen mated to individual rams between March and April.

Lambing occured between August and September. Shortly after birth each lamb was tagged then birth date, sex, birth rank and dam identification were recorded. Lambs were weaned and weighed in late November and shorn in mid December. From lamb shearing until hogget shearing in early October, ram and ewe hoggets were grazed separately. Within sex, hoggets from both lines were grazed together on rye grass-white clover pastures. Hogget fleeces, including bellies and pieces, were individually weighed and recorded. Live weights were taken directly off shears. A sample of wool from the right midside of each fleece was collected and labelled for later determination of descriptive traits, clean yield and fibre diameter.

Selection of FW and C animals to enter experiments was purely on a random basis. Whenever possible, all available animals were measured. Measurements of seasonal wool growth and seasonal reproduction were conducted under the standard management practices of the flock. No effort was made to alter the nutrition or growth rates of lambs on pasture.

3.2 Analytical techniques employed

3.2.1 Data collection and correction

All data were edited prior to analysis to remove records which did not physically conform to the requirements. This included removing all hoggets with incomplete seasonal data (Chapter 5), removing animals with unknown values for sire, birth date, dam, birth rank and weaning weight. Ewes which were injured or died during the breeding season were not considered in the comparison of incidence of oestrus (Chapter 7). In practise, very few records were omitted, especially in indoor trials.

After preliminary screening of records, all data were plotted against sheep number (unrelated variable) for the identification of outlying values due to miscoding. Variables requiring extra computation were calculated using Fortran programs to minimize errors. Statistical analyses were performed using both SAS (Statistical Analysis System, SAS Institute, Cary, NC, USA) and REG (Generalized Regression Package, A. Gilmour, N.S.W. Dept of Agriculture, 1985).

3.2.2 Univariate and Multivariate analysis of variance

Much of the data analysed in these experiments represents repeated observations on the same animals. Although this type of data could be analysed using univariate analysis of variance (ANOVA) at each discrete sampling, or using univariate (typically split-plot) ANOVA considering time as a design factor, these approaches do not avail themselves of all the information which is available. Using these approaches may lead to erroneous error terms (split-plot) or less powerful tests of main effects (separate ANOVA) (Box, 1950; Danford et al., 1960; Cole and Grizzle, 1966; Gill and Hafs, 1971; Bryant and Gillings, 1985). The preferred method of analysing these data is to apply multivariate analysis of variance (MANOVA). One type of MANOVA which is particularly suited to growth data is referred to as Repeated Measures Analysis (RMA).

When some yield variable y is measured over p periods, on the same animal, then to do separate ANOVAs would be to disregard the correlations which exist across the p-dimensioned vectors of y. Thus, each animal is represented by a vector rather than a single observation. Sums of squares and crossproducts, in ANOVA, are replaced by a matrix consisting of sums of squares for each y (on the diagonal) and sums of crossproducts between all y's on the off-diagonals. The advantage of this technique is that direct comparisons of time effects, and more powerful tests of main effects are made because all main effect (repeated) data is included. The interaction of main effects with time can also be assessed.

In the univariate ANOVA, hypotheses about main effects were made via an F-test, formed by a ratio of mean squares. In the multivariate case, tests of hypothesis are made on H (hypothesis) and E (error) matrices. These matrices are dimensioned pxp. H and E matrices are formed by the appropriate multiplication of identity and contrast matrices to account for n animals and k coefficients. A number of different contrast matrices can be used to generate hypotheses about main effects and interactions.

Once H and E are formed, the general test of main effects can be done by a variety of methods (Morrison, 1976; Chatfield and Collins, 1980). Although no one of these methods has won universal acceptance, the method of Wilks (1946) using the likelihood approach of Neyman and Pearson (1928) is straightforward and fairly robust (Box, 1950; Danford et al., 1960). Where simple ratios of mean squares (SSQ/df) form hypothesis tests in ANOVA, the determinants of the H and E matrices form a test ratio in MANOVA where,

$$\Gamma = \frac{|E|}{|H + E|}$$

and $M = n \ln (1/\Gamma)$

$A1 = (p + (k+1) + 1) / 2n$

to form the test statistic $(1-A1)M$

which is distributed as Chi-square with $p(k-1)$ degrees of freedom.

3.2.3 Tests of Assumptions in MANOVA

The only assumption crucial to MANOVA is homogeneity of the variance-covariance (VCV) matrices - similar to a matrix extension of Barlett's test. As this statistic was not available through REG or SAS, it was calculated from the matrices of sums of squares and crossproducts (SSQCP), which can be output from the REG or SAS programs according to the method of Box (1950). In no case was there significant deviation from homogeneity. This statistic is calculated as below:

Let n_t = number of animals per treatment

p = number of periods

k = number of treatments

N = total number of animals

$|E_t|$ = the determinant of the within treatment group error VCV matrix

$|E|$ = the determinant of the error VCV matrix

The determinants of a VCV matrix can be found directly from the determinants of the SSQCP matrix

$$|VCV| = |SSQCP| / (df)^p \qquad \text{note: } df(E)=N-k,\ df(E_t)=n_t-1$$

and

$$A1 = \frac{2p^2 + 3p - 1}{6(p+1)(k-1)} \left[\sum_{t=1}^{k} \frac{1}{n_t-1} - \frac{1}{N-k} \right]$$

and

$$M = (N-k) \ln |E| - \Sigma \left[(n_t-1) \ln |E_t| \right]$$

The test criteria (1-A1)M is distributed as Chi-squared with f_1 df where $f_1 = (1/2)(k-1)(p)(p+1)$.

Discussions of the interaction between time and main effects refer to the departure from parallelism of treatment effects. This parallelism does not mean linearity across time. It refers to the presence or absence of constant differences between treatments across time periods. MANOVA is capable of making these comparisons, while they are difficult to quantify otherwise.

In addition to MANOVA, univariate analyses were conducted, as part of RMA, at each time interval in order to determine when, in the production cycle, significant selection line differences were occuring.

THE PERFORMANCE OF FW AND C HOGGETS FED LUCERNE DIETS WITH AND WITHOUT FORMALDEHYDE-PROTECTED CASEIN

4.1 Introduction

The inherent difficulty in obtaining field measurements on productive characters such as feed intake, metabolic or digestive ability, and efficiency lend some appeal to pen-feeding experiments and their use as preliminary guides to more exhaustive field research. Knowledge of these characters is essential to provide a basis for later field comparisons where estimates of intake may be based entirely on faecal output, and the underlying assumption of no significant differences in dry matter or nitrogen digestive ability.

Selection for fleece weight in Merinos has brought about a correlated increase in the efficiency of conversion of food to wool. The correlated responses in intake and body size have been variable (Butler and Maxwell, 1984). Similar studies using Romney sheep (Clark et al.,1965; Wodzicka-Tomasewska, 1966) have reported that within flock differences between sheep with high or low fleece weight were due to differences in the efficiency of conversion of food to wool.

Wool and body growth have been shown to respond positively to abomasal supplementation with casein or S-amino acids (Reis, 1979). Fleece weight selected Merinos are more efficient at directing these supplements towards wool growth (Williams et al.,1972). Equivalent studies with selection lines in Romneys have only recently been reported (McClelland et al., 1986; Clark, 1987; McCutcheon et al., 1987).

Prior to this trial, FW and C sheep had only been studied in one indoor experiment. Using data from an experiment on 12 FW and 12 C rams fed cut pasture ad libitum, McClelland et al., (1986) found FW sheep to be inferior to C sheep in the apparent ability to digest dry matter (60.1±0.9% vs. 62.8±0.6%.). Data on wool and body growth in these same rams yielded a significant positive relationship between intake and wool growth in FW rams and a significant negative relationship among C rams. C rams also maintained significantly higher growth rates during the trial. These and other results indicated that the advantage of FW rams was due, at least in part, to differences in the ability to direct absorbed nutrients toward wool growth. Line differences in wool growth were more pronounced among sheep with higher intakes.

The purpose of this study was to examine the relative wool growth, liveweight gain, apparent digestive ability, and utilisation of dietary protein by FW and C Romney rams.

4.2 Materials and Methods

4.2.1 Experimental plan

Nine FW and nine C ram hoggets, born 1983, were chosen at random off pasture and brought indoors. Rams were housed and fed in individual digestability crates for the duration of the experiment.

The experiment, a total of 18 weeks beginning May 01/1984, was divided into 3 subperiods (P1, P2, P3) each of 6 weeks. The first two weeks of each period were used to adjust rams to the experimental diets and to stabilize intakes. Wool growth, liveweight gain and digestive ability were measured in the last 4, 4 and 2 weeks of each 6 week period, respectively.

P1 was a uniformity, or covariance period, during which all sheep received an equal weight of feed, calculated to be above maintainance. Wool growth in P1 was used as a covariate in the analysis of P2 and P3 data.

During P2, three sheep from each line were assigned at random to receive either 0, 30 or 60 g per day of formaldehyde protected casein in the feed in addition to the basal diet fed in P1.

An additional 2-week adjustment period (not included in these analyses) was placed between P2 and P3 to allow for the gradual transition from fine to long cut lucerne diets. In each of four 3-day stages, the proportion of new feed was increased by 25% and the level of feeding was raised by 100gms.

During P3, all sheep continued to be fed a similar amount of higher quality diet.

4.2.2. Feeding

In periods P1 and P2 each sheep received 1000g per day (air dry basis) of protein extracted lucerne meal obtained from Zanpro Lucerne (NZ) Ltd. The diet was finely ground and unpelleted. During period P3 each sheep was fed 1400 gms per day (air dry basis) of chaffed lucerne. Pure casein, obtained from the Dairy Research Institute, Palmerson North, was treated by soaking 200kg of casein in 1000l of cold water to which 5l of 40% formaldehyde had been added. After 60 minutes agitation, the casein was dried to 10% moisture. The formaldehyde casein, thus obtained, was stored under refrigeration and mixed thoroughly with individual daily presscake rations (P2) before feeding.

Sheep were fed once daily at 08:30 hours after removal of refused feed from the previous day. During periods P1 and P2, daily refusals were dried at 120 °F for 24 hours and then weighed. During period P3 some sheep refused a greater proportion of stalk than leaf so refusals were dried overnight, ground in a hammer mill fitted with a coarse screen and refed the following day. Feed samples, in all periods, were taken daily and bulked over 2 weeks. Feed samples were dried, as above, in order to obtain mean daily dry matter intakes for each sheep. Water was provided ad libitum in 81 buckets attached to the digestability crates but water intakes were not recorded.

The experimental protocol involved the estimation of wool growth from clipped shoulder and midside skin patches, the determination of body weight by regular fortnightly weighings and the estimation of nitrogen and dry matter digestibilty of the various rations.

4.2.3. Wool growth rate

Right shoulder and right midside wool patches were shorn at the beginning and end of the last 4 weeks of each period. Wool was clipped from a square patch (≈10cm by ≈10cm) on the right shoulder and midside of each sheep. Oster clippers fitted with No.0000 blades were used to remove the wool grown on the patch in each period. A similar patch was opened on the left shoulder and was intended to capture data on wool production in the transition periods. This data was eventually discarded as transitory periods were considered to be difficult to interpret. Also, the transition between P2 and P3 was an additional 2 weeks longer than between P1 and P2, and some sheep had difficulty adjusting to a chopped diet after press-cake feeding. Two patches were clipped at 2 or 4 weekly intervals to coincide with uninterupted wool growth measurment during the last 28 days on a particular diet. Only the four week samples were processed to estimate wool growth. The first two weeks of these periods allowed a brief time for wool growth to adjust to dietary changes. One shoulder was at all times replicating the midside sample.

The dimensions of each patch were measured at each clipping using Vernier calipers with extended arms. The length of each side and the diagonal of each patch were measured and recorded. The surface of the patch was calculated as the sum of two triangles. This precaution was necessary as some of the skin sample areas were remarkably non-rectangular.

All wool samples were stored in labelled open envelopes in a climate controlled laboratory (20° C,65%RH) and were conditioned for at least 48 hours prior to weighing. Samples were weighed, scoured by a four bowl and detergent water method while contained in individual fine mesh bags, dried in a blast of warm air, conditioned to 16% regain and weighed again.

Wool growth rates (greasy and clean) were expressed as mg per cm^2 per day. Rams were not shorn at the beginning and end of the 18 week trial as hogget fleece weights from these experimental rams were required by the flock management protocol and subsequent selection. As total wool growth during the experiment was not known it was not possible to express wool growth in terms of total gms per day.

An attempt was made to measure the length of the pile on wool growth patches using the same Vernier calopers which measured the patch area. This proved unsucessful and the technique and measurements were abandoned.

4.2.4 Live weight

Live weight was measured at fortnightly intervals beginning with the first day of the trial. To minimize live weight errors arising from differences in gut fill, sheep were always weighed prior to feeding at 08:00 hours. Live weights and subsequent measures of live weight gain included differences in fleece carried. As mentioned obove, it was not possible to partition the total fleece produced in each period and subtract this in order to obtain fleece-free live weights. Gains are expressed as absolute changes over 28 day periods in order to more clearly demonstrate the associated live weight changes.

4.2.5 Digestibility of dry matter and nitrogen

Nitrogen and dry matter digestibility were determined by the total collection of faeces and urine on every ram during 10-day periods in the last two weeks of each dietary period as outlined previously. Faeces were collected daily, stored at 5° C, bulked over 5 days and then weighed. Two sub-samples, of approximately 200g, were taken per sheep from each of the two 5-day samples. Sub-samples were weighed before and after drying at 110° F, for approximately 72 hours, to determine dry matter content. Six to seven small grab samples from each fresh total 5-day output were pooled and freeze-dried for subsequent nitrogen (N) determinations. Urine was collected into buckets containing 10 ml of 2.0M H_2SO_4. Urine volume was measured daily and 1% of the daily output was sampled to form a representative 5-day composite sample, also for N determination. Samples of feed, urine and faeces were analysed for total nitrogen by the Kjeldahl method.

4.2.6 Analytical Methods

Data were analysed by ANOVA and MANOVA (Repeated Measures Analysis) as described previously.

Several different covariates were used to remove complicating variables. Initial weight at the start of each period was used as a covariate in the assessment of liveweight gain. Although sheep were fed constant amounts of feed designed to be completely consumed each day, sometimes significant refusals were collected such that dry matter intake (DMI) was used as a covariate in the analysis of apparent dry matter (DMDIG), and nitrogen (NDIG), digestability and wool growth. Similarly, total nitrogen intake was used as a covariate in the analysis of total urinary nitrogen excretion (TUN).

Each period was analysed separately at first, then all measures of wool production, all measures of digestability and all measures of liveweight gain were combined in a repeated measures analysis including diet effects (even though diets were in effect for P2 only. By carrying diets as a design factor in MANOVA, the true diet effect is assessed by the interaction of time with diet. With such small numbers of sheep per diet and line (3), it may have been possible that animals were ineffectively randomized. A significant diet by time interaction may be a more effective method of determining non-parallel performance between true treated and untreated periods.

No fixed effect corrections (dam age, birth rank, rearing rank) were applied to the data as this would have resulted in singular matrices due to large numbers of classes and very few animals per class.

The model can be generalized as follows:

Model 4.1:

$$y_{ijk} = \mu + a_i + b_1X1_{ijk} + b_2X2_{ijk} + l_j + e_{ijk}$$

where,

y_{ijk} = an observation on various productive traits of the k^{th} C or FW or ram hogget in selection line j,

μ = an unobserved population mean,

a_i = the fixed effect of the i^{th} diet

b_1 = the regression of y_{ijk} on $X1_{ijk}$ where,
$X1_{ijk}$ = the observed initial weight of the ijkth individual and,
b_2 = the regression of y_{ijk} on $X2_{ijk}$ where,
$X2_{ijk}$ = the observed dry matter intake of the ijkth individual,
l_j = the fixed effect of the jth selection line, and
e_{ijk} = the random residual associated with the ijkth individual

For P2, in addition to the above, the model included fixed effects of diet and the interaction of diet and selection line. For P2 and P3 and multivariate analysis of wool growth, wool growth in P1 replaced initial weight as a covariate and dry matter intake remained in the model.

MANOVA on across period data used the above model, with the inclusion of diet and diet X selection line interaction, extended to p-dimensional space, where p=3, for P1, P2 and P3 replicates.

4.3 Results and discussion

The bags used to wash wool samples were found to have too coarse a weave to effectively contain short clipped wool fibres. As all samples were washed prior to this discovery, significant loss of fibres likely occured during processing. The loss rate was determined by washing clean, solvent extracted samples and comparing sample weights before and after. As the effect of this error on the estimates of clean wool production on individual sheep could not be determined, greasy wool production figures will be used in all subsequent results. Clean wool growth will be discussed in the text.

No significant effect of wool sample location on wool growth rate was found. It was then decided to include data on all locations as replicates to increase the power of testing for selection line and diet differences. Wool growth means in Table 4.1 are averaged across location.

Least squares means for initial weight (IWT), liveweight gain (LWG), greasy wool production (GWOOL), DMDIG, daily urine volume (UVOL), TUN, and NDIG by selection line and diet (P2 only), are presented in Tables 4.1 a,b and c for P1, P2 and P3, respectively.

Shoulder greasy wool production, by diet group, in P1, P2 and P3 are shown in Figure 4.1. Shoulder and midside results were similar. Shoulder results were chosen for reporting as the dimensions of the patch, across samplings, remained more constant than midside patches and appeared to be a more discerning measure of wool growth.

4.3.1 Apparent digestive ability

No significant selection line effects on the ability to digest dry matter, or nitrogen, were demonstrated in any of the periods studied. Individual rams within line were a larger source of variation than selection line. This result does not agree with the earlier digestibility trial using rams on ad libitum feeding of cut pasture (McClelland et al., 1986). DMDIG in that trial, could have been affected by failure to account for all variation in DMI, because of the relatively small number of animals per group (8) and the relatively large range in DMI (912 to 1676 g/d). Rams were fed equally in this trial and refused feed was not significantly different between FW and C rams, as expected there were no differences in DMI or digestible dry matter intake between lines.

The results of the current trial agree with the conclusions of Piper and Dolling (1969) and Williams (1979) who found that the ability to digest nutrients had not been altered by selection for fleece weight in Merinos.

Similarly, no differences were found in NDIG, in any of the periods, and there was no significant interaction between selection line and diet during P2. The ability of FW rams to respond to additional dietary supply of amino acids, is therefore not related to the proportion of ingested nutrients absorbed and any significant differences in wool or body growth are likely attributable to differences in feed conversion efficiency

During P2, diets differed significantly ($p<.05$) in the digestability of nitrogen, but not of dry matter.

4.3.2 Live weight and liveweight gain

Large within line variation in liveweight existed. The line differences in initial weight at the beginning of P1, P2 and P3 were not significantly different between lines. To what extent these differences reflect liveweights under grazing conditions is not known. FW hoggets have, historically, been 2 kg heavier than C hoggets at the time of hogget shearing (Blair, 1986). Liveweight differences in small indoor trials are affected by sampling.

Liveweight gain, was not significantly different between FW and C rams in P1 and P2, but the greater liveweight gain of FW hoggets in P3 was highly significant. By the end of P3, FW rams weighed the same as C rams, as they had at the start of the experiment. For unknown reasons, FW rams gained slightly less than C rams during P2 but the difference was not significant.

Comparisons of liveweight gain were limited by the restricted feeding regimen employed in this trial. The primary objective being to evaluate digestive ability, it was decided to opt for equal feeding with few refusals.

In the trial conducted in 1983, (McClelland et al., 1986), FW and C rams displayed a similar relationship between DMI and liveweight gain. Superior growth rates in P3 can only be attributed to improved efficiency of converting feed to gain.

4.3.3 Urine volume

An unexpected result was the increased urine output of FW rams relative to controls. This difference was significant at $p<0.01$ in P1, at $p<0.05$ in P2 and approached significance in P3 ($p<0.10$). Although water intake was not measured, it is assumed that differences in urine output reflect differences in water intake. The nitrogen concentration of FW urine was correspondingly reduced such that the total urinary nitrogen excretion was not significantly different between genotypes.

Genetic differences in water consumption or turnover have been documented in the literature. Dolling and Carpenter (1963) and McFarlane et al., (1966) have both reported higher water intakes in F+ Merinos. McFarlane et al., (1966) suggested that higher water turnover may correlate with the use of water in cellular intermediary metabolism as F+ sheep produced 15% more wool over the same period in his trial. He postulates a relationship with total energy turnover and suggests the possibility of greater renal output of water in F+ sheep.

Subsequent to this current trial, McCutcheon et al., (1987) demonstrated a higher creatinine clearance rate (indicative of greater glomerular filtration rate) in FW compared to C rams. The biological significance of these differences remains unclear.

4.3.4 Wool growth

Mean shoulder results are presented in Figure 4.1. Similar trends were noted for midside samples. Greasy wool growth of FW rams was greater, in all periods. Clean wool growth was significantly different in P2 and P3.

C rams showed no significant response in greasy or clean wool growth the casein supplementation as the regression of P2 wool growth rate on P1 wool growth rate was equal for all dietary levels of casein (slope $=0.900 \pm 0.297$). Amongst FW rams, these regressions were heterogeneous with steeper slopes (0.261 ± 0.222; 0.652 ± 0.292; 2.326 ± 0.327 respectively) as the dietary level of casein increased from 0 to 30 to 60 g/d.

In P1, the relationship of greasy wool growth to DMI/kg$^{0.75}$ was positive in FW rams but near zero in C rams ($p<0.05$). In P2, and P3 similar relationships existed and approached significance at $p=0.06$.

Differences in wool production between sheep or between lines may be due to differences in intake, digestive ability or the the efficiency of conversion of food to wool. This experiment was consistent with the results of Wodzicka-Tomaszewska (1966) in which Romney sheep differed primarily in the efficiency of conversion of feed to wool. In Merino flocks, there have been consistent reports of higher efficiency of conversion of food to wool and only sporadic reports of increased feed intake as a response to selection for fleece weight.

As with Merino selection flocks (Williams, 1979) and within-flock Romney comparisons (Clark et al., 1965), differences in wool production indicated that FW sheep were able to direct a higher proportion of absorbed nutrients towards fleece growth, this difference being greater at higher intakes. Similar partitioning differences have been demonstrated between Romney sheep with high or low winter wool growth (Hawker and Crosbie, 1985). Diverging regressions of wool growth on intake between F+ and C sheep were reported by Hamilton and Langlands (1969) with increased allowances for sheep on pasture.

The responses to casein supplementation were not as large as those reported in Merinos (Reis, 1979). Reis (1979) also suggests that near maximal increases in wool growth rate are obtained at supplementations of 120 g/d. Selection line by diet interactions existed as C rams receiving 30 or 60 g/d of casein did not significantly outperform the 0 g/d controls. FW rams on casein diets increased wool growth relative to 0 g/d controls.

In this study, casein supplementation was tested over winter and several authors have shown that the ability of Romneys to respond to increased nutrition is substantially reduced over winter (Sumner, 1979; Hawker and Crosbie, 1985).

The extent to which inherent differences in the seasonal cycle of wool growth have been confounded with selection line comparisons is not known.

Table 4.1 Least squares means of performance traits of FW and C rams fed lucerne diets.

a. Preliminary period, P1 (1000g/d lucerne presscake)

Variable	C	FW	sig.
IWT (kg)	30.1±0.9	29.3±1.42	ns
LWG (kg)	1.26±.23	1.20±.26	ns
GWOOL (mg/cm^2/d)	1.31±.06	1.50±.09	*
DMDIG (%)	58.4 ±.4	57.5 ±.3	ns
NDIG (%)	66.6 ±.7	65.8 ±.8	ns
UVOL (ml/d)	1355.±96.	2133.±287.	**
TUN (g/d)	7.5±0.1	7.4±0.4	ns

Table 4.1 b. Chopped lucerne (1400g/d), P3

Variable	C	FW	sig.
IWT (kg)	40.6±0.7	38.8±0.9	ns
LWG (kg)	1.42±.41	3.23±.38	***
GWOOL (mg/cm^2/d)	2.02±.14	2.56±.11	**
DMDIG (%)	59.4 ±.3	59.6 ±.4	ns
NDIG (%)	69.1 ±.5	69.9 ±.4	ns
UVOL (ml/d)	1527.±210.	2096.±230.	p<.10
TUN (g/d)	9.5±0.2	9.1±0.4	ns

Table 4.1 c. P2 ± Formaldehyde protected casein

	Variable	C	FW
0 g/d	IWT (kg)	34.6±0.6	32.7±0.9
	LWG (kg)	1.61±.41	0.60±.38
	GWOOL (mg/cm^2/d)	1.62±.47	1.68±.83
	DMDIG (%)	59.5 ±.3	60.8 ±.4
	NDIG (%)	67.2 ±.7	68.1 ±.6
	UVOL (ml/d)	1463.±210.	2567.±230.
	TUN (g/d)	7.0±0.6	8.0±0.7
30 g/d	IWT (kg)	34.2±0.7	34.2±0.7
	LWG (kg)	1.42±.41	1.63±.42
	GWOOL (mg/cm^2/d)	1.91±.76	1.86±.45
	DMDIG (%)	63.4 ±.3	63.3 ±.3
	NDIG (%)	71.9 ±.5	71.0 ±.4
	UVOL (ml/d)	1524.±210.	2138.±230.
	TUN (g/d)	10.2±0.7	9.9±0.4
60 g/d	IWT (kg)	35.1±0.7	33.4±0.9
	LWG (kg)	1.90±.23	3.2.38
	GWOOL (mg/cm^2/d)	1.50±.95	2.37±.42
	DMDIG (%)	63.6±.3	61.9 ±.7
	NDIG (%)	74.1 ±.5	73.5 ±.4
	UVOL (ml/d)	1985.±210.	2004.±230.
	TUN (g/d)	13.4±1.2	11.8±0.6

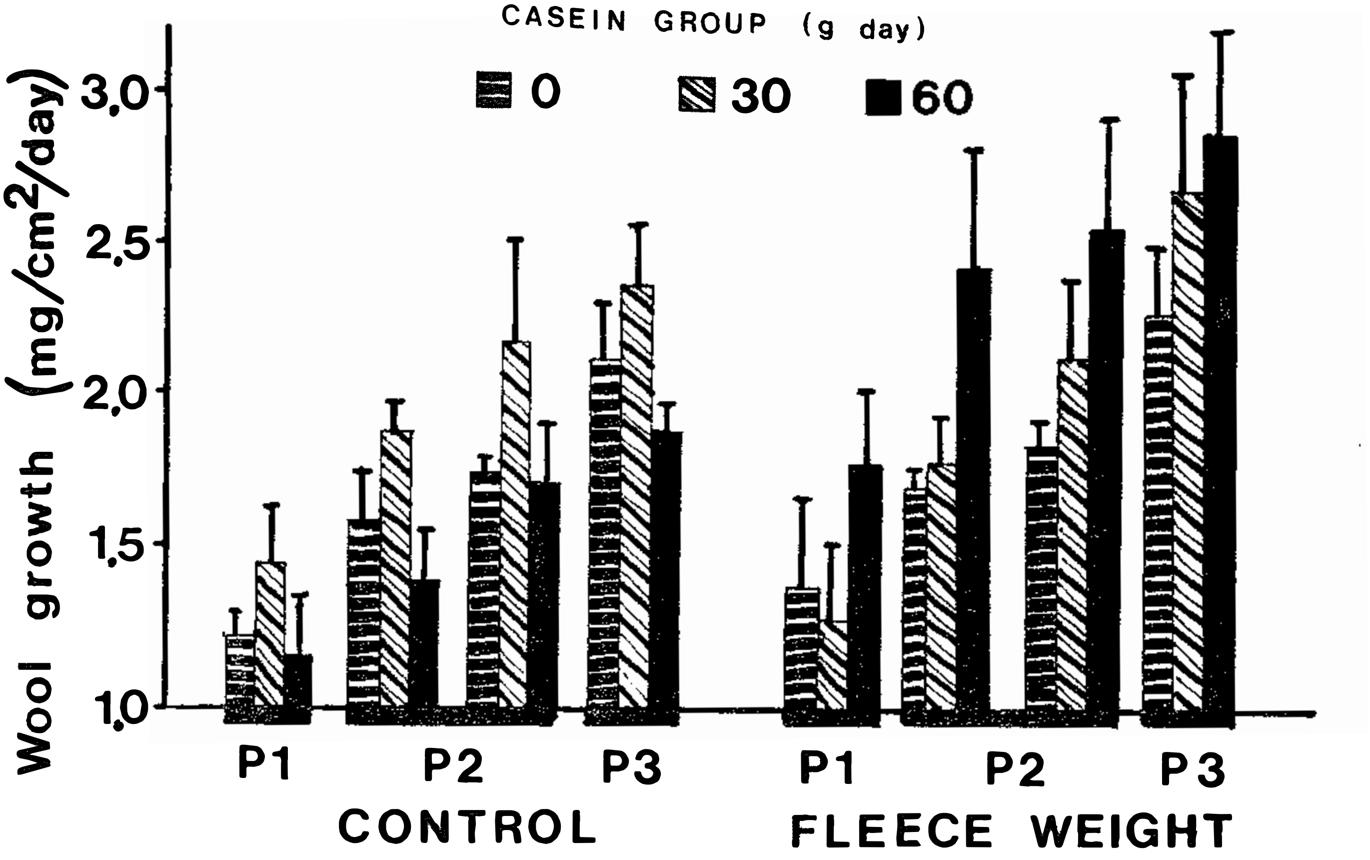

Figure 4.1 Mean shoulder greasy wool growth of fleece weight selected (FW) and control (C) rams during uniform feeding (1kg/d) in P1, casein supplementation in P2, and uniform feeding (1.4kg/d) in P3.(Diet details may be found in the text)

4.4 Conclusions

The results suggest that the advantage of FW over C rams is due, in part, to differences in the ability to direct absorbed nutrients towards wool growth. This difference becomes more evident with higher feeding levels. The C flock advantage in digestive ability reported previously, was not demonstrated in this trial. The possibility that differences in "foraging ability" , selectivity or other adaptive characters may operate under pasture conditions cannot be ignored.

The performance of these animals under pasture conditions needs to be more fully explored especially with reference to patterns of intake, wool growth and live weight gain over their first productive year.

Further investigations into water metabolism of FW and C sheep may also be warranted given consistent differences in daily urine output reported here.

SEASONALITY OF WOOL GROWTH

5.1 Introduction and review of literature

Although it has long been recognized that wool growth is not uniform throughout the year, the various factors which contribute to the observed pattern have yet to be fully unravelled. In the absence of controlled environments it was difficult for early workers to separate the effects of seasonal pasture growth, changing temperature, daylength, pregnancy and lactation and the effect of shearing itself on the observed wool growth patterns.

The annual rhythm of wool growth displayed by most modern breeds of sheep is largely a vestige of the archaic mechanism of fleece shedding. This rhythm of wool/hair growth is now known to be kept in phase with season by photoperiodic control in sheep and in other mammals (such as mink, deer, ferrets, voles and hamsters) which exhibit changes in their pelage and reproductive activity according to the season.

Breeds of sheep, as in strains of other mammals, differ in their response to photoperiodic, nutritional and thermal stimuli. These, and differences in fleece characteristics between animals, contribute to the genetically determined component of the seasonal cycle.

The physiological mechanisms by which photoperiod exerts its control on the rhythm of wool growth are poorly understood. Associated mechanisms involved in the control of reproductive cycles have only recently been elucidated. Evidence in both fields would implicate the pineal gland and its effects, via light/dark controlled secretions, on the action of various endocrine organs and their subsequent effects on wool growth and reproduction.

The seasonal pattern of wool growth is pertinent to the comparison of unselected and fleece weight-selected sheep as it relates to: staple strength; possible seasonal differences in the ability to discriminate between genotypes; the seasonality of reproduction; seasonal patterns of feed intake and body growth and the ability of animals to respond to nutritional factors.

5.1.1 Nutritional and climatic effects

5.1.1.1 Historical

Wodzicka (1960) summarized early German work which established that wool growth was greatest in the summer months after spring shearing. Hence, it was thought that the irregularity of wool growth was a shearing, rather than a seasonal, effect. Other workers (Hardy and Tennyson, 1930; Burns 1931a,b; Duerden and Mare, 1931) had previously confirmed seasonal trends by measuring length growth rate. Seasonal trends in fibre diameter were also observed (Hardy and Tennyson, 1930). In these studies, nutrition was largely uncontrolled. Galpin (1948) reported substantial seasonal differences in midside patch production in Romney sheep but did not report feeding levels.

Wilson (1931) and Bell et al. (1936) recognized the correlation between wool growth rate and feed availability. Ewes were also observed to have reduced wool growth during lactation (Bell et al., 1936). In Mediterranean environments, where feed was often superior in winter months, the rhythm of wool growth was not shown (Frazer, 1931).

Canadian workers thought that the bitter cold of the Canadian winter might be the cause of low winter production (Bowstead and Larose, 1938; Larose and Tweedie, 1938;

Sackville and Bowstead, 1938). They kept Rambouillet ewes in heated and unheated pens for up to 3 months but were unable to alter winter production. As the feeding levels were not stated, it is difficult to draw direct conclusions about the effects of temperature (varying as much as 29°C between pens) from this work.

5.1.1.2 Shearing Responses

Although early researchers thought that shearing had a direct effect on wool growth, it has since been demonstrated that the shearing response is mediated through a change in intake following shearing. Early observations by Carter (1944, unpublished data) showed that appetite increased markedly after shearing and declined steadily until the next shearing when shearing. In other studies (Daly and Carter, 1955; Schinckel, 1960; Wodzicka, 1960; Wheeler, Reardon and Lambourne, 1963; Weston, 1970; Bottomley, 1979) the increase in intake post-shearing has been well documented.

Wodzicka-Tomasewska (1960) was unable to show greater annual wool growth in frequently shorn sheep but McGuirk et al. (1966) and Bigham (1974) demonstrated that annual wool production increased as shearing frequency increased. Bottomley (1979) reviewed the factors affecting the extent of this post-shearing rise in intake. Wheeler et al. (1977) compared wool growth in covered and uncovered sheep and showed that a thermo-regulatory response, rather than a response to shearing per se. was responsible for increased wool growth after shearing.

5.1.1.3 Nutrition

Since the first observations in the 1930's, numerous authors have tied the variability in seasonal wool growth to seasonal variation in pasture availability (Marston, 1948;

Schinckel, 1956; Hutchinson and Porter, 1958; Roe et al., 1959; Stewart et al. 1961; Sharkey et al., 1962; Williams and Schinckel, 1962; Arnold et al., 1964; McFarlane, 1965; Reis and Williams, 1965). However, Wheeler et al. (1963) were unable to demonstrate a clear relationship between pasture availability and digestible organic matter intake in the Merinos they studied. Notwithstanding this result, it seems that the wool growth rhythm displayed by Merinos is more sensitive to nutrition than the rhythms of other breeds in which altered annual intake patterns do not remove or reverse the normal pattern of wool growth (Coop, 1953; Wildman, 1957; Story and Ross, 1960; Doney and Smith, 1961a; Slee and Carter, 1961; Bennett et al., 1962a,b; Williams, 1964; Hutchinson 1965; Ross 1965; Doney 1966; Doney and Eadie 1967; Doney and Evans, 1968; 1970).

Ryder (1956) concluded that the stimulus for fibre shedding is seasonal rather than nutritional in Masham sheep although Lyne (1964)was able to increase shedding in Merinos fed a poor diet. Slee (1965) showed that although poor nutrition could impede shedding in Wiltshire Horns, adequate nutrition merely allowed shedding to proceed under the influence of other factors.

Arnold et al. (1964) and Sumner and Wickham (1969) found that higher stocking rates accentuated the rhythm of wool growth through a greater and prolonged winter depression.

Pregnancy and lactation, through their high nutritive demands and drains on body reserves, also reduce winter wool growth further and postpone the rise in spring (Coop, 1953; Slen and Whiting, 1956; Story and Ross, 1960; Stewart et al., 1961; Ross, 1965; Hawker and Kennedy, 1978b). The effect is greater in ewes bearing more than one offspring (Slen and Whiting, 1956; Ross, 1965)

That the annual rhythm of wool growth in many breeds is not removed by constant feeding, or feeding to equal body weight, indicates its control by non-nutritional factors. Nutrition modifies the inherent pattern established by other environmental and physiological factors.

5.1.1.4 Temperature

Ferguson et al. (1949) studied the wool growth rate of Camden Park Merinos and Corriedales given a constant intake of a uniform diet and found a positive association between environmental air temperature and fibre length growth rate. They suggested that vasodilation caused increased blood flow to the skin which increased wool growth in warmer temperatures. Ferguson (1949) in an extension of this idea, performed unilateral thoracic sympathectomies on sheep to destroy the vasoconstriction response. Increased wool growth on the operated side was elicited for up to 10 weeks.

Coop (1953) and Coop and Hart (1953), also using ewes on controlled feeding, found that seasonal changes in length and diameter were not affected by keeping ewes in a room 13°F above outside temperature during winter. They did note the correlation between outside temperature and daylength as a possible force behind seasonal variation in wool growth.

Wodzicka (1960) supported the result of Ferguson et al. (1949) in the absence of a demonstrative effect of photoperiod in her experiment. Morris (1961) reversed the annual temperature cycle and found no effect on the wool growth cycle in Romney Marsh sheep. Bennett et al. (1962 a,b), using Southdowns and Merinos, found no obvious effects of temperature on wool growth, providing that the sheep had adequate wool cover.

Although wool growth is not under the control of temperature, some local effects of temperature, as evidenced on frequently clipped patches, may exist.

Differing wool growth on clipped patches exposed to natural or induced cold conditions (Bennett et al., 1962; Wodzicka-Tomasewska, 1966; Doney and Griffiths, 1967; Wodzicka-Tomasewska and Bigham, 1968; Downes and Hutchinson, 1969; Lyne et al., 1970) were due to a short term reduction in length growth rate while fibre diameter was largely unaffected. In most of these studies the surrounding pile was kept short offering minimal protection to the clipped patch. Sharkey et al. (1962) offered no explanation as to why the average diameter of clipped samples was 2 microns greater than adjacent long staples in Corriedales. Rudall (1933) noted increase hairness after shearing in Romney lambs which appeared to be linked to local temperature effects.

Coop (1953) found no difference between adjacent patches clipped either every month or every 3 months. Downes and Lyne (1961), using radiographic techniques, showed that clipping per se. had no effect once temperature effects were minimized. Other researchers have found no effect of frequent clipping on wool growth (Doney and Smith, 1961a; Bigham 1974) or in blood flow to the skin (Setchell and Waites, 1965). Bigham does not comment on the contradiction of his (1974) results with those of an earlier study (Wodzicka-Tomasewska and Bigham 1968). The earlier study was done indoors under constant feeding, whereas the later work was done outdoors under free grazing conditions. Under ad libitum feeding, sheep are able to maintain thermoneutrality by increasing intake after shearing. Locomotion also helps to maintain deep body and peripheral tissue temperature.

5.1.1.5 Photoperiod

Early work established that daylength regulated seasonal shedding and coat changes in the ferret (Bisonette 1935) and other mammals such as the silver fox, mink, weasel and horse (Bisonette and Wilson 1939, Bassett et al. 1944, Bisonette and Bailey 1944, Burkhardt 1947, Hammond 1951,1952 1953). Yeates (1954 a,b) reviewed much of this early work and in later experiments (Yeates 1955,1957) showed that moulting cycles in cattle were associated with daylength.

In sheep, as mentioned previously, Coop and Hart cooperated on one of the first wool growth and photoperiod experiments. A number of reports were published (Hart 1953; Coop 1953; Coop and Hart 1953) showing that wet Corriedale ewes exposed to 8 hours of light (L):16 hours of dark (D) grew more wool in winter and spring than ewes under natural light on a similar diet. The rhythm of wool growth in the constant daylength group persisted for over 2 years. Assuming that the eye was the receptive organ, Hart (1955) hooded sheep for a period of two years. The animals were still subjected to the annual temperature rhythm but the rhythm of wool growth dissappeared after 1.5 years.

Wildman (1957) subjected rams and wethers to an 8L:16D constant regime for about 2 years and found increased production in all seasons, which is in contrast to previous and subsequent work by others. Morris (1961) was able to reverse the annual cycle of wool growth by accentuating and reversing daylength. The amplitude of seasonal wool growth was increased in the accentuated cycle. The fact that 2 years were required to reverse the rhythm was used to explain the failure of Wodzicka (1960) to alter wool growth during 12 months of constant daylength.

In an extension of his earlier work, Hart (1961) included dry ewes in the 8L:16D group, hooded ewes, ewes under continuous light and ewes on a 2L:4D cycle. Continuous light, supplied by artificial lighting, had no effect on the wool growth rhythm, suggesting that sheep could distinquish between light of varying intensity. Failure to provide adequate intensity of light may also have caused misleading results in other studies. The latent period of response to other treatments was 3-5 months and ewes on the 2L:4D schedule responded quicker than those on 8L:16D, even though both groups received equal daily hours of light and dark. Hart (1961) suggested that the thyroid gland may be involved in the regulation of wool growth. Other workers (Bennett et al. 1962 a,b; Hart et al. 1963; Williams 1964, Hutchinson 1965) confirmed the response of wool growth to photoperiodic changes. Differences in light intensity were believed to affect the shape of the attained curve and the immediacy of its establishment.

Rougeot (1957,1961) showed that the shedding and growth cycles of the kemp follicles of Limousine sheep could be readily controlled by daylength. Reviews of photoperiodic effects on wool growth and shedding are given by Hutchinson (1965;1976), Ryder and Stephenson (1968), Nagorcka (1979) and Panaretto (1979).

More recently, Ryder and Lincoln (1976) studied the effect of alternating periods of short (8L:16D) and long (16L:8D) days on fleece growth and shedding in Soay sheep. Delays in response were 2-3 months after changing daylength. Eight to 12 weeks of long days was sufficient to activate follicles in all animals, whereas 4 weeks exposure to short days was enough to reduce follicular activity. Lincoln et al. (1980) found both wool and horn growth in this breed to be under photoperiodic control. Kay and Ryder (1978) were able to elicit a twice annual shedding and regrowth of hair in Red deer exposed to a six month cycle of day length. Shortening of the cycle was wholly brought about by reducing the retention time of the mature coat.

It has been well demonstrated, both in sheep and in other mammals that photoperiod is the central regulator of wool and hair growth. The responses to a change in photoperiod are not immediate and genetic differences between animals can alter the expressivity of the wool growth rhythm. the interpretation of light rhythms and their effects on the endocrine system are discussed in Sections 5.3 and 5.4. The effect of individual hormones on wool growth is discussed later.

5.1.2 Hair and wool growth cycles

5.1.2.1 Shedding

Several forms of hair growth cycle exist. Many fur bearing animals and ungulates such as deer, cattle and primitive sheep undergo a complete moult either once a year (in spring) or twice a year (in spring and autumn). Ryder and Stephenson (1968) have discussed these moulting cycles in some detail. Although most breeds of sheep do not have a definite moult, many sheep do show appreciable shedding, either of wool or kemp fibres.

In domestic breeds, the proportion of fibres undergoing replacement is lower and spread over a longer time than in wild sheep and so no definite moult is apparent. Differences in shedding between breeds is partially due to differing proportions of the main fibre types. Seasonal changes in the rate of wool growth represent a less dramatic manifestation of ancient shedding cycles (Hutchinson and Wodzicka -Tomasewska 1962, Hutchinson 1965,1976; Ryder and Stephenson 1968). Margolena (1960) related reduced winter wool growth to a reduction in the rate of cell division in the follicle bulb.

5.1.2.2 Natural adaption

Johnson (1984), among others, has reviewed the adaptive nature of seasonal coat changes in mammals. In wild animals, the most dramatic seasonal changes in pelage involve a change of colour which aids in both temperature regulation and protective camouflage. Whether or not a colour change occurs, seasonal moulting produces coats of varying density and structure which are adapted to the environment. Domestication tends to disengage the seasonal, hormonal and moult cycles. In the extreme case of laboratory rodents there is no seasonal moult and no seasonal changes in the endocrine system although hair growth can still be influenced by hormones.

In breeds of sheep which undergo annual shedding of the entire fleece such as the Mouflon (Ryder 1960), the Wiltshire Horn (Slee 1963,1965; Ryder 1969,1973), the Shetland (Ryder and Stephenson (1968) and the Soay (Boyd et al.1964, Ryder and Stephenson 1968; Ryder 1971; Ryder and Lincoln 1976), the moult progresses in such a way as to never leave the animal without protective covering.

Previously domesticated populations of sheep which become feral differ from their parent stocks in many aspects of wool production. Fleece weights, follicle density and secondary:primary (S:P) ratio and staple length are reduced in feral populations. To a lesser extent, self-shedding is also often re-established (Rudge, 1984; Bigham and Cockrem, 1984).

The adaptive advantage of fleece shedding in spring could be related to thermal regulation or to the advantages of not carrying an ever-increasing amount of wool which would absorb large amounts of water, reduce freedom of movement and be a risk to skin health and be a physical barrier to breeding. Hutchinson and Wodzicka-Tomasewska (1961) have reviewed the functioning of the fleece in thermal regulation.

5.1.2.3 Breed formation

Ryder and Stephenson (1968) and Ryder (1984) discussed the evolution and domestication of sheep with reference to genetic variation in hair and wool growth cycles. Evolution in sheep, which has been engineered by man through selective breeding, has changed only the part of the sheep's coat which is valuable to him; whereas, the rest often continues with shedding cycles. The relative emphasis placed on meat, wool and climatic adaptation during breed formation, and subsequent selection, has also altered the responsiveness of sheep to climatic and environmental stimuli and the proportion of primary and secondary follicles in the skin.

Ryder (1960) studied the seasonal changes in the coat of wild Mouflon sheep from whom most domestic sheep are thought to have been derived. Although the entire fleece was shed in spring only 40-60% of the secondary fibres showed brush ends at this time. This indicated that the underwool of wild sheep already showed a tendency towards a growth phase longer than one year. The outer kemps (corresponding to primaries) formed brush ends in the autumn which were shed the following spring as follicular activity resumed. Similar patterns occur in British breeds which shed their fleece. Domestication per se has not always altered this ancient cycle, as shedding relieves the need to shear sheep and fine underwool can easily be harvested by hand in early spring, before primary fibres are shed (Ryder and Stephenson 1968).

The extent of fibre shedding in a variety of British breeds has been reviewed by Ryder (1957,1958) and Ryder and Stephenson (1968). In hill breeds such as the Scottish Blackface and the Herdwick, shedding of both primary and secondary fibres reached as high as 60% in late winter. Down breeds such as the Suffolk and Shropshire also had relatively high (30-84%) proportions of shed fibres. Less shedding seems to occur amongst Longwool breeds, but evidence is limited. In Merinos, fibre shedding is extremely rare (1%) (Ryder, 1962) indicating a growth cycle of about 8 years.

5.1.2.4 Breed differences in seasonality of wool growth

From the above evidence, it would appear that where characteristics other than wool have been favoured in breed formation there is a greater persistence of shedding. Breeds that shed the most also show the greatest seasonal variation in wool growth. Nagorcka (1979) summarized seasonal variation in wool growth displayed by a number of breeds in various locations where the amount of food, or liveweight, had remained constant throughout the year. The unit of comparison was amplitude, defined by Hutchinson and Wodzicka-Tomasewska (1961) as (H-L)/((H+L)/2) where H and L are the highest and lowest rates of wool growth, respectively.

Although the Merino and the Rambouillet show minimal shedding of fleece wool, leg kemps do go through a shedding cycle (Bennett et al., 1962a,b). For this reason, Hutchinson (1965) suggested that the two cycles may be under separate control.

The existence of seasonal patterns of clean wool growth in the absence of nutritional or temperature effects have been demonstrated in previous sections. This variation is due to concomitant changes in length and diameter, although minimum and maximum times for length often precede those of fibre diameter (Story and Ross, 1960). Seasonal changes also occur in the production of associated skin secretions and in the sulphur (S) content of wool. In so much as S-content and wax and suint production are under genetic control, breed cycles in chemical composition of the greasy fleece may reflect different responses to seasonal environments.

5.1.2.5 Associated secretions

Both primary and secondary follicles have associated sebaceous glands that produce wool wax or grease; however, sudiferous glands, which produce suint, are only associated with primary follicles. Daly and Carter (1955) observed in four breeds, that wax and suint production increased with intake. Furthermore, wax output decreased as temperature rose and suint output increased as the fleece grew.

Story and Ross (1960) found that wax and suint content of monthly clipped samples from grazing Romneys followed a similar, although less marked, pattern to wool growth. This difference in amplitude reduces the clean yield of winter grown wool relative to that grown in summer. These trends may be difficult to detect in field studies under high rainfall conditions. Hutchinson (1962) compared wax and suint production between grazing and constant diet pen-fed Merinos. In both groups the production of wax and suint followed that of wool growth, although suint production did so to a lesser extent than wax. The production of suint was possibly affected more by temperature than wax production.

5.1.2.6 Sulphur content of wool

Early work on the sulphur content of wool has been reviewed by Ross (1961c) and Reis (1965). As early as 1926, the sulphur content of various samples of clean, dry wool was found to vary between 3 - 4.1% (Barritt and King 1926,1929). Changes in sulphur content along the staple were related to the availability and quality of pasture and minimal changes were displayed by sheep on a constant diet (Bonsma, 1931). Other workers (Marston, 1928; Fletcher et al., 1963) found little or no seasonal change in sulphur content of wool. Copper deficiency was also related to a reduction in the sulphur content.

Later, Ross (1961c) found a seasonal rhythm in wool sulphur content in four-monthly samples from grazing Romneys that inversely followed the seasonal wool production. In another study,(Ross, 1964) the sulphur content was frequently, but not invariably, inversely related to wool growth. Ross (1964) concluded that pronounced individual differences in sulphur content existed and that the availability of sulphur was probably not a factor limiting production.

Reis and Schinckel (1961a,1964) showed that wool growth and the sulphur content of wool were increased with additional abomasal supplies of sulphur-containing amino acids. Reis (1965) confirmed this relationship. Reis and Williams (1965), also using Merinos, showed that the positive relationship between wool growth and wool sulphur content in grazing sheep was related to nutritional, not climatic, cycles. They also suggested that the sulphur content of wool may have an intrinsic minimum, such that dietary deficiencies could reduce wool growth further, without reducing sulphur content beyond this minimum. Sumner (1979) found a positive association between wool growth, fibre diameter, and sulphur content in a variety of breeds maintained indoors in longterm studies.

Others have compared the seasonal cycle of sulphur content in various breeds subjected to altered nutritional regimes (Reis and Williams, 1965; Piper and Dolling,1966; Doney and Evans,1968,1970). These studies will be reviewed in the following section.

5.1.3 Genetic differences in response to seasonal and nutritional cycles.

5.1.3.1 Photoperiodic sensitivity

Photoperiodic sensitivity plays a substantial role in producing wool growth patterns characteristic of each breed. The reduced dependence of the Merino cycle has been demonstrated earlier and is perhaps a product of its mediterranean origins and adaptation (natural or directed) to seasonal migration and autumn lambing (Ryder and Stephenson 1968). Although other equatorial breeds share the Merino's ability to breed year-round, little is known of the wool growth cycle in these breeds.

The northern exception to strongly photoperiodic reproduction is the Dorset Horn. No published estimates of its seasonal wool growth pattern were found. The development of an extended breeding season, renowned as early as the 1700's (Ryder and Stephenson 1968) is curious given its supposed close ancestry to the Soay.

Evidence from northern and southern strains of white-footed mice (Connecticut and Georgia) showed that melatonin, a pineal indol-amine involved in photoperiodic regulation, had little effect on moulting or reproductive patterns in the southern mice, but was capable of inducing moult to winter pelage and loss of reproductive competence in the northern mice (Heath and Lynch 1982). It is possible that similar intra-specific differences in the sensitivity of the endocrine system to melatonin occur within or between breeds of sheep, but experiments to this end have not been reported. Genetic differences in the seasonal response of wool growth to environmental effects seem to be related to these differences in photoperiodic sensitivity, although the precise mechanisms are unclear.

5.1.3.2 Breed by season interactions in response to nutritional effects

Wool growth

The interpretation of annual rhythms of wool growth in different breeds and different environments is made difficult by the inability to separate possible seasonal interactions between breeds and nutritional and seasonal effects. Breed comparisons on sequential nutritional regimes can include interactions with season.

When Daly and Carter (1955) imposed progressively restrictive intakes on Merino, Polwarth, Corriedale and Lincoln ewes they observed (in descending order of magnitude) a reduction in clean wool growth. In this experiment, generous feeding was provided in the Australian winter (July) and full restriction was complete by summer (December). From other studies, it is likely that the Lincoln sheep were being relatively more held back (in July) by non-nutritional factors and thus, were less affected overall, by the reduction in nutrition from winter to summer.

Doney (1966) addressed this topic directly by offering Cheviots and 3/4 Merinos either level, natural or reversed annual intake cycles. In Merinos, the between sheep variation in intake was reflected by differences in wool growth in all periods, but in Cheviot sheep intake and wool growth were related in summer but not in winter. The effect of additional nutrition in winter on wool growth has been shown to be minimal in Scottish Blackface sheep (Doney 1964) and in the Soay (Doney, unpublished). His results suggested that the genetic differences in metabolic responses to "unspecified seasonal factors" might be removed by intensive selection for increased wool growth. In a later study, Doney and Evans (1970) fed Romney and Blackface ewes to achieve different patterns of live-weight change from mating to parturition and achieved a wool growth response in Romneys, but not in the Blackface sheep.

Although breed responses to nutrition have been shown to vary in the winter, Doney and Eadie (1967) and Bigham et al. (1978a,b) have shown that wool growth over the summer period varied most, both within and between breeds on pasture. Also, summer nutrition had a greater influence on total fleece production than performance in winter. Bigham et al. (1978) concurred with Sumner (1977,1979) that breed comparisons in short term studies may depend greatly on the time of the year during which the studies are conducted.

In-depth comparisons of seasonal wool growth in selection lines have not been reported. Using sheep with previously high or low fleece weight (6 sheep each) on two pasture types, Reis and Williams (1965) showed greater seasonal variation in clean wool growth in phenotypically high than low producing sheep, the absolute difference being greater in periods of high rather than low production.

Hawker et al. (1985), on the basis of four samples per year, could not detect a difference in the annual pattern of wool growth between control and high hogget greasy fleece weight selection lines, as the entire curve seemed to be lifted in the selection line. Hawker and Crosbie (1985), separated Romney and Perendale ewes which had either high (W+) or low (W-) winter wool growth, and fed them at either high or low levels in the following summer and winter. There were marked wool growth differences in winter between W+ and W- ewes. Wool growth differences did not exist in the summer. The W+ ewes also responded to high levels of winter feeding while W- ewes did not. Thus, phenotypic separation, on the basis of winter wool growth, was successful in identifying sheep with different seasonal responses to nutrition and repeatable differences in winter wool production.

Sulphur content

The first evidence that the sulphur content of wool may be under genetic control was found by Gillespie (1965) in the examination of mutant and normal wool fibres produced by fleece mosaicism, a somatic mutation thought to occur in early embryonic development (Lang 1952, Fraser and Short

1958). Mutant (long) fibres had higher percentages of sulphur overall, characterized by a lower proportion of high sulphur proteins and a higher proportion of medium sulphur proteins than the normal shorter wool fibres. Gillespie (1965) also found that lustre mutant Merinos (Short 1958) incorporated more high sulphur proteins into wool fibres than normal sibs on similar diets. This difference was thought to be due to a larger proportion of para cortex in these lustrous fibres, the para cortex being the segment in normal Merino wool thought to be richest in high sulphur proteins.

Reis and Williams (1965), comparing their results on the seasonality of wool sulphur content with those of Ross (1961,1964), concluded that differences between the results may be due to the more sensitive seasonality of wool growth in Romneys compared to Merinos ie. effects other than low dietary sulphur content depressed wool growth in Romney sheep. Reis and Williams (1965) also found that high producing sheep had higher feed efficiencies and lower sulphur content in the wool. The high producers had greater seasonal variation in sulphur content, possibly due to a higher level of sulphur substrates being available to low producers. During times of nutritional stress, the sulphur content from high producers fell the most, as high producers maintained greater wool growth under these conditions.

Piper and Dolling (1966) compared high and low fleece weight selection lines grazed together on low quality pastures. The correlation between sulphur content and wool growth was (-.69 and +.28) within low and high selection lines, respectively. The low line also had larger variation in sulphur content and as sulphur was likely not limiting their wool growth they displayed the normal wool growth-sulphur content relationship. In contrast, the high fleece weight line was likely near its minimum level of wool sulphur content. These results suggested differences in the efficiency of utilization of sulphur at the follicular level. Gillespie (1965) in a review of much of his own work, showed that high producers had lower overall wool sulphur content characterized by lower proportions of high sulphur proteins in the fibre matrix.

Doney and Evans (1968;1970) compared Merino with Cheviot sheep and Scottish Blackface with Romney sheep for their wool growth and wool sulphur content under various nutritional planes over winter. Significant breed differences in the wool growth-sulphur content relationship were reported which supported the conclusions of Reis and Williams (1965). In all reported studies, large within group differences in sulphur content existed and were, in many cases, greater than the differences between groups.

5.1.4 Hormonal effects

Reviews of the hormonal regulation of wool growth have been prepared by Downes and Wallace (1965), Ferguson, Wallace and Lindler (1965), Ryder and Stephenson (1968) and Wallace (1979). Ebling and Hale (1983) have also reviewed this topic but with emphasis on species differences and human hair growth.

Ferguson (1958) distinguished between three types of hormone action. First, hormones may have a permissive role, where secretions are necessary for wool growth to take place but variation in secretion is without effect. Secondly, there is a regulatory role where variation in secretion rate controls the level of wool production and probably shedding. Thirdly, some hormones are capable of eliciting a pharmacological effect and can promote wool growth if administered artificially in amounts greater than those in normal secretion. In early studies the effects of gland removal and subsequent replacement therapy yielded much knowledge but was hampered by heterogeneous hormone preparations and the difficulty of measuring specific hormone concentrations in plasma.

5.1.4.1 Pituitary and associated target gland hormones

The pituitary is the central gland of the endocrine system. Some of the pituitary hormones act by stimulating other endocrine glands. For this reason, the target tissues and their secretions will be discussed along with their controlling pituitary hormones.

Ferguson (1951) described a technique for hypophysectomy in the sheep and found that wool growth was reduced to very low levels following this procedure. In most cases wool growth ceased completely after 4-26 weeks (Ferguson et al. 1965; Girard 1969) indicating that at least one of the pituitary hormones must be present for wool growth to occur.

Thyroid stimulating hormone (TSH) and thyroid hormones

The thyroid gland reacts to the pituitary hormone TSH by releasing Thyroxine (T4) and Triodothyronine (T3). T3 is more biologically active than T4 and T4 is altered to T3 by body tissues (Fisher et al. 1972). In hypophysectomized sheep, daily subcutaneous administration of T4 can restore wool growth to pre-operative levels, but cannot raise it above this (Ferguson et al. 1965). The wool growth of thyroxine-maintained hypophysectomized sheep still varies between individuals, being proportional to pre-operative levels; therefore, this variation must be due to differences in the structure or density of follicles in the skin or other systemic factors.

Thyroidectomy reduces wool growth to approximately 60% of pre-operative levels, due entirely to a reduction in fibre length growth rate (Simpson, 1924; Marston and Pierce, 1932; Ferguson, 1951; Theriez and Rougeot, 1962). In contrast to hypophysectomized sheep, wool growth in thyroidectomized sheep can be raised above pre-operative rates by increasing the dose of T4 (Ferguson et al. 1965), suggesting that some other pituitary hormone is necessary for thyroid hormones to express their full physiological activity. Downes and Wallace (1965) demonstrated a direct effect of thyroxine on wool growth, suggesting that thyroxine can increase the output of wool follicles appart from systemic effects such as changes in appetite or general metabolism. Not all attempts to modify thyroxine levels have resulted in changes in the activity of the wool follicle (Ryder 1973,1979).

Coop and Clark (1958) showed seasonal effects on thyroxine response with effects being shown in midsummer to autumn, but not in midwinter or early summer. Hart (1961) found differences in the thyroid glands of various light treatment groups, but as the gland weights and wool growth were not always positively related he concluded that there must be a latency of response. Wallace (1979) concluded that thyroid hormones were not involved in the seasonality of wool growth while Ryder (1979) and Lincoln et al. (1980) found a strong positive correlation between wool growth and circulating levels of thyroxine. Rougeot et al. (1984) quote associations between thyroxine and moulting periods in the mink and in the harbour seal. Khateeb and Johnson (1971) concluded from work with voles that the seasonal regulation of hair activity is due to the interaction of thyroxine with other hormones such as adrenal and gonadal steroids.

These results suggest that thyroxine exhibits permissive, regulatory and pharmacological effects on wool growth. Photoperiodic control of thyroid hormones will be discussed in subsequent sections.

Adrenocorticotrophic hormone (ACTH) and Cortisol

ACTH exerts its physiological action by increasing the secretion of steriods from the adrenal gland. One class of these steroids, the glucocorticoids, may stimulate wool growth when present in very small amounts (Downes and Wallace 1965; Chapman and Bassett 1970) and when given in the whole animal (rather than locally to the dermis) may depend on the ability to increase feed intake. At higher levels, corticosteroids inhibit follicular activity resulting in decreased fibre diameter and length growth rate and increased shedding (Lindler and Ferguson 1956; Ferguson et al. 1965; Panaretto et al. 1975). Increased adreno-cortical activity in times of physical or psychological stress can be sometimes responsible for "break" or "tenderness" in the fleece. Panaretto and Wallace (1978a,b) investigated the use of powerful synthetic analogues of corticosteroids for chemical defleecing but their results were not sufficiently predictable for commercial use.

Ebling and Hale (1983) commented that the ability of corticosteroids to affect follicular activity was surprising in light of Ward and Kasmarik's (1979) result that wool roots were unable to metabolize cortisol as they lack 11B-hydroxysteroid dehydrogenase which is present in other parts of the skin. The 17B form is, however, ubiquitous. Wallace (1979) quoted his own unpublished work showing that cortisol depresses the uptake of cysteine into wool fibres.

Lindler and Ferguson (1956) suggested that adrenocortical activity may be responsible for the decreased wool growth in winter but adrenalectomised ewes on constant replacement therapy still exhibited some seasonality of wool growth. Riviere et al. (1977) attributed the moulting period in harbour seals to fluctuations in the balance of cortisol and thyroxine, with thyroxine increasing from June to July (the moulting period) and cortisol decreasing over this period. Ferguson et al. (1965) also showed that cortisol influenced the wool growth response to thyroxine whereas cortisol at higher circulating levels prevented any response to thyroxine.

Growth Hormone

Growth hormone is not thought to act through a secondary organ, but it does stimulate the secretion of one or more polypeptides, known as somatomedins, primarily from the liver but also from most other tissues examined. Growth hormone cannot initiate wool growth in hypophysectomised sheep maintained on T4 (Ferguson et al.1965). In normal sheep growth hormone was able to stimulate wool growth after the growth hormone injections ceased (Ferguson, 1951;1954; Ferguson et al., 1965; Wheatley et al., 1966; Reklewska, 1974; Wynn et al., 1979). These changes occured primarily through an increase in fibre diameter. Contrary to the results of Labban (1957), growth hormone did not change the number of follicles in any of the above studies. Many studies showed a depression in wool growth during the period of hormone injections. Wynn et al., (1979) attributed this to an increase in tissue protein retention during treatment followed by protein mobilization after growth hormone injections ceased.

Intradermal injections of growth hormone (Downes and Wallace 1965) did not alter wool growth rate, therefore, growth hormone is unlikely to have a direct effect on the follicle. It also seems unlikely that growth hormone is involved in the seasonality of wool growth (Wallace 1979).

Prolactin

Wallace (1979) concluded that prolactin was unlikely to be involved in wool growth. The injection of prolactin into normal or hypophysectomised sheep (Ferguson et al. 1965) did not affect wool growth. Very low and very high intradermal injections of prolactin increased length growth rate of wool fibres, while intermediate levels resulted in a decrease (Downes and Wallace, 1965). Prolactin cycles in the field are positively associated with the annual temperature cycle, and with the wool growth cycle but Smith et al. (1977) were more willing to accept the former, rather than latter, as the direct association.

Rougeot et al. (1984) considered prolactin to be involved in the wool growth cycle. In mink and in sheep, spring moult coincided with a seasonal increase in plasma prolactin (Martinet et al., 1982; Ravault, 1976) and autumn moult in mink is associated with low or decreasing levels of prolactin. In experimental conditions, mink kept under 16L:8D from summer solstice underwent a moult but to another summer coat. Under similar conditions, but with daily injections of ergocriptin (a prolactin inhibitor) a normal autumn moult occurred. Under 8L:16D prolactin was unable to elicit a spring, rather than autumn, moult.

Gonadotrophic hormones

The gonadotrophins stimulate the ovaries and testes to secrete physiologically active steroids. Very little work has been done on the effects of sex hormones on wool growth in sheep. Gonadal and wool growth cycles are both influenced by photoperiod, but no evidence suggests that sex hormones directly affect wool growth other than through a response in feed intake.

Ferguson (1951) found no effect of orchidectomy on wool growth or from testosterone implants in sheep fed a constant ration. Slen and Connell (1958) found no effects due to the administration of testosterone or progesterone. Although Slen and Connell found oestradiol to reduce length growth rate, it is difficult to separate direct effects and those mediated through accompanying changes in the pituitary and adrenal glands. Draper et al.(1966) found that oestradiol reduced wool growth only when feed was restricted.

Ferguson et al. (1965) concluded that oestrogens, androgens and progesterone, at physiological concentrations, are unlikely to affect wool growth.

Other pituitary hormones

There is no evidence that oxytocin or vasopressin, secreted by the posterior lobe of the pituitary, affect wool growth (Wallace 1979). Ferguson et al. (1965) showed evidence that a pituitary fraction, devoid of other pituitary hormone action was able to stimulate wool growth in the hypophysectomized sheep.

5.1.4.2 Catecholamines

Catecholamines such as adrenaline and noradrenaline are secreted in response to neural stimulation. Ferguson (1949), showed that wool growth increased after sympathectomy in sheep. Blood flow to the skin increased due to vasodilation, after the vasoconstricting effects of noradrenaline from the nerve endings ceased. Adrenalectomy does not affect wool growth (Ferguson et al. 1965) but the amount of noradrenaline secreted at the sympathetic nerve ending could control wool growth through vasoconstriction of the skin's blood vessels (Wallace 1979). Other unpublished evidence, cited by Wallace (1979), indicated that intradermal injections of adrenaline or noradrenaline depress the rate of uptake of L^{35}S-cystine into wool fibres plucked from around injection sites. The results suggested that its effect was via a temporary reduction in blood flow.

5.1.5 Role of the pineal gland in wool growth cycles

Many of the reviews on hormones and wool growth have ignored the pineal gland, although pinealectomy has been used in studies with sheep since the late 1960's. Existence of the pineal gland has been recognized for centuries but serious endocrinological work with this gland began only in the 1950's. Pineal research, though far from complete, has begun to elucidate the mechanisms of photoperiodic control of endocrine systems and their relationship to cycles of wool/hair growth and reproduction.

5.1.5.1 The discovery of pineal function

Prior to 1954, the two commonly known facts about the pineal gland were that it tends to calcify, and thus can be used as a landmark in brain X-rays, and that Descartes had bestowed on it the honour of being the seat of man's soul. Otherwise it was generally believed to be a functionless, evolutionary vestige. Brainard (1978) reviewed pineal research in what he refers to as "the decade of transformation" from 1954 to 1965.

Interest in the pineal gland increased after the publication of an extensive review (Kitay and Altschule 1954) which summarized more than 1800 references. They concluded that the pineal was involved in gonadal function, in light-induced pigmentation responses and possibly in brain-behavioral anomalies. Independently, and unaware of Kitay and Altschules' book, Lerner began investigations in 1951 to isolate a pineal hormone. His work was based on an earlier report (McCord and Allen 1917) that pineal extracts counteracted the darkening effect of melanophore stimulating hormone in frog skin. His publication (Lerner et al., 1958) identified a potent pineal hormone, melatonin, as the methoxy derivative of serotonin, and set into motion a great number of studies of pineal stucture and function, the momentum of which has not visibly diminished.

By 1965, the innervation of the pineal by sympathetic nerves; the depressant action of melatonin on thyroid secretion; the light dependant nature of pineal enzymatic reactions and the ability of pinealectomy to remove short photoperiod induced gonadal changes were well established, such that the pineal was termed a "neuroendocrine transducer" by Wurtman and Alexrod (1965).

Wurtman (1978) emphasized that the most regrettable aspect of much pineal research had been the concentrated use of rats as the experimental animals. Selective breeding and inbreeding of these stocks have resulted in an animal of negligible photoperiodic sensitivity, and therefore it may not constitute the most appropriate animal model. Other seasonal animals may have elicited better results. The fact that much evidence arises from long-day breeding species has also, at times, confused the story of the role of melatonin in reproduction and hair growth.

Excellent reviews of pineal anatomy and function can be found in Nir, Reiter and Wurtman (1978) and Relkin (1983). Many of these reviews concentrate on gonadotrophic responses in laboratory and wild animals, and applications to human physiology. Although the pineal indole, melatonin, has received most of the publicity other pineal indole-amines and polypeptides are secreted by the pineal gland but their physiological actions have not been as widely studied.

5.1.5.2 Melatonin and photoperiodic time-measurement

It may be worthwhile to spend a small amount of time outlining the ways in which melatonin is involved in photoperiodic time-measurement. Two distinct hypotheses have been proposed. In the first, it is the total duration of melatonin exposure each day which dictates the response. The second hypothesis has the timing of a daily rhythm in sensitivity to melatonin relative to the period of melatonin secretion determining the response.

The first hypothesis is supported by experiments in which exogenous melatonin has been given to increase the duration of exposure to melatonin. Carter and Goldman (1981) and Goldman (1982), working with Djungarian hampsters, and Bittman et al. (1982) with Suffolk sheep have used programmed infusions of melatonin to show that when blood levels are continually elevated for more than 12 hours each day for several weeks, a short day response is seen. Remember that melatonin is released from the pineal during darkness hours. If blood levels are elevated for short periods, even if more than once per day, then a long day response is seen.

Tamarkin et al. (1976) showed that the timing of injections was crucial, with afternoon rather than morning extensions being required. Almeida and Lincoln (1982) supported the involvment of circadian rhythms. Rollag and Niswender (1976) and Kennaway et al., (1983) found that melatonin secretion continued to "free run" to a 24 hour rhythm in constant darkness, but was suppressed by continuous light. Timing effects have also been noted by Watson-Whitmeyer and Stetson (1983). In pinealectomized hampsters no time effect was observed (Tamarkin et al., 1977; Goldman et al., 1979).

5.1.5.3 Melatonin and hair, wool and horn growth cycles

Pineal involvement (via melatonin) in the regulation of hair growth in mice was demonstrated by Houssay et al. (1966) who observed that pinealectomy accelerated the passage of waves of hair growth, and subcutaneous melatonin injections to intact or pinealectomized animals retarded them. Rust and Meyer (1969) induced melatonin implanted weasels to moult to a winter coat when animals were held in photoperiods which promoted summer coat formation in control animals. Similarly, melatonin implanted white-footed mice held in summer environmental conditions underwent an "autumn" moult to winter coats (Lynch and Epstein, 1976; Heath and Lynch, 1981;1982).

Hoffmann (1973) delayed, but did not prevent, a spring moult in winter-maintained, melatonin-implanted, Siberian hampsters exposed to long photoperiods. The replacement coat, although closer to summer structure, was white (winter) coloured. In animals maintained on short photoperiods there were no differences between melatonin-treated and control animals. Logan and Weatherhead (1980) concluded from studies of cultured hampster follicles, that pineal indole-amines may act directly on melanogenesis, but other photoperiod related effects on hair growth are likely mediated via the pituitary and other endocrine organs. Mink, subcutaneously implanted with melatonin, were delayed in the spring moult or were early in the autumn moult also demonstrating the ability of melatonin to mimic the action of short days (Allain and Rougeot, 1980; Allain et al., 1981; Rougeot et al., 1984; Rose et al., 1984)

Pineal research in sheep has concentrated on its role in seasonal reproduction and the onset of puberty. Wool growth research has been quite incomplete. It seems regrettable that wool growth studies have not been coupled with most of these reproductive projects.

Lincoln et al. (1980), using Soay rams, studied the effects of superior cervical ganglionectomy (which destroys innervation of the pineal gland) on wool and horn growth in alternating 16-week periods of short (8L:16D) and long (16L:8D) days for three years. In intact rams both wool and horn growth followed the imposed light regimes. During short days, the rate of wool and horn growth declined and during long days, moulting of the old coat coincided with the phase of increasing wool growth. In ganglionectomized rams, wool and horn growth did not respond to photoperiodic changes but, rather, followed long term changes in plasma levels of various pituitary hormones. Orally administered melatonin has been shown to induce antler maturation in white-tailed deer (Bubenik, 1983).

Lincoln (1983) noted that although melatonin was a convenient method of inducing winter changes during the summer, the reverse effects were not so simply achieved. Accordingly, some method of blocking the action of melatonin in the brain, or to inhibit its release was needed to counteract the effects of natural winter.

5.1.5.4 Pineal-hormone interactions

The overall effect of the pineal gland on thyroid function would appear to be inhibitory. Several studies with laboratory species, reviewed by Relkin (1983) showed that the administration of melatonin to rats reduced thyroid weights and decreased the secretion rate of thyroxine. Pinealectomy leads to thyroid hypertrophy and increased thyroxine secretion. These workers thought that melatonin acted directly on the thyroid. Other studies in Relkin's review, have shown melatonin to act on the hypothalamic-pituitary level where TRH release and subsequent effects on TSH were reduced by the administration of melatonin. Other studies found a positive feedback of the thyroid on the pineal. In general, long days should result in higher thyroxine levels than short days. This has been verified by Ryder (1979) and Lincoln et al. (1980).

The effect of the pineal on the adrenals is unclear and may be species dependant. In rats, the pineal inhibits both adrenal corticosteroid synthesis and secretion, the latter decrease being partly the result of accelerated degradation.

Melatonin appears to exert its effects both directly and via the feedback response on ACTH.

The effects of melatonin on diurnal variation have been conflicting (Relkin, 1983). The seasonal effects on serum concentrations of glucocorticoids in large animals are not well established owing to confounding effects of stress and diurnal variation (Thun et al., 1981). Long days lowered serum glucocorticoids in cattle (Leining et al., 1980) and in sheep (Brinklow and Forbes, 1984a). Pinealectomy reduced this decline in sheep (Brinklow and Forbes, 1984b). Other studies have reported little or no photoperiodic effects in sheep (Kennaway et al., 1981; Lincoln et al., 1982). Long days elevated serum glucocorticoids in pigs (Barnett et al., 1981; Kraeling et al., 1983).

Photoperiodic effects on growth hormone also vary greatly between reports and between species. In rats, enhanced pineal activity reduced the production and release of growth hormone in some studies (Relkin, 1983). In cattle, photoperiod has not had any demonstrative effect on growth hormone (Peters and Tucker, 1978). In non-pregnant goats, growth hormone concentrations were higher in long than in short day treatments (Tergui et al., 1984). Results from deer are conflicting.

Prolactin is considered to be the metabolic hormone most responsive to seasonal influences (Tucker, 1982). Studies in rats and mice, reviewed by Relkin (1983) have produced conflicting results. Under natural conditions, elevated serum concentrations of prolactin have been associated with spring and summer and depressed concentrations have been observed during autumn and winter in cattle (Koprowski and Tucker, 1973), sheep (Ravault, 1976; Munro et al., 1980; Bose et al., 1982), goats (Buttle, 1974), deer (Mirarchi et al., 1978) and wild pigs (Ravault et al., 1982). Prolactin concentrations in heifers, under constant photoperiod, rise and fall with similar changes in temperature (Wetteman and Tucker, 1974). Bull calves, maintained at constant temperature, also varied prolactin concentrations with daylength. Similar studies with sheep have shown that prolactin concentrations increase with increased daylength (Pelletier, 1973; Forbes et al., 1975;1979; Lincoln et al., 1978). Superior ganglionectomy reduces or removes the photoperiod induced prolactin response in sheep (Barrell and Lapwood, 1979; Brown and Forbes, 1980; Lincoln et al., 1982; Brinklow and Forbes, 1984a,b). Continuous light is not necessary for stimulation of prolactin release as a photoinducible phase of prolactin synthesis exists about 17 hours after dawn in sheep (Ravault and Ortavant, 1977; Thimonier et al., 1978; Schanbacher and Crouse, 1981; Brinklow and Forbes, 1984a.b).

5.1.5.5 Summary

The mechanisms that regulate the photoperiodic rhythm of wool growth in sheep are poorly understood. What does seem likely is that the pineal gland interacts with the endocrine system to alter the circulating levels of metabolic hormones which then affect wool growth. Exactly which hormones and which aspects of their levels are important have not been clearly shown. From the evidence presented, the thyroid gland, possibly interacting with the adrenals, seems the most likely influence on seasonal wool growth. The role of prolactin certainly needs to be more clearly defined.

Strains of sheep, with differing photoperiodic sensitivity should be studied to determine at which level this sensitivity is being manifest. Is it a difference in pineal activity, a difference in the response of the endocrine system to pineal secretions, or is it at the level of the productive tissues?

5.1.6 Measuring the seasonality of wool growth

Three main techniques exist for measuring wool growth over short periods. Whole animal shearing is inappropriate as it may complicate natural cycles with the additional influences of temperature regulation, altered intake, and damage to the skin. Changes in the rate of wool growth in experimental sheep are usually measured by clipping the wool at regular intervals from a defined area of skin; by dye-banding the wool at skin level with permanent dye; or by labelling the wool with ^{35}S-labelled cysteine via intravenous injection. All methods have inherent advantages and disadvantages and the efficacy may depend on time intervals involved and the uniformity of fibre growth in the fleece.

5.1.6.1 The tattooed patch technique

The tattooed patch technique involves regular (usually monthly) clipping of all wool on a delineated patch (approximately 100cm^2). Continuous sampling of the production of the same follicles increases the accuracy of within sheep comparisons. The whole fleece:patch production can be used to partition whole fleece growth, which is appropriate for both within- and between-animal comparisons. Failure to retain a constant patch size alters the ratio of patch:fleece production.

Although clipping per se had no effect on the rate of wool growth on midside patches, Downes and Lyne (1961) and Wodzicka-Tomaszewska and Bigham (1968) concluded that local cooling of the patch could reduce wool growth and exaggerate the seasonal amplitude of wool growth. However, in the latter of these studies the whole animal was shorn every 16 wks, and this would prevent the rest of the fleece from insulating the patch. The patch technique also lags behind follicle output due to the 5-10 day emergence time of the fibre (Downes and Sharry, 1971).

5.1.6.2 Dye-banding

Dye-banding was developed by Chapman and Wheeler (1963) using a weak aqueous solution of Durafur Black R which has the capacity to dye greasy wool at skin temperature. Dye-banding also leaves the proprioclimate of the skin undisturbed. As discussed by Squires (1964) and Clark and Kohn (1964) a correlation of 0.88 -0.97 exists between dye-banding and clipping results in Merino sheep. Dye-banding gives easy readings of fibre length and interval diameters could be obtained by sampling dyed staples.

However, Langlands and Wheeler (1968) and Wheeler et al. (1977) emphasized the difficulty of predicting the weight of wool from length and diameter measurements. The technique is also affected by shedding, wear and the tendency of individual fibres in the staple to grow at different rates. Wheeler et al. (1977) suggest that the technique may be unsatisfactory for coarse, open or medullated fleeces.

5.1.6.3 Radioisotope labelling

Labelling of wool with radioisotopes was first described by Downes and Lyne (1959). Further evaluation of this radioautographic technique using ^{35}S-cysteine was carried out by Downes and Lyne (1961) and Downes and Sharry (1971). The advantage of the techniques lies in very short term studies in which accurate information on daily incorporation of nutrients into fibres is required. As the wool is labelled in the follicle, samples for study are not removed until sometime after the end of the experiment. Periods as short as four days can be measured. The disadvantage, aside from cost, is that measurements are required on several hundred individual fibres as some fibres grow at 3x the rate of others. The other shortcoming is that infusions of labelled cysteine may themselves alter the normal growth of fibre by providing substrates at rates or levels not physiologically normal.

5.1.7. Summary

The annual variation in wool growth is significant for a number of reasons. The seasonality of wool growth appears to be controlled by a number of physiological systems which ultimately are reflected in the entire animal. Hormonal involvment in the annual cycle is not likely limited to local effects on the skin , but is involved on a larger scale with intake and metabolic function.

Studies dealing with different breeds, or selected lines may be affected by seasonal differences in the relative level of performance. Seasonality of wool growth is also likely reflected in other seasonal traits such as reproduction, efficiency and intake. The underlying seasonality of many aspects of sheep performance, and differences in seasonal responses between groups, is essential to studying most aspects of sheep performance.

5.1.8 Objectives of the current trial

The objectives of the current trial were:
1) to determine the correlated responses in the seasonality of wool growth to selection for high hogget greasy fleece weight;
2) to quantify the importance of sources of variation such as sex, birth rank, dam age, and selection line; and,
3) to provide a database for later comparison with seasonality of reproduction, the estimation of feed intake and the measurement of staple strength.

5.2 Materials and Methods

5.2.1 Experimental plan

The study was conducted between December 11th, 1984 and October 23rd, 1985 on 1984 born ram and ewe hoggets from the FW and C lines. These sheep were about 4 months old at the start of the trial and 14 months old at the conclusion. On December 11th, 1984 wool was removed from a right midside patch (approximately 8cm by 8cm) on all available FW and C lambs. Fleeces were weighed at lamb shearing on December 12,1984. On December 13th, 1984 a dyeband was applied along an 8cm line approximately 2 cm directly above the dorsal edge of the midside patch.

Wool sampling, dyebanding and measurements of live weight were conducted every 4 weeks between lamb and hogget shearing on October 23rd, 1985. Only those sheep which survived until the conclusion of the experiment were considered in the analysis, as patch production was used to partition the hogget fleece weight into 28-day units. Complete measurements were also needed for the estimation of amplitude traits. Throughout the experiment sheep were lost due to death and misplacement. The final dataset consisted of 54 Control (C) and 72 Fleece weight selected (FW) hoggets. As ewe and ram hoggets were grazed separately rams and ewes were sampled on adjacent days.

5.2.2 Sampling routine

Between 15:00 and 17:00 hours on the day before sampling, hoggets were put in a shed overnight without access to food or water. Between 08:30 and 09:30 hours live weights were taken and recorded on all sheep. Wool sampling began at 09:30 hours and continued throughout the day. Sampling was completed between 15:00 and 17:30 hours at which time the sheep were returned to pasture.

Each sheep was laid on its side on a table for sampling. Wool was clipped from the midside patch, then patch size was measured with calipers. At no time was the patch area difficult to identify and extreme care was taken not to expand the patch area during clipping. As a precaution, the boundaries of each patch were defined by tattooing in mid-February.

The length of wool grown during the period was measured to the nearest mm as the distance between the skin and the bottom of the previous dyeband on unstretched staples. A new dyeband was applied and the sheep was released. Dye was prepared according to Chapman and Wheeler (1963) and applied with a standard Pastueur pipette drawn along the skin. Excess dye was removed by suction after the pipette had been emptied of remaining dye. Approximately .5 ml of dye was applied to each sheep.

5.2.3 Sample processing and calculated variables

Wool samples were conditioned, weighed, scoured and reweighed as outlined in chapter 4.2.3 except that finely woven silk bags replaced the mesh bags used in that experiment. Residual grease measurements obtained from ether extraction of scoured samples yielded between 0.6% and 2.2 % residue indicating that the scouring procedure was adequate.

Clean samples were then carded on hand carders to free matted fibres. Fibre diameter was determined by the Air-flow method (Anderson, 1954). Fibre diameter was recorded as the mean of 2 readings on one subsample. During winter months some of the clean samples weighed less than 2 gms so the adapted air flow apparatus and method described by Sumner (1969) for 1 gm samples were used. Fibre diameter of these "light" samples was recorded as the mean of four readings on one subsample.

Complete dye-banded staples were removed for reference from half the dye-banded area on May 30th and 31st, 1985. The second half-year's dyebanded staples and full year dye-banded staples and surrounding wool were removed at the last sampling on the 16th and 17th of October, 1985 to prevent contamination of the fleece with black fibres. These staples were saved and used to estimate staple strength (Chapter 8).

Clean wool growth (g per day) in each month of the year was estimated from monthly clean samples. Each month's clean patch wool weight was expressed as a proportion of the total clean wool grown by the patch. The clean fleece weight was then multiplied by each month's proportional growth.

Greasy fleece weight was multiplied by these same proportions to estimate the monthly change in greasy fleece weight. These values were used to obtain fleece-free live weights at each sampling. Live weights and live weight changes reported subsequently are on a fleece-free basis unless otherwise indicated.

Other traits calculated from the data included the amplitude (H-L)/((H+L)/2), where H and L refer to the highest and lowest values for a particular trait within animal. Amplitudes of seasonal changes in clean wool per day (CPD), fibre diameter (FD) and length per day (LPD) are designated as CPDAMP, FDAMP and LPDAMP. Other variables included the month of the lowest values for particular traits and are MLCPD, MLLPD, and MLFD.

5.2.4 Statistical Methods

Data for single measurement traits such as greasy fleece weight (GFW), lamb fleece weight (LFW), weaning weight (WW), post shearing live weight (PSLW), CPDAMP, FDAMP, LPDAMP, MLCPD, MLLPD and MLFD were analysed by analysis of variance according to the following model:

Model 5.1

$$y_{ijklm} = \mu + b_1 X_{ijklm} + r_i + d_j + t_k + l_l + e_{ijklm}$$

where

y_{ijklm} = an observation of wool or weight characteristic on the m^{th} sheep of sex k, selection line l, dam age j and birth rank i

μ = an overall mean,

b_1 = the regression coefficient of y_{ijklm} on X_{ijklm} where,

X_{ijklm} = an observed individual birthdate,

r_i = the fixed effect of the i^{th} birthrank class

d_j = the fixed effect of the j^{th} age of dam class

t_k = the fixed effect of the k^{th} sex,

l_l = the fixed effect of the l^{th} selection line, and

e_{ijklm} = the random residual associated with an observation on the m^{th} sheep of sex k, selection line l, with dam age j and birth rank i.

Multivariate analyses were conducted on monthly bodyweights, and monthly measurements of CPD, LPD, FD. The underlying linear model was similar to Model 5.1 but included p-dimensional time effects and the interactions between time and design factors. In most cases, interactions between main effects were nonsignificant and were dropped from the model, with the exception of line X sex, which is reported where significant. Null hypotheses were tested using the Chi-squared statistic as described by Morrison (1976).

5.3 Results and discussion

5.3.1 Liveweight

The least squares means (by selection line) for weaning weight (WW), post-shearing liveweight (PSLW), and monthly weights during January through to October are given, along with their standard errors and indications of significance, in Table 5.1.

5.3.1.1 Fixed effects

Although mean liveweights are not presented for each month for each level of fixed effects, the relative importance of these effects and the associated changes with advancing lamb age can be derived from the repeated measures analysis of variance. As these effects were not of central interest in this study, it was felt that presentation of all subclass means would be needlessly repetitive.

Date of birth was a significant ($p<0.001$)covariate for liveweight throughout the measurement period. The regression coefficient did not change significantly ($0.05<p<0.10$) across time. Values of this regression varied from a low of 141±40 g/day of age in February to a high of 227±60 g/day of age in April. The covariate reflects differences in cumulative weight per day of age and was not expected to vary widely given the relatively flat growth curves presented in Table 5.1.

Single-born lambs were consistently heavier ($p<0.001$) than twin-born lambs although the magnitude of this difference varied across time ($p<0.01$) and ranged from 3.8±.8 kg at weaning to a low of 2.1±.6 kg in July and August. By the time of hogget shearing, the average difference between single- and twin-born lambs had risen to 2.9±.7 kg. Similar results have been reported by Ch'ang (1967), Sumner (1969) and Bigham et al. (1978a).

Lambs born to 3 and 4 year old ewes were consistently heavier than lambs born to 2 and 3 year old ewes although the overall effect of dam age across time was not significant ($0.05<p<0.10$). The effect of dam age did not change significantly over time ($p>0.30$) although the trend was decreasing differences as the lambs became older.

Ram lambs were consistently heavier ($p<0.001$) than ewe lambs and the relative advantage was not constant ($p<0.001$) over time. The difference between ram and ewe lambs was 2.2±.4

kg at weaning and rose markedly over January, February and March (5.2±.6 kg), declined over winter (4.2±.5 kg) and increased again near hogget shearing (5.3±.5 kg). Sex differences in growth patterns cannot be directly attributed to sex in this study as ram and ewe lambs were grazed separately on different blocks of the Massey University farm. Monthly changes in pasture quality and quantity were not standardized across sex.

5.3.1.2 Seasonal trends and line effects

Generally, lambs grew steadily over January, February and March. Little change (0.2 - 1.6 kg) in liveweight occurred over winter. FW lambs began growing again in July while C lambs did not gain significant weight until August. The relative advantage of FW over C lambs became significant in late May and continued through to hogget shearing. The relative advantage (FW-C)/C is also given in Table 5.1. and ranged from a minimum of -1.33% in January to a maximum of 6.99% in October. As in Sumner's (1969) data, body weight plateaus coincided with periods of decreased wool growth and the return of positive growth rates was accompanied by increased wool production as seen in the subsequent discussion.

5.3.2 Wool growth

The least squares means and standard errors by selection line and month for CPD, LPD and FD are presented, respectively, in Tables 5.2a,b and c along with significance levels, minimum and maximum values (clean wool growth only), and the relative advantage of FW over C animals. These data for CPD, LPD and FD are also presented, respectively, in Figures 5.1a,b and c (by selection line) and Figures 5.2a,b and c (by selection line and sex). As with liveweight data, subclass means for fixed effects are not presented but will be discussed.

5.3.2.1 Fixed effects

Clean wool production was significantly affected by date born ($p<0.001$), dam age ($p<0.01$) and sex of lamb ($p<0.001$). The effect of date born was not consistent across time ($p<0.001$) and varied in sign with no discernable trend except a tendency to be negative. Later born lambs having lower clean wool production per month than earlier born lambs. The effect of dam age was also inconsistent across time ($P<0.05$) with only 3 year old dams being consistently superior. Clean wool production was not significantly affected by birth rank ($p>0.50$). Sex had a major effect on CPD ($p<0.001$) and was inconsistent across time ($p<0.001$). Ram lambs were superior to ewe lambs from lamb shearing until March. Rerankings of ewes and rams were common over winter with ram lambs becoming clearly superior from August onwards to hogget shearing (Figure 5.2a). As mentioned in the previous section, it is difficult to interpret sex effects in this data due to the grazing practices adopted as University farm protocol.

Fibre length growth rate (LPD) was significantly affected by date of birth ($p<0.001$) and sex of lamb ($p<0.05$). Date of birth effects were consistently negative but did vary slightly ($p<0.05$) across time with no consistent trends. Sex effects were not at all consistent across time ($p<0.001$) and varied in sign (Figure 5.2b). The effects of dam age ($p>0.80$) and birth rank ($p>.10$) were not significant and did not vary with time.

Fibre diameter was significantly affected by date of birth ($p<0.01$) with later born lambs tending to have finer fibres. Although the magnitude of this trend was not consistent across time ($p<.01$) it was consistent in sign. Fibre diameter during the year was not affected by dam age, birth rank or sex of lamb. The effect of sex was not consistent across time ($p<0.001$) with females having greater fibre diameters than rams only during the period from April to August (Figure 5.2c). Reasons for these trends by sex are unclear, as stated previously.

5.3.2.2 Seasonal patterns

All three wool traits showed significant seasonal variation. In both lines, and in all traits, production increased from December to January, plateaued briefly in February then declined until April-June and increased steadily afterwards. Similar hogget patterns (ranges and times of minimum production) for Romney sheep were reported by Bigham et al. (1978b) and Sumner (1979, 1983).

Absolute values of clean wool production, as opposed to production per area of skin, were used in this trial because the nature of the data allowed accurate partitioning of clean fleece weight. Since the same follicles are being sampled at each clipping (within a tattooed patch), the comparison of period to period production is quite accurate. When this production was divided by the area of the patch, large discrepancies began to emerge in the data. Many of these problems are possibly related to the difficult task of accurately measuring patch area. Measurement of per area of skin production also falsely entrains body growth and wool production into a negative relationship.

Most studies (Ferguson et al., 1949; Story and Ross, 1960; Stuart et al., 1961; Arnold et al., 1964; McFarlane, 1965; Ross, 1965; Doney and Eadie, 1967; Williams and Suijdendorp, 1968; Horton and Wickham, 1979; Hawker et al., 1984,1985) on seasonal variation in wool growth have been conducted on mature sheep and the values and patterns are not directly comparable to hogget data. Generally, the seasonal cycle in FD appears to lag behind that of LPD as found by Story and Ross (1960), Ross (1965) and Sumner (1969) .

Least squares means and their associated standard errors (by selection line) for the amplitude and month of minimum production for clean wool growth, length and fibre diameter are shown in Table 5.3 along with greasy hogget fleece weight (GFW), clean hogget fleece weight (CFW), lamb greasy fleece weight (LFW) and the ratio of clean hogget fleece weight to PSLW.

The amplitude of clean wool growth corresponds closely to Hart's (1961) estimate of 85% for Corriedale ewes in Christchurch. Values calculated from reported studies elsewhere (Story and Ross, 1960;Ross, 1965; Bigham et al., 1978a) range from 43% to 114% for clean wool growth in mature Romney ewes, indicating that values (88%-119%) obtained in this study are well within realistic limits. The amplitude of LPD (52%-58%) corresponds well to Story and Ross (1960) at 49% and Ross (1960) at 40%-47%. Similarly, FDAMP in this study (26%-29%) seems to be in the range of Story and Ross (1960) at 38% and Ross (1965) at 15%-24%.

Correlations amongst seasonal wool growth variables pooled (where homogeneous) across genotypes are given in Table 5.4. Correlations significantly different from zero are marked with an asterisk (*). Clean fleece weight was highly correlated with minimum CPD. In a simple regression analysis, June CPD alone was able to explain 76% of the variation in clean fleece weight. This indicates that superiority for clean fleece weight is highly related to winter wool production in these data. Amplitude variables were negatively correlated with greasy and clean fleece weight meaning that sheep with less seasonal variation in wool growth measures tended to have higher fleece weights. The opposite relationship was found in the Merino by Reis and Williams (1965) who concluded that sheep with phenotypically high fleece weight showed greater variation in seasonal wool growth. The relationship between amplitude and wool growth in this experiment was not dependent on selection line.

5.3.2.3 Selection line effects

As shown in Tables 5.2 and 5.3, FW sheep maintained higher overall seasonal levels of production, maintained higher minimum levels of production in winter, and had similar (FDAMP) or reduced (CPDAMP,LPDAMP) amplitudes of wool growth characteristics. The increased body growth of FW sheep in late winter would normally suggest that intakes were higher for FW sheep in winter. The possibility of increased efficiency of wool and body growth cannot, however, be disregarded.

In the study of Hawker and Crosbie (1985), ewes with a history of high winter wool growth (W+) were maintained at high or low feeding levels the subsequent winter. W+ ewes outperformed W- ewes at both feeding levels, the differences being more pronounced under high feeding. The significance of Hawker and Crosbie's work is that winter production differences may be due more to efficiency than to intake.

In this study, as in Hawker and Crosbie (1985), the largest proportional difference between the lines occurred during winter even though the largest absolute difference occurred during the last month prior to hogget shearing. Some authors (Doney and Eadie, 1967; Bigham et al., 1978; Hawker et al., 1984) suggest that within and between breed/group comparisons are more discerning at higher levels of production.

These results suggest that, depending on the purpose of pen-fed studies, the time to conduct trials dealing with metabolic/hormonal differences between lines is in winter, when proportionate differences between groups are largest. If FW sheep are truly less seasonal than C sheep, as the data suggest, then they should be more likely to respond to nutritional stimulus during this period. Although adult differences in late spring/early summer wool growth were not measured in this trial, the relative contribution of this section of the curve should be considered. In many respects, the FW line has similar productive characteristics to the W+ lines of Hawker and Crosbie (1985).It should be investigated whether or not the seasonal pattern of wool growth can be removed even further, in FW sheep compared to C, by supplemental winter feeding.

In agreement with our findings, Doney (1964) suggested that genetic differences in metabolic responses to "unspecified seasonal factors" might be removed by intensive selection for wool growth. In contrast, Hawker et al. (1985) could not detect a difference in the annual pattern of wool growth between screened high and low fleece weight lines, as the entire curve seemed to be lifted in the high fleece weight group.

Over the course of the repeated clippings of the midside skin area, it was noted that FW and C animals had observable differences in the colour of skin beneath the patch. Although these differences were difficult to quantify an effort was made, on two separate sampling times, to identify the genotype of each sheep merely by examining skin colour (no obvious line identifications were present - allocations to line were checked against sheep numbers on the data sheets). On both occasions, selection line was correctly identified in 8 out of 10 animals. FW sheep had much brighter skin colour characterised by visible pinkness. C sheep had chalky skin without pink hues and with a prevalence of brown or grey hues. Although the significance of this observation is unclear, further investigation into differences in skin temperature, or surface circulation may be warranted.

Given the increased reproductive season, and extended period of high ovulation rate in the W+ ewes of Montgomery and Hawker (1987), and the high relationship of winter wool growth to hogget fleece weight in this trial, measures of winter wool growth may yet prove valuable as additional selection criteria in ram or ewe selection.

Plate 5.1 Dye-banded staples in relation to the midside patch

Table 5.1 Least squares means(LSM), standard errors, percentage advantage ((FW-C)/C)*100. and significance of monthly liveweight, weaning weight (WW) and post shearing liveweight (PSLW) by selection line.

Month	C LSM	FW LSM	sig.	% (FW-C)/C
WW	21.8±.4	21.5±.3	ns	-1.33
JAN	24.1±.4	24.2±.5	ns	0.41
FEB	27.2±.3	27.5±.5	ns	1.10
MAR	29.2±.4	29.9±.5	ns	2.40
APR	29.1±.3	29.8±.4	ns	2.41
MAY	30.0±.4	30.9±.3	*	3.00
JUN	29.3±.4	31.2±.3	**	6.48
JUL	33.3±.3	34.8±.4	**	4.50
AUG	33.5±.4	35.8±.4	**	6.87
SEP	38.6±.5	41.3±.4	**	6.99
OCT	41.3±.5	42.6±.4	**	3.15
PSLW	40.9±.5	43.1±.4	**	5.38

* $p<0.05$

** $p<0.01$

*** $p<0.001$

Table 5.2 Seasonal wool growth of C and FW hoggets: least squares means (LSM), standard errors, significance, and percentage advantage ((FW-C)/C)*100.

a. Clean wool growth (g/day) [1]

	CONTROL			FLEECE WEIGHT			% (FW-C)
Month	LSM	Min	Max	LSM	Min	Max	C
DEC	8.14±.37	4.39	13.75	9.85±.32	5.22	15.88	21.01
JAN	11.02±.48	5.88	16.11	12.93±.42	7.06	18.09	17.33
FEB	10.03±.40	5.38	16.82	11.73±.35	7.02	16.88	16.95
MAR	7.67±.39	4.58	12.40	8.98±.34	5.07	13.98	17.08
APR	6.88±.39	2.97	12.83	8.43±.35	4.61	13.55	22.53
MAY	7.66±.35	4.08	11.13	9.66±.31	6.49	13.72	26.11
JUN	5.92±.37	2.92	9.12	8.54±.33	4.80	13.20	44.26
JUL	6.77±.39	4.11	11.94	10.49±.35	5.89	14.40	54.95
AUG	7.27±.46	4.78	11.57	10.48±.40	5.21	15.26	44.15
SEP	9.20±.54	4.25	14.73	12.97±.47	7.93	23.33	40.98
OCT	12.46±.53	6.68	20.20	16.94±.46	9.12	25.46	35.96

[1] all monthly clean wool growth values are significantly affected by selection line ($p<.001$)

Table 5.2 Seasonal wool growth of C and FW hoggets: least squares means (LSM), standard errors, significance, and percentage advantage ((FW-C)/C)*100.

b. Length per day (mm/day)

Month	C LSM	FW LSM	sig.	% (FW-C)/C
DEC	.47±.01	.50±.01	**	7.07
JAN	.51±.01	.55±.01	***	7.50
FEB	.48±.01	.53±.01	***	9.58
MAR	.46±.01	.49±.01	*	6.32
APR	.45±.01	.47±.01	*	5.61
MAY	.45±.01	.50±.01	***	10.71
JUN	.39±.01	.46±.01	***	16.75
JUL	.46±.01	.52±.01	***	14.44
AUG	.47±.01	.52±.01	***	11.94
SEP	.52±.01	.58±.01	***	11.54
OCT	.57±.01	.62±.01	***	8.06

* $p<0.05$
** $p<0.01$
*** $p<0.001$

Table 5.2 Seasonal wool growth of C and FW hoggets: least squares means (LSM), standard errors, significance, and percentage advantage ((FW-C)/C)*100.

c. Average fibre diameter (µm)

Month	C LSM	FW LSM	sig.	% (FW-C)/C
DEC	30.2±.4	31.0±.4	*	2.64
JAN	33.0±.5	33.7±.4	p<.10	2.12
FEB	33.3±.4	33.9±.4	p<.10	1.80
MAR	31.3±.5	31.5±.4	ns	0.64
APR	30.1±.5	30.7±.4	ns	1.99
MAY	31.0±.5	32.4±.5	***	4.52
JUN	29.6±.6	31.8±.5	***	7.43
JUL	30.1±.5	33.3±.5	***	10.63
AUG	30.4±.6	33.2±.5	***	9.21
SEP	32.6±.6	35.2±.5	***	7.98
OCT	35.7±.5	38.3±.5	***	7.28

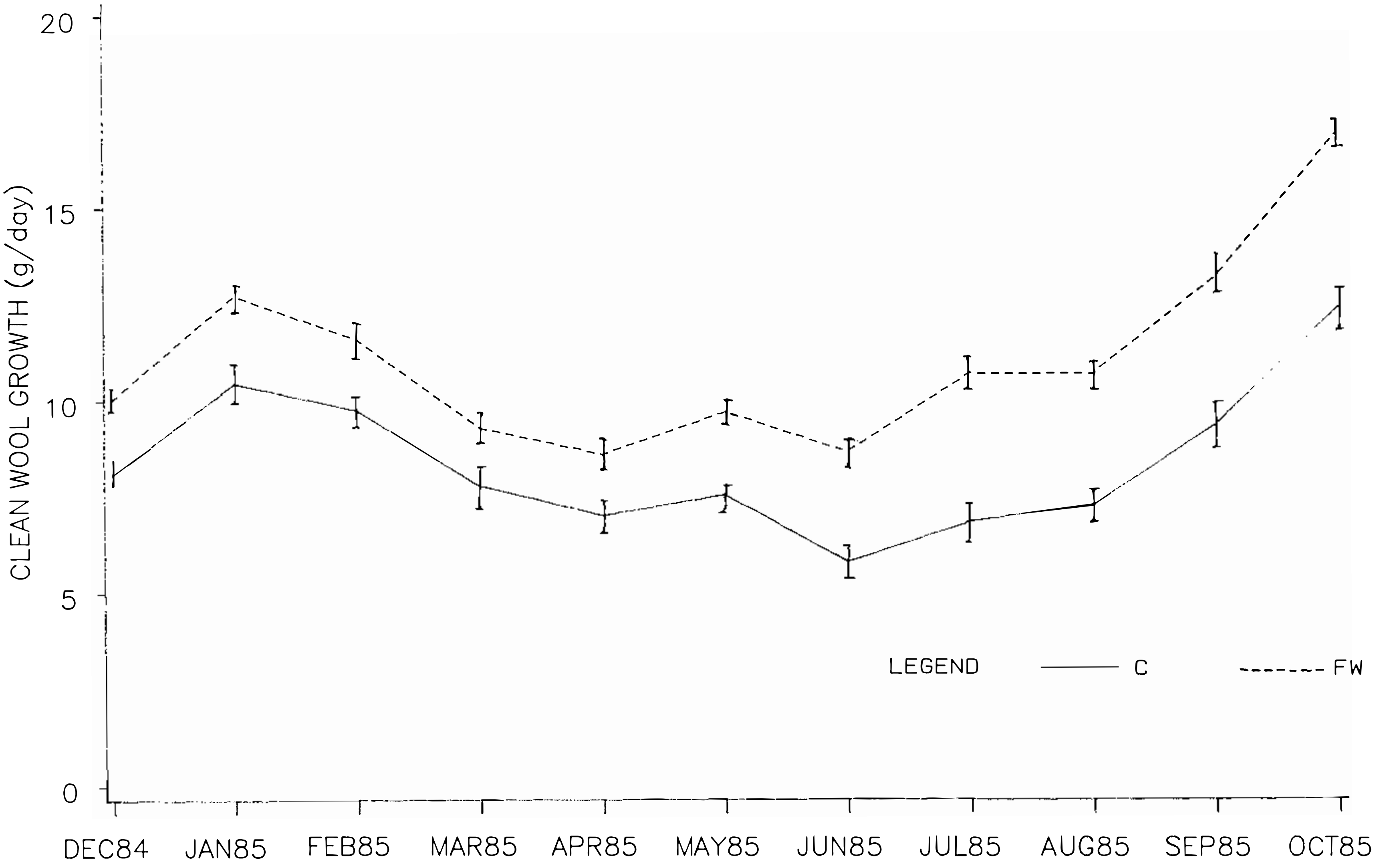

Figure 5.1 Seaonal pattern of wool growth in FW and C hoggets.
a. Seasonal variation in clean wool growth (g/day).

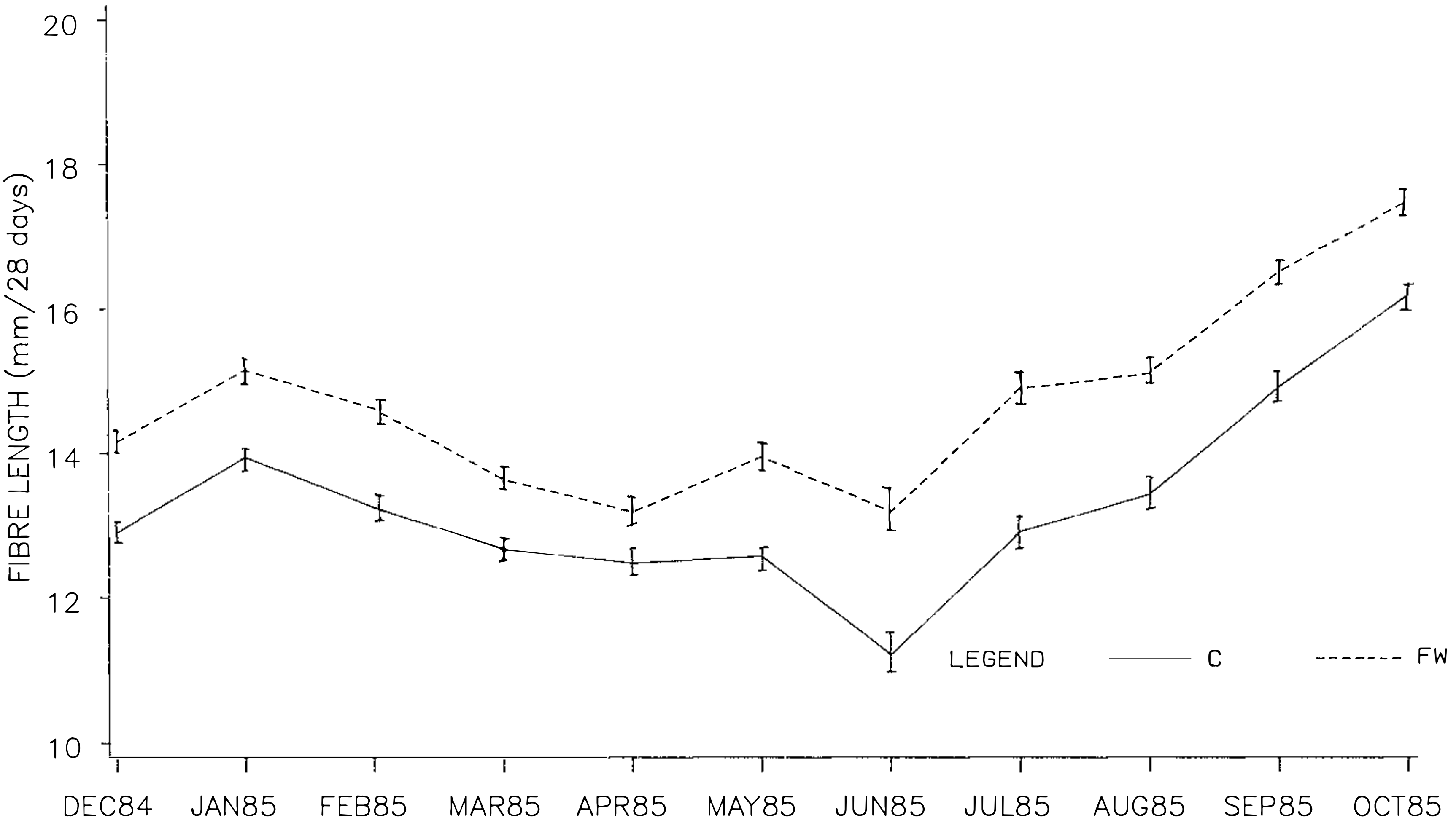

Figure 5.1 Seasonal pattern of wool growth in FW and C hoggets.
b. Seasonal variation in length per 28 days (mm).

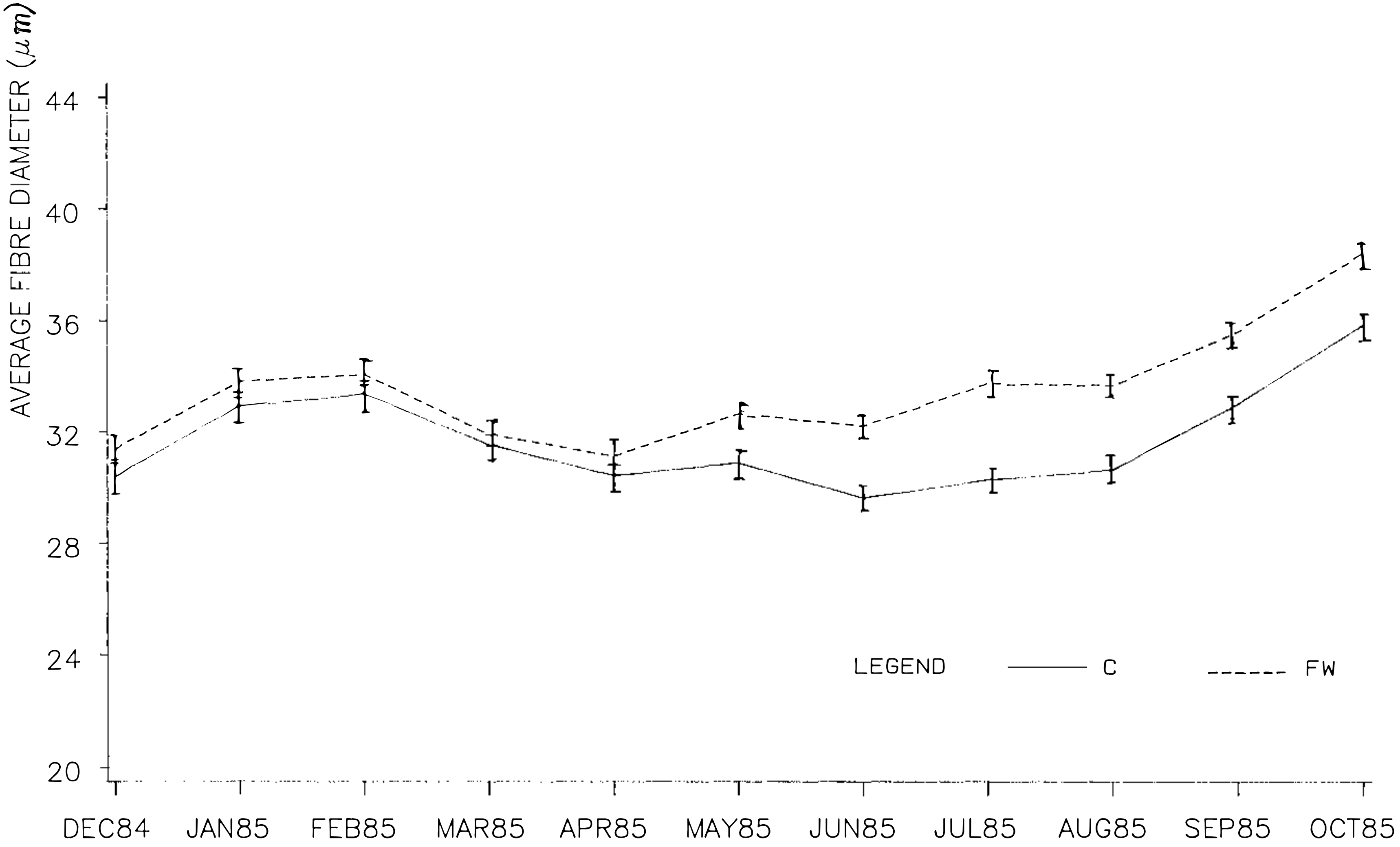

Figure 5.1 Seasonal pattern of wool growth in FW and C hoggets.
c. Seasonal variation in fibre diameter (μm)

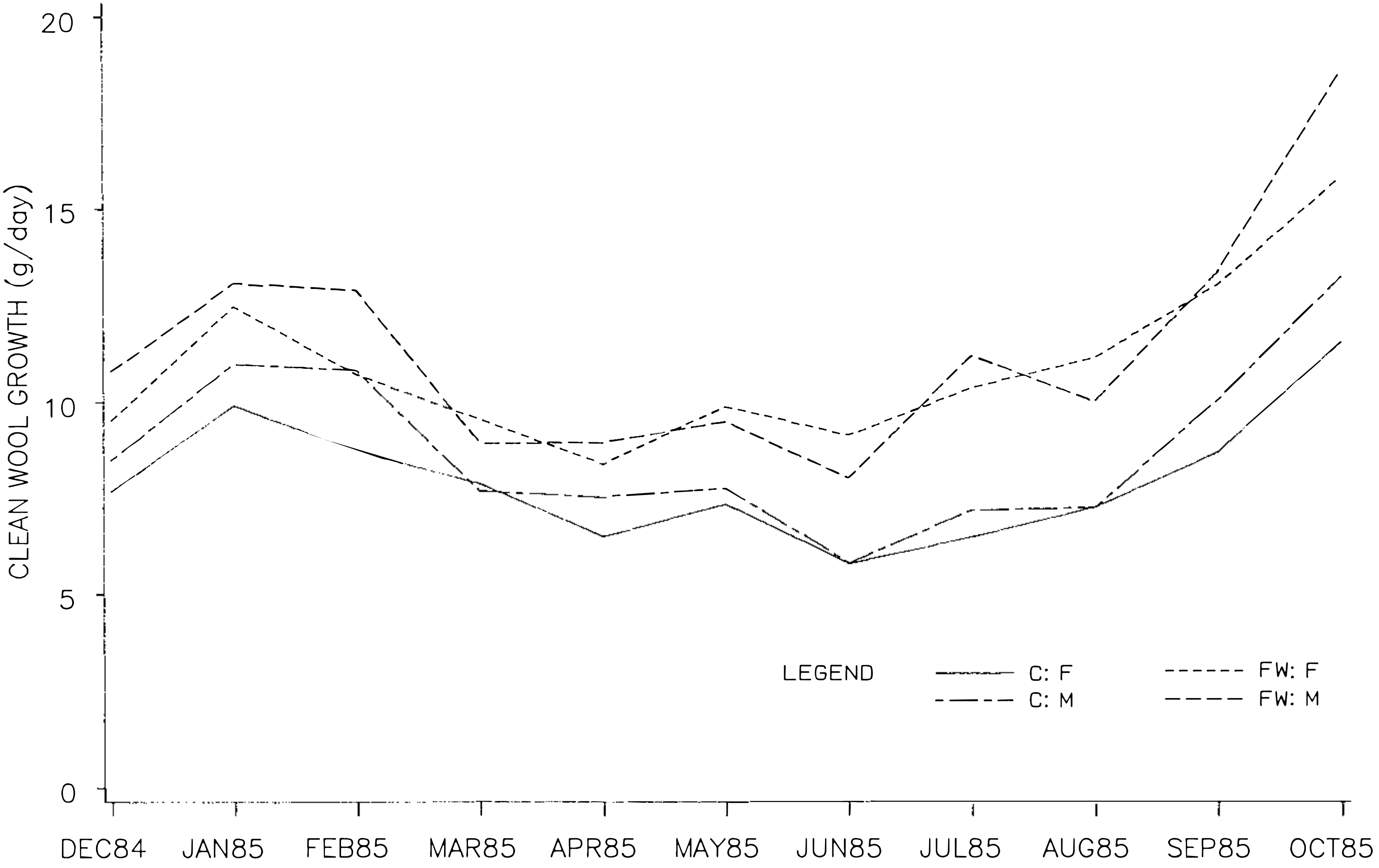

Figure 5.2 Seasonal pattern of wool growth in FW and C ram and ewe hoggets.
a. Seasonal variation in clean wool growth (g/day).

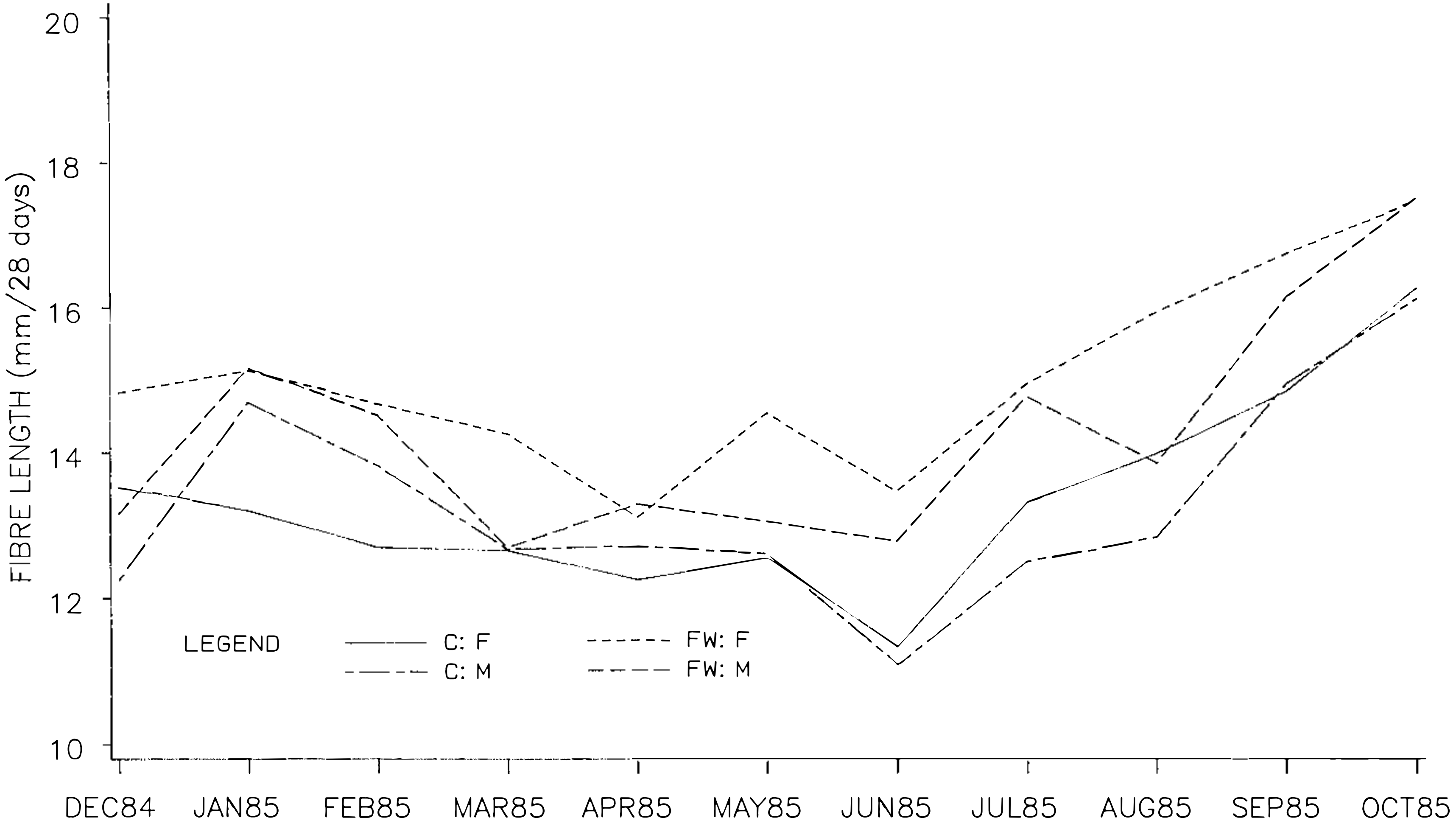

Figure 5.2 Seasonal pattern of wool growth in FW and C ram and ewe hoggets.
b. Seasonal variation in length per 28 days (mm).

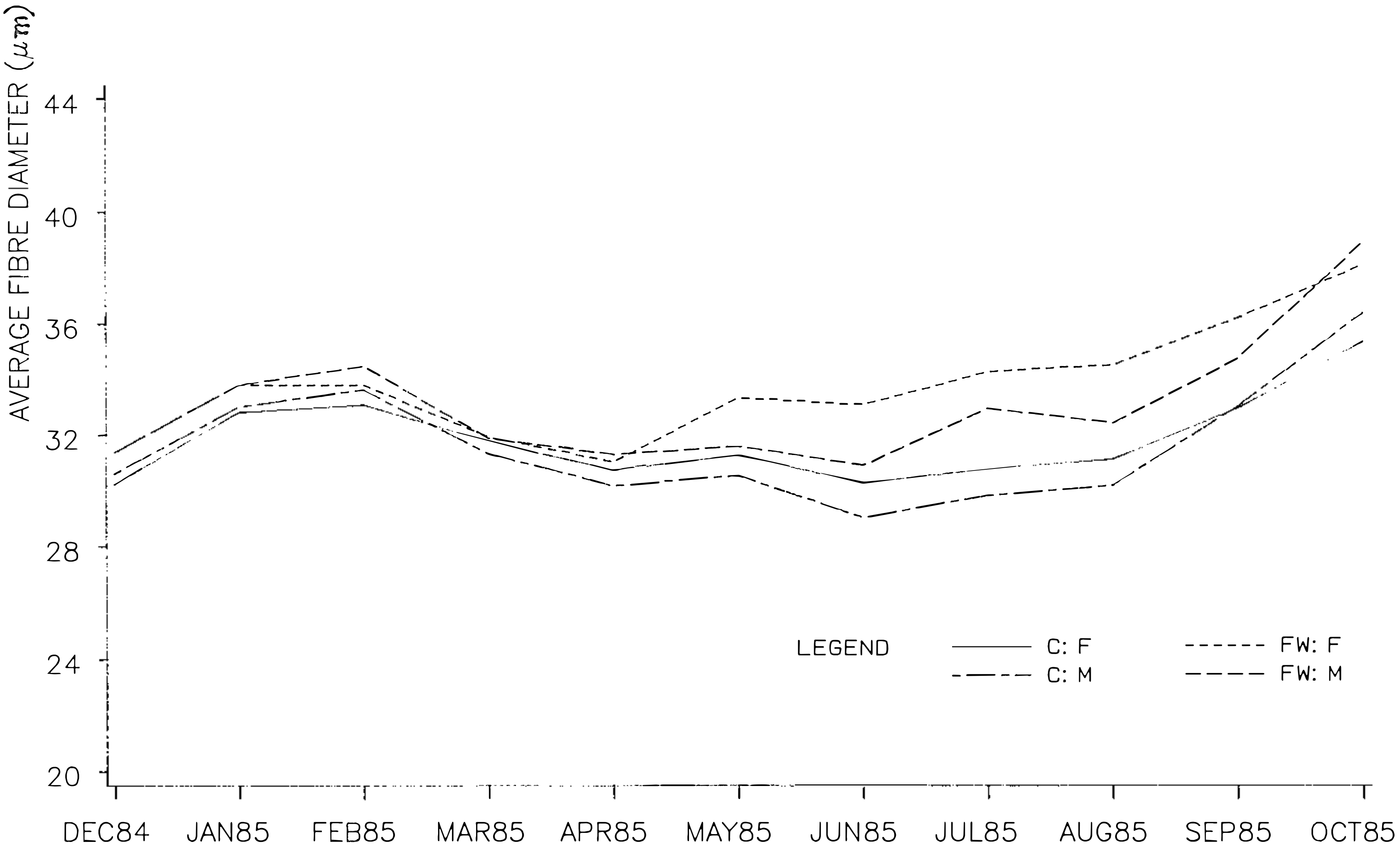

Figure 5.2 Seasonal pattern of wool growth in FW and C ram and ewe hoggets.
c. Seasonal variation in fibre diameter (μm)

Table 5.3 Characteristics of the seasonal pattern of wool growth, greasy fleece weight (GFW), clean fleece weight (CFW), greasy lamb fleece weight (LFW) and average fibre diameter (FD) in C and FW sheep. Least squares means, standard errors, and percentage advantage (FW-C)/C)*100.

Trait	C LSM	FW LSM	sig.	(FW±C)/C
CPDAMP(%)	119.16±6.27	88.78±5.49	***	-25.48
LPDAMP(%)	58.73±2.37	52.37±2.09	*	-10.83
FDAMP (%)	26.82±0.88	28.63±0.77	p<.10	6.75
MLCPD	4.62±.46	6.26±.56	**	
MLLPD	5.17±.39	4.82±.34	ns	
MLFD	5.08±.47	3.66±.40	**	
LFW (kg)	0.98±.02	1.10±.02	***	12.24
GFW (kg)	3.62±.07	4.78±.06	***	32.04
CFW (kg)	2.57±.06	3.40±.05	***	32.33
FD (µm)	31.74±.25	33.40±.22	***	5.20

* $p<0.05$

** $p<0.01$

*** $p<0.001$

Table 5.4 Pooled (where homogeneous) or within line (C/FW) correlations between wool growth characteristics (corrected for DB, BR, DA and SEX)[1]

	LCPD	LLPD	FDAMP	CPDAMP	LPDAMP	MFD	GFW	CFW	SL	MLFD	MLCPD	MLLPD
LFD	.63*	.26*	-.58*	-.58*	-.33*	.78*	.37*	.45*	.16	-.11	-.17	-.04
LCPD		.57*	-.43*	-.73*	-.53*	.47*	.73*	.80*	.30*	-.21*	-.13	-.4*/.1
LLPD			-.09	-.36*	-.74*	.27*	.39*	.51*	.59*	-.20*	-.4*/.1	-.5*/.2
FDAMP				.63*/.81*	.30*	-.14	-.06	-.08	.09	-.15	-.08	-.05
CPDAMP					.60*	-.27*	-.21*	-.26*	-.06	.09	.05	.11
LPDAMP						-.20*	-.22*	-.28*	-.23*	.13	.12	.38*/-.1
FD							.43*	.53*	.30*	-.15	-.19*	.02
GFW								.94*	.31*	-.17	-.19*	-.09
CFW									.44*	-.16	-.15	-.24*/.1
SL										-.06	-.07	-.14/-.17
MLFD											.73*/.42*	.37*
MLCPD												.37*

[1] * correlations significantly different from zero ($p<0.05$)

where,

LFD	minimum monthly fibre diameter
LCPD	minimum monthly clean wool growth
LLPD	minimum monthly length growth
MLFD	month of minimum fibre diameter
MLCPD	month of minimum clean wool growth
MLLPD	month of minimum length growth

5.4 Conclusions and recommendations for further study

In this trial, wool growth of FW sheep was superior to C sheep during the entire production period from lamb- to hogget-shearing. Differences were most pronounced in the periods of lowest wool growth with FW sheep producing 52% more clean wool and 18% more clean wool than C hoggets in July and February, respectively. Relative superiority of FW hoggets for FD was, likewise, highest in July (10.63%) compared to 0.64% in March. Relative superiority for length growth rate was highest (16.75%) in June.

The consistency of these results and the high correlation between measures of winter wool growth and CFW lead to the conclusion that some aspect of winter physiology has been dramatically altered in response to selection for hogget greasy fleece weight. A response in winter production may not have been found if selection, in this or other flocks, was based on fleece weights which incorporate only periods of summer wool growth into the selection criteria. Selection on later (Dec or January) fleece weights might have permitted spring/summer variation in wool growth to exert a more pronounced influence on the selection criteria than winter wool growth did in this study. The selection of sheep on hogget winter wool growth (June, July, August) may be effective as an additional criteria in increasing hogget and lifetime fleece weight.

If selection line differences exist, as suggested by Clark (1987) and McCutcheon et al. (1987), in the requirement or metabolism of S-containing amino acids, then a lower requirement of FW sheep for S-containing amino acids may have exerted a positive permissive influence on winter wool growth in FW sheep. Reis and Williams (1965) found that the S-content from high producing sheep fell more during time of nutritional stress as high producers maintained greater wool growth under these conditions. Similar results were reported by Piper and Dolling (1966) and showed greater seasonal variation in S-content of wools from fleece-weight selected Merinos. A study of the S-content of monthly fleece samples from these flocks would be of great assistance in understanding seasonal responses between selection lines.

Similarly, it would be of interest to subject sheep from the FW and C lines to artificially short photoperiods during summer (or treat the animals with melatonin). A trial of this nature would help to establish whether differences in winter wool growth are due mainly to altered photoperiodic response, or to the ability of FW sheep to make better metabolic use of limited feed resources in winter. If the study was conducted at various levels of nutrition, the interaction of seasonal and nutritional factors could be elucidated. Any study of this nature should include comparisons of wool S-content.

This study has not determined the nature of seasonal influences on winter wool growth in the fleece weight selected line. These relationships may become clearer after comparison of intake, efficiency on pasture (Chapter 6) and seasonal reproduction (Chapter 7).

DRY MATTER INTAKE AND GROSS EFFICIENCY OF WOOL AND BODY GROWTH OF FW AND C HOGGETS ON PASTURE

6.1 Introduction

In commercial flocks, the objective of fleece weight selection is to improve the efficiency of wool production. This efficiency has been increased in Merino F+ flocks in Australia (McGuirk, 1980). Vercoe and Frisch (1982) argued that sheep represent animals well adapted to grazing conditions. Furthermore, they suggest tha when a sheep's usual environment is disrupted, such as placing it indoors for feeding or changing the animals with which it socialises, one of the responses is the removal of those conditions which stimulate feeding behaviour on pasture. They suggest that failures to demonstrate differences in intake, unless conducted out of doors, do little to improve our knowledge of sheep biology, which is a balance between production potential and productive adaption to the environment.

Whether differences in the intake of FW versus C sheep exist on pasture remains to be determined. In any case, it is certainly preferable to conduct these comparisons, as Vercoe and Frisch suggest, under free grazing situations.

6.2 Materials and Methods

Experimental plan

The study was conducted between January and October of 1985 on 1984-born ram hoggets from the FW and C lines. These rams were a subset of rams involved in the experiment described in Chapter 5. In January of 1985, 15 FW and 15 C rams were chosen at random from their respective lines and harnessed for total collection of faeces over a 14-day period.

The decision was made, after the January collection, to sample 4 ram progeny from each of the four sires represented in each line (a total of 32 sheep) while maintaining as many of the January sampled rams as possible. This change was thought to give a more judicious sampling of genetic material from each of the lines. Where a surplus of sire offspring had been sampled in January they were randomly deleted and extra offspring, in other sire groups, were added on the same random basis. These 32 ram hoggets were harnessed repeatedly for total faecal collection during 2 weeks in each of April, July and October of 1985.

Collections were during the middle 2 weeks of each 4 week wool growth period (chapter 5). Collection months were chosen to coincide approximately with season, the four collections representing summer, autumn, winter and spring. Pasture sampling for herbage allowance was completed immediately prior to each faecal collection.

6.2.2 Harness and bag design.

Harnesses and bags were designed, tested and built prior to the experiment. Harnesses and bags used are illustrated in Plate 6.1., being adaptations of those reported by Arnold (1963) and Scoffield (1970).

A thin plastic bag was pegged inside each outer bag so that faeces could be easily removed and transported to the laboratory. Quick release buckles facilitated removal and replacement of the bags and the polymerized fabric of the outer bags withstood repeated washings and considerable abuse by the sheep. Harnesses and bags did not fit well if rams were lighter than 22 kg. As rams and fleeces grew it was necessary to add extension straps along the back.

6.2.3 Collection routine

One week after weighing and wool sampling rams were mustered into temporary yards set up in the paddock. Harnesses, without collection bags, were fitted to each ram (day 1). On day 2, at 08:00 hours, harnesses were tightened and collection bags and liners were put in place. At 08:00 hours on days 3 and 4 faeces were collected and bags were checked carefully for any signs of faecal loss. Faeces from days 3 and 4 were weighed and discarded.

Days 5-14 constituted the measured collection period. Faeces were removed and liners replaced each day between 08:00 and 09:30 hours. All bags and harnesses were removed on day 14.

Each day during the collection period, faeces were weighed and duplicate samples (100-200 gms) were weighed before and after drying at 140° F for 72 hours to determine dry matter content. In some collection periods low dry matter content of faeces required the drying times to be extended.

6.2.4 Pasture sampling

On day 1 of the collection period 20 random patches of pasture were cut to ground level within a 25cm by 75 cm frame. Grass was dried at 120° F for 48 hours and weighed to determine the herbage allowance on pasture. Subsamples of herbage were ground in a hammer mill fitted with a fine screen. Subsamples were used to determine dry matter digestibility by in vitro digestion.

6.2.5 Wool and body growth

Data from the experiment in chapter 5 were merged with intake data to estimate the gross efficiency of wool and body growth. Efficiency was measured as the weight of wool or body tissue deposited daily divided by daily dry matter intake or digestible dry matter intake.

6.2.6 Statistical methods

Data were analysed within and across periods. The within period analyses of intake included initial body weight at that collection period, as a covariate. Univariate analysis of variance at each time period, as well as repeated measures analyses across the last three collections, were carried out.

The model included the effects of initial weight, birth date, dam age, birth rank, and was similar to those used in Chapter 5.

The effect of body weight as a covariate was similar for both lines, such that separate regressions were not required.

6.3 Results and Discussion

6.3.1 Measures of intake

The rams did not appear to be bothered by the addition of harnesses and bags, and returned to normal grazing after collection of faeces (Plate 6.2). Although some faecal losses were evident on the first or second pre-collection days, by the third day all bags appeared to be tight and relatively leak free.

The April collection period was quite severely affected by ryegrass staggers. Some rams were not behaving normally and faecal outputs were reduced due to abnormal grazing. The effect of staggers on different rams was difficult to quantify and could not be removed from the analysis.

Pasture availability was reasonable in most seasons, but herbage allowance of 1100kgDM/ha in July may have caused some ingestion of soil which would bias upwards the estimates of dry matter intake (DMI) and bias downwards the estimates of wool and body growth efficiency. Organic matter content of faecal samples was not performed so that digestable organic matter intake could not be estimated. Pasture allowances and estimated dry matter and organic matter digestibilities of the herbage samples are presented in Table 6.1 a.

Dry matter intakes and digestible dry matter intakes (DDMI) are given in table 6.1c. No selection line differences in either DMI or DDMI were detected in any season. The mean digestible dry matter intakes across lines being 0.67, 1.27 , 1.84 and 1.65 kg/day in January, April, July and October, respectively.

Herbage allowances and dry matter digestibilities of the pasture at these times were 4500, 3500, 1100 and 1900 kgDM/ha and 68, 78, 74 and 79% on a dry matter basis. DDMI may have been biased downwards if lambs selected diets of higher digestibility than that of the whole sward.

Repeated measures analysis of intakes over the last three periods also failed to identify selection line differences in intake on pasture.

Although selection line differences in initial liveweight were significant in all periods (Table 6.1b) there was no difference in the relationship between liveweight and intake in the selected lines.

6.3.2 Efficiency of liveweight gain

The average daily gains of FW and C rams during the collection months and the calculated efficiency of those gains, relative to digestible dry matter intake, are given in Table 6.2 . Average daily gain and the consequent efficiencies of liveweight gain did not differ between selected lines in any of the periods measured.

Whole flock differences in rate of gain were significant in early spring (Chapter 5), but these line differences were not demonstrated in the subsampled rams. Late winter/early spring differences in liveweight gain do not account entirely for difference in hogget liveweight between lines, rather, over the entire course of the winter, the FW line gradually increases its weight advantage over C rams.

6.3.3 Wool growth and wool growth efficiency

The clean wool growth (CWOOL) and the efficiency of clean wool growth in FW and C lines is given in Table 6.2b.. Differences in clean wool growth during January were not significant in the subsampled rams, even though whole flock differences in clean wool growth over the same period were significant. During late summer, even whole flock differences were not widely separated (differences of 1.7g/d) so it is not surprising that differences of this size were not significant in the smaller subsample. Similarly, lines did not vary in the efficiency of wool growth in this first collection.

Although the difference in wool growth in subsampled rams during April appeared to reflect the differences found in the whole flock (C:FW is 7.0:8.5 g/d in the whole flock) the effect of rye-grass staggers may have been responsible for the inability to detect significant differences in the efficiency of wool growth during this period. Differences approached significance (p=.08) and it is unfortunate that the comparison was not unencumbered by extraneous effects.

Selection line differences in the efficiency of wool production during mid winter (July) were highly significant and the relative advantage (FW-C)/C of FW rams was 67%. The wool production of FW and C rams accurately reflected equivalent whole flock comparisons (C:FW is 7.1:10.8 g/d in the whole flock). This large difference in the efficiency of winter wool growth indicates that FW sheep are not as restricted, by photoperiodic or nutritional variables, as C sheep over winter.

The ability of FW sheep to respond to additional dietary protein (Chapter 4) was also evaluated in winter months. Differences in that experiment may have reflected seasonal differences between genotypes, in which exaggerated differences in efficiency are demonstrated during winter months.

Increased efficiency over winter is responsible, in the absence of intake differences, for sustained winter wool production in the FW line. This sustained winter wool production may have additional benefits in the resultant staple strength of FW and C fleeces, which will be evaluated in chapter 8.

During October, the largest absolute differences in wool production occur between FW and C hoggets. The efficiency of wool growth during this period was also highly significant in these data. Although the subsampled rams did not display the same magnitude of wool growth differences as were seen in the whole flock (C:FW is 12.5:17 g/day in whole flock comparisons), differences in wool growth between C and FW subsampled rams were also highly significant, as were the resultant efficiencies. The relative advantage of FW over C rams for October wool growth efficiency was 33%.

The relative differences between lines in wool growth efficiency, as well as the absolute efficiencies are well within the ranges quoted in the literature (Butler and Maxwell, 1984). It is difficult to comment on the trends in efficiency from 4-14 months of age. The high wool growth efficiency of young animals is not discussed widely in the literature, and relative to efficiencies calculated at later ages, appears quite high. In young animals, the skin represents a relatively large productive organ, such that relative to intakes, skin output of wool fibre represents a relatively large productive component.

These results are in agreement with a number of Australian studies reviewed earlier and summarized by Williams (1979,1987). Selection for fleece weight has resulted in significant increases in wool production, in the presence of insignificant differences in measureable feed intake, the net result being an increase in the efficiency of conversion of feed to wool.

Table 6.1 Measures of pasture, liveweight and intake by season and line

a) Pasture availability and digestibility

Pasture Measurements

Month	Available herbage (kgDM/ha)	Dry matter digestibility (%)	Organic matter digestibility (%)
January	4500	68.2	66.3
April	3500	78.3	72.4
July	1100	74.1	68.2
October	1900	79.2	73.5

Plate 6.1 Faecal collection bags (with liners) and harnesses

Plate 6.2 Harnessed rams returned to grazing

Table 6.1 Measures of pasture, liveweight and intake by season and line

b) Monthly intial liveweight and liveweight $^{.75}$

Month	Initial wt (kg)			Initial wt$^{.75}$ (kg$^{.75}$)	
	C	FW		C	FW
January	29.8±1.1	29.0±1.3	ns	12.7	12.5
April	33.9±1.2	34.5±1.1	ns	14.1	14.2
July	33.4±1.4	37.6±1.5	*	14.2	15.2
October	44.9±1.3	48.0±1.4	*	17.3	18.2

Table 6.1 Measures of pasture, liveweight and intake by season and line

c) Digestible dry matter intake (DDMI) and DDMI/wt$^{.75}$

Month	DDMI (kg)			DDMI/wt$^{.75}$	
	C	FW		C	FW
January	0.655±.022	0.687±.023	ns	51.6	54.9
April	1.257±.141	1.315±.218	ns	89.1	92.6
July	2.011±.629	1.955±.369	ns	141.6	128.6
October	1.621±.358	1.765±.336	ns	93.6	96.7

Table 6.2 Production and productive efficiency by line and season

a) Average daily gain (ADG) and efficiency of gain ADGEFF calculated relative to DDMI, in g/kg DDMI.

Month	ADG (g/d)		ADGEFF (g/kgDDMI)		
	C	FW	C	FW	
January	124±10	128±11	189±20	186±15	ns
April	34±20	67±15	27±15	51±16	ns
July	89±10	84±11	44± 6	43±5	ns
October	192±10	186± 9	118± 7	105±6	ns

b) Clean wool growth (CWOOL) in g/d and the efficiency of clean wool growth (CWOOLEFF) in g/kg DDMI

Month	CWOOL (g/d)		CWOOLEFF (g/kg)		
	C	FW	C	FW	
January	13.0±.6	13.9±.6	19.8±.4	20.2±.5	ns
April	7.8±.4	9.4±.7	6.4±.4	7.3±.5	p<.10
July	6.8±.4	11.3±.5	5.2±.4	8.7±.4	***
October	13.2±.4	19.0±.4	10.5±.4	14.0±.4	***

6.4 Conclusions

Selection for fleece weight appears to have resulted in improved efficiency. This result was consistent over a number of seasons, although it was only significant in winter, and spring, in these comparisons. In other seasons, the failure of the subsampled group to reflect changes in wool production of the entire flock, or the complicating effects of rye-grass staggers on animal intake may have affected the ability to discern differences in efficiency.

The large relative differences in efficiency over winter months may indicate altered seasonal responses in FW sheep or may reflect differences in the composition of wool grown during times of nutritional stress. Vercoe and Frisch (1982) describe a successful animal in terms of potential advantage, demonstrated during non-stressed production, and adaptive potential that is related to the ability to sustain production during times of nutritional or environmental stresses. It would appear that FW sheep have both potential and adaptive advantages over C sheep, being able to perform equally well during the poor winter and good spring conditions.

These results are in agreement with those of other researchers with Merinos, summarized by Williams (1979). Selection for fleece weight does not appear to have altered the intake of FW sheep in the absence of differences in liveweight. The efficiency of conversion of feed to wool is increased, under pasture and pen-fed comparisons, as a result of selection for fleece weight.

INCIDENCE AND DURATION OF HOGGET OESTRUS

7.1 Introduction and review of literature

7.1.1 The importance of reproductive rate to efficient sheep production

Low reproductive rate is a major factor limiting the productivity of sheep enterprises. The biological and economic efficiency of sheep production would likely increase with improved reproductive performance as the relatively large fixed cost of ewe maintainance (Coop, 1961) would be spread over a larger number of saleable offspring (Dickerson, 1970; Large, 1970: McGuirk, 1976; Bindon and Piper, 1976; Dalton and Rae, 1978; Woolaston and Butler, 1987). Ultimately, low reproductive rate will reduce the rate of genetic progress in any character under selection as loss of selection pressure results from low numbers of available replacements.

Although several measures of reproductive rate exist, the number of lambs weaned per ewe joined per year (NLW/EJ) is an informative assessment of the annual reproductive performance of the ewe flock. The NLW/EJ is a composite trait representing four components as follows:

$$\text{Reproductive rate} = \text{Ewe survival} \text{ X } \text{Ewe fertility} \text{ X } \text{Litter size} \text{ X } \text{Lamb survival}$$

written as $$\frac{NLW}{EJ} = \frac{EPL}{EJ} \text{ X } \frac{EL}{EPL} \text{ X } \frac{NLB}{EL} \text{ X } \frac{NLW}{NLB}$$

where: EPL = ewes present at lambing
EL = ewes lambing, and
NLB = number of lambs born.

Furthermore, litter size is also a composite trait subdivided as follows:

$$\text{Litter size} = \text{Ovulation rate} \text{ X } \text{Zygotic fertility} \text{ X } \text{Embryonic survival}$$

written as $$\frac{NLB}{EL} = \frac{OR}{EL} \times \frac{NFE}{OR} \times \frac{NLB}{NFE}$$

where, in addition: OR = ovulation rate, and
NFE = number of fertilised embryos.

Increased reproductive rate can be achieved by altered management, direct manipulation or by the judicious application of genetic principles to any combination of the above components or related physiological traits. Genetic improvement of reproductive components may not lead to increased reproductive performance in situations where environmental constraints, natural selection or concurrent selection for other productive characters is allowed to discriminate against individuals of high genetic merit for reproduction (Bielharz, 1986; Bielharz and Luxford, 1987).

7.1.2 Factors affecting the onset and duration of oestrus in ewe hoggets

Extensive reviews of the breed, line and environmental factors affecting the attainment of puberty in ewe lambs have been presented elsewhere (Dyrmundsson, 1973; 1981; 1983; Rattray, 1977; Land, 1978b; Lees, 1979; McMillan, 1981). Only environmental factors will be briefly summarised here.

Definition of puberty:

The most common practical definition of puberty in ewe lambs is the first occurrence of behavioral oestrus (Dyrmundsson, 1973). As numerous authors have demonstrated subsequently that oestrus and ovulation are not always concomitant events in ewe lambs (Edey et al., 1977; 1978; Hare and Bryant, 1982), some authors have preferred to include the condition of permitting insemination at an ovulatory oestrus in the definition of puberty (Edey et al., 1978; Quirke, 1981). The former definition will be considered satisfactory in this study.

7.1.2.1 Endocrinology and photoperiod effects

The endocrine events leading to ovulation in cyclic ewes can be summarised (very simply) as follows:

1. The release of gonadotrophins (Luteinising Hormone (LH) and Follicle Stimulating Hormone (FSH)) from the pituitary is regulated by a neurohormone (Gonadotrophin Releasing Hormone (GnRH)) from the hypothalamus. These gonadotrophins stimulate the growth of ovarian follicles.

2. Growing follicles, in turn, synthesize a range of steroid and peptide hormones, including oestradiol and inhibin, which exert a negative-feedback action on the release of pituitary gonadotrophins. Progesterone, produced by the corpus luteum during the luteal phase of the cycle, also exerts a negative feedback action on the release of LH and enhances the inhibitory effects of oestradiol.

3. Very high levels of oestradiol, such as are produced by the growing ovarian follicle near the end of the cycle, are also responsible for the pre-ovulatory surge of LH which consummates the ovulatory process by releasing the egg from the mature follicle. This positive feedback of oestradiol is facilitated by a fall in progesterone levels resulting from a release of prostaglandins from the uterus.

In the last decade, much research has focused on the endocrine control of seasonal anoestrus in sheep and the onset of puberty in young sheep. Ovarian steroid secretion during anoestrus has been reviewed by Karsch et al. (1984) who found that follicles which develop during anoestrus have an apparently normal capacity to secrete oestradiol. Anoestrus was found to be related to decreased magnitude and spike frequency of episodic LH secretion. They proposed that during anoestrus, the sensitivity of the hypothalamo-pituitary axis to oestradiol was lowered. Foster and Ryan (1979a,b) noted that the onset of oestrus at puberty and the occurrence of oestrus at the beginning of the breeding season of adult ewes might both be related to a pronounced decrease in the response of the hypothalamus to the negative feedback action of oestradiol on subsequent release of GnRH. They proposed that "puberty" could almost be considered an annual process in the ewe.

Since 1979, a plethora of information has been published and reviewed on the physiological effects of melatonin, an indole-amine released from the pineal gland during darkness hours. It is thought that melatonin may be the chemical responsible for this variation in sensitivity of the hypothalamic-pituitary axis to oestradiol, and hence the seasonality of reproduction and puberty in sheep (Foster and Ryan, 1981; Bittman et al., 1983a; 1983b; Bittman and Karsch, 1984; Karsch et al., 1984; Kennaway, 1984; Foster et al., 1986). Others are working to devise methods which will allow the time of onset of oestrus activity to be manipulated directly by the strategic treatment of ewes (Arendt et al., 1983) and ewe lambs (Kennaway and Gilmore, 1984; Nowak and Rodway,1985) with exogenous melatonin. Exogenous melatonin treatment, although requiring long term administration via oral, subcutaneous, ruminal or vaginal routes, may still prove to be a viable management option due to the relatively low cost of manufacturing synthetic melatonin.

This area of research will not be discussed at length; however, a few points are worth noting.

i) Ewe lambs require an 11-15 week period of exposure to long days in which to establish a circadian sensitivity to melatonin (Yellon and Foster, 1982;1985). Without this long-day exposure puberty is delayed. In breeds with pronounced seasonality, puberty may be delayed until the following autumn/winter as is the case in lambs born and reared out of season (Kennaway, 1984).

ii) The transition into adulthood is not sudden but, rather, is characterised by shortened or incomplete cycles during which part of the endocrine system becomes "primed" to the presence and action of progesterone (Foster et al. 1984). One or more of these cycles may involve silent ovulations (Foote et al., 1970; Foster and Ryan, 1979a,b;Hare and Bryant, 1982). The first ovulatory oestrus occurs subsequent to these irregular cycles. Similar "transitional" cycles are often seen in adult ewes (Karsch et al., 1984).

iii) Ewe hogget live weight, growth rate, and age interact with the above dynamic system such that the exposure of the young ewe to the appropriate photoperiodic stimuli does not necessarily guarantee that the lamb will attain puberty. These interactions may be dependent on genetic factors (Rattray, 1977; Land, 1978b).

iv) Cessation of oestrus activity in both ewes and ewe lambs seems to be a result of refractoriness of the hypothalamic-pituitary axis to the effects of melatonin.

7.1.2.2 Age and liveweight

Care must be taken in generalising about the minimum age or liveweight required for the attainment of puberty as age, birth rank, season of birth, growth rate and genetic effects can all interact with photoperiodic conditions. Several New Zealand studies have shown that animals reaching puberty in the first autumn/winter tend to be heavier than those which do not (Ch'ang and Raeside, 1957; Hight et al., 1973; Meyer and French, 1979; Baker et al., 1981; McMillan and McDonald, 1983; Asofi, 1984). In other studies little or no difference was found (Baker et al., 1979; Quirke, 1979).

Animals born later in the season will tend to reach puberty at a younger age and lower liveweight than those born earlier in the year as critical photoperiodic effects are experienced by early- and late-born lambs at similar times of the year (Hulet et al., 1969; Dyrmundsson, 1973; 1981; 1983; Dickerson and Laster, 1975; Cedillo et al., 1977; Baker et al., 1979; Quirke, 1981). Early-born ewes, perhaps due to a liveweight advantage, reach puberty earlier than late-born ewes (Dyrmundsson and Lees, 1972a).

Twin born lambs are often older and lighter at first oestrus, particularly if late born, due to the combined effects of lower body weight and/or body weight gain (Hulet et al., 1969; Baker et al., 1978; Dyrmundsson and Lees, (1972a).

7.1.2.3 Presence of the ram

Although sudden introduction of rams into groups of prepubertal ewes can lead to oestrus synchronization, the date of first oestrus is usually unaltered (Dyrmundsson and Lees, 1972b).

7.1.3 Selection for improved reproductive performance

7.1.3.1 Direct selection

Early reviews of genetic influences on reproduction in sheep were quite pessimistic (Reeve and Robertson, 1953) and, although breed differences were recognised, individual variation was considered inconsequential. Later work showed that direct selection for increased fertility would likely yield only limited improvement, primarily because the maximum level of performance is 100%, but also because heritability and repeatability values for fertility were very low (Young et al., 1963; Turner, 1969; McGuirk, 1976; Land, 1977; 1978a). The other, perhaps more important inference, was that fecundity showed sufficient genetic variation, and repeatability, to warrant direct selection.

Genetic differences in fecundity between and within most breeds of sheep are considered to be due to many genes of small effect. Selection for increased fecundity is assumed to produce small incremental changes in a phenotypically discrete character. The exception to this is the Booroola Merino where a single gene, the F-gene, of major additive effect is responsible for much of the observed variation in ovulation rate in this population (Piper and Bindon, 1982). Recent work on the mechanics of ovarian follicular development (Driancourt et al., 1986; Driancourt and Fry, 1988) has shown that selection for high ovulation rate in Booroolas, Finns and Romanovs has led to three distinct ovulatory mechanisms, each of which helps to control the final observed ovulation rate. As our understanding of ovulation rate increases it may be possible to select directly for underlying hormonal and physiological traits.

A number of fertility/fecundity selection flocks were independently established in New Zealand (Wallace, 1958; 1964; Clarke, 1972; 1977) and Australia (Turner 1962; 1969;

Young, et al. 1963; McGuirk, 1976). The central limitations of these systems were soon pointed out, namely:

i) characters were sex-limited and rams had to be selected on the basis of the performance of female relatives,

ii) age of the ewe exerted considerable influence on the level of performance and heritability,

iii) the ram's contribution to conception rate often masked important variation in ewe traits, and

iv) fertility and fecundity were themselves influenced by the ewe lamb's birth status.

Even given these complications, annual genetic gains of 1-2 lambs docked per 100 ewes joined have been achieved in three separate selection experiments (Turner, 1968; Dun and Eastoe, 1970; Clarke, 1972).

7.1.3.2 Indirect selection

The difficulties inherent in improving reproductive rate by direct selection have prompted many studies into methods of indirect selection or selection for component traits, especially measures of fertility/fecundity evident at an earlier age, in an attempt to obviate the problems outlined above. Potential selection criteria have been reviewed by Bindon and Piper (1976), Land (1977), Bradford (1985), Purvis (1987) and (in Romneys) Dalton and Rae (1978), and include:

i) plasma LH and FSH levels,
ii) testis growth and diameter,
iii) ovulation rate,
iv) number of hogget oestruses, and
v) liveweight at weaning or 14-months.

FSH and LH have the advantage of being measurable in both sexes at an early age; however, the pulsatile nature of LH release means that one blood sample is unlikely to be a reliable indicator of LH status. Measurement of FSH concentration permits discrimination between ewe lambs of varying merit for fertility/fecundity but not between ram lambs (Bindon and Piper, 1976; Ricordeau et al. 1984). Excellent discussions of FSH and LH levels and their interactions with genetic and environmental factors can be found in Findlay and Bindon (1976), Land (1978b) and Land and Carr (1979).

In search of a character in rams which may be related to component of female reproduction, Land (1973) and Islam and Land (1977) studied testis growth rate and diameter in breeds and crosses differing in fecundity. This work, and preliminary results from a divergent large versus small testis diameter selection trial, are summarised by Land (1978b). An increase in adult testis diameter was accompanied by a delayed end to the breeding season and higher ovulation rate in the large testis line. Increased juvenile testis diameter, and early testis growth rate, were associated with increased ovulation rate and earlier onset of the breeding season. The heritability of testis diameter in sheep has ranged from 0.1 to 0.6 and adjustment for date of birth and birth rank are required (Kilgour et al., 1985; Purvis, 1987).

The prospect of utilising ovulation rate (measured by endoscopy) as a selection criterion has recently received more attention (Bradford, 1972; Hight et al., 1973; Hanrahan, 1974; Bindon and Piper, 1976). Ovulation rate is highly repeatable both within (.69) and between (.15 to .78) years (Turner, 1962; Hanrahan, 1976). The highest estimates of repeatability were obtained in high fecundity breeds such as the Finnish Landrace. The heritability of ovulation rate has not been reliably assessed. Although the relationship between ovulation rate and litter size is less than unity (Hanrahan, 1976) it appears safe to conclude that litter size will increase following selection for ovulation rate. Smith et al. (1987) have demonstrated a close genetic relationship between naturally occurring ovulation rates and those induced by Pregnant Mare Serum Gonadotrophin (PMSG). Treatment with PMSG had the advantage of allowing ovulation rate to be expressed in a proportion of otherwise anovular prepubertal ewe lambs. A practical programme for the use of ovulation rate to improve fecundity is outlined by Hull and Hanning (1980).

Like ovulation rate or fertility, the number of times a ewe or ewe hogget displays oestrus is a measure of ovarian activity. Heritability estimates for the number of hogget oestruses in New Zealand Romneys, summarised by Dalton and Rae (1978), are higher than those of other reproductive traits measured in mature ewes. The number of hogget oestruses has also been positively related to subsequent reproductive rate in a number of within (Ch'ang and Rae, 1970; 1972; Bindon and Piper, 1976), and between breed studies (Dyrmundsson, 1973). The percentage of ewe hoggets displaying oestrus is another way of describing oestrus occurrence in hoggets. Higher subsequent reproductive performance in ewes able to show oestrus in their first autumn has been widely demonstrated (Hulet et al., 1969; Hight and Jury, 1976; Baker et al. 1987).

A recent review of the genetic and physiological relationships between growth and reproduction in mammals concluded that mature and yearling liveweight had strong genetic correlations (.44 to .78) with the number of lambs born per ewe mated or per ewe lambing (Brien, 1986). Genetic correlations with weaning weight were also positive but of lesser magnitude (.17 to .37). Barlow and Hodges (1976) showed similar ewe lamb reproductive performance in lines simultaneously selected for reproductive rate, weaning weight and clean fleece weight or selected on weaning weight alone. Recent work by Davis (1987), in Merinos, demonstrated correlated responses to selection for increased weaning weight in all reproductive traits except fertility and prolificacy. The correlated response resulted from increased lamb survival and rearing ability of the dams. Comparisons of Ruakura lines differing in reproductive rate have not always demonstrated differences in weaning weight while 14-month weight was usually higher in the higher fecundity lines (Clarke, 1972; Dalton and Rae, 1978; Baker et al., 1987).

7.1.4 Relationships between wool growth and reproduction

Estimates of the genetic correlation between hogget greasy fleece weight and subsequent lamb production have varied from strongly negative (-.85) to strongly positive (+.92) in studies by Kennedy (1967), Blair (1981) and Davis and Kinghorn (1986). Estimates published prior to 1978 (most of them negative) have been reviewed by Lewer (1978). Lewer's own estimates of the genetic correlation between number of lambs weaned and hogget greasy fleeceweight were negative but variable, and ranged from -.54 to -.04. None of the genetic correlations was significantly different from zero. Turner (1972) concluded that available estimates of this genetic correlation were not sufficiently antagonistic to prevent simultaneous selection for wool, meat and reproduction. On the basis of Merino parameters, judicious cross-breeding may be a better method to improve all three traits as quickly as possible (Turner, 1972). She also commented on the highly variable reported genetic correlations between fleeceweight and reproduction and noted that failure to account fully for birth rank effects may bias this correlation downwards.

An association between the seasonality of wool growth and length of the reproductive season was found by Montgomery (1987) and Montgomery and Hawker (1987). These authors demonstrated higher ovulation rates and a prolonged breeding season in Romney and Perendale ewes with a history of high, rather than low, winter wool growth. They also commented on the relevance of their results to across breed comparisons of the seasonality of wool growth and reproduction. Heath and Lynch (1982) demonstrated analogous intra-specific differences in sensitivity of hair growth and reproduction to exogenous melatonin in strains of white footed mice from northern and southern regions of the United States. It remains to be shown whether breed differences in the sensitivity of physiological systems to photoperiod relate to differences in the level or pattern of production of melatonin, or the response of endocrine or target tissues to circulating melatonin concentration.

Selection for high hogget greasy fleece weight in the Massey University PT Romney flock has been accompanied by correlated responses in weaning weight, hogget liveweight and the number of lambs born and reared per ewe lifetime (Blair, 1981; Blair et al., 1984). The pathways through which selection for increased fleeceweight has led to increased lamb production in this flock have not yet been elucidated. Preliminary analyses of 1982-, 1983- and 1984-born two-tooth lambing records have failed to show significant differences in either fertility (EL/EPL) or fecundity (LB/EL). This implies that differences in lifetime reproductive performance are due to lambing performance at later lambings. Turner (1969) has shown that differences in lamb production were often not evident until the second or later lambings.

Increased reproductive performance in FW ewes may relate to advantages in liveweight or to other indirect effects such as the related responses of wool growth and reproduction to photoperiodic effects. As noted by Blair (1981) it is also possible that fixation of some gene (or genes) favorable for lamb production has occurred.

7.1.5 Objectives of the current research

The objectives of this trial were to:

1) examine the onset and duration of oestrus in fleeceweight-selected (FW) and control (C) Romney hoggets,

2) determine the contribution of within- and between-line differences in liveweight, liveweight gain and age to the observed differences in the onset and duration of oestrus, and

3) to observe the relationship between the incidence of hogget oestrus, wool growth and subsequent reproduction.

7.2 MATERIALS AND METHODS

7.2.1 Experimental plan

The experiment was conducted on the "Pahiatua block" farm of Massey University. A total of 148 ewe hoggets born either 1984(86) or 1985(62) from the fleeceweight-selected (FW) and control (C) subflocks were used in the study. In 1985 and 1986 there were 61(30,31) C hoggets and 87(56,31) FW hoggets present throughout the breeding season (defined as 03 April to 24 July). In each year, hoggets from the two subflocks were grazed together. Figure 7.1 shows a calendar of events for the two years of data collection. Ewe lambs born 1984 were involved in concurrent wool growth (Chapter 5), and staple strength (Chapter 8) studies.

7.2.2 Recording of reproductive activity and growth

Ewe hoggets were run with vasectomised South Suffolk cross ram lambs from 03 April until 24 July in both 1985 and 1986. In order to maintain a constant ram:ewe ratio in the two years, three rams were used in 1985 while only two were needed in 1986. Ram lambs were well grown by the start of the breeding season. Ram marker crayons and colour were changed every fortnight and checked during the intervening week to ensure effectiveness. Observation and recording of marked ewe hoggets was done at the end of each 14-day mating period.

Ewe hoggets were weighed monthly after an overnight (16 hour) fast indoors. During the fasting period, rams were kept separate from the ewes to avoid mismarkings in the crowded shed conditions.

Seven mating periods, with four crayon colours available, meant that very heavy marks had to be scrubbed out with soapy water, and light marks removed by hand clipping, before subsequent colour rounds were begun. Colour rotations, different in the two years, are also shown in Figure 7.1. In 1985, ewe lambs showed no signs of oestrus in the first mating period so ram crayons were freshend up and used again in the next period. No ewe lambs appeared to be cycling after 26 June, 1985. From 26 June, 1985 until 24 July, 1985 the rams remained fitted with soft purple crayons but no marks were found. Yellow crayons were not used in 1986 because of difficulty in detecting light yellow marks.

A number of additional variables were formed from the tupping and liveweight data including:

Oestrus display variables:

- age at first tup (days)
- weight at first tup (kg)
- length of the breeding season (number of mating periods, 1-7)
- number of mating marks (1-7)
- period of first marking (1-7)
- period of last marking (1-7)
- oestrous displayed at any time (0=no,1=yes)

Liveweight gains (kg):

- post-weaning gain (04 Apr weight - weaning weight)
- autumn gain (24 July weight - 04 April weight)
- April gain
- May gain
- June gain
- July gain
- gain to shearing (Post shearing weight - 24 July weight)

Liveweights were not corrected for differences in the weight of fleece carried as monthly wool growth (needed to obtain fleece-free body weights) was only available for 1984-born hoggets. All liveweights, with the exception of post-shearing liveweight (14 months of age), overestimate true fleece-free liveweights and all liveweight gains are, correspondingly, biased.

7.2.3 Statistical methods

7.2.3.1 Continuous characters

Univariate analyses of variance were performed on all records of hogget fleece weight, June clean wool growth, weaning weight, monthly weights during the breeding season, post-shearing liveweight, liveweight gains over the post-weaning, breeding and post-breeding seasons and monthly liveweight gain over the breeding season. The preliminary analyses included all main effects and first order interactions. Second or higher order interactions were assumed negligible. Subsequent to these preliminary analyses, interactions which were consistently non-significant were omitted from the model to give:

Model 7.1 $y_{ijklmn} = \mu + a_i + bX_{ijklmn} + r_j + d_k + l_l + p_m + al_{il} + rl_{jl} + lp_{lm} + e_{ijklmn}$

where, y_{ijklmn} = an observation on the n^{th} individual of m^{th} puberty status, j^{th} birth rank, k^{th} dam age, l^{th} selection line and born in the i^{th} year,

μ = the unobserved population mean,

a_i = the fixed effect of the i^{th} year,

b = the regression of y_{ijklmn} on X_{ijklmn},

where,

X_{ijklmn} = an observed individual birth date,

r_j = the fixed effect of the j^{th} birth rank,

d_k = the fixed effect of the k^{th} age of dam

l_l = the fixed effect of the l^{th} selection line,

p_m = the fixed effect of the m^{th} puberty status,

al_{il} = the fixed effect of the interaction between year and selection line,

rl_{jl} = the fixed effect of the interaction between birth rank and selection line,
lp_{lm} = the fixed effect of the interaction between selection line and puberty status, and
e_{ijklmn} = the random residual associated with an observation on the $ijklmn^{th}$ individual.

Univariate analyses were also performed only on records of sheep which had displayed oestrus as a hogget to estimate the effect of selection line and other factors on age af first oestrus, weight at first oestrus, the number of hogget oestruses, the length of the breeding season and the period of first and last marking. The model used was similar to Model 7.1 with the exclusion of p_m and its interactions.

Multivariate analyses, notably repeat-measures analysis, were conducted on monthly liveweights and liveweight gains during the breeding season, as well as on post-weaning, breeding and post-breeding seasonal liveweight gains. As outlined in Chapter 3, repeated measures analyses were used to obtain more powerful tests of mean differences between levels of the main effects in the model and to obtain direct estimates of time effects. The underlying linear model included main effects, time effects and interactions as outlined in Model 7.1 with the inclusion of p-dimensional time effects and the interactions between time and design factors. Repeated measures analyses have been described in Chapter 3. Null hypotheses were tested using the Chi-squared statistic as described by Morrison (1976).

On a within-time basis these residuals were assumed to be individually and independently distributed, there being covariances amongst individual residuals across times due to the repeated nature of the sampling.

7.2.3.2 Discrete characters

Occurrence versus non-occurrence of hogget oestrus was analyzed as a binary variable by the method of iterative re-weighted least squares in an analysis of deviance (Gilmour, 1985). The dependent variables were transformed, prior to analysis, using the logit transformation.The deviances were tested as Chi-square variables.

When covariates are included in logit models, the regression coefficients cannot be simply interpreted as in a linear regression model. As these regression coefficients were not of primary interest in this study, they will not be discussed further, except to mention their statistical significance.

The model used to describe the occurrence versus non-occurrence of hogget oestrus was as follows:

Model 7.2:

$$y_{ijkl} = \mu + a_i + b_1X1_{ijkl} + b_2X2_{ijkl} + r_j + l_k + e_{ijkl}$$

where,

y_{ijkl} = an observation on the incidence of oestrus in the l^{th} ewe hogget born in year i, of birth rank j, in selection line k,

μ = an unobserved population mean,

a_i = the fixed effect of the i^{th} year

b_1 = the regression of y_{ijkl} on $X1_{ijkl}$ where,

$X1_{ijkl}$ = the observed birth date of the $ijkl^{th}$ individual, and

b_2 = the regression of y_{ijkl} on $X2_{ijkl}$ where,

$X2_{ijkl}$ = the observed 30 May liveweight of the $ijkl^{th}$ individual,

r_j = the fixed effect of the j^{th} birth rank,

l_k = the fixed effect of the l^{th} selection line, and

e_{ijkl} = the random residual associated with the ijklth individual

Two-tooth lambing records were analysed as a binomial variable, and the effect of previous oestrus status on two-tooth fertility/ fecundity was determined by:

<u>Model 7.3</u> $y_{ijk} = \mu + bX_{ijk} + l_i + p_j + lp_{ij} + e_{ijk}$

where,

y_{ijk} = an observed lambing record of the kth ewe of mth puberty status from the lth line, born in 1984,

μ = an unobserved population mean,

b = the regression of y_{ijkl} on X_{ijk}, where,

X_{ijk} = an individual autumn pre-mating liveweight,

l_i = the fixed effect of the ith selection line,

p_j = the fixed effect of the jth puberty status,

lp_{ij} = the interaction of selection line and puberty status, and

e_{ijk} = the random residual associated with the ijkth observation.

7.3 <u>RESULTS</u>

7.3.1 <u>Liveweight</u>

Mean liveweights of hoggets at weaning and hogget shearing and during the intervening breeding season are presented in Table 7.1a while the repeated measures analysis is in Table 7.1b.

Examination of the repeated measures analyses of breeding season liveweights showed highly significant month, year and month by year effects. Dam age, date of birth and selection line also significantly affected hogget liveweights. Significant month by selection line interactions arose from increased selection line segregation as the breeding season progressed. Line differences became significant by 29 May, and FW hoggets remained heavier than C hogget until hogget shearing. The overall effect of birth rank was not significant. A significant birth rank by selection line interaction resulted from twin-born hoggets of both lines being similar in weight, whereas, single-born FW hoggets were heavier than single-born C hoggets. This interaction was independant of months. Cyclic ewe hoggets were heavier than acyclic hoggets throughout the entire breeding season. Remaining first order interactions were non-significant.

Weaning weight and post-shearing liveweight were analysed by separate analyses of variance. Single-born lambs were 3 kg heavier at weaning than twin-born lambs. Five-year old ewes weaned lambs which were 2-3 kg heavier than those born to 2-, 3- or 4-year old ewes. Hoggets which cycled were 1 kg heavier, at weaning and throughout the autumn, than acyclic hoggets. By the time of hogget shearing no liveweight differences were found between cyclic and acyclic ewes.

Significant interactions existed between hogget oestrus display status and and selection line. Acyclic and cyclic C ewe hoggets did not significantly differ in liveweight at any time of the year, but acyclic FW hoggets were 2 kg lighter than cyclic FW ewes from weaning through to June. After this time, the difference in liveweight was reduced to 1 kg.

7.3.2 Liveweight gain

Monthly liveweight gains during the breeding season were analyzed separately and by repeated measures analysis. Post-weaning gains, gains over the breeding season and gains from July to hogget shearing were studied in a similar manner. Mean liveweight gains are presented in Table 7.2a and the repeated measures analyses are presented in 7.2b and 7.2c.

7.3.2.1 Monthly weight gain in the breeding season.

Differences in liveweight gain over the four months in the breeding season were highly significant as were year and month by year-effect. Selection line differences were also significant with FW hoggets gaining 300-900 gms more than C sheep over four-week periods. Although there was no difference in liveweight gain between cyclic and non-cyclic hoggets, there was a suggestion of a line by cyclic status interaction (p<.10) such that non-cyclic FW sheep were gaining more than non-cyclic C hoggets. No differences in liveweight gain existed between FW and C cyclic hoggets. Selection line by year interactions were significant (p<.05) such that in 1985, selection line differences in liveweight gain were much larger than in 1986. In both years, line differences in liveweight gain were most pronounced in May and June.

7.3.2.2 Gains post-weaning, over the breeding season and post-breeding season

Differences in liveweight gain by season were highly significant (p<.001) reflecting different areas of the growth curve. Gains in all periods were affected by year (p<.001) and significant season by year interactions were present. Twin-born lambs gained more than single born lambs (p<.05) especially in the post-weaning period. Lambs born later in the year had greater growth rates than early-born lambs (p<.001). The effect of date of birth on liveweight gain varied with the season, the effect decreasing as lambs became older. Cyclic and non-cyclic ewes did not differ in liveweight gain when weaning to hogget shearing was the interval

7.3.3 Puberty

Table 7.3a shows the percentage of ewe hoggets in oestrus, classified by selection line and year. The analysis of deviance (Table 7.3b) proved to be quite volatile with respect to order of fit and the distribution of input data for various traits. Date of birth and selection line significantly affected the attainment of puberty in these data.

7.3.3.1 Onset of oestrus

The time of onset of the breeding season, assessed as the 14-day period in which the first tupping marks were observed, was significantly affected by year. In 1985, the mean period of first oestrus was 4.01±.27 while in 1986 it was period 2.37±.19. These corresponded to the last two weeks of May (1985) and the last two weeks of April (1986). Time of onset of the breeding season was unaffected by date of birth, dam age, birth rank, or selection line and there were no significant interactions. The model explained 42.5% of the variation in date of first oestrus.

Onset of the breeding season was also estimated by the age at first oestrus. As tupping marks were read quite infrequently (fortnightly), the smallest effective difference that can be interpreted is also 14 days. Hoggets born in 1984 reached puberty 23 days later than 1985-born hoggets (267±4 versus 244±3 days). For every day later in the year that lambs were born, the age at first oestrus was reduced by .88±.23 days. The model explained 33.9% of the variation in age at first oestrus.

The weight of hoggets at their first oestrus was significantly affected by date of birth and selection line. Liveweight at first oestrus decreased by 207±44g for each day later in the year that hoggets were born. FW hoggets were 1.7 kg heavier than C hoggets at their first oestrus. The model explained 31.9% of the variation in weight at first oestrus.

7.3.3.2 Duration of oestrus

The number of observed oestruses (NTUP) and the number of periods over which oestrus was displayed (LTUP) were both used to describe the length of the breeding season. The model explained 23% of the variation in each of these traits. Both NTUP and LTUP were highly affected by year, the means being (1.56±.28; 1.63±.35) and (2.41±.19 : 2.88±.24) in 1985 and 1986, respectively. Selection line effects (C:FW) for NTUP (1.83±.28 : 2.16±.17) and LTUP (2.04±.35 : 2.48±.21) approached significance ($p<.10$). No selection line by year interactions were significant. When years were analysed separately selection line effects were non-significant in 1985 while the associated selection line probabilities for NTUP and LTUP in 1986 were 5.1% and 6.8%.

7.3.4 Relationship of hogget oestrus to wool growth

Mean greasy hogget fleece weights for each year, selection line and oestrus status are given in Table 7.4. Hogget greasy fleece weight was unaffected by whether or not the ewe had previously displayed oestrus. No interactions existed between selection line and oestrus status.

Winter clean wool growth, defined as clean wool growth during June, was unaffected by hogget oestrus status and no interactions existed amongst other factors.

7.3.5 Relationship of hogget oestrus to two-tooth lambing performance

The presence or absence of hogget oestrus produced marginally ($.05<p<.10$) significant effects on two-tooth lambing performance. Of the two-tooth ewes present at lambing, slightly less than half of them had already been cyclic as hoggets. Of the previously cyclic FW ewes, all lambed. Eighty percent of previously cyclic C hoggets and 65-69% of the previously non-cyclic ewes lambed (Table 7.5). In the C ewes, previously acyclic ewe hoggets left more progeny than previously cyclic hoggets; whereas, the converse was true of FW hoggets.

Of the ewes lambing (40/52) 6 FW ewes and 1 C ewe gave birth to twins. Line differences in prolificacy approached significance ($.05<p<.10$). High lamb mortality in the 1986 season resulted in 26% losses (15 lambs) from birth to weaning.

Figure 7.1 Calendar of events for ewe hoggets

```
23 AUG 84-  lambs born  12 AUG 85-
08 OCT 84        |      26 SEP 85
                 |
26 NOV 84 lambs weaned  22 NOV 85
                 |
12 DEC 84  lambs shorn  20 DEC 85
                 |
           weigh hoggets
04 APR 85  crayons on rams  03 APR 86
           &join with rams
  yellow         |              green
17 APR 85  read marks &     17 APR 86
           change crayons
  yellow         |              blue
01 MAY 85  weigh hoggets    01 MAY 86
           & read marks
           & change crayons
  green          |              red
15 MAY 85  read marks &     15 MAY 86
           change crayons
  blue           |              green
29 MAY 85  weigh hoggets    29 MAY 86
           & read marks
           & change crayons
  red            |              blue
12 JUN 85  read marks &     12 JUN 86
           change crayons
  green          |              red
26 JUN 85  weigh hoggets     26 JUN 86
           & read marks
           & change crayons
  purple         |              green
10 JUL 85  read marks &      10 JUL 86
           change crayons
  purple         |              purple
24 JUL 85  weigh hoggets     24 JUL 86
           & read marks
           & remove crayons
                 |
17 OCT 85  shear hoggets     27 SEP 86
           & weigh hoggets
```

Table 7.1 The liveweight of ewe hoggets (kg)

7.1a Year, birth rank, dam age, selection line and oestrus status least squares means.

Classification	n	Weaning	04APR	01MAY	29MAY	26JUN	24JUL	PSW[1]
Overall	148	20.7±.3	28.2±.3	29.7±.3	30.3±.3	30.4±.4	31.0±.3	33.7±.3
Year 1985	86	21.7±.3	28.2±.4	29.0±.4	29.4±.4	30.0±.4	32.2±.4	39.4±.4
1986	62	19.2±.4	28.3±.6	30.6±.5	31.2±.5	30.9±.6	29.9±.6	25.7±.6
born single	72	22.0±.4	28.9±.4	30.4±.4	31.0±.4	31.0±.5	31.6±.4	33.5±.5
twin	76	18.9±.3	27.5±.5	29.0±.4	29.6±.4	29.9±.5	30.5±.5	31.9±.4
Dam 2yr	35	19.9±.5	28.3±.6	29.3±.6	29.8±.6	30.5±.7	30.8±.6	31.8±.6
3yr	38	19.7±.5	27.3±.6	29.0±.6	29.4±.6	29.8±.6	29.9±.6	31.5±.6
4yr	32	20.9±.5	28.3±.7	29.5±.6	30.5±.6	30.1±.7	31.0±.6	32.2±.6
5yr	43	22.2±.5	29.1±.6	30.8±.6	31.5±.6	31.5±.7	32.4±.6	34.2±.7
Line C	61	20.2±.4	27.9±.5	29.4±.4	29.7±.4	29.5±.5	30.1±.5	31.5±.5
FW	87	20.6±.3	28.5±.4	30.0±.4	30.9±.4	31.4±.5	32.0±.4	33.5±.4
Oestrus Acyclic	64	19.7±.4	27.6±.5	29.0±.5	29.7±.5	29.6±.6	30.5±.5	32.0±.6
Cyclic	84	20.6±.3	28.7±.5	30.4±.4	30.9±.4	31.3±.5	31.6±.4	33.1±.5
C Acyclic	34	20.3±.3	27.9±.7	29.2±.6	29.6±.6	29.1±.7	29.8±.7	31.3±.8
Cyclic	27	20.0±.3	27.7±.7	29.7±.7	29.8±.6	30.1±.8	30.5±.7	31.9±.7
FW Acyclic	30	19.2±.2	27.3±.7	29.2±.7	30.2±.6	30.7±.7	31.6±.7	32.5±.6
Cyclic	57	21.3±.3	29.7±.5	31.1±.4	32.0±.4	32.6±.5	32.8.±5	34.1.±7
C Single	35	21.6±.5	27.8±.6	29.5±.6	29.7±.5	29.4±.6	30.0±.6	31.7±.6
Twin	26	19.3±.6	28.1±.7	29.3±.7	29.7±.6	29.5±.7	30.2±.7	31.5±.6
FW Single	37	22.4±.5	29.9±.6	31.3±.6	32.4±.6	32.6±.7	33.3±.6	34.7±.6
Twin	50	18.2±.4	27.0±.5	28.6±.5	29.5±.5	30.2±.6	30.7±.5	31.9±.7

[1] PSW is post shearing live weight at hogget shearing

Table 7.1b Repeated measures analysis of liveweight

Source	df	Chi-Square	
FULL MODEL	10	329.0	***
FULL MODEL TIMES	60	576.5	***
YEAR	1	33.9	***
DATE OF BIRTH	1	311.3	***
AGE OF DAM	3	6.7	P<.10
SELECTION LINE	1	6.1	*
YES/NO OESTRUS CYCLES	1	17.7	***
YES/NO OESTRUS x LINE	1	0.2	ns
YEAR x LINE	1	0.1	ns
TIMES X YEAR	6	217.6	***
TIMES X AGE OF DAM	18	26.2	P<.10
TIMES x BIRTH DATE	6	1.1	ns
TIMES X LINE	6	27.9	***
TIMES X YES/NO OESTRUS	6	11.5	P<.10
TIMES X YEAR X LINE	6	7.1	ns
TIMES X LINE X BIRTH DATE	6	3.7	ns
TIMES X LINE x YES/NO OESTR	6	5.9	ns

* P<.05
** P<.01
*** P<.001

Table 7.2 Liveweight gain of ewe hoggets (kg).

7.2a Year, birth rank, dam age, selection line and oestrus status least squares means

Classification		n	PWG[1]	APR-JUL	APR	MAY	JUN	JUL	JUL-PSW[2]
Overall		148	8.0±.2	2.7±.2	1.5±.2	0.6±.1	0.2±.2	0.4±.2	1.4±.1
Year	1985	86	6.6±.3	4.1±.3	0.9±.2	0.4±.2	0.6±.2	2.1±.2	7.0±.3
	1986	62	9.4±.3	1.3±.3	2.2±.2	0.8±.2	-0.2±.3	-1.2±.3	-4.2±.3
Born	Single	72	7.1±.3	2.6±.3	1.6±.2	0.6±.2	0.0±.2	0.4±.2	1.5±.2
	Twin	76	8.9±.3	2.8±.3	1.5±.2	0.6±.2	0.4±.2	0.4±.2	1.3±.2
Dam	2yr	35	8.6±.4	2.4±.4	1.1±.3	0.5±.2	0.8±.3	0.1±.3	1.2±.2
	3yr	38	7.7±.4	2.9±.4	1.8±.3	0.4±.3	0.4±.3	0.0±.3	1.5±.3
	4yr	32	7.5±.5	2.6±.4	1.3±.3	1.0±.2	-0.3±.3	0.7±.3	1.3±.3
	5yr	43	8.3±.1	2.9±.4	1.8±.3	0.6±.2	0.0±.3	0.9±.3	1.6±.2
Line	C	61	7.5±.3	2.1±.3	1.5±.2	0.3±.2	-0.1±.2	0.5±.2	1.5±.2
	FW	87	8.5±.3	3.3±.3	1.5±.2	0.9±.2	0.6±.2	0.4±.2	1.2±.3
Oestrus	Acyclic	64	7.9±.4	2.8±.3	1.5±.2	0.7±.2	0.0±.2	0.7±.3	1.3±.3
	Cyclic	84	8.2±.3	2.7±.3	1.6±.2	0.5±.2	0.4±.2	0.2±.2	1.4±.3
1985	C	36	6.3±.5	3.0±.4	0.8±.3	0.0±.3	0.1±.3	2.1±.4	7.1±.3
	FW	50	6.9±.4	5.1±.3	0.9±.2	0.8±.2	1.1±.2	2.1±.3	6.8±.5
1986	C	25	8.7±.5	1.2±.4	2.2±.3	0.6±.3	-0.4±.3	-1.2±.3	-4.0±.4
	FW	37	10.2±.5	1.4±.5	2.1±.4	1.1±.3	0.0±.4	-1.3±.4	-4.4±.5

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[1] Post weaning gain

[2] Post shearing

Table 7.2b Repeated measures analysis of seasonal liveweight gains

Source	df	Chi-Square
FULL MODEL	10	217.1 ***
FULL MODEL TIMES	20	232.2 ***
YEAR	1	125.1 ***
DATE OF BIRTH	1	153.8 ***
AGE OF DAM	3	1.5 ns
SELECTION LINE	1	2.7 ns
YES/NO OESTRUS CYCLES	1	0.6 ns
YES/NO OESTRUS x LINE	1	2.7 ns
YEAR x LINE	1	0.4 ns
TIMES X YEAR	2	98.5 ***
TIMES X AGE OF DAM	6	2.8 ns
TIMES X LINE	2	5.7 p<.10
TIMES X YES/NO OESTRUS	2	6.1 *
TIMES X YEAR X LINE	2	3.3 ns
TIMES X LINE X BIRTH RANK	2	2.7 ns
TIMES X LINE x YES/NO OESTR	2	0.7 ns

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* P<.05
** P<.01
*** P<.001

Table 7.2c Repeated measures analysis of monthly liveweight gains during the breeding season.

Source	df	Chi-Square	
FULL MODEL	10	71.9	***
FULL MODEL TIMES	30	174.2	***
YEAR	1	53.5	***
DATE OF BIRTH	1	0.1	ns
AGE OF DAM	3	4.4	ns
SELECTION LINE	1	10.1	**
YES/NO OESTRUS CYCLES	1	0.7	ns
YES/NO OESTRUS x LINE	1	3.1	p<.10
YEAR x LINE	1	6.1	*
TIMES X YEAR	3	144.8	***
TIMES X AGE OF DAM	9	14.5	ns
TIMES X LINE	3	5.7	ns
TIMES X YES/NO OESTRUS	3	2.6	ns
TIMES X YEAR X LINE	3	0.5	ns
TIMES X LINE X BIRTH DATE	3	1.1	ns
TIMES X LINE x YES/NO OESTR	2	0.5	ns

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* P<.05
** P<.01
*** P<.001

Table 7.3a Percentage of ewe lambs in oestrus by selection line.

Line	1985	1986	Overall
Control	23.7	64.5	44.3
Fleece Weight	53.6	87.1	65.5
Overall	43.0	75.8	56.8

Table 7.3b Analysis of deviance for yes/no display of oestrus as a hogget.

Source	df	Deviance	
YEAR	1	16.31	***
BIRTH DATE	1	17.9	***
LIVEWEIGHT	1	9.14	**
BIRTH RANK	1	2.14	ns
SELECTION LINE	1	7.05	**

*** P<.001
** P<.01
* P<.05
ns non significant.

Table 7.4 Clean hogget fleece weight (CFW) and winter wool growth (June g clean wool/head/day) in cyclic and acyclic FW and C hoggets.

Classification		CFW (kg)	June wool (g/day)
Overall		3.0±.1	7.8±.3
Year	1985	4.1±.1	7.8±.3
	1986	3.1±.1	---
born	single	3.7±.1	7.6±.4
	twin	3.6±.1	8.1±.4
Dam	2yr	3.7±.1	7.9±.5
	3yr	3.6±.1	7.8±.5
	4yr	3.4±.1	8.5±.5
	5yr	3.8±.1	7.1±.5
Line	C	3.1±.1	6.4±.5
	FW	4.1±.1	9.3±.3
Oestrus	Acyclic	3.6±.1	7.7±.3
	Cyclic	3.6±.1	8.0±.5

Table 7.5 Two-tooth lambing performance of ewes which were either cyclic or acyclic as hoggets in FW and C lines (n).

Selection Line	Pubertal Status	Percentage Lambing	Percentage Twin-bearing	
C(25)	Cyclic (5)	80% (4)	25% (1)	4%
	Acyclic(20)	65% (13)	0% (0)	
FW(27)	Cyclic (14)	100% (14)	29% (4)	22%
	Acyclic (13)	69% (9)	22% (2)	

7.4 DISCUSSION

7.4.1 Ewe hogget liveweight

The mean liveweight of ewe hoggets during the breeding season was less than the 33-35 kg normally recommended target weight (Dalton, 1981). Although liveweight was measured on fasted ewes, the liveweights of 30 kg in May, June and July are less than those reported in other studies of Romney ewe hoggets at Massey University (McMillan, 1981; Asofi, 1984).

The liveweight advantage of single- over twin-born lambs was less than that reported at weaning (Baker et al., 1974) or during autumn (Ch'ang and Rae, 1961; 1970; Baker et al., 1979). The use of birth rank, rather than rearing rank, is assumed not to have greatly affected the results as only 11 lambs born as twins remained as singles at weaning. Ch'ang and Rae (1970) and Baker et al. (1974) have estimated that liveweight differences between twins reared as singles and twins reared as twins were between 25% and 50% of the magnitude of twin- vs. single-born comparisons.

Throughout the entire interval from weaning to hogget shearing FW ewe hoggets were heavier than C hoggets, the difference becoming and remaining significant by June. This difference (+1 kg) includes differences in the weight of wool carried. Historically, FW hoggets are 1.5 - 2 kg heavier than C hoggets after hogget shearing (Blair, 1986). As discussed in Chapter 5, this difference accrues slowly, is usually significant by late autumn or early winter, and increases slightly in early spring prior to hogget shearing.

Oestrous FW hoggets were approximately 2 kg heavier than acyclic FW lambs while oestrous and anoestrous C lambs did not differ in liveweight. Differences in autumn liveweight of 2 to 3 kg between oestrus and non-oestrus ewe hoggests have been reported for Romney lambs elsewhere (Ch'ang and Raeside, 1957; Hight et al., 1973; Asofi, 1984). McMillan (1981) found no difference in weight between oestrous and anoestrous Border Leicester X Romney lambs while oestrous Romney lambs were 5-6 kg heavier at joining than anoestrous lambs. Allison (1975) has also demonstrated breed differences in weight between marked and unmarked ewe lambs even when breed differences in joining liveweight were small. The possible neuroendocrine pathways through which body weight and growth information influence the sensitivity of the prepubertal sheep's hypothalamus to the negative feedback of oestradiol on LH secretion are reviewed and discussed by Foster et al. (1986).

7.4.2 Liveweight gain

Post-weaning liveweight gains were greater in 1986 but gains over the breeding and post-breeding seasons were substantially lower in 1986 than in 1985. These differing patterns of body growth were due, in part, to a dry autumn in 1985, which reduced pasture growth until May, and partly due to a poor winter and overstocking of the research block property with cattle, in 1986.

Twin-born lambs had higher liveweight gains over all seasons which indicated compensatory post-weaning growth. As noted in other studies this difference in liveweight gain decreases with increasing age (Ch'ang and Rae, 1970; Hight and Jury, 1971; McMillian, 1981).

Significant selection line differences (FW > C) existed only in May and June, the differences in all other periods being non-significant. Generally, under conditions for adequate growth, FW animals grew faster than C animals. In periods of poorer nutrition line differences were undetectable.

7.4.3 Puberty

7.4.3.1 Incidence of oestrus

The levels of oestrous activity in FW (65.5%) and C (44.3%) Romney ewe hoggets were comparable to those of other New Zealand Romney studies (Ch'ang and Raeside, 1957 (72%); Hight et al., 1973 (55%); Allison et al., 1975 (43%); Meyer and French, 1979 (25%); McMillan, 1981 (89%); Asofi, 1984 (79%)). Variation in the incidence of oestrous between studies is often attributed to differences in autumn liveweight (Moore and McMillan, 1984). The mean incidence of oestrus (57%) in this study appears reasonable given autumn liveweights of about 30 kg.

Care must be taken when display of oestrous, rather than the establishment of regular ovarian cycles, is the trait used to describe puberty. The recording of oestrous display relies on adequate seasonal preparation and libido of the rams, physical and visual proximity of ewes and rams in the paddock and the reliability and condition of the ram's marking device. Also, ovulations in prepubertal ewes may not always be accompanied by outward behavioral oestrus (Hare and Bryant, 1982). The author also assumes that these phenomena occur equally in FW and C sheep.

Both appropriate photoperiodic and liveweight signals are required for the onset of puberty. Malnourished females have functional photoreceptive mechanisms but an appropriate response to permissive photoperiod will be manifest only when they achieve the appropriate physiological size. As mentioned earlier, this manifestation involves a reduction in hypothalamic sensitivity to the negative feedback action of oestradiol on LH secretion (Foster et al. 1986).

It is possible that genetic variation exists in the "trigger" liveweight required to initiate oestrous cycles in photoperiodically receptive ewes. Genetic variation in photoperiodic sensitivity is also possible and is supported by evidence in various strains of mice (Heath and Lynch, 1982). As discussed by Montgomery and Hawker (1986), the inter-connection of common neuroendocrine mechanisms affecting both wool growth and reproduction may have some relevance given the higher winter wool growth (Chapter 5) and winter wool growth efficiency (Chapter 6) of FW sheep. The 1 kg liveweight advantage of FW ewe hoggets seems insufficient to account for the 20-25% advantage in number of oestrous ewes. Moore and McMillan (1984) suggest a 3% advantage for each 1 kg increase in weight, although the linearity of this relationship over a range of liveweights was not discussed. In some way, FW sheep may have an altered response or sensitivity to melatonin. Differences in production, or clearance rates from cerebral tissues, of melatonin are also possible. Without discussing the ramifications of his result, Hales (pers. comm.) has found higher (2X normal) blood flow rates to the pineal gland of fleeceweight-selected Merinos while that in C sheep was considered "normal".

Foster et al. (1986) maintain that nutritional cues are translated more directly, and hence more rapidly, than photoperiodic cues such that sudden increases in nutrition are often quite expedient in hastening puberty. The increased growth rates and liveweights during the early breeding season of 1986 may have been responsible for the earlier onset of oestrus in 1985- vs. 1984-born ewes. In agreement with McMillan (1981) the peak oestrus activity was in late May during both years.

7.4.3.2 Duration of the breeding season

The mean number of oestrus cycles (1.6) agrees well with other published estimates for Romney ewe lambs in New Zealand (Ch'ang and Raeside, 1957 (2.7); Hight et al. 1973 (1.4); Baker et al. 1974 (1.7)). Higher values (3.5) have been found by McMillan (1981).

The duration of the breeding season in ewe hoggets has practical implications. Ch'ang and Rae (1970; 1972) have advocated its use in early indirect selection for fecundity. Montgomery and Hawker (1987) have demonstrated a positive relationship between ovulation rate and the length of the breeding season in adult ewes. Where mating of hoggets is practised, multiple cycles allow recording of the returns to service. The measurement of ovulation rate, in indirect selection for fecundity (Hull and Hanning, 1980), by laparoscopy is also facilitated by measurements at consecutive oestruses.

Although the number of oestruses recorded in this study ranged from 1 to 6, the year of data collection was the only factor controlling significant variation. Selection line effects were suggested by the data, as FW sheep had more cycles and displayed oestrus over a longer period than C sheep, but this effect was significant only at the 10% level.

7.4.4 Relationship to other productive characters

Although tentatively supporting the results of Montgomery and Hawker (1987), no conclusions can be drawn about the relationships between winter wool growth, ovulation rate or length of the breeding season in FW and C sheep from these data. Both winter wool growth and hogget fleece weight were unrelated to reproductive characteristics in the hoggets studied. The possibility that these factors may be related in adult sheep is not discredited. Ewe hoggets differ from adults in many ways which may disguise relationships between these traits. First, the endocrine system of young sheep is experiencing photoperiodic cues for the first time. Secondly, energetic demands for body growth may influence wool growth and reproductive patterns.

On the basis of ewes present at lambing, the higher twinning rate of FW sheep appeared to be related to the higher proportion of FW ewes which were cyclic as hoggets. Lambing data for 1985-born sheep were not available but should be examined to augment the 1984-born data.

The mean two-tooth lambing performance of this flock has been historically low (Wickham, pers. comm.) and is possibly related to low two-tooth liveweights. The adverse grazing conditions of late-autumn and winter of 1986, as discussed earlier may have proved especially hard on 1984-born lambing two-tooths.

7.5 CONCLUSIONS

Selection for high hogget greasy fleece weight appears to have increased the percentage of ewe hoggets attaining puberty in their first autumn. This 20-25% increase has not been due to large differences in autumn liveweight, as selection line differences (1kg) attain significance only by early June, which is later than the peak of oestrous activity in ewe hoggets.

It is likely that liveweight-reproduction relationships have been altered in the two flocks, as oestrous and anoestrous C hoggets did not differ in liveweight while oestrous FW hoggets were approximately 2 kg heavier than anoestrous FW ewes. The suggestion has been made that FW and C sheep may respond differently to photoperiodic cues or that the interaction of photoperiod and liveweight "triggers" may be different in the two lines.

The age of FW or C sheep at first oestrus was unaltered by selection as was the mean date of first oestrus, these values being approximate, due to the fortnightly recording adopted in the study. Increased length of the breeding season in FW ewes was suggested ($p<0.10$) by the data, but may be related to significantly greater liveweight during late autumn.

The reproductive performance of 1984- and 1985-born lambs should be followed throughout their lifetime and related to the incidence of hogget oestrous. Further study of reproductive performance, as related to ovulation rate and autumn liveweight, is warranted in this flock. The lifetime lambing performance of ewes should also be re-assessed so as to discern between the combined effects of fertility and fecundity on the 30% advantage of FW ewes in lifetime performance for number of lambs born or reared.

STAPLE STRENGTH OF FW AND C HOGGET WOOL AND ITS RELATIONSHIP TO THE SEASONAL PATTERN OF HOGGET WOOL GROWTH AND STRENGTH OF ADULT WOOL

8.1 Introduction and review of literature

8.1.1 Economic importance

Interest in staple strength as a productive characteristic should ultimately relate to the processing performance and market value of wool. Physical characteristics such as length and diameter will also affect market value and will interact with staple strength. Although Henderson (1955), Ross (1960) and Bigham et al. (1983) have identified fleece unsoundness and its related defects as a major fault of New Zealand wool, there has been little direct evidence on the importance of staple strength in determining lot price. Ross (1982) suggested that tender wools and their associated faults, such as cotting and discolouration, resulted in a financial loss to New Zealand wool producers of $50m - $100m annually. These figures represent 5-10% of the value of the national clip. However, there are no reliable statistical analyses of prices of Romney-type wools described as sound or tender indicating that price differentials as large as the $0.14 - $0.27 per kg implied above apply to the entire national clip. According to figures published in the N.Z.W.B. Statistical Handbook (1985/86) 28,587 tonnes of wool was classified as tender or cotted. The majority of this wool was in the Romcross 33-37µm range and represented 11% of the production in this category. Using average prices for the above classes, also published in the N.Z.W.B. Handbook, a discount of about $7m appears to have been incurred. Even if a total cost to New Zealand of $10 m annually was related to tender wool, fleece tenderness would still be considered a major wool fault.

8.1.2 Processing significance

The processing significance of staple strength has been studied extensively in Australian fine wools (Douglas, 1984; TEAM, 1985) and in New Zealand Romcross wools (Ross et al., 1961; Bratt, 1965; Ross and Meikle, 1985). Manufacturers are concerned with the fibre diameter and length of wool as they partly determine its uses and value (Ross, 1960; 1982). At higher fibre diameters the length of fibres present in carded slivers primarily determines value. High strength yarns, characterized by longer mean fibre length, are certainly preferable in modern high speed processing machinery. Fibre length after carding is a function of the length and strength of greasy wool, the degree of fibre entanglement before carding, the position of any tender region in the staple and the conditions of the carding process (Gee, 1978; Wood, 1984).

The length and strength of greasy wool and the position of break in the staple will have the greatest effects on fibre length after carding. A break near the butt or tip of the staple will reduce fibre length in the top and increase noilage as short fibres are removed in combing. A break near the centre of the staple may not increase noilage if the remaining halves of the broken fibres are of sufficient length but there may be a major decrease in mean fibre length. An increase in noilage reduces top yield while a decrease in fibre length in the top reduces its subsequent processing performance. The relative economic importance of these two factors depends on the proportion of unsound fibres and the length of fibres before carding (Douglas, 1984b).

Fibre length after carding has a more significant effect on spinning performance and yarn strength of worsted and semi-worsted than woollen- spun yarns. Although tops of high uniform length may reduce worsted processing performance these uniform lots are never achieved unless wools are sorted on both length and strength prior to carding (Bratt, 1965). Tops of shorter mean fibre length have lower spinning performance and ultimate yarn/fabric strength (Ross et al., 1961; Bratt et al., 1964). The effect of staple break on processing performance (top yield and strength) is likely to be most severe when the break is 25% to 40% along the length of the staple (Bratt et al., 1964; Wickham, 1968).

8.1.3 Causes of poor strength

A marked seasonal rhythm of wool production exists in long-woolled breeds of sheep in New Zealand. This rhythm is characterized by reductions in the diameter, cross sectional area, length and subsequent weight of fibres grown by sheep during winter months. Even when nutrition is held constant throughout the year wool growth (g/d) is two to ten times greater in summer than in winter months (Ross, 1962, 1965; Geenty et al., 1984). This seasonality is of central importance to staple strength as individual wool fibres tend to break at their narrowest point (Fitzgerald et al. 1984). Even so, Orwin et al. (1980,1985) concluded that the exact location of the break may be difficult to predict. Monthly diameter measurements may not, however, be adequate in identifying short periods of restricted fibre growth which have serious effects on staple strength. These short periods of severe wool growth check can cause otherwise superior wool producers to have fleeces of low tensile strength (Ross, 1965).

Hoggets have less variation in monthly mean fibre diameter throughout the year than adult ewes (Bigham et al., 1978a). The lower incidence of fleece tenderness in hogget wool is also due to differences in ewe and hogget feeding levels over winter and the absence of pregnancy and lactation which place additional demands on the supply of nutrients for wool growth to the ewes.

Minimum fibre diameter may not be the only component of fibre strength. Orwin et al. (1980; 1985), Carnaby (1984) and Fitzgerald (1984) have demonstrated differences in intrinsic strength (load/area) between fibres and between sheep which may relate to cortex composition or protein profiles within fibres. Tenderness in uniformly growing wool can also arise from damage to the intercellular cement of wool fibres caused by bacterial invasion of the skin surface during moist, warm conditions (Roberts et al., 1960). In extreme cases, copper deficiency can lead to the production of straight wool of very low tensile strength commonly known as 'steely wool' (Henderson, 1968).

8.1.4 Measurement of staple strength

The strength of individual staples has, historically, been estimated by either the "ring" of the staple as it is flicked between the fingers, or the hand-pull required to break it. These two subjective tests can be greatly affected by the force exerted by individual appraisers, the thickness of the staple selected and the position of weakness in the staple (Roberts et al., 1960; Rottenbury, 1979).

If break is to be considered an important wool fault then any long term research programme which aims to reduce the incidence of break in New Zealand wool should be based on more objective and repeatable measures of staple strength. Ross (1960; 1961a), Heuer (1979), and Douglas (1984a) have outlined a variety of objective tests for staple strength. Many are based on the force, in Newtons, required to break the staple relative to the staple's linear density, in kilotex. These methods require the staple to be held between one fixed and one movable jaw. The staple is then extended under force until most or all of the intervening fibres are broken. The values of staple strength obtained by various researchers will vary due to machine factors such as the test length between the jaws, the rate of staple extension and the jaw design. Most of these factors are related to the type of equipment used (Hueur, 1979). Irrespective of the method used, staples within a fleece will vary in strength due to the weight/density of tested staples, the configuration of the staple between the jaws and the effects of body position on staple weathering and wool growth characteristics (Ross, 1960; 1961a,b; 1982; Ross and Meikle, 1985).

The reported correlations between subjective and objective measures of staple strength have ranged from 0.65 to 0.90 (Ross, 1960; Rottenbury, 1979); however, many subjective tests are unable to distinguish between a wide range of strengths when staple strength is above 35 or 40 N/ktex (Roberts et al., 1960: Rottenbury, 1979) and staple size is more critical to strength assessment. The ability to distinguish, not only between sheep with superior or inferior staple strength but also, to distinguish accurately between sheep of intermediate staple strength may be important in sheep improvement programmes.

8.1.5 Improvement of staple strength

Although it is possible to improve staple strength by altering the pattern of feed intake throughout the year, this practice does not constitute an economic solution. Hawker and Crosbie (1985) were able to virtually eliminate the seasonal pattern of wool growth by feeding a high plane of nutrition over winter followed by a low plane over summer. In another experiment Hawker (1985c) obtained a 74% increase in wool growth and a 24% increase in staple strength through a 150% increase in feeding level over an 8 week winter period. These regimes, although interesting from a research standpoint, would be impractical on-farm for a number of reasons:

1) Feed resources under grazing conditions are greatest in spring and autumn and lowest over winter (depending on weather and location).

2) To maximise wool and lamb production ewes should be well fed over summer-autumn.

3) The efficiency of wool growth and its responsiveness to the plane of nutrition are at least twice as great in summer as they are in winter (Sumner, 1979; Geenty et al., 1984; Hawker et al., 1984).

4) Winter feed is best used for the breeding ewes.

The position of tenderness in the staple is affected by the relationship between shearing date and the time of minimum wool growth (Ross, 1961a,b). In adult ewes, the most direct way to improve the strength of marketed fleece wool would be to shear prior to lambing when wool growth and fibre diameter are at their minimum. This may not be practical for all management situations as shearing in late winter increases feed demands at a time of limited pasture growth and increases the risk of post-shearing lamb and ewe losses (Sumner, 1984; 1986).

Given that management practices are only a temporary solution to improving staple strength, much discussion has recently taken place in New Zealand on the role of staple strength in sheep breeding policies (Rae, 1982; Ross et al., 1982; Bigham et al., 1983; Wickham and McPherson, 1985). The inclusion of staple strength as a selection criterion in sheep improvement programmes (rather than as a commonly accepted selection objective) requires knowledge of its genetic and phenotypic relationships to other productive characters (within age) and to staple strength and fleece traits over the sheep's lifetime. The heritability of various measures of staple strength should also be assessed. If a positive genetic correlation exists between fleeceweight and staple strength then correlated responses in staple strength should accompany selection for fleeceweight. As staple strength measurement is both tedious and expensive indirect selection for staple strength, either through fleeceweight or associated wool growth characteristics, may obviate the need to test staple strength on a widespread basis.

Heritability estimates for staple strength have been moderate to high (0.2-0.6) (Bigham et al., 1983; Bigham 1984) suggesting that staple strength should respond to direct selection. However, the costs of measurement could possibly exceed the benefits from selection. Chopra (1979) produced estimates of the heritability of hand-pull grade in Romney hoggets ranging from 0.0 to 0.22.

Positive genetic correlations between staple strength and greasy fleeceweight of 0.3 have been reported by Bigham (1984) while Chopra (1979) calculated a genetic correlation of 0.74 between hand-pull grade and fleeceweight. Given heritabilities of 0.3 and 0.4 for greasy fleeceweight and staple strength respectively, and genetic correlations of 0.3 to 0.7, indirect selection for staple strength would be 25% to 60% as efficient as direct selection. Based on selection practices in the Massey University PT fleeceweight selection flock (Blair, 1986), the parameters above should result in correlated responses of 1.7 N/ktex or 0.2 units of hand-pull grade per generation.

The effectiveness of any staple strength selection programme in raising the level of strength in the entire Romcross clip may also depend on the genetic and phenotypic correlations between hogget and adult staple strength. These correlations may be influenced by the relative shearing dates at both ages. Strength of pre-lamb shorn wools could possibly result more from differences in average fibre properties than on differences in winter wool growth. The correlation between maximum and minimum staple strength is low (.26) and of varying significance (Ross, 1965; Ross and Meikle, 1985). Average winter wool growth may contribute less to staple strength in post-lamb shorn wools than the presence of, or response to, short term nutritional or physiological stress.

8.1.6 Objectives of the current trial

(1) to examine the correlated responses in staple strength to selection for high greasy fleeceweight in Massey University's Romney fleeceweight selection flock (Blair et al., 1985);

(2) to quantify the importance of sources of variation in staple strength such as sheep, sire and selection line;

(3) to relate the objective measures of staple strength in hogget fleece wool to their known monthly patterns of wool growth;

(4) to determine the relationship between hand-pull grade and staple strength;

(5) to determine the relationship between ewe hogget and two-tooth staple strength.

8.2 MATERIALS AND METHODS

8.2.1 Experimental plan

Staples from a midside sample of the hogget fleece from 1984-born rams and ewes, of the fleeceweight-selected (FW) and control (C) lines, were tested for maximum load on a Hounsfield tensometer. These sheep had complete records on monthly wool growth (Chapter 5). The staples used had been dye-banded monthly and were removed on 17 October 1985 just prior to hogget shearing. Replacement FW and C ewes present in the flock as two-tooth ewes in 1986 were midside sampled at ewe shearing on 21 October 1986. Staples from this midside sample were also tested for maximum load. The numbers of FW and C ewe and ram hoggets tested are given in Table 8.1 as are the numbers of FW and C ewes re-tested as two-tooths.

8.2.2 Equipment used

A Hounsfield tensometer, originally equipped with a spring-loaded mercury manual readout and motor drive unit, was modified to allow automatic recording of the maximum load. The modified machine was set up as illustrated schematically in Figure 8.1. The spring-loaded scale was disconnected and an electronic expansion-cell was inserted between the frame of the machine and the fixed wool clamp. The expansion-cell was connected to an AG-300 digital display unit which translated the analogue signals from the expansion-cell to digital signals. The AG-300 provided a visual display of the load sustained by the staple as it was being pulled. An Epson HX-20 portable micro-computer received load measurements from the AG-300 at the rate of 4 per second and was programmed to automatically record the maximum load. Staples were pulled by a motor-driven shaft at the rate of 5 cm per minute such that between 250 and 500 total load measurements were received.

8.2.3 Measurement of staple strength

All measurements were taken in a humidity controlled laboratory (20±2° C, 68±2%RH). Ten staples from the greasy midside sample were selected for testing. Prior to measuring these staples, an additional staple was broken by hand-pull to determine the region of break. Butt ends of the staples were securely clamped between the fixed jaws and the staple tip was secured in the movable jaws. Staples were positioned so that the area of break would be within the 8 cm tested region.

Staples were extended until the load displayed on the AG-300 had visibly decreased from maximum and staples showed evidence of breakage. Fibres from between the jaws were cut free and weighed to the nearest mg. If fibre slippage was evident during the pull the staple was removed and the measurements discarded. Clean weight of wool tested was estimated from the clean yield of midside samples taken at shearing. Maximum load was expressed in N/ktex.

Staple strength and month of staple break of hogget samples were also estimated by hand-pull. Hand-pull strength grades were on a scale of 1 to 9. A single value was recorded after 1 to 4 staples were broken by hand. The description of these hand-pull grades is given in Table 8.2. Month of break was determined by hand-breaking at least three dye-banded staples per sheep. In cases where staples broke in a diffuse area the month in the centre of the break region was recorded.

8.2.4 Statistical methods

A number of linear models were used to analyze staple strength and hand-pull grade data. The first model (8.1) included individual staple measurements to enable the estimation of within- and between- sheep variances. This model ignored fixed effects other than sex and selection line as it was thought that correction factors based on multiple records might not necessarily reflect correction factors based on sheep means. The second model (8.2) was used to estimate sire and error variances for hand-pull grade, month of break and sheep mean values for staple strength. This model included fixed effects which had been found, in preliminary analyses, to have significant effects on one or more of the traits studied. Model 8.3 was designed to obtain least squares means for staple strength and wool growth characteristics in each hand-pull grade class in order to assess their effect on subjective strength classes. The final model (8.4) was used to estimate the regression of two-tooth staple strength on hogget staple strength after adjustment for two-tooth lambing status.

The repeatability and heritability of staple strength across 10 staples from each sheep was estimated in the following nested model:

<u>Model 8.1</u> $y_{ijklm} = \mu + t_i + l_j + s_{jk} + sh_{ijkl} + e_{ijklm}$

where,

y_{ijklm} = the observed staple strength of the m^{th} staple from the l^{th} sheep in each i^{th} sex, j^{th} line and jk^{th} sire class,

μ = an overall mean,

t_i = the fixed effect of the i^{th} sex,

l_j = the fixed effect of the j^{th} selection line,

s_{jk} = the random effect of the k^{th} sire within each j^{th} selection line,

sh_{ijkl} = the random effect of the l^{th} sheep of sex i within each jk^{th} sire subclass, and

e_{ijklm} = the random residual associated with each m^{th} staple from the l^{th} sheep in each i^{th} sex, j^{th} line and jk^{th} sire class.

Variance components for random sire and sheep components were obtained by equating each mean square to its expectation where:

error variance(σ_e^2) = Error Mean Square (EMS),
sheep variance(σ_{sh}^2) = (Sheep MS - EMS) / 10.,
sire variance(σ_s^2)= (Sire MS - EMS -10 σ_{sh}^2))/153.09,

heritability(h^2) = (4 σ_s^2) / (σ_e^2 + σ_{sh}^2 + σ_s^2),and
repeatability(R^2) = σ_{sh}^2 / (σ_e^2 + σ_{sh}^2).

Sire and error variances for hand-pull grade, month of break and sheep mean staple strength were obtained from the following model:

Model 8.2

$y_{ijklmn} = \mu + b_1X_{ijkl} + r_i + d_j + t_k + l_l + s_{lm} + e_{ijklmn}$

where,

y_{ijklmn} = the observed staple strength/hand-pull grade or month of break of the n^{th} sheep belonging to to the m^{th} sire, l^{th} selection line, k^{th} sex, j^{th} dam age and i^{th} birthrank classes,

μ = overall mean,

b_1 = regression coefficient of y_{ijklmn} on X_{ijklmn}

where,

X_{ijklmn} = observed individual birthdate,

r_i = fixed effect of the i^{th} birthrank class,

d_j = fixed effect of the j^{th} age of dam class,

t_k = fixed effect of the k^{th} sex,

l_l = fixed effect of the l^{th} selection line,

s_{lm} = random effect of the m^{th} sire within each l^{th} selection line, and

e_{ijklmn} = random residual associated with the $ijklmn^{th}$ observation.

Equating each mean square to its expectation yielded:

error variance (σ_e^2) = Error Mean Square (EMS),

sire variance (σ_s^2) = (Sire MS - EMS) / 15.309,

and heritability (h^2) = ($4\sigma_s^2$) / ($\sigma_s^2 + \sigma_e^2$)

Correlations between birth date, birth rank, dam age and sex corrected residuals for staple strength and wool growth characteristics were calculated within selection line and tested for homogeneity and pooled, if homogeneous, by Z-transformation according to Steele and Torrie (1980, p282).

Least squares means for staple strength and wool growth characters by hand-pull grade class were obtained from the following model:

Model 8.3

$y_{ijklmn} = \mu + b_1X_{ijklmn} + r_i + d_j + t_k + l_l + h_m + e_{ijklmn}$

where,

y_{ijklmn} = an observation of strength or wool growth characteristic on the n^{th} sheep of sex k, selection line l, dam age j and birth rank i and hand-pull grade k,

μ = an overall mean,

b_1 = the regression coefficient of y_{ijklmn} on X_{ijklmn} where,

X_{ijklmn} = an observed individual birthdate,

r_i = the fixed effect of the i^{th} birthrank class,

d_j = the fixed effect of the j^{th} age of dam class,

t_k = the fixed effect of sex k,

l_l = the fixed effect of selection line l,

h_m = the fixed effect of hand-pull grade m, and

e_{ijklmn} = the random residual associated with an observation on the n^{th} sheep of sex k, selection line l and hand-pull grade m.

Two-tooth and hogget staple strength were analysed according to the following model, where lambing status 1=dry, 2=single and 3=twins:

<u>Model 8.4</u> $y_{ijk} = \mu + p_i + l_j + b_1 X_{ijk} + e_{ijk}$

where,

y_{ijk} = an observed staple strength on the k^{th} two-tooth ewe of lambing status i and selection line j,

μ = an overall mean,

p_i = the fixed effect of two-tooth lambing status,

l_j = the fixed effect of selection line j,

b_1 = the linear regression coefficient of y_{ijkl} on,

X_{ijk} = the observed hogget staple strength, and

e_{ijk} = the random residual associated with the k^{th} twotooth ewe of lambing status i from selection line j.

8.3 RESULTS

8.3.1 Sources of variation in hand-pull grade and staple strength of hogget samples

Neither hand-pull grade (PULL) nor staple strength (STR) were significantly affected by birth date or age of dam (Figure 8.3). Hand-pull grade did not differ between single- and twin-born lambs but staple strength was significantly greater in single- than in twin- born hoggets (25.7±1.9 vs. 21.8±1.7 N/ktex). Ram and ewe hoggets did not differ in staple strength but hand-pull grade was greater in ewe hoggets (6.04±0.20 vs. 5.15±0.21). No interactions existed between the fixed effects of sex, selection line, birth rank or dam age and the regression of STR or PULL on birthdate was homogeneous across all fixed effects. In order to more readily compare strength and wool growth variables all subsequent analyses, unless otherwise stated, refer to data corrected for the fixed effects above. Although dam age and birth date did not significantly affect either PULL or STR they were included in subsequent analyses in order to obtain staple strength measures corrected for the same effects as many of the wool growth characteristics.

As shown in Table 8.3 staple strength was significantly greater in FW than in C hoggets ($.01 < p < .05$, $R^2=11.5\%$) but differences in hand-pull grade were not clearly significant ($.05 < p < .10$, $R^2=17.7\%$). Selection line accounted for 4.5% and 1.9% of the total sums of squares for staple strength and hand-pull grade, respectively. The distributions of staple strength and hand-pull grade in FW and C sheep are given in Figures 8.2 (a,b).

The effect of sire (within line) was significant for staple strength ($0.01 < p < 0.05$) and hand-pull grade ($0.01 < p < 0.05$). The proportions of the total sums of squares accounted for by fixed effects, selection line and sire within selection line are shown in Figures 8.3 (a,b) along with the relevant sums of squares. The heritability of staple strength was 0.47±0.34 from sire and error variances of 13.5798 (N/ktex)^2 and 102.3398 (N/ktex)^2 respectively. The heritability of hand-pull grade was 0.38±0.30 from sire and error variances of 0.1404 (classes)^2 and 1.3448 (classes)^2 respectively. The relatively large standard errors are likely due to the small number of sires represented in the data.

Using staple strengths from all 10 measured staples per sheep yielded variance estimates of 105.73 (N/kext)^2 between- and 30.32 (N/ktext)^2 within- sheep to give an across staple repeatability of 77.7%.
Sire variance in this model, which was uncorrected for fixed effects other than sex, was 10.89 (N/ktex)^2 yielding a heritability of 0.30±0.26 . The proportions of the total sums of squares accounted for by staples within sheep, sheep, sire, selection line and sex in Model 8.1 are given in Figure 8.3(c) along with the relevant sums of squares.

8.3.2 Sire and selection line effects on staple strength and their relationship to the seasonal pattern of hogget wool growth.

Selection line least squares means (from Model 8.2) for STR, PULL and the fleece characteristics including:

Winter wool growth traits:

- lowest monthly fibre diameter (LFD),
- lowest monthly clean wool growth per day (LCPD),
- lowest monthly length growth rate per day (LLPD);

Amplitude traits:

- amplitude of fibre diameter (FDAMP),
- amplitude of clean wool growth (CPDAMP),
- amplitude of length growth rate (LPDAMP);

Average wool growth traits:

- mean annual fibre diameter (MFD),
- greasy fleeceweight (GFW),
- clean fleeceweight (CFW),
- staple length (SL);

'Month of' traits:

- month of staple break (MB),
- month of lowest fibre diameter (MLFD),
- month of lowest clean wool growth (MLCPD),
- month of lowest length growth rate (MLLPD)

are given in Table 8.3 along with their standard errors.

In order to assess the contribution of these wool growth characteristics to selection line differences in staple strength, the simple correlations among all variables were first examined within each selection line. An upper-diagonal matrix of pooled (where homogeneous) and within-line (where heterogeneous) correlation coefficients is presented in Table 8.4. Heterogeneous within-line correlations existed most predominantly in the 'month of' variables such as MB, MLFD, MLCPD and MLLPD.

An examination of the first two rows of Table 8.4 shows that winter wool growth traits had the highest correlations with staple strength (0.38 to 0.42). Correlations between staple strength and amplitude traits were of similar magnitude but opposite sign to those of winter wool growth traits (-0.34 to -0.44). Average wool growth traits were positively correlated to staple strength (0.19 to 0.27). 'Month of' traits, with the exception of MLLPD in FW sheep, were not significantly related to staple strength. The correlations between PULL and wool growth measures were very similar to those just presented. Correlations among wool growth characters have been presented and discussed in earlier sections.

The contribution of various wool growth characteristics to line differences in STR and PULL was also tested by analysis of variance using sequential sums of squares from a model where the covariate preceded selection line effects. All dependent and independent variables were corrected for all fixed effects except selection line. The ability of the covariate to remove selection line differences in STR or PULL was judged by the probability associated with the selection line mean square and the multiple correlation coefficient (R^2) of the model.

The regressions of STR or PULL on measures of wool growth were all homogeneous across genotypes. The regression coefficients, R^2 values, and subsequent probability associated with selection line effects are given in Table 8.5. As regressions for STR and PULL showed similar trends, only the regressions involving STR will be presented here. All regressions of staple strength on wool growth characteristics were significant when fitted prior to or following genotype effects. Pre-adjustment for the effects of CFW, GFW, MFD, SL, LFD, LCPD and LLPD rendered selection line differences in staple strength non-significant indicating that these traits contributed, either directly or through their correlation to other traits, to selection line differences in staple strength.

As might be expected from the simple correlations presented in Table 8.4, measures of winter wool growth gave the highest R^2 values (19% to 21%) relative to 8% to 12% for average wool growth traits. R^2 values for the regression of staple strength on amplitude traits ranged from 16% to 23%. In no instance did amplitude traits remove selection line differences. Pre-adjustment for FDAMP raised the significance of selection line effects. The month of minimum production or month of wool break had no effect on selection line differences in staple strength.

Month of staple break was highly heritable (0.50±0.32) but bore no clear relation to staple strength in either FW or C sheep (Table 8.4). Control sheep tended to have weaker wool if the break was closer to the butt of the staple but the correlation was only significant at the 10% level. In both C and FW sheep the 'month of' variables were positively correlated but relationships amongst these variables were stronger in C than FW sheep. Most notably, MB was uncorrelated with MLFD in FW sheep while the correlation in C sheep was 0.41 . In both FW and C sheep, later month of staple break was accompanied by lower minimum fibre length growth, higher amplitude of length growth, lower amplitude of fibre diameter and lower average fibre diameter and staple length.

The distributions of FW and C sheep for MB, MLFD, MLCPD and MLLPD are given in Figure 8.4 . Control sheep distributions for all traits and the FW distribution for MB were characterized by strong central tendency, the mode and the mean being in close agreement. Distributions of FW sheep for MLFD, MLCPD and MLLPD were split with the majority of observations falling into either months 5 or 7. In Chapter 5, FW hoggets were found to reach minimum wool growth approximately 5 weeks earlier than C hoggets. However, month of break was only 2 weeks earlier in FW than C hoggets.

8.3.3 The relationship between hand-pull grade and staple strength

As given in Table 8.4, the correlation between hand-pull grade and staple strength was 0.58 so that 34% of the variation in measured staple strength was accounted for by variation in subjective assessment. Least squares means for staple strength and wool growth characteristics for each hand-pull grade class are given in Table 8.6. Also shown in this table are the range of staple strengths represented in each hand-pull grade and the staple linear density in ktex.

Mean staple strength increased with hand-pull grade. Mean differences between all classes except 5 and 6, and 2/3 and 4, were significant. The variation in measured strength within each class is indicated by the range. With the exception of the lowest strength class, the range in remaining classes was near to 30 N/ktex. Very similar ranges existed for classes 4,5 and 6.

Hand-pull grade was positively associated with mean clean wool growth and winter wool growth. Increased hand-pull grade was also characterized by a decrease in amplitude of wool growth. Hand-pull grade did not appear to be affected by the average linear density of staples selected or by 'month of' variables.

8.3.4 The relationship between ewe hogget and two-tooth staple strength

Over the 40 ewes measured as hoggets and again as two-tooths the correlation between raw values of ewe and hogget staple strength was 0.34. The correlation was significantly higher for FW (0.43) than C ewes (0.22). Hogget staple strength alone explained 12% of the variation in subsequent ewe strength. An additional 3.5% was explained by selection line effects. Lambing status as two-tooths (dry,single or twin) did not significantly affect staple strength in these data. Average strength was not significantly different in FW and C two-tooth ewes, the means being 12.7±3.0 N/ktex and 10.2±1.5 N/ktex, respectively.

Table 8.1 Number of hoggets tested, and two tooths re-tested for staple strength in the fleeceweight-selected (FW) and Control (C) lines.

		SELECTION LINE		
		C	FW	
HOGGET:	RAMS	27	28	55
	EWES	27	43	70
TWO-TOOTH:	EWES	20	20	40
		54	71	125

Table 8.2 Description of hand-pull grades for staple soundness

1	Much of fleece lost
2	Very weak - obvious "break"
3	Slight pull to break
4	Moderate pull to break
5	Good pull to break
6	Slight pull to break 1/2 staple
7	Good pull to break 1/2 staple
8	Good pull to break 1/4 staple
9	Sound (1/4 staple)

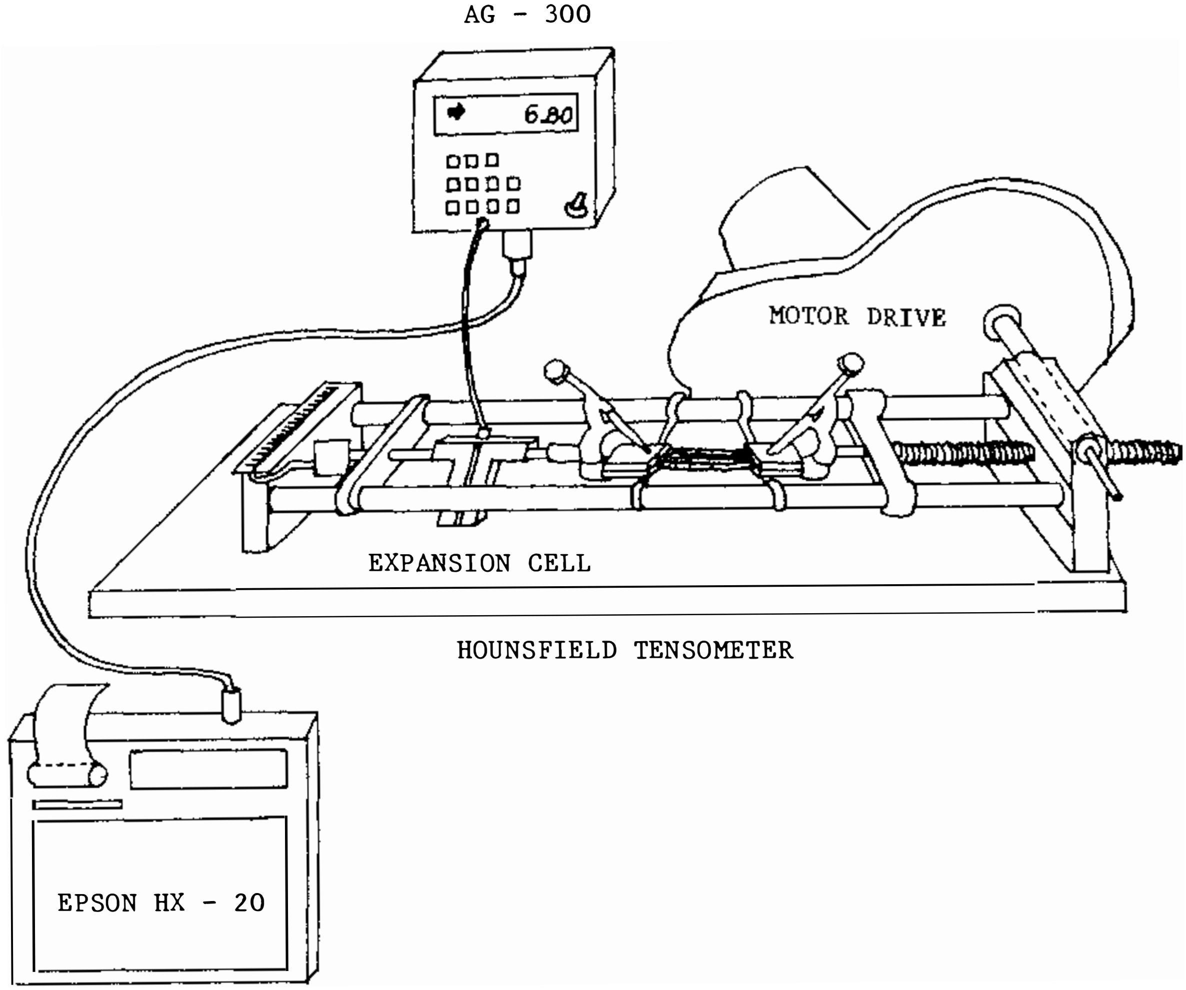


Figure 8.1 SCHEMATIC REPRESENTATION OF THE HOUNSFIELD TENSOMETER AND LOAD RECORDING EQUIPMENT

Table 8.3 Selection line least squares means, standard errors, and significance for staple strength, hand-pull grade and wool growth characteristics.

	SELECTION LINE		
Trait considered	C	FW	sig[2].
STR (N/ktex)	22.2 ± 1.2	27.8 ± 1.3	*
PULL (class)	5.4 ± 0.2	5.8 ± 0.1	$p<.10$
LFD (μm)	28.7 ± 0.3	30.3 ± 0.3	***
LCPD (g/d)	5.4 ± 0.2	7.7 ± 0.2	***
LLPD (mm/d)	.38 ± .01	.43 ± .0	***
FDAMP (%)	22.1 ± 0.7	23.5 ± 0.7	ns
CPDAMP (%)	80.3 ± 2.3	74.4 ± 2.0	$p<.10$
LPDAMP (%)	43.5 ± 1.5	39.6 ± 1.3	ns
MFD (μm)	31.1 ± 0.3	33.5 ± 0.3	***
GFW (kg)	3.6 ± 0.1	4.6 ± 0.1	***
CFW (kg)	2.6 ± 0.1	3.4 ± 0.1	***
SL (cm)	12.8 ± 0.2	14.6 ± 0.2	***
MB (month)[1]	6.8 ± 0.2	6.3 ± 0.1	$p<.10$
MLFD (month)	7.1 ± 0.2	5.8 ± 0.2	***
MLCPD (month)	6.8 ± 0.2	5.9 ± 0.2	***
MLLPD (month)	5.9 ± 0.2	5.4 ± 0.2	ns

[1] where month represents 28-day periods, and period 1 ended 09, January 1985.

[2] * $p<0.05$
** $p<0.01$
*** $p<0.001$

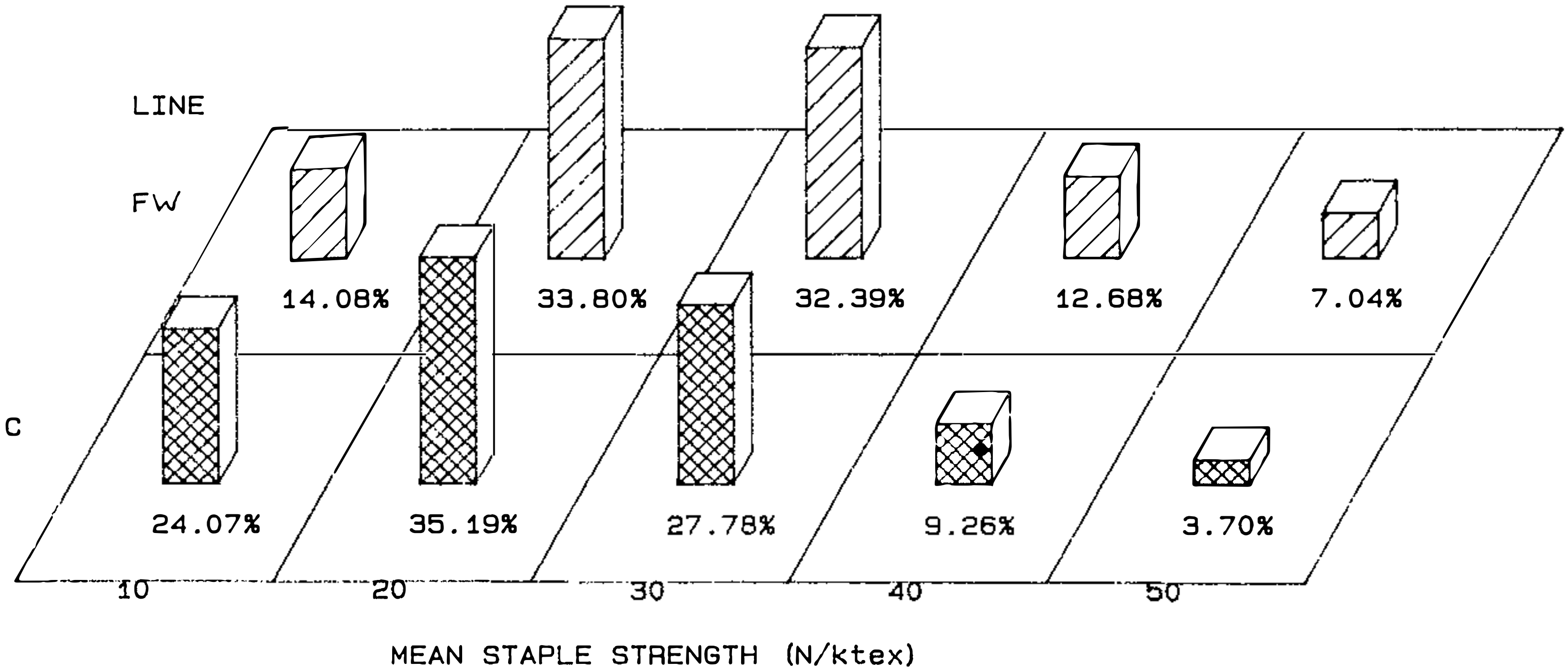


FIGURE 8.2 PERCENTAGE WITHIN LINE DISTRIBUTIONS IN FW AND C HOGGETS
a) MEAN STAPLE STRENGTH

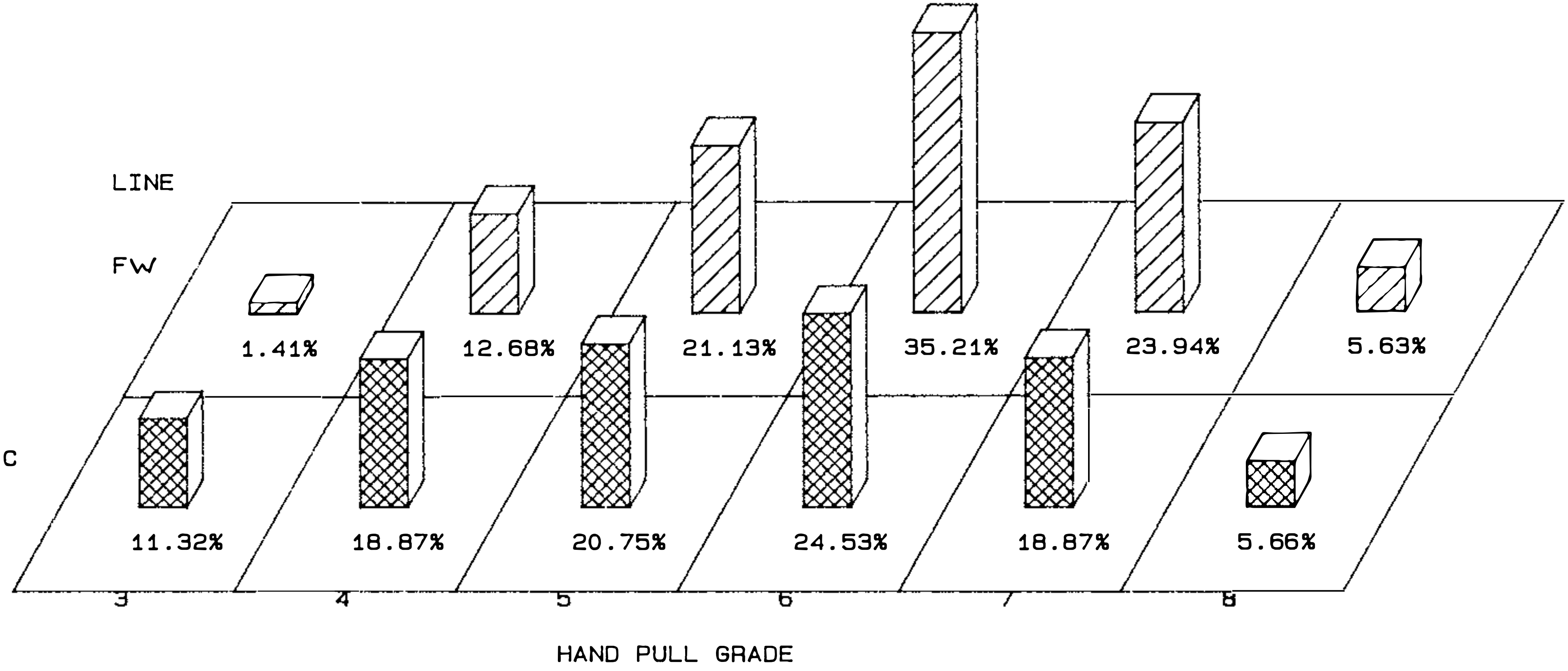
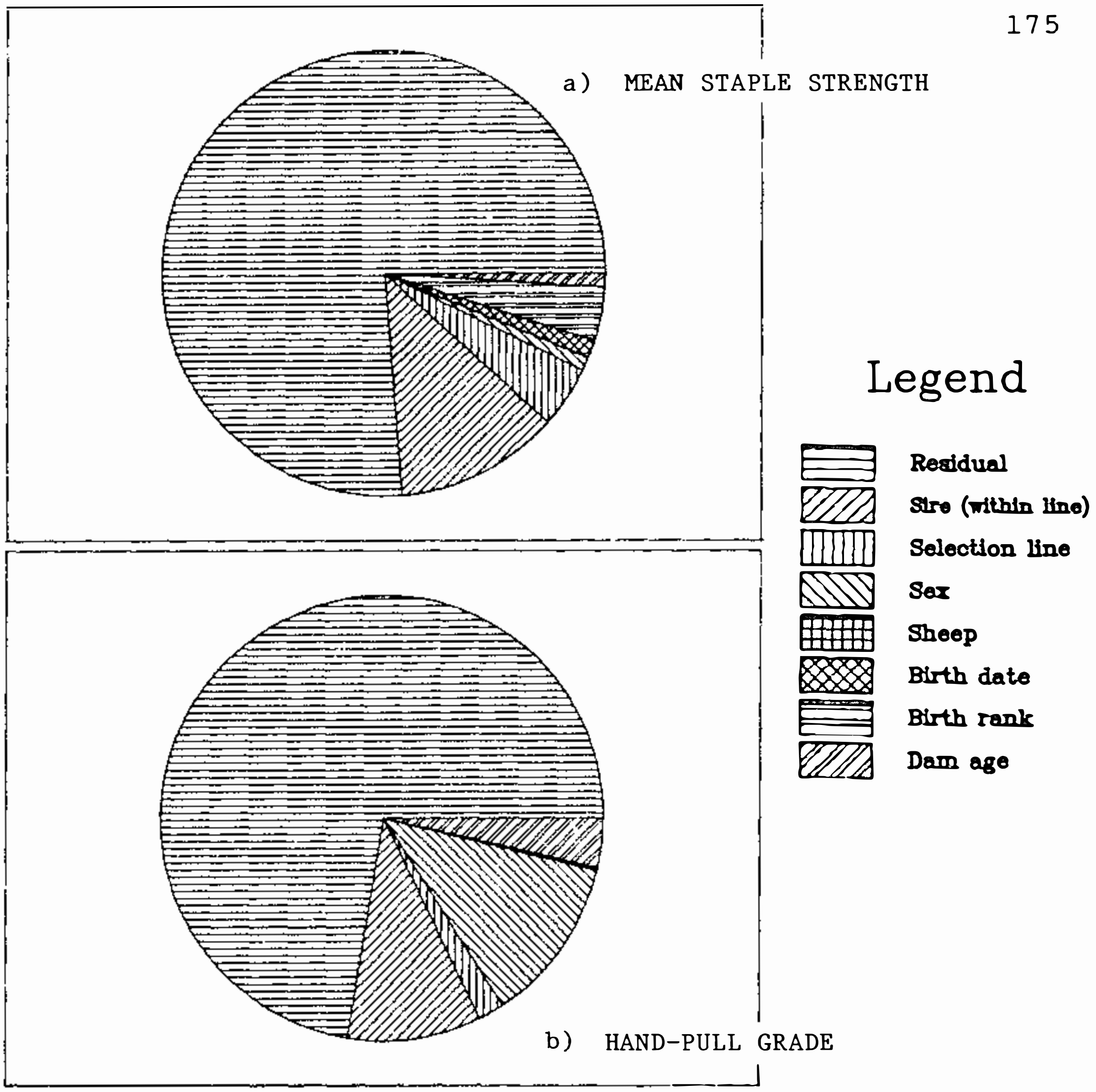
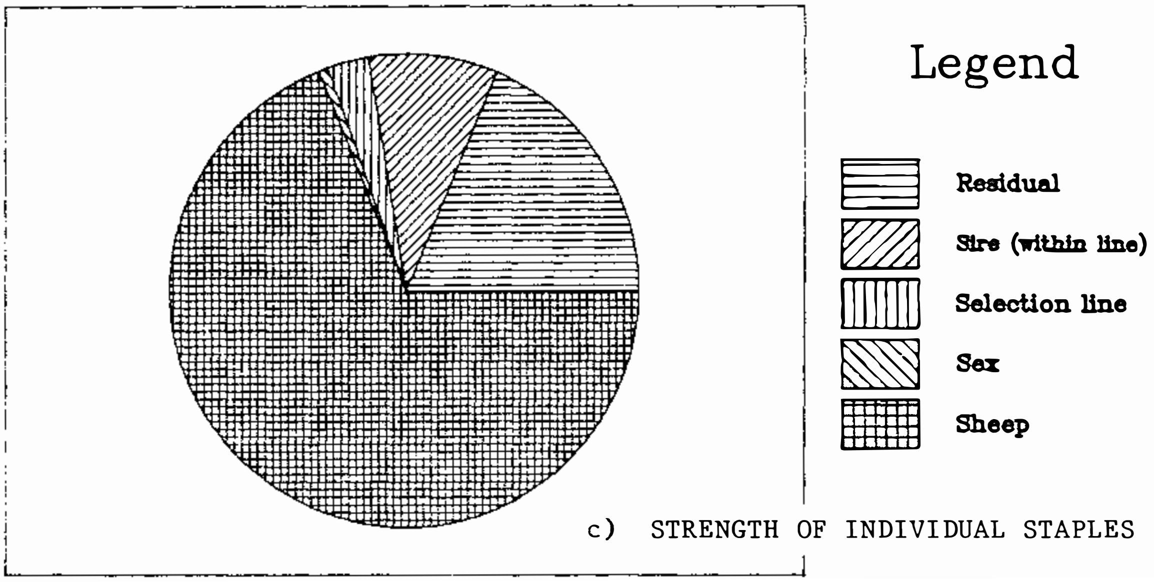


FIGURE 8.2 PERCENTAGE WITHIN LINE DISTRIBUTIONS IN FW AND C HOGGETS
b) HAND PULL GRADE



a) MEAN STAPLE STRENGTH

b) HAND-PULL GRADE



c) STRENGTH OF INDIVIDUAL STAPLES

Figure 8.3 SUBDIVISION OF THE TOTAL SUMS OF SQUARES FOR MEASURES OF STAPLE STRENGTH

Table 8.4 Pooled (where homogeneous) or within line (C/FW) correlations between measures of staple strength and wool growth characteristics (corrected for DB, BR, DA and SEX)

	PULL	LFD	LCPD	LLPD	FDAMP	CPDAMP	LPDAMP	MFD	GFW	CFW	SL	MB	MLFD	MLCPD	MLLPD
STR	.58*	.42*	.38*	.42*	-.34*	-.36*	-.44*	.27*	.19*	.24*	.26*	-.22/.12	.09	.17	-.1/.41*
PULL		.37*	.37*	.28*	-.25*	-.35*	-.38*	.28*	.20*	.26*	.22*	-.07	.08	.11	.10
LFD			.63*	.26*	-.58*	-.58*	-.33*	.78*	.37*	.45*	.16	-.06	-.11	-.17	-.04
LCPD				.57*	-.43*	-.73*	-.53*	.47*	.73*	.80*	.30*	-.09	-.21*	-.13	-.4*/.1
LLPD					-.09	-.36*	-.74*	.27*	.39*	.51*	.59*	-.24*	-.20*	-.4*/.1	-.5*/.2
FDAMP						.63*/.81*	.30*	-.14	-.06	-.08	.09	-.18*	-.15	-.08	-.05
CPDAMP							.60*	-.27*	-.21*	-.26*	-.06	.00	.09	.05	.11
LPDAMP								-.20*	-.22*	-.28*	-.23*	.26*	.13	.12	.38*/-.1
MFD									.43*	.53*	.30*	-.26*	-.15	-.19*	.02
GFW										.94*	.31*	-.16	-.17	-.19*	-.09
CFW											.44*	-.16	-.16	-.15	-.24*/.1
SL												-.22*	-.06	-.07	-.14/-.17
MB													.4*/.1	.35*	.17
MLFD														.73*/.42*	.37*
MLCPD															.37*

Table 8.5 Regression coefficients, R^2 values, and the significance of selection line differences in staple strength following preadjustment for wool growth characteristics.

COVARIATE	b ± S.E	prob(selection line)	R^2
LFD (µm)	2.10 ± 0.41	p=.38	21.4 %
LCPD (g/d)	2.66 ± 0.58	p=.56	18.8 %
LLPD (mm/d)	81.33 ±16.06	p=.51	21.2 %
MFD (µm)	1.26 ± 0.40	p=.32	11.6 %
GFW (kg)	3.41 ± 1.71	p=.65	7.7 %
CFW (kg)	5.40 ± 2.02	p=.85	9.9 %
FDAMP (%)	-.67 ± 0.17	p=.002	15.8 %
CPDAMP (%)	-.23 ± 0.15	p=.06	17.1 %
LPDAMP (%)	-.43 ± 0.08	p=.06	22.9 %

note: prior to covariate adjustment selection line differences were significant at p=.04.

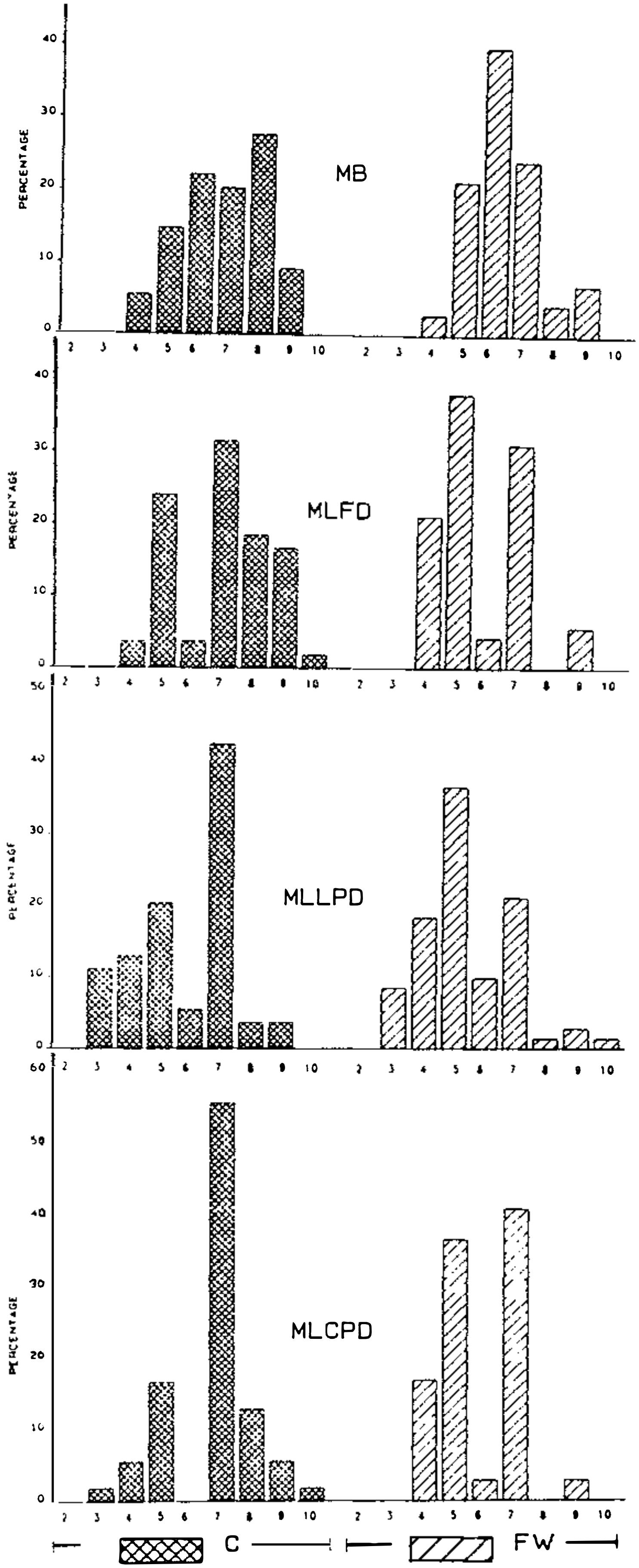


Figure 8.4 DISTRIBUTIONS OF FLEECE WEIGHT SELECTED (FW) AND CONTROL (C) HOGGETS FOR MB, MLFD, MLLPD AND MLCPD

note: 2,3,4...10 are 28-day periods where period 1 ended 9 Jan, 1985

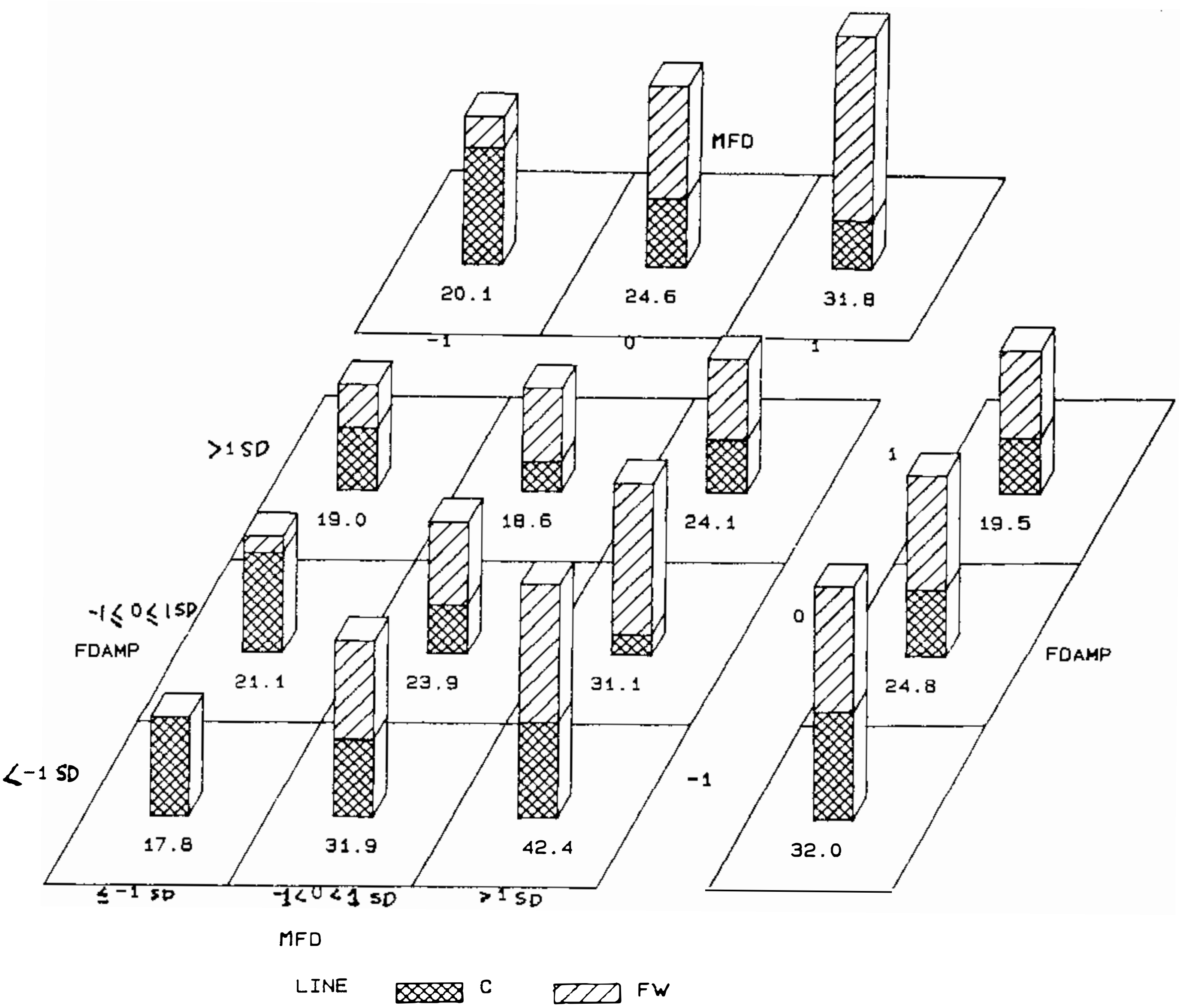


Figure 8.5 MEAN STAPLE STRENGTH AND THE PROPORTION OF FLEECE WEIGHT SELECTED (FW) AND CONTROL (C) HOGGETS IN STANDARD DEVIATION (SD) CLASSES FOR PAIRS OF WOOL GROWTH CHARACTERISTICS.

a) FDAMP and MFD (Fibre diameter amplitude and mean fibre diameter)

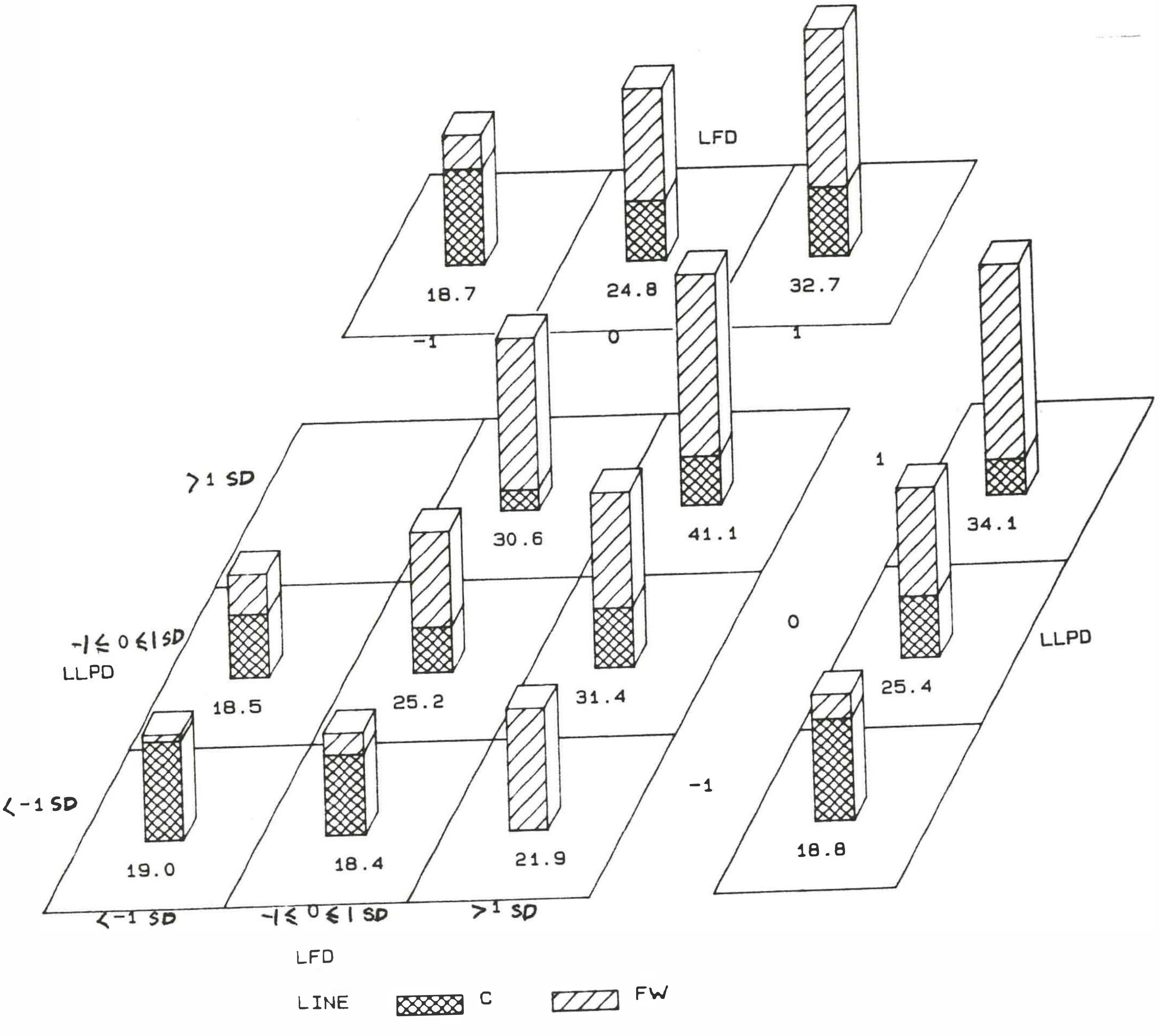


Figure 8.5 MEAN STAPLE STRENGTH AND THE PROPORTION OF FLEECE WEIGHT SELECTED (FW) AND CONTROL (C) HOGGETS IN STANDARD DEVIATION (SD) CLASSES FOR PAIRS OF WOOL GROWTH CHARACTERISTICS

b) LLPD and LFD (Lowest length growth rate and lowest fibre diameter)

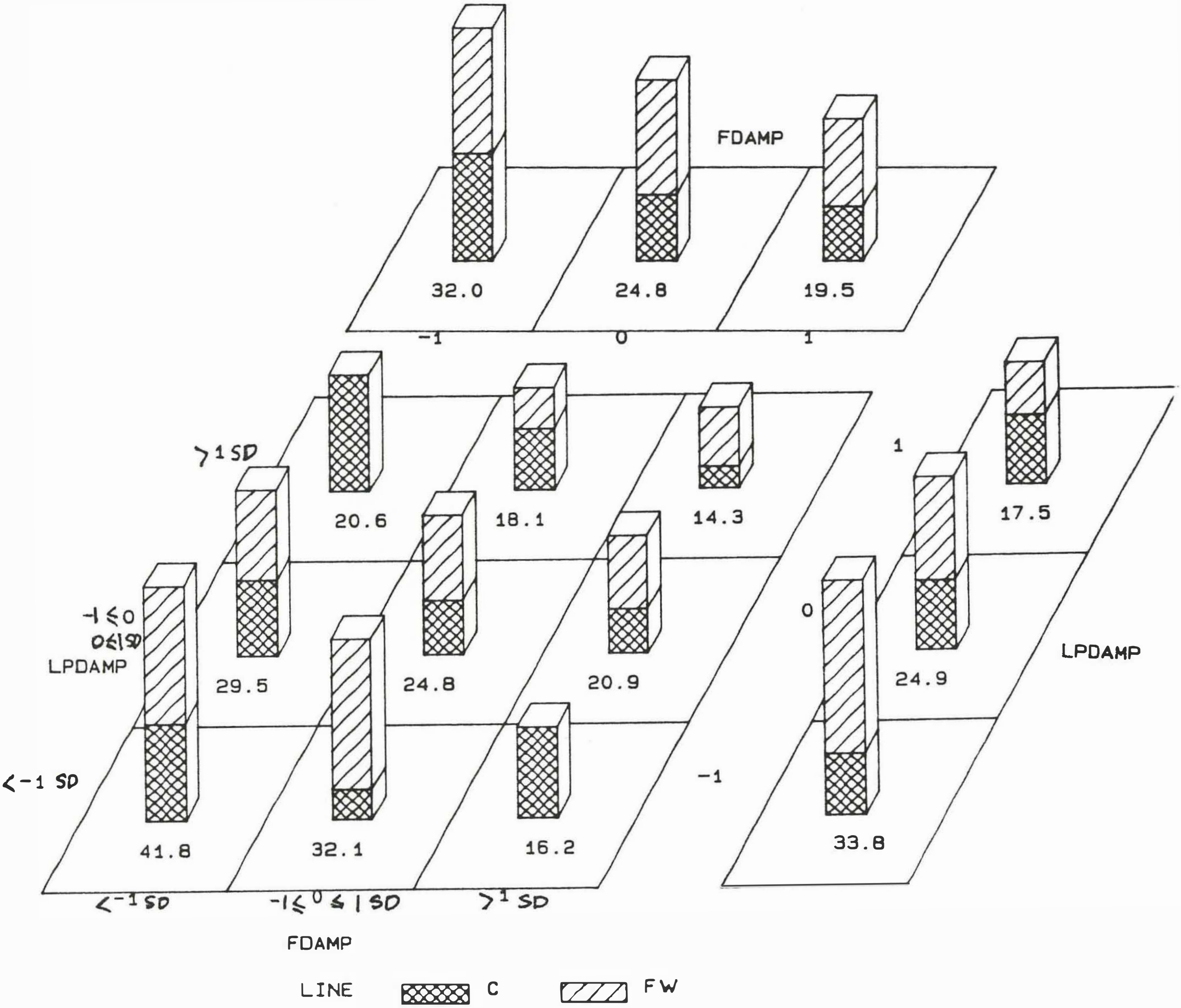


Figure 8.5 MEAN STAPLE STRENGTH AND THE PROPORTION OF FLEECE WEIGHT SELECTED (FW) AND CONTROL (C) HOGGETS IN STANDARD DEVIATION (SD) CLASSES FOR PAIRS OF WOOL GROWTH CHARACTERISTICS

c) LPDAMP and FDAMP (Length growth amplitude and fibre diameter amplitude)

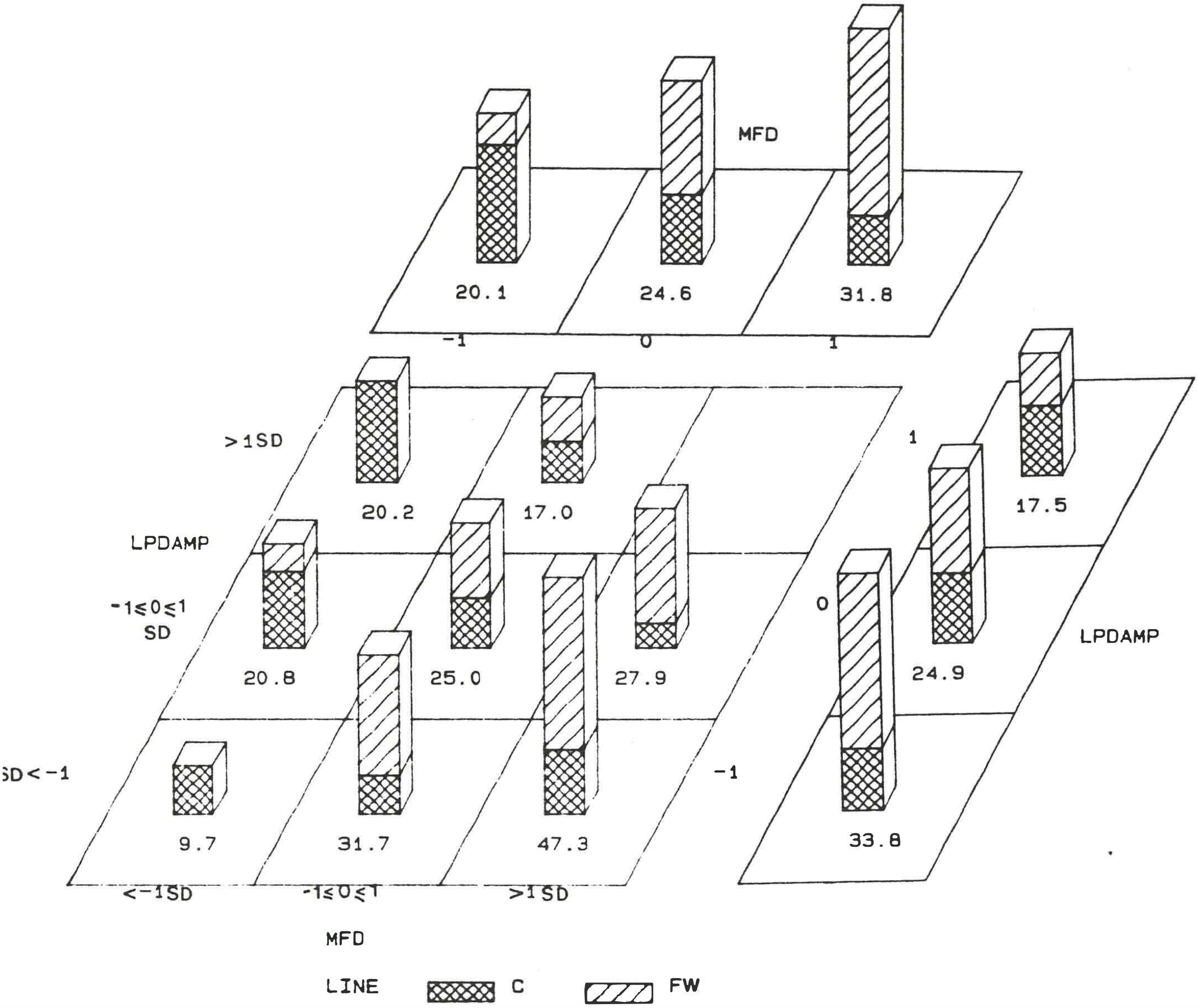


Figure 8.5 MEAN STAPLE STRENGTH AND THE PROPORTION OF FLEECE WEIGHT SELECTED (FW) AND CONTROL (C) HOGGETS IN STANDARD DEVIATION (SD) CLASSES FOR PAIRS OF WOOL GROWTH CHARACTERISTICS

d) LPDAMP and MFD (Length growth amplitude and mean fibre diameter)

Table 8.6 Least squares means for staple strength and wool growth characteristics for each hand pull grade class

	HAND-PULL GRADE						
	2 & 3	4	5	6	7	8	
Observations	7	19	26	38	27	7	sig[1]
STR (N/ktex)	12.5±3.4	17.4±2.1	23.0±1.8	24.4±1.5	32.3±1.8	40.6±3.4	**
STR range	8.3-16.3	8.7-41.2	9.3-47.3	10.0-43.5	8.9-57.7	22.7-59.0	
LFD (μm)	27.8±0.8	29.0±0.5	28.7±0.4	29.8±0.3	30.3±0.4	31.9±0.8	**
LCPD (g/day)	5.0±0.6	6.4±0.3	5.9±0.3	7.0±0.2	6.9±0.3	8.3±0.5	***
LLPD (mm/day)	.387±.02	.389±.01	.380±.01	.408±.01	.424±.01	.435±.02	*
FDAMP (%)	28.1±2.0	22.7±1.2	24.5±1.1	22.4±0.9	21.0±1.1	18.3±2.0	*
CPDAMP (%)	100.1±5.9	76.6±3.5	85.2±3.1	74.8±2.5	72.7±3.1	59.4±5.8	***
LPDAMP (%)	52.6±3.9	43.7±2.3	46.8±2.0	39.8±1.7	35.6±2.1	34.4±3.9	***
MFD (um)	31.7±0.9	31.9±0.5	31.7±0.4	32.6±0.4	33.1±0.5	34.4±0.8	*
GFW (kg)	3.9±0.2	4.0±0.1	4.0±0.1	4.3±0.1	4.1±0.1	4.5±0.2	ns
CFW (kg)	2.9±0.2	2.9±0.1	2.9±0.1	3.1±0.1	3.0±0.1	3.4±0.2	*
SL (cm)	14.6±0.7	13.4±0.4	12.9±0.3	13.7±0.3	14.4±0.3	15.3±0.6	**
MB (month)	6.5±0.5	6.3±0.3	6.9±0.2	6.6±0.2	6.3±0.2	6.0±0.5	ns
MLFD (month)	6.2±0.6	6.1±0.3	6.3±0.2	6.3±0.2	6.5±0.2	6.6±0.6	ns
MLCPD (month)	5.7±0.5	6.0±0.3	6.7±0.3	6.0±0.2	6.3±0.2	7.0±0.5	ns
MLLPD (month)	5.9±0.6	5.3±0.4	5.4±0.3	5.6±0.2	5.0±0.3	5.8±0.6	ns
Staple density (ktex)	0.9±0.2	1.1±0.1	0.9±0.1	1.1±0.1	1.2±0.1	1.1±0.2	

note: month refers to 28-day periods where period 1 ended 09 January 1985.

[1] * $p<0.05$
** $p<0.01$
*** $p<0.001$
ns non significant

8.4 DISCUSSION

8.4.1 Sources of variation in staple strength

8.4.1.1 Within sheep

Any attempt to evaluate staple strength is fraught with concerns relating to appropriate sampling and measuring procedures. Staple measurements are affected by biological and environmental variation over the body of the sheep and variation in fibre diameter, crimp, length and orientation of fibres within the staple itself. Variation in the length, weight or configuration of staples (both within and between sheep), mechanical variables of strength testing equipment (such as test length, breaking speed and clamp design) and the units of measurement employed can all affect the accuracy and precision of wool strength measurement. Hand assesment of staple strength is further affected by differences in the thickness of staples selected and human errors of judgement.

Ross (1961a) and Ross and Meikle (1985) concluded that samples taken from the normal midside position would give a representative measure of the staple strength over the body. Samples subjected to greater weathering (as indicated by higher alkali solubility), such as withers and back samples, had lower staple strength than the remainder of the fleece (Ross, 1961a). Ross and Meikle (1985), using a smaller number of samples, were unable to demonstrate significant body region effects. Rottenbury (1979) showed that variation between and within regions of the fleece contributed 19% and 20% of whole fleece variability in staple strength. Although samples in this study were taken from the midside position, the samples were subject to some weathering due to their location directly above the shaven midside patch. This weathering would have been most severe on staple tips and, as such, should not have greatly affected the results. Mean staple strength ranged from 8 to 60 N/ktex in the hoggets studied. This range appears fairly realistic given the relatively small sample size and quoted biological limits of 0 to 90 N/ktex (Rottenbury, 1979).

Maximum load may not be the most accurate measure of staple strength as some fibres within the staple will have ruptured before others have reached full extension. As staple strength depends on individual fibre strength, variability in fibre crimp and the breaking extension of individual fibres within staples, Ross (1960; 1961a) has argued that the total energy required to break the staple may be a more informative measure of staple strength. Although, in general, the two measures are highly (0.66 - 0.9) correlated the correlation is often lower in weaker staples (Ross, 1960; Ross, Cockrem and Wickham, (unpublished), Gourdie et al., (unpublished)). Ross (1960; 1984) showed that in staples with double peaking load curves, where the different breaking loads and extensions of short and long fibres within the staple are very distinct, maximum load is likely a severe underestimate of the true staple strength. In staples which display double peaked load curves as many as half of the fibres being extended may have already broken by the time maximum load is achieved.

Although load curves were not recorded in this study, the constant pull and continuous load readout gave a visual impression of the underlying curve. Distinct double peaked load curves were evident in a number of samples, especially those ultimately sustaining less than about 20 N/ktex of maximum load. The relative frequency of these type of samples in the two selection lines was not established. Ross (1984) agreed that the percentage of double peaked curves decreases dramatically when wools are above 19 N/ktex.

Bigham (1984) reported variance components of 80 (N/ktex)^2 and 120 (N/ktex)^2 within- and between-sheep giving a repeatability of 60%, a figure somewhat less than the 77% repeatability found in this trial. Bigham (1984) does not quote the mean or range of staple strengths represented in his data but Ross (1961a) found greater within-site variability in weaker staples. Within-site repeatabilities ranging from 62% to 92% have been reported for different mobs of Merinos (Rottenbury, 1979).

8.4.1.2 Within and between sires

Staple strength was moderately heritable (.30 - .47) in this trial, agreeing well with estimates quoted by Bigham et al. (1983), Bigham (1984) and Orwin et al. (1986). The heritability of hand-pull soundness grade was in the same range (.38) although lower estimates (.1-.2), based on a similar grading system, have been shown elsewhere (Chopra, 1979; Newman, (unpublished)).

8.4.2 Selection line and the seasonal pattern of wool growth

8.4.2.1 Correlated response to fleeceweight selection

Genetic correlations were not estimated from these data as estimates of genetic correlations are remarkably unstable in small datasets. Genetic correlations between fleeceweight and staple strength of .3 to .7 have been reported (Chopra, 1979; Bigham et al., 1983) indicating that a correlated increase in staple strength should accompany selection for higher fleeceweight.

Staples from FW sheep were, on average, 6 N/ktex stronger than those of C sheep. Compared to the expected correlated response of 1.7 N/ktex per generation, or 16.3 N/ktex over 9.6 generations, the actual correlated response has been somewhat less. Predicted correlated response could have been overestimated if the genetic correlation between hogget greasy fleeceweight and staple strength is less than 0.3, or if the heritability of either trait is less than the values used (GFW h^2 = 0.3; STR h^2 = 0.4). If, as was suggested by Blair et al. (1985), the heritability of either trait is lower in ram than in ewe hoggets, this would also lead to an overestimate of the expected correlated response. In the screened high fleeceweight flock at Woodlands Agricultural Research Station (Hawker and Littlejohn, 1986) high fleeceweight hoggets had staple strengths ≈ 3 N/ktex greater than randomly selected hoggets. The phenotypic difference in hogget fleeceweight in both the high and random Woodlands groups and the Romney lines studied here was ≈ 1 kg. As the genetic difference in fleeceweight between Woodlands groups is expected to be substantially less than 1 kg, the reported difference in staple strength on a genetic basis, agrees quite well with that found here.

Bigham et al. (1983) showed evidence of differences in staple strength between various commercial and experimental strains of Romneys which they attributed to differences in fibre diameter. Although not presented, differences in fleeceweight or other fleece characteristics may have also contributed to strain differences in staple strength.

8.4.2.2 Relationship between strength and wool growth characteristics

The correlations of staple strength with average or minimum wool growth characteristics found here (Table 8.4) were slightly lower than those quoted in the literature although published correlations were obtained from mature ewe records (Ross, Cockrem and Wickham, (unpublished); Sumner, 1969; Bigham et al., 1983; Geenty et al., 1984; Hawker, 1986; Hawker and Crosbie, 1985). Regressions of staple strength on wool growth characteristics were also somewhat lower than published estimates from mature ewes. The degree to which these relationships become stronger in two-tooth compared with hogget fleeces is unknown. Average winter wool production is higher, and the amplitude of production much lower, in hoggets than in older ewes (Bigham et al., 1978a) such that LFD and LLPD in mature sheep may exert a greater influence on staple strength. Amplitudes, as measured in this study, only reflect differences up until the time of hogget shearing. The magnitude of monthly wool production differences in FW and C sheep beyond this time as hoggets, and as adult ewes, is unknown.

Geenty et al. (1984) found that staple strength increased by 12 N/ktex for every 1g/day increase in clean wool growth of sheep fed uniformly indoors. They were unable to demonstrate any relationship in sheep fed uniformly out of doors. Hawker and Littlejohn (1986) quote a regression coefficient of 5.1 N/ktex per g of clean wool per day (R^2 = 38%) in their hogget data. The estimate of 1.62 N/ktex per g of average clean wool growth reported here is considerably lower than either of these estimates. Hawker (1985c) and Hawker and Crosbie (1985) were able to explain 50% - 80% of the variation in staple strength of non-pregnant Romney and Perendale ewes by the level of clean wool growth over winter. In the above studies, staple strength increased 2.5 - 9.0 N/ktex for every 1 g/day increase in clean wool growth over winter. The estimate of 2.7 N/ktex per g/day found in this study is within the quoted range although the equivalent R^2 value was only 10%.

The other, perhaps most important, aspect of Hawker and Crosbie's (1985) trial was that W+ (high winter wool growth) sheep produced more wool than W- (low winter wool growth sheep) even though the relative wool production of W+ sheep was lower over summer months. The implication of their work was that fleeceweight and amplitude of wool growth might be inversely related. Their conclusion is consistent with the correlations in Table 8.4 although more data on complete wool growth cycles in FW and C sheep would help to verify this relationship. The amplitude of wool growth in hoggets is not readily interpretable. The sheep in Hawker's trial have demonstrated repeatable winter wool growth performance but it remains to be shown whether or not these seasonal wool growth characters are successfully transmitted to their offspring.

Despite the fact than wool fibres tend to break at their narrowest point, not more than than 40% of the variation in staple strength has, historically, been explained by minimum fibre diameter as reviewed by (Bigham et al., 1983). Horton (1978) found marked short term nutritional effects on fibre diameter and subsequent breaking point in sheep subjected to a sudden change in dietary regimen over winter. Sudden changes in diet were thought to upset rumen microbial populations causing short term changes in nutrient supply. Staple strength was also affected, in Horton's study, by monthly minimum fibre diameter as dietary change and break point did not correspond in all sheep. Henderson (1955) and Ross (1965) suggested that winter or minimum fibre diameter was an important component of staple strength although winter fibre diameter, measured at 54-day or 28-day intervals, did not improve the prediction of mean staple strength from clean wool growth in other work (Bigham et al., 1978b; Geenty et al., 1984). The results obtained here showed that minimum fibre diameter had a more marked effect on staple strength than average fibre diameter, based on the respective regression coefficients (2.1 vs. 1.2 N/ktex per μm) and correlations (0.42 vs. 0.27). the expression of minimum fibre dimensions in terms of cross sectional area rather than diameter did not alter any of the the results or conclusions in this trial.

Increased staple strength in the FW line was accompanied by greater winter length, weight and diameter of wool grown. These heavier FW fleeces were longer and coarser than those of C sheep. Sire differences in staple strength were not as clearly related to differences in wool growth characteristics. No single factor appeared to adequately account for sire rankings for staple strength either within or across selection lines.

The ability of preadjustment for various wool growth characteristics to remove selection line differences in staple strength indicates that these traits contributed, either directly or through their association with other wool growth characteristics, to the correlated response in staple strength.

Although increased minimum fibre diameter contributed to selection line differences in staple strength, its contribution was more through an increase in average fibre diameter than through reduced amplitude of fibre diameter changes. Fibre diameter amplitude was marginally greater in FW sheep. As noted in previous discussion, the absolute and relative values for amplitude measures should be treated cautiously as wool growth data, in this experiment, did not encompass the expected time of maximum wool growth in December through February following hogget shearing. The amplitude of fibre diameter was lower in FW sheep if the local maximum in February following lamb shearing was compared with the minimum over winter.

8.4.2.3 Interactions between wool growth characteristics in describing strength

In order to observe the joint effects of changes in mean and amplitude of wool growth characteristics on staple strength the data were converted into standard normal deviates. Observations within one standard deviation (SD) either side of the mean were coded as '0' and those greater than one SD from the mean on negative and positive extremes were coded as '-1' or '+1' respectively. Data were arranged into 3-way contingency tables with wool growth measures forming 2 sides of the table and genotype or staple strength constituting the third dimension. Grids were analysed by the G-test (log-likelihood test) as outlined by Sokal and Rohlf (1969) and Kullback (1959) to test for independence and interaction of grid dimensions. These tests were used solely to aid in the interpretation of results. Figures 8.5 a) through d) show the response of staple strength to simultaneous changes in pairs of wool growth characteristics. The height of each bar represents the mean staple strength of sheep in each cell of the grid. Also shown in these figures are the within-cell proportions of observations represented by FW and C sheep. The mean response of staple strength to each wool growth characteristic can be seen in the attached (3x1) grids at the top and side of each figure. Mean response bars are a reflection of the regression coefficients in Table 8.5.

The outward changes in staple strength associated with grid combinations of FDAMP and MFD were as expected. As fibre diameter varied less from month to month (decreased FDAMP) changes in mean fibre diameter exerted a more pronounced effect on staple strength. Similarly, as mean fibre diameter increased, the effect of increased FDAMP on staple strength appeared to be more severe. In the absence of selection line differences in FDAMP the greater staple strength of FW sheep appeared to be primarily related to differences in MFD.

When the effects of minimum length and minimum fibre diameter were compared staple strength increased equally with increased minimum growth for either trait such that long thick winter-grown fibres had the greatest strength. No sheep grew extremely long and extremely thin wool and only one FW sheep grew extremely thick and short wool over winter, suggesting a close biological link between winter levels for both traits. The increased strength of FW sheep was related to greater length and diameter of winter-grown wool.

When the amplitudes of length and diameter were examined together a strong interaction was found. The effect of LPDAMP on staple strength was greatly reduced at high amplitudes of fibre diameter and the effect of FDAMP was greatly diminished in the presence of marked amplitudes of fibre length. The distributions of FW and C sheep were equal across most cells of the grid with the exceptions of high-low combinations where only C sheep were present and medium FDAMP combined with low LPDAMP where FW sheep predominated.

Coarser staples had lower LPDAMP. The effect of LPDAMP on strength was greatest when MFD was higher. The advantage of FW sheep in staple strength was related to increased MFD and its tendency, in FW sheep, to be strongly associated with low LPDAMP.

Although many other possible combinations of effects could have been studied the staple strength advantage of FW sheep seemed to be related to higher MFD in combination with reduced amplitudes of other wool characters and optimum combinations of length and diameter of wool grown over winter.

The effect of one wool growth characteristic on strength was often modified under changing mean values of other wool growth traits. This created a system of interacting effects more dynamic than the static relationships implied in the simple linear regressions presented in Section 8.4.2.2 . If more data had been available multivariate approaches such as canonical correlation or canonical variates analysis might have been more suitable for examining these inter-relationships between variables.

8.4.2.4 Relationship between month of break and wool growth characteristics

In C sheep, MLFD was closely related to both MB and MLCPD whereas, in FW sheep, these relationships were less evident. It could be that short periods of restricted growth have had a greater influence on the breaking region of FW sheep. Alternatively, the occurence of two relatively weak regions along the staples of FW sheep may have given rise to a diffuse breaking region causing the intervening month to be recorded (see Figure 8.4). Rottenbury (1979) found that sound wools break in a less clearly defined region than tender wools. However, this discrepancy between month of break and month of lowest fibre growth may also reflect errors in detecting relatively small changes in fibre diameter or length on a month to month basis.

Control hoggets reaching minimum wool growth later in the year had lower absolute length and weight per day minimums than C sheep reaching minimum wool growth earlier in the season. The month of lowest fibre diameter and lowest length growth rate were more closely related in C than in FW hoggets. These differing associations in FW and C sheep between month and level of minimum wool growth have probably given rise to the tentative relationship between later month of break and lower staple strength in C sheep which was absent in FW sheep.

8.4.2.5 Other factors contributing to staple strength

The possibility exists that factors other than fibre growth patterns are affecting differences in staple strength in FW and C sheep.

1. Intrinsic strength: The low proportion of variation in staple strength which is explained by wool growth characteristics (max.38%) may indicate that wool fibres from FW and C sheep differ in intrinsic strength. Intrinsic strength is largely independant of cross sectional area. Possible causes may relate to cortical cell types, as proposed by Orwin et al. (1980; 1985), or to differences in protein/amino acid composition of wool. These effects on staple strength (proportion and arrangement of ortho- and para-cortex and sulphur content of cortical cell types) are inter-related not only between sheep but also within the growing fibre (Carnaby, 1984; Fitzgerald, 1984). The relationship between wool sulphur content and staple strength has not been fully resolved and may depend on relative changes in both the proportion of para-cortex and the balance of proteins within the matrix. This area of research may prove rewarding but the implications with respect to selection line effects are unclear at this time.

Seasonal and average differences in wool sulphur content between the lines have not yet been extensively studied but a study which included sulphur analyses on October-grown wool from 5 FW and 5 C sheep (McCutcheon et al., (1987)) was unable to demonstrate selection line differences in sulphur content. Piper and Dolling (1966) compared high (F+) and low (F-) fleeceweight-selected lines of Merinos grazed together on low quality pasture. The correlations between sulphur concentration and monthly wool growth were -0.69 and 0.28 for F- and F+ lines. The low line also had greater seasonal variation in wool sulphur-concentration and as sulphur supply was not limiting to wool growth they exhibited the normal wool growth:sulphur % relationship. In contrast, the F+ line was likely near its biological minimum level of sulphur concentration. The lower concentration of sulphur in high producing Merinos is related to a decrease in the proportion of high-sulphur proteins in the fibre matrix.

2. Techniques of measuring wool growth: The low R^2 of predicting staple strength in these data could also relate to the inability of the techniques employed to identify short term changes in fibre dimensions which, although not enduring long enough to affect average monthly measurements, may have profound effects on fibre and staple strength. For example, a weak region may only be 1mm long over a guage length of 8 cm. More accurate measurements on fibre diameter changes, such as are possible with modern computer-assisted image analysis, may greatly improve our ability to identify structural changes influencing staple strength. Low R^2 may also be a consequence of the many errors associated with staple strength measurement and the determination of length and diameter from small samples.

3. Follicle population: Variation in primary and secondary follicle growth parameters, as well as their ratios within the follicle population of FW and C sheep, may have also contributed to differences in and errors in the measurement of staple strength.

4. Environmental effects: Bacterial invasion of the skin surface can also reduce staple strength, without causing overt changes in fibre dimensions, through damage to the intercellular cement of the fibre. This enzymatic damage is also related to the incidence of wool faults such as cotting and, staining. Fleeces with more open staple structure may also be more subject to weathering than fleeces with a more dense staple arrangement (Ross, 1962)..

8.4.3 The relationship between hand-pull grade and staple strength

Both the high phenotypic correlation (.58) between hand-pull grade and staple strength (Table 8.4) and the similarity of response of hand-pull grade and staple strength to wool growth characteristics (Tables 8.3, 8.6) would imply that reasonable progress in staple strength should accompany selection for higher hand-pull grade. Phenotypic correlations of .65 have been reported by Ross (1960) and genetic correlations of .54 have been found by Newman (unpublished). In Australian studies, where hand-pull grade has been cross-checked with standard samples, the correlation between hand-pull grade and staple strength has been as high as .9 (Rottenbury, 1979). Unless staple splitting practices are standardized while hand-testing fleece samples for soundness, a great deal of error can be introduced, especially with respect to mis-classification of high strength staples.

Temporary errors in assessment were possibly a large source of sex differences in hand-pull grade (in the absence of measurable differences in strength) found in this trial. Ewe and ram hoggets were assessed on separate days. Although Rottenbury (1979) found large differences in the staple linear density and subsequent hand-pull grade both between and within operators, the size of staples selected appears to have been relatively constant in these data (Table 8.6).

8.4.4 Ewe hogget and two-tooth staple strength

The weak relationship between hogget and two-tooth staple strength found in this study should be viewed with caution as very few sheep were involved and the strength of October shorn two-tooth samples was very low. Many samples were so badly cotted that it was difficult to remove individual staples without losing the staple butt.

Very little information is available on the relationship between hogget and lifetime staple strength. Newman (unpublished) has found repeatabilities of .26 between hogget and two-tooth or lifetime staple strength relative to a repeatability of .38 between two-tooth and lifetime staple strength. Repeatabilities of hand-pull grades were somewhat lower (.14 vs. .20) . All sheep were shorn post-lambing in October. Ross(1965) quoted repeatabilities of 0.21 and 0.50 indicating that selection for high hogget staple strength might not necessarily improve staple strength in the ewe clip. The genetic and phenotypic correlations between hogget and subsequent staple strength need to be more fully examined before the effect of selection policies in hoggets on subsequent performance can be predicted.

No effect of lambing status on staple strength was evident in the small number of sheep studied. Stevens and Wright (1951), Lambourne (1956), Hight et al. (1976), Bigham et al. (1978b), Horton and Wickham (1979) and Hawker (1984) reported increased numbers of unsound fleeces with increasing number of lambs born and reared. In contrast, Ross (1965) found twin-bearing ewes to have 10% higher staple strengths than single-bearing ewes. Hawker (1984) also showed that the effect of lambing status on staple strength was reduced by delaying lambing dates so that photoperiodic and physiological influences were separated.

8.5 SUMMARY AND CONCLUSIONS

Both staple strength and hand-pull grade were moderately heritable and, as such, should respond to direct selection.

The correlated response in staple strength of ≈ 6 N/ktex indicates the presence of positive genetic correlations between staple strength and fleeceweight and/or their contributing traits. Although greasy fleeceweight had a relatively low phenotypic correlation with staple strength the effect of selection for greasy fleeceweight has been to increase staple strength by increasing the length, diameter and subsequent weight, of fibres grown over winter months with small concomitant and complementary decreases in the amplitude of fibre length and wool weight. Increased mean fibre diameter of FW sheep also contributed to increased strength.

Hand-pull grade was strongly correlated to measured staple strength and should be a useful alternative measurement technique if used with diligent attention to staple selection, the number of staples tested and cross referencing to previous lots of tested samples. If more precise measurements are required, such as might be required in ram selection, then objective measurements would be recommended.

Staple strength in two-tooths was not closely related to staple strength in the same animals as hoggets. Further study of the relationship between hogget and two-tooth staple strength is warranted before hogget staple strength is included as a selection criterion in sheep improvement programmes.

The implication of these and previous results is that selection for high winter wool growth (May-July) may be an effective method of improving both staple strength and fleeceweight of hoggets by genetic means. This does not imply, however, that equivalent or greater response in both characters could not be achieved through other selection methods based solely on fleeceweight or on fleeceweight in combination with staple strength or hand-pull grade. In any selection programme the cost of obtaining data on specific traits should not outweigh the benefits from their inclusion as selection criteria.

GENERAL DISCUSSION AND CONCLUSIONS

A single trait fleece weight selection flock, the Massey University PT flock, has provided an excellent basis for the study of physiological and productive differences between selected lines. Genetic resources such as this do not often exist. Massey University, and her associated administrators, as well as the researchers involved with the initiation of this selection flock, are to be commended for commiting and contributing resources for the maintenance of these flocks over long terms. A study of the nature reported here, would not have been effective using screened populations.

Initial objectives and eventual pursuits do not always coincide. The original purpose of preliminary investigations was to do detailed physiological comparisons of the lines, especially as these studies related to protein digestion and metabolism. With this objective, a long indoor trial was initiated to determine if differences in the apparent ability to digest nutrients did or did not exist in this flock.

The conduct of pen trials can be a frustrating experience. Decisions about ad libitum vs. controlled feeding and the number of animals per line required are nearly impossible to make without some a priori knowledge of differences in productive responses between groups. The nature of these trials requires fairly long term feeding and caring indoors, and there is the additional complication of across season comparisons being potentially confounded with treatments applied in series.

Notwithstanding these afflictions, some very useful results were obtained from the indoor trial. In three repeated observation periods and under diets of varying quantity and quality, a difference in FW and C sheep in the apparent ability to digest ingested nutrients was not demonstrated. Furthermore, FW rams were capable of utilizing additional supplies of amino acids towards wool growth, while the wool growth of C rams did not respond. Significant differences in wool production were obtained over the entire course of the experiment, which ran over winter. And finally, some intriguing results related to urine output were obtained that led to useful subsequent investigations by other authors (Clark, 1987; McCutcheon et al., 1987).

Reassuringly, these results were also in agreement with many Australian Merino comparisons (Williams, 1979) so the field was open to pursue other interests with confidence.

As thoughts progressed and congealed, the notion of comparing and studying these animals throughout the wool growth period that contributed to their ultimate selection/rejection as replacement animals became appealing.

The work of (the late) Hugh Hawker (Hawker and Crosbie, 1985) was particularly enticing, as most other studies had pursued the nature of productive differences under the conditions of maximum growth, the route determined to be most elucidating in Merino comparisons. Merinos and Romneys are quite different beasts, not only in the quality and fibre properties of their fleeces, but also in the nature and extent of photoperiodic influences on productive traits such as wool growth and reproduction.

With these thoughts in mind, it seemed unlikely that young FW and C hoggets, sheared in late December of their first year, could manage to produce significant differences in hogget fleece weight unless they were capable of sustained superiority over winter. Also, it was possible that the entire seasonal production curve could have been lifted (as suggested by Hawker et al.(1985), in FW lines.

The positive correlated response in number of lambs born (Blair et al., 1985), seemed difficult to explain solely on the basis of liveweight differences. As both wool growth and reproduction can be modified by photoperiod, the concept of estimating differences in the seasonality of both of these traits in FW and C hoggets became appealing. It was possible, at the same time, and on the same animals, to evaluate differences in intake and wool growth efficiency under grazing conditions.

The results of efficiency trials confirmed those demonstrated in the indoor trial. FW and C rams did not differ significantly in DMI in any season outdoors, nor were there any differences in the efficiency of body growth or in average daily gains. FW rams did maintain higher wool growth and wool growth efficiency in all measured periods although differences in wool growth and efficiency were not significant in January, and January and April, respectively. In conflict with most Merino studies, where differences in wool growth and wool growth efficiency are often greatest under the most advantageous environments, in the Romney rams studied here, the absolute difference (3.5g wool/kg DDMI)in wool production efficiency was equal in July and October, but proportionately greatest in July (67% relative advantage in July: 33% relative advantage in October), the period of minimum wool growth.

It appears clear, that selection for higher fleece weight has produced animals capable of better metabolic utilization of nutrients throughout the year, but these differences were most pronounced over winter months.

Measures of the level and amplitude (88.8% in FW vs. 119.2% in C sheep) of seasonal wool growth confirmed that FW hoggets not only produce significantly more wool than C hoggets in all months up to hogget shearing, but that the absolute, as well as relative advantage in many traits was greatest in winter months. Winter wool production (June, July and August) of FW sheep averaged 46% above C levels. Absolute differences in clean wool production between FW and C lines were greatest in the month just prior to hogget shearing (4.5g/d) and least in the month just after lamb shearing (1.7g/d) and June (1.7g/d). Winter (June or July) clean wool production was able, in the absence of any other variables, to describe close to 80% of the variation in clean hogget fleece weight. It may be that measures of winter wool production would be a valuable trait for prescreening of breeding stock. This trait was not significantly related to hogget reproductive traits in this study, but differences did exist between the selected lines.

Selection for high hogget greasy fleece weight has increased the percentage of ewe hoggets attaining puberty in their first autumn. This 20-25% increase was not due to selection line differences in liveweight as liveweight differences only became significant in early June, long past the peak of oestrus activity in ewe hoggets.

Although the ability of FW hoggets to reach behavioural oestrus in autumn appeared to be related to subsequent ewe reproduction, the underlying causes of a reproductive correlated response in the Massey PT flock first needs to be adequately segregated into differences in fertility and fecundity between lines. Without this information, no definite conclusions can be drawn.

Studies into the staple strength of fleece wools from these flocks were not directly related to physiological comparisons; rather, the opportunity existed to study a trait (staple strength) which is generally accepted to be highly related to the seasonal growth of wool. As staple strength is also a productive character with considerable economic weight, the relationships between seasonal wool growth and staple strength were studied relative to selection line differences, and correlated selection response.

Although greasy fleeceweight had a relatively low phenotypic correlation with staple strength, the effect of selection for greasy fleeceweight was to increase staple strength by increasing the length, diameter and subsequent weight, of fibres grown over winter months with small and complementary decreases in the amplitude of these traits. Although the amplitude of fibre diameter changes was slightly larger in FW than C sheep, this resulted from large increases in fibre diameter over spring, rather than from extreme decreases in fibre diameter over winter.

There remains considerable scope for continued investigations in these flocks. Of first concern would be the estimation of seasonal trends in the sulphur content of fleece wool in these lines, as changes in sulphur content are central to the theory of altered requirements for sulphur containing amino acids in these flocks. The monthly samples archived from this study should provide an excellent first resource for this purpose.

Further examination of reproductive differences between FW and C flocks should include the observation of oestrus and ovulation rate, and their changes with season in open, mature FW and C ewes. The results of Montgomery and Hawker (1987) would suggest that FW ewes may have extended breeding season, with accompanied sustained ovulation rates later into the season.

REFERENCES

Ahmed, W., R.B. Dun and R.J. Winston (1963). The efficiency of conversion of feed to wool in Merino flocks selected for and against fleece weight. Australian Journal of Experimental Agriculture and Animal Husbandry 3:269-275.

Allain, D., J. Rougeot (1980). Induction of autumn moult in mink (Mustela vison Peale and Beauvois) with melatonin. Reproduction Nutrition Development 20(1A):197-201.

Allain, D., L. Martinet, J. Rougeot (1981). Effects of melatonin implants on changes in the coat, plasma prolactin levels and testis cycle in the mink (Mustela vison Peale and Beavois). Photoperiodism and Reproduction in Vertebrates les colloqiums de l'INRA 6:263-271.

Allison, A.J. (1975). Flock mating in sheep. I. Effects of number of ewes joined per ram on mating behavior and fertility. New Zealand Journal of Agricultural Research 18:1-8.

Almeida, O.F.X., G.A. Lincoln (1982). Photoperiodic regulation of reproductive activity in the ram : evidence for the involvement of circadian rhythms in melatonin and prolactin secretion. Biology of Reproduction 27:1062-1075.

Almeida, O.F.X., G.A. Lincoln (1984). Central mechanisms in the control of seasonal breeding. Acta Zoologica Fennica 171:151-156.

Arendt, J., A.M. Symons, C.A. Laud, and S.J. Pryde (1983). Melatonin can induce early onset of the breeding season in ewes. Journal of Endocrinology 97:395-400.

Arnold, G.W., W.R. McManus, I.G. Bush (1964). Studies in the wool production of grazing sheep: 1. Seasonal variation in feed intake, liveweight and wool production. Australian Journal of Experimental Agriculture and Animal Husbandry 4:392-403.

Asofi, M.K. (1984). A study on the breeding performance of Romney and Border Leicester cross Romney ewe hoggets and two year old ewes. Thesis, Ph.D., Massey University, Palmerston North, New Zealand.

Baker, R.L., J.N. Clarke and A.H. Carter (1974). Sources of variation for wool, body weight and oestrous characters in Romney hoggets. Proceedings of the New Zealand Society of Animal Production 34:19-22.

Baker, R.L., J.N. Clarke, A.H. Carter and G.D. Diprose

(1979). Genetic and phenotypic parameters in New Zealand Romney sheep. I. Body weights, fleece weights and oestrus activity. New Zealand Journal of Agricultural Research 22:9-21.

Baker, R.L., J.N. Clarke and G.D. Diprose (1981). Effect of mating Romney ewe hoggets on lifetime production - preliminary results. Proceedings of the New Zealand Society of Animal Production 41:198-203.

Baker, R.L., T.G. Harvey, J.N. Clarke and H.H. Meyer (1987). Genetic variation among some selected New Zealand strains and breeds of sheep. Proceedings of the 4th Asian Australasian Association of Animal Production Animal Science Congress, Hamilton, New Zealand p.385.

Barlow, R. (1974). Selection for clean fleece weight in Merino sheep II. Correlated responses to selection. Australian Journal of Agricultural Research 25:973-994.

Barlow, R. and C.J. Hodges (1976). Reproductive performance of ewe lambs: genetic correlation with weaning weight and subsequent reproductive performance. Australian Journal of Experimental Agriculture and Animal Husbandry 16:321-324.

Barnett, J.L., C.G. Winfield, G.M. Cronin, A.W. Makin (1981). Effects of photoperiod and feeding on plasma corticosteriod concentrations and maximum corticosteriod binding capacity in pigs. Australian Journal Biological Science 34:577-562.

Barrell, G.K. (1983). How daylight affects reproduction in sheep. New Zealand Veterinary Journal 31:137-138.

Barrell, G.K., K.R. Lapwood (1979). Effects of pinealectomy on the secretion of luteinizing hormone, testosterone and prolactin in rams exposed to various lighting regimes. Journal of Endocinology 80:397-405.

Barritt, J., A.T. King (1926). The sulphur content of wool.I. Inherent variations according to the type of wool. Journal of the Textile Institute 17:T386-395.

Barritt, J., A.T. King (1929). The sulphur content of wool. II. Distribution of sulphur along the fibre, variation with colour and the effect of exposure to ultra-violet light. Journal of the Textile Institute 20:T151-158.

Barry, T.N., P.F. Fennessy and S.J. Duncan (1973). Effect of formaldehyde treatment on the chemical composition and nutritive value of silage. III. Voluntary intake, live-weight gain, and wool growth in sheep fed the silages with and without intravenous peritoneal supplementation with DL-methionine. New Zealand Journal of Agricultural Research 16:64-68.

Bassett, C.F., O.P. Pearson, F. Wilke (1944). The effect of artificially increased length of day on moult, growth and priming of silver fox pelts. American Fur Breeder 17:32.

Bell, O.S., D.A. Spencer, J.I. Hardy (1936). Ohio Agricultural Experiment Station Bulletin NO. 571.

Bennett, J.W., J.C.D. Hutchinson and M. Wodzicka-Tomaszewska (1962a). Climate and wool growth. Proceedings of the Australian Society of Animal Production 4:32-33.

Bennett, J.W., J.C.D.Hutchinson and M. Wodzicka-Tomaszewska (1962b). Annual rhythm of wool growth. Nature 194:651-652.

Bielhartz, R. G. (1986). The pivotal role of reproduction in animal improvement. Proc. 3rd World Congress on Genetics Applied to Livestock Production. XI:49-54.

Bielhartz, R.G. and Luxford, B.G. (1987). Inheritance of reproduction affects gains possible in commercially important traits. Proceedings of the 6th Australian Association of Animal Breeding and Genetics Conference, Perth, WA., Feb 9-11. p.253-256.

Bigham, M.L. (1974). Effects of shearing interval on fleece weight and wool growth on a delineated midside patch. New Zealand Journal of Agricultural Research 17:407-410.

Bigham, M.L. (1984).(comment) Lincoln College Wool Bulletin No.1. Proceedings of of a Seminar on Staple Strength, August 1984.

Bigham, M.L., R.M.W. Sumner and D.C. Dalton (1978a). Wool production of different breeds on mixed aged ewes on hill country. New Zealand Journal of Agricultural Research 21:119-126.

Bigham, M.L., R.M.W. Sumner, K.J. Elliot (1978b). Seasonal wool production of Romney, Coopworth, Perendale, Cheviot, and Corriedale wethers. New Zealand Journal of Agricultural Research 21:377-382.

Bigham, M.L., R.M.W. Sumner, H. Hawker and J.M. Fitzgerald (1983). Fleece tenderness - A review. Proceedings of the New Zealand Society of Animal Production 43:73-78.

Bindon, B.M., and L.R. Piper (1976). Assessment of new and traditional techniques of selection for reproductive rate. In: Sheep Breeding, Proceedings of the 1976 International Congress, Muresk and Perth, W.A. Ed. Tomes, G.J.; Robertson, D.E. and Lightfoot, R.J., pp.322-329.

Bissonnette, T.H. (1935). Relations of hair cycles in ferrets to changes in the anterior hypophysis and to light cycles. Anatomical Record 63:159-168.

Bissonnette, T.H. and E. Wilson (1939). Shortening daylight periods between May 15 and Sept 12 and the pelt cycle of the mink. Science 89:418-419.

Bissonnette, T.H., and E.E. Bailey (1944). Experimental modification and control of moults and changes of coat colour in weasels by controlled lighting. Annals New York Academy of Science 45:221-260.

Bittman, E.L. (1984). Melatonin and photoperiodic time measurement: Evidence from rodents and ruminants. In "The pineal gland", Ed. R.J. Reiter, Raven Press, New York. pp.155-192.

Bittman, E.L., F.J. Karsch, R.J. Dempsey (1982). Pineal melatonin mediates photoperiodic drive of seasonal changes in pulsatile LH secretion in sheep. Abstract 983, 64th Annual Meeting of the Endocrine Society, San Francisco.

Bittman, E.L., R.J. Dempsey and F.J. Karsch (1983a). Pineal melatonin secretion drives the reproductive response to daylength in the ewe. Endocrinology 113:2276-2283.

Bittman, E.L., F.J. Karsch and J.R. Hopkins (1983b). Role of the pineal gland in ovine photoperiodism: Regulation of seasonal breeding and negative feedback effects of estradiol upon luteinizing hormone secretion. Endocrinology 113:329-336.

Bittman, E.L. and Karsch, F.J. (1984). Nightly duration of pineal melatonin secretion determines the reproductive response to inhibitory day length in the ewe. Biology of Reproduction 30:585-593.

Blair, H.T. (1981). Response to selection for open face and greasy fleece weight in Romney sheep. Thesis, Ph.D., Massey University, Palmerston North, New Zealand.

Blair, H.T. (1986). Responses to 27 years of selection for yearling fleece weight. Proceedings of the 3rd World Congress of Genetics Applied to Livestock Production XII:215-220.

Blair, H.T., D.J. Garrick, A.L. Rae and G.A. Wickham (1984). Selection responses in New Zealand Romney sheep I. Selection for wool free faces. New Zealand Journal of Agricultural Research 27:329-336.

Blair, H.T., D.J. Garrick, A.L. Rae and G.A. Wickham (1985).

Selection responses in New Zealand Romney sheep II. Selection for yearling greasy fleeceweight. New Zealand Journal of Agricultural Research 28:257-264.

Bliss, C.I. (1958). Periodic regression in biology and climatology. Conneticut Agriculture Experiment Station Bulletin #615.

Bodin, L., B. Bibe, M. Blanc and G. Ricordeau. (1986). Parametre genetiques de la concentration plasmatique en FSH de agnelles de race Lacaune viande. Genetique, Selection, Evolution. 18:55-62.

Bonsma, F.N (1931). The sulphur content of some South African wools. Journal of the Textile Institute 22:T305-313.

Bose, M.J., J. Djiane, P. Durand, J. Pelletier, J.P. Ravault (1982). Influence of season on mean plasma levels of prolactin, placental lactogen hormone and luteinizing hormone during the second half of gestation in the ewe. Reproduction, Nutrition, Development 22:485-493.

Bottomley, G.A. (1979). Weather conditions and wool growth. In "Physiological and Environmental Limitations to Wool Growth", Eds. J.L. Black and P.J. Reis, U.N.E. publishing unit: Armidale, N.S.W. pp.115-125.

Bowstead, J.E. and P. Larose (1938). Wool growth and quality as affected by certain nutritional and climatic factors. III. Results and Conclusions. Canadian Journal of Research, D 16:361-374.

Box, G.E.P. (1950). Problems in the analysis of growth and wear curves. Biometrics 6:362-389.

Boyd, J.M., J.M. Doney, R.G. Guhn, P.A. Jewell (1964). The Soay sheep on the island of Hirta, St. Kilda. A study of a feral population. Proceedings of the Zoological Society of London 142:129-163.

Bradbury, J.H. (1973). The structure and chemistry of keratin fibres. Advances in Protein Chemistry 27:111-211.

Bradford, G.E. (1972). Genetic control of litter size in sheep. Journal of Reproduction and Fertility, Supplement 15:23-41.

Bradford, G.E. (1985). Selection for litter size. In: "Genetics of reproduction in sheep". Edited by R.B. Land and D.W. Robinson, Butterworths, London. p 3-18.

Brainard, G.C. (1978). Pineal Research: The decade of transformation. Journal of Neural Transmission ,Supplement. "The pineal gland". Proceedings of the

International Symposium, Jerusalem, Ed. I. Nir, R.J. Reiter and R.J.Wurtman.

Bratt, R.L. (1965). The effect of staple strength on worsted processing III. Fibre length distribution and spinning. Journal of the Textile Institute 56:62-72.

Bratt, R.L., D.A. Ross and L.F. Story (1964). The effect of staple strength on worsted processing II. Carding and combing of 58.60's. Journal of the Textile Institute 56:T165-174.

Brien, F.D. (1986). A review of the genetic and physiological relationships between growth and reproduction in mammals. Animal Breeding Abstracts 54:975-997.

Brinklow, B.R. and J.M. Forbes (1984a). Effect of pinealectomy on the plasma concentrations of prolactin, cortisol and testosterone in sheep in short and skeleton long photoperiods. Journal of Endocinology 100:287-293.

Brinklow, B.R. and J.M. Forbes (1984b). The effect of short and skeleton long photoperiods on the plasma concentrations of prolactin and cortisol in sheep. Reproduction, Nutrition, Development 24:107-112.

Brown, T.H. (1971). The effect of three factors on the incidence of tender wool in deferred grazing management. Australian Journal of Experimental Agriculture and Animal Husbandry 11:607-613.

Brown, W.B. and J.M. Forbes (1980). Diurnal variations of plasma prolactin in growing sheep under two lighting regimes and the effect of pinealectomy. Journal of Endocrinology 84:91-99.

Bryant, E. and D. Gillings (1985). Statistical analysis of longitudinal repeated measures designs. Biostatistics :251-282.

Bubenik, G.J. (1983). Shift of seasonal cycle in White-tailed deer by oral administration of melatonin. Journal of Experimental Zoology 225:155-156.

Burkhardt, J. (1947). Transition from anoestrus in the mare and the effect of artificial lighting. Journal of Agricultural Science 37:64-68.

Burns, R.H. (1931a,b).J.Text.Instit. 22:T98 22:T456

Butler, L.G. and W.M.C. Maxwell (1984). A review of the efficiency of conversion of feed into wool. Animal Breeding Abstracts 52:475-485.

Buttle, H.L. (1974). Seasonal variation of prolactin in plasma of male goats. Journal of Reproduction and Fertility 37:95-99.

Carnaby, G. (1984). Relationship of ortho- and para- cortex and staple strength. Lincoln College Wool Bulletin No.1. Report of a seminar on staple strength. p 49-52.

Carter, D.S. and B.D. Goldman (1981). Antigonadal and progonadal effects of programmed melatonin infusion into juvenile Djungarian hamsters (Phodopus sungoris). Biology of Reproduction 24:Abstr.23.

Cedillo, R.M., W. Hohenboken and J. Drummond (1977). Genetic and environmental effects on age at first oestrus and on wool production of crossbred ewe lambs. Journal of Animal Science 44:948-957.

Ch'ang, T.S. (1961). Reproductive performance of New Zealand Romney sheep grazed on Red clover (Trifolium pratense) pastures. Journal of Agricultural Science, Cambridge 57:123-129.

Ch'ang, T.S. (1967). Indirect selection for higher fertility of the Romney ewe. Sheepfarming Annual 1967:7-13.

Ch'ang, T.S. (1968). Early recognition of fertility in the ewe. Wool technology and sheep breeding 15:11-13.

Ch'ang, T.S. and J.I. Raeside (1957). A study on the breeding season of Romney ewe lambs. Proceedings of the New Zealand Society of Animal Production 17:80-87.

Ch'ang, T.S. and A.L. Rae (1970). The genetic basis of growth, reproduction and maternal environment in Romney ewes. I. Genetic variation in hogget characters and fertility of the ewe. Australian Journal of Agricultural Research 21:115-129.

Ch'ang, T.S. and A.L. Rae (1972). The genetic basis of growth, reproduction and maternal environment in Romney ewes. I. Genetic covariation between hogget characters, fertility and maternal env of the ewe. Australian Journal of Agricultural Research 23:149-165.

Chapman, R.E. and J.L. Wheeler (1963). Dye banding : A technique for fleece growth studies. Australian Journal of Science 26:53-54.

Chapman, R.E. and J.M. Bassett (1970). The effects of prolonged administration of cortisol on the skin of sheep on different planes of nutrition. Journal of Endocrinology 48:649-663.

Chatfield, C. and A.J. Collins (1980) Introduction to multivariate analysis. University Press. Cambridge.

Chesworth, J.M. and M.P. Easdon (1983). Effect of diet and season on steroid hormones in the ruminant. Journal of Steroid Biochemistry 19:715-723.

Chopra, S.C. (1979). Genotype-environmental interactions and genetic parameters in New Zealand Romney sheep. Thesis, Ph.D., Massey University, Palmerston North, New Zealand.

Clark, N.T. and G.D. Kohn (1964). The measurement of seasonal wool production -- a comparison between midside sampling and a dye-banding technique. Australian Journal of Experimental Agriculture and Animal Husbandry 4:90-91.

Clarke, J.N. (1972). Current levels of performance in the Ruakura Fertility flock of Romney sheep. Proceedings of the New Zealand Society of Animal Production 32:99-111.

Clark, C.M. (1987) Physiological responses to selection for greasy fleeceweight in Romney sheep. M. Agr. Sc. Thesis, Massey University, Palmerson North

Clarke, J.N. (1977). In: Annual Report of the Research Division 1976-1977, New Zealand Ministry of Agriculture and Fisheries, Wellington, New Zealand. p228-230.

Cockrem, F.R.M. (1979). A review of the influence of liveweight and flushing on fertility made in the context of efficient sheep production. Proceedings of the New Zealand Society of Animal Production 39:23-42.

Cole, J.W.L. and J.E. Grizzle (1966) Applications of multivariate analysis of variance to repeated measurements experiments. Biometrics 22:810-828.

Coop, I.E. (1953). Wool growth as affected by nutrition and by climatic factors. Journal of Agricultural Science, Cambridge 43:456-472.

Coop, I.E. (1961). The energy requirements of sheep. Proceedings of the New Zealand Society of Animal Production 21:79-91.

Coop, I.E. and D.S. Hart (1953). Environmental factors affecting wool growth. Proceedings of the New Zealand Society of Animal Production 13:113-119.

Coop, I.E. and V.R. Clark (1958). The effect of thyroxine on wool growth and lamb production. New Zealand Journal of Agricultural Research 1:365-381.

Dalton, D.C. and Rae, A.L. (1978). The New Zealand Romney sheep: A review of productive performance. Animal Breeding Abstracts 46:657-680.

Daly, R.A. and H.B. Carter (1955). The fleece growth of young Lincoln, Corriedale, Polwarth and fine Merino maiden ewes under housed conditions and unrestricted and progressively restricted feeding on a standard diet. Australian Journal of Agricultural Research 6:476-513.

Danford, M.B., H.M. Hughes and R.C. McNee (1960). On the analysis of repeated-measurements experiments. Biometrics 16:547-565.

Davis, G.P. (1987). Direct and correlated responses to selection on weaning weight in Merinos. Proceedings of the 6th Australian Association of Animal Breeding and Genetics Conference, Perth, WA., Feb 9-13. p.83-86.

Davis, G.P. and B.P. Kinghorn (1986). Genetic and phenotypic parameters for growth, wool production and reproductive traits in a line of Merino sheep. Proceedings of the 3rd World Congress on Genetics Applied to LivestockProduction. Vol XI:145-150.

Dickerson, G.E. (1970). Efficiency of animal production - Moulding thebiological components. British Journal of Animal Science 30:849-856.

Dickerson, G.E. and Laster, D.B. (1975). Breed, heterosis and environmental influences on growth and puberty in ewe lambs. Journal of Animal Science 41:1-9.

Dolling, C.H.S. and M.T. Carpenter (1963). Water consumption at pasture of Merino sheep selected for high wool production. Proceedings of the Australian Scociety of Animal Production. 4:172-174.

Dolling, C.H.S. and R.W. Moore (1960). Efficiency of conversion of food to wool I. Correlated response to selection for high and low clean wool weight per head. Australian Journal of Agricultural Research 11:836-844.

Dolling, C.H.S. and L.R. Piper (1968). Efficiency of conversion of food to wool III. Wool production of ewes selected for high clean wool weight and of random control ewes on restricted and unrestricted food intake in pens. Australian Journal of Agricultural Research 19:1009-1028.

Doney, J.M. (1964). The fleece of the Scottish Blackface sheep. IV. The effects of pregnancy, lactation and nutrition on seasonal wool production. Journal of Agricultural Science, Cambridge 62:59-66.

Doney, J.M. (1966). Breed differences in response of wool growth to annual nutritional and climatic cycles. Journal of Agricultural Science, Cambridge 67:25-30.

Doney, J.M. and W.F. Smith (1961a). The fleece of the Scottish Blackface sheep. 1. Seasonal changes in wool production and fleece structure. Journal of Agricultural Sciences,Cambridge 56:365-374.

Doney, J.M. and W.F. Smith (1961b). The fleece of the Scottish Blackface sheep. 2.Variation in fleece components over the body of the sheep. Journal of Agricultural Science, Cambridge 56:375-378.

Doney, J.M. and J. Eadie (1967) . The wool growth response to the annual cycle of grazing intake in Cheviot wethers. Journal of Agricultural Science, Cambridge 69:411-416.

Doney, J.M. and J.G. Griffiths (1967) . Wool growth regulation by local skin cooling. Animal Production 9:393-397.

Doney, J.M. and C.C. Evans (1968). The influence of season and nutrition on the sulphur content of wool from Merino and Cheviot sheep. Journal of Agricultural Science, Cambridge 70:111-116.

Doney, J.M. and C.C. Evans (1970). The influence of nutrition during winter on growth rate and sulphur content of wool of pregnant Scottish Blackface and Romney ewes. Journal of Agricultural Science, Cambridge 75:133-136.

Douglas, S. (1984a). Staple strength and wool marketing in Australia Lincoln College Wool Bulletin no.1. Report of a seminar on Staple strength, Ed. D.A. Ross and L.F. Story, p 55-71.

Douglas, S. (1984b). Trials on the processing significance of staple strength Lincoln College Wool Bulletin no. 1. Report of a seminar on staple strength, Ed. D.A. Ross and L.F. Story. p 79-92.

Downes, A.M. and A.G. Lyne (1961). Studies on the rate of wool growth using 35S-cystine Australian Journal Biological Science 14:120-130.

Downes, A.M. and A.L.C. Wallace (1965). Local effects on wool growth of intradermal injections of hormones. In: "Biology of the skin and hair growth". Eds. A.G. Lyne and B.F. Short, Angus and Robertson, Sydney. pp. 679-704.

Downes, A.M. and J.C.D. Hutchinson (1969). Effect of low skin surface temperature on wool growth. Journal of Agricultural Science, Cambridge 72:155-158.

Downes, A.M. and L.F. Sharry (1971). Measurement of wool growth and its response to nutritional changes. Australian Journal of Biological Science 24:117-130.

Draper, S.A., N.B. Haynes and G.E. Lamming (1966). Effect of plane of nutrition on change in rate of wool growt h in sheep induced by hexoestrol. Nature, London 210:222-223.

Driancourt, M.A., I.K. Gauld, M. Terqui and R. Webb. (1986). Variations in patterns of follicle development in prolific breeds of sheep. Journal of Reproduction and Fertility 79:565-576.

Driancourt, M.A. and R.C. Fry. (1988). Differentiation of ovulatory follicles in sheep. Journal of Animal Science 66(Suppl.2):9-20.

Duerden, J.E. and G.S. Mare (1931). Union of South Africa Department of Agriculture Reprint #35.

Dun, R.B. and Eastoe, R.D. (1970). Science and the Merino breeder. New South Wales Government Printer, Ultimo. p. 141.

Dunlop, A.A., C.H.S. Dolling and J.F. Kennedy (1960). Efficiency of conversion of food to wool in five Merino strains. Australian Journal of Agricultural Research 11:576-584.

Dunlop, A.A., C.H.S. Dolling and M.T. Carpenter (1966). Efficiency of conversion of food to wool at two nutritional levels by three Merino strains. Australian Journal of Agricultural Research 17:81-89.

Dyrmundsson, O.R. (1973). Puberty and early reproductive performance in sheep. I. Ewe lambs. Animal Breeding Abstracts 41:273-284.

Dyrmundsson, O.R. (1981). Natural factors affecting puberty and reproductive performance in ewe lambs: A review. Livestock Production Science 8:55-65.

Dyrmundsson, O.R. (1983). The influence of environmental factors on the attainment of puberty in ewe lambs. In: Sheep Production. W. Haresign, Ed., Butterworths, London . pp.393-407.

Dyrmundsson, O.R. and Lees, J.L. (1972a). Attainment of puberty and reproductive performance in Clun Forest ewe lambs. Journal of Agricultural Science, Cambridge, 79:39-45.

Dyrmundsson, O.R. and Lees, J.L. (1972b). Effect of rams on the onset of breeding in Clun Forest ewe lambs. Journal of Agricultural Science, Cambridge, 79:269-271.

Ebling, F.J. and P.A. Hale (1983). Hormones and hair growth. In: "Biochemistry and physiology of the skin",Editor, Lowell A. Goldsmith Vol1:522-552.

Edey, T.N., T.T. Chu, R. Kilgour, J.F. Smith and H.R. Tervit (1977). Oestrus without ovulation in pubertal ewes. Theriogenology, 7:11-15.

Edey, T.N.; Kilgour, R. and Bremner, Kaye. (1978). Sexual behavior and reproductive performance of ewe lambs at and after puberty. Journal of Agricultural Science, Cambridge. 90:83-91.

Ferguson, K.A. (1949). The effect of sympathectomy on wool growth. Australian Journal of Scientific Research B:2:438-443.

Ferguson, K.A. (1951). The effect of hypophysectomy on wool growth. Journal of Endocrinology 7:1-17.

Ferguson, K.A. (1951). Thesis, Ph.D., University of Cambridge, England.

Ferguson, K.A. (1954). Prolonged stimulation of wool growth following injection of ox growth hormone. Nature, London 174:411.

Ferguson, K.A. (1958). The influence of thyroxine on wool growth. Proceedings of the New Zealand Society of Animal Production 18:128-140.

Ferguson, K.A., H.B. Carter and M.H. Hardy (1949). Studies of comparative fleece growth in sheep. 1. The quantitative nature of inherent differences in wool growth rate. Australian Journal of Scientific Research B:2:42-81.

Ferguson, K.A., A.L.C. Wallace and H.R. Lindner (1965). Hormonal regulation of wool growth. In: "Biology of the skin and hair growth". Eds. A.G. Lyne and B.F. Short, Angus and Robertson, Sydney. pp. 655-678.

Findlay, J.K. and Bindon, B.M. (1976). Plasma FSH in Merino lambs selected for fecundity. Journal of Reproduction and Fertility, 46:515-516.

Fisher, D.A., I.J. Chopra and J.H. Dussault (1972). Extrathymoidal conversion of thyroxine to triiodothyronine in sheep. Endocrinology 91:1141-1144.

Fitzgerald, J.M. (1984). Fibre structure and soundness. Lincoln College Wool Bulletin no.1. Report of a seminar on staple strength. Ed. D.A. Ross and L.F. Story p 52-53.

Fitzgerald, J.M., D.C. Smeaton and K.T. Jagusch (1984).

Fleece tenderness: the effect of nutrition, age and lambing status on pregnant Romney and Coopworth mixed-age ewes. Proceedings of New Zealand Society of Animal Production 44:53-56.

Fletcher, J.C., A. Robson and J. Todd (1963). The sulphur balance in wool. Biochemical Journal 87:560-567.

Foote, W.C., N. Sefidbakht and M.A. Madson (1970). Pubertal estrus and ovulation and subsequent estrous cycle patterns in the ewe. Journal of Animal Science 30:86-90.

Forbes, J.M., P.M. Driver, A.A. El Shahat, T.G. Boaz, C.G. Scanes (1975). The effect of daylength and level of feeding on serum prolac tin on growing lambs. Journal of Endocrinology 64:549-556.

Forbes, J.M., P.M. Driver, W.B. Brown, C.G. Scanes, I.C. Hart (1979). The effects of daylength on the growth of lambs.2. Blood concentration of growth hormone, prolactin, insulin and thyroxine, and the effect of feeding. Animal Production 29:43-51.

Foster, D.L. (1981). Mechanism for delay of first ovulation in lambs born in the wrong season (Fall). Biology of Reproduction, 25:85-92.

Foster, D.L. (1983). Photoperiod and sexual maturation of the female lamb: early exposure to short days perturbs oestradiol feedback inhibition of LH secretion and produces abnormal ovarian cycles. Endocrinology 112:11-17.

Foster, D. and K. Ryan (1979a). Mechanisms governing onset of ovarian cyclicity at puberty in the lamb. Annals de Biologie animale et Biochemistry et Biophysique 19:1369-1380.

Foster, D.L. and Ryan, Kathleen. (1979b). Endocrine mechanisms governing transition into adulthood: A marked decrease in inhibitory feedback action of oestradiol on tonic secretion of LH in the lamb during puberty. Endocrinology 105:896-904.

Foster, D.L. and Ryan, Kathleen, D. (1981). Endocrine mechanisms governing transition into adulthood in female sheep. Journal of Reproduction and Fertility, Supplement 30:75-90.

Foster, D.L.; Yellon, S.M. and Olster, D.H. (1984). Endocrine physiology of puberty in the female sheep. Proceedings of the 10th International congress of Animal Reproduction and Artificial Insemination VII:16-23.

Foster, D.L., S.M. Yellon and D.H. Olster (1985). Internal and external determinants of the timing of puberty in the female. Journal of Reproduction and Fertility 75:327-344.

Foster, D.L., F.J. Karsch, D.H. Olster, K.D. Ryan and S.M. Yellon (1986). Determinants of puberty in a seasonal breeder. Recent Progress in Hormone Research 42:331-377.

Fraser, A.G., B.F. Short (1958). Studies of sheep mosaic for fleece type I. Patterns and origin of mosaicism. Australian Journal of Biological Science 11:200-208.

Frazer, K.M. (1931). Journal of the Council of Scientific and Industrial Research in Australia 4:204-231.

Galpin, N. (1947). Study of wool growth. I. Weight of wool. Journal of Agricultural Science,Cambridge 37:275-286.

Galpin, N. (1948). Study of wool growth. II. mean fibre thickness, density of population, the area of skin covered by fibre and the mean fibre length Journal of Agricultural Science, Cambridge 38:303-313.

Gee, E. (1978). Staple strength as a measure of the soundness of wool - A preliminary note. S.A.W.T.R.I. Technical Report #429

Geenty, K.G., D.F.G. Orwin, J.L. Woods, S.R. Young, M.C. Smith (1984). Seasonal wool production and staple strength of Romney ewes. Proceedings of New Zealand Society of Animal Production 44:57-59.

Geenty, K.G., D.F.G. Orwin, J.L. Woods, S.R. Young and M.C. Smith (1984). Seasonal wool production and staple strength of Romney ewes. Proceedings of New Zealand Society of Animal Production 44:57-59.

Gill, J.L. and H.D. Hafs (1971) Analysis of repeated measurements of animals. Journal of Animal Science, 33:331-336.

Gillespie, J.M. (1965). The high sulphur proteins of normal and aberrant keratins. In: "Biology of the skin and hair growth". Eds. A.G. Lyne and B.F. Short, Angus and Robertson, Sydney. pp. 375-398.

Gilmour, A.R. (1985) REG: A generalized linear models programme. Miscellaneous bulletin No. 1., Division of Agricultural Services, N.S.W. Department of Agriculture, N.S.W., Australia.

Gilmour, A.R., R.D. Anderson, and A.L. Rae (1985). The analysis of binomial data by a generalized linear mixed model. Biometrika 72:593-599.

Girard, J. (1969). (Resumption of wool growth induced by thyroxine injection in hypophysectomized <<Ile de France>> ewes). Annales de Biologie,animal Biochemique,Biophysique 9:497-512.

Goldman, B.D. (1982). Society for the Study of Reproduction 26,Supp 1:Abstr 22

Goldman,B.D., V. Hall, C. Hollister, P. Roychoudhury, L. Tamarkin and W. Westrom (1979). Effects of melatonin on thee reproductive system in intact and pinealectomized male hamsters maintained under various photoperiods. Endocrinology 104:82-88.

Graham, N.McC. (1968) The metabolic rate of Merino rams bred for high or low wool production. Australian Journal of Agricultural Research 19:821-824.

Hamilton, B.A. and J.P. Langlands (1969) Efficiency of wool production of grazing sheep. I. Differences between Merinos selected for high and low fleece weight. Australian Journal of Experimental Agricultre and Animal Husbandry 9:249-253.

Hammond, J. (1951). Control by light of reproduction in ferrets and mink. Nature 167:150-151.

Hammond, J. (1952). Control of reproduction and pelt changes in ferrets; some experiments with animals kept entirely upon artificial light. Journal of Agricultural Science 42:293-303.

Hammond, J. (1953). "Effects of artificial lighting on the reproductive and pelt changes of the mink".Monograph, Heffer, Cambridge.

Hanrahan, J.P. (1974). Ovulation rate as a selection criteria for fecundity in sheep. Proceedings of the 1st World Congress of Genetics Applied to Livestock Production, III:1033-1037.

Hanrahan, J.P. (1976). Repeatability of ovulation rate and its relationship with litter size in four sheep breeds. Proceedings of the 27th meeting of the European Association of Animal Production, Zurich, 630,538 ppl-8.

Hardy, J.I. and J.B. Tennyson (1930). Journal of Agricultural Research 40:457-468.

Hare, Louise and M.J. Bryant (1982). Characteristics of oestrus cycles and plasma progesterone profiles of young female sheep during their first breeding season. Animal Production 35:1-7.

Hart, D.S. (1953). Additional photoperiodic response in sheep. Nature 171:133-134.

Hart, D.S. (1955). The photoperiodic and hormone response of wool growth in sheep. Proceedings of the New Zealand Society of Animal Production 15:57-65.

Hart, D.S. (1961). The effect of light-dark sequences on wool growth. Journal of Agricultural Science 56:235-243.

Hart, D.S., J.W. Bennett, J.C.D. Hutchinson, M. Wodzicka-Tomazewska (1963). Reversed photoperiodic seasons and wool growth. Nature 198:310-311.

Hawker, H. (1984). Twins and triplets don't hurt wool production. New Zealand Farmer 105(7):114-115.

Hawker, H. (1985a). Liveweight and wool characteristics of Romney ewe hoggets screened on high fleece weight. Annual Report 1983/84. Southern South Island Region. Agricultural Research Division. New Zealand Ministry of Agriculture and Fisheries. p. 263.

Hawker, H. (1985b). Effects of nutrition in winter and summer on the wool growth of Romney and Perendale ewes. Annual Report 1983/84. Southern South Island Region. Agricultural Research Division. New Zealand Ministry of Agriculture and Fisheries. p. 264-265.

Hawker, H. (1985c). Effects of season and nutrition on wool growth. New Zealand Wool Board. Proceedings of a Wool Production Seminar, June 1985, 4(1-16).

Hawker, H. (1986). Breeding for more efficient fibre production. W.R.O.N.Z. Proceedings of a Wool Production Seminar 5:48-53.

Hawker, H. and J.P. Kennedy (1978a). Puberty and subsequent oestrous activity in young Merino ewes. Australian Journal of Experimental Agriculture and Animal Husbandry 18:347-354.

Hawker, H. and J.P. Kennedy (1978b). Influence of season and of reproductive status on the wool growth of Merino ewes in an arid environment. Australian Journal of Experimental Agriculture and Animal Husbandry 18:648-652.

Hawker, H., S.F. Crosbie, K.F. Thompson and J.E. McEwan (1984). Effects of season on the wool growth response of Romney ewes to pasture allowance. Proceedings of the Australian Society of Animal Production 15:380-383.

Hawker, H. and S.F. Crosbie (1985). Effects of level of nutrition in winter and summer on the wool growth of

Romney and Perendale ewes with a history of high or low winter wool growth. Proceedings of the New Zealand Society of Animal Production 45:225-228.

Hawker, H., J.C. McEwan and J.N. Clark (1985). The influence of selection for hogget greasy fleece weight on wool growth patterns. Annual Report 1983/84, Southern South Island Region, Agricultural Research Division, New Zealand Ministry of Agriculture and Fisheries, p.266.

Hawker, H. and Littlejohn, R.P. (1986). Liveweights, fleeceweights and wool characteristics of screened high fleeceweight and randomly selected Romney ewe hoggets. Proceedings of the New Zealand Society of Animal Production 46:219-223.

Heath, H.W. and G.R. Lynch (1981). Effects of 18 weeks of daily melatonin injection on reproduc tion and temperature regulation in the mouse, (Peromyscus leucopus). Journal of Experimental Zoology 216:193-195.

Heath, H.W. and G.R. Lynch (1982). Intraspecific differences for melatonin-induced reproductive regression and the seasonal moult in "peromyscus-leucopus". General and Comparative Endocrinology 48:289-295.

Henderson, A.E. (1955). Faults in New Zealand wool. Lincoln College Technical Publication No. 12.

Henderson, A.E. (1968). Growing better wool. A.H. and A.W. Reed, Wellington

Henderson, A.E., J. McG. Bryden, F.E. Mazzitelli and K.E. Milligan (1970). Protein supplementation and wool growth.Proceedings of the New Zealand Society of Animal Production 30:186-201.

Heuer, P.A. (1979). Staple strength measurement equipment. C.S.I.R.O. Division of Textile Physics. Proceedings of a seminar on staple length and staple strength of greasy wool, Ryde NSW p 63-78.

Heydenrych, H.J., L.P. Voosloo and D.J.B. Meisenheimer (1977). Selection response in South African Merino sheep selected either for high clean fleece mass or for a wider S/P ratio. Agroanimalia 9: 67-73.

Hight, G.K. and K.E. Jury (1971). Hill Country sheep production. III. Sources of variation in Romney and Border Leiscester X Romney lambs and hoggets. New Zealand Journal of Agricultural Research 14:669-686.

Hight, G.K., D.R. Lang and K.E. Jury (1973). Hill Country sheep production. V. Occurence of oestrus and ovulation rate of Romney and Border Leicester X Romney ewe hoggets. New Zealand Journal of Agricultural Research

16:509-517.

Hight, G.K. and Jury, K.E. (1976). Hill Country sheep production. VIII. Relationship of hogget and two-year-old oestrus and ovulation rate to subsequent fertility in Romney and Border Leicester X Romney ewes. New Zealand Journal of Agricultural Research 19:281-288.

Hight, G.K., J.J.Atkinson, R.M.W. Sumner and M.L. Bigham (1976). Hill country sheep production VIII. Wool traits of Romney and Border Leicester x Romney ewes. New Zealand Journal of Agricultural Research 19:197-210.

Hill, M.K. (1970). The effect of plane of nutrition on seasonal variation in the efficiency of wool growth in Merino sheep. Proceedings of the Australian Society of Animal Production 8:527-530.

Hoffmann, K. (1973). The influence of photoperiod and melatonin on testis size, body weight and pelage colour in the Djungarian hamster (Phodopus sungoris). Journal of Comparative Physiology 85:267-282.

Horton, C.T. (1978). Some aspects of winter grazing systems on wool production. Thesis, M.Agr.Sci., Massey University, Palmerston North, New Zealand.

Horton, C.T. and G.A. Wickham (1979). The effects of winter grazing systems on some wool traits . Proceedings of the New Zealand Society of Animal Production 39:106-114.

Houssay, B.B., J.H. Pazo C.E. Epper (1966). Effects of the pineal gland upon the hair cycles in mice. Journal of Investigative Dermatology 47:230-234.

Hulet, C.V., E.L. Wiggins and S.K. Ercanbrack (1969). Oestrus in range lambs and its relationship to lifetime reproductive performance. Journal of Animal Science 28:246-252.

Hull, F.T.L. and R.K.T. Hanning (1980). A plan for improving the fecundity of a flock by indirect selection. Proceedings of the New Zealand Society of Animal Production, 40:240-247.

Hutchinson, J.C.D. (1965). Photoperiodic control of the annual rhythm of wool growth. In; "Biology of the skin and hair growth". Eds. A.G. Lyne and B.F. Short, Angus and Robertson, Sydney.

Hutchinson, J.C.D. (1976). Photoperiodic effects on hair and wool growth of domestic animals. Progress in Biometeorology B vol 1 pt 2:47-60.

Hutchinson, J.C.D., M. Wodzicka-Tomaszewska (1961). Climate physiology of sheep Animal Br.Abstr. 29,1:1-14

Hutchinson, K.J. (1961) Measurements of wool production and its physiological components in a group of South Australian Merino sheep. Australian Journal of Agricultural Research 12:696-714.

Hutchinson, K.J. (1962). Climate corrections to the seasonal wool growth rhythm of sheep grazing in a Southern Australian environment. Proceedings of the Australian Society of Animal Production 4:34-37.

Hutchinson, K.J. and R.B. Porter (1958). Growth and wool production of Merino hoggets related to grazing intake in a South Australian environment. Proceedings of the Australian Society of Animal Production 2:33-41.

Hynd, P.I. (1989) Effects of nutrition on wool follicle cell kinetics in sheep differing in efficiency of wool production. Australian Journal of Agricultural Research 40:409-417.

Islam, A.B.M.M. and R.B. Land (1977). Seasonal variation in testis diameter and sperm output of rams of different prolificacy. Animal Production 25:311-319.

Johnson, E. (1984). Seasonal adaptive coat changes in mammals. Acta Zoologica Fennica 171:7-12.

Johnsson, I.D., I.C. Hart and B.W. Butler-Hogg (1985). The effects of exogenous bovine growth hormone and bromocriptine on growth, body development, fleece weight and plasma concentrations of Growth hormone, Insulin and Prolactin in ewe lambs. Animal Production 41:207-217.

Joubert, D.M. (1963). Puberty in female farm animals. Animal Breeding Abstracts 31:295-306.

Karsch, F.J., E.L. Bittman, D.L. Foster, R.L. Goodman, S.J. Légan and J.E. Robinson (1984). Neuroendocrine basis of seasonal reproduction. Recent Progress in Hormone Research 40:185-232.

Kay, R.N.B. and M.L.Ryder (1978). Coat growth in Red deer (Cervus elaphus) exposed to a day length cycle of six months duration. Journal of the Zoological Society, London, 185:505-510.

Kennaway, D.J. (1984). Pineal function in ungulates. Pineal Research Reviews 2:113-140.

Kennaway, D.J., J.M. Obst, E.A. Dunstan, H.G. Friesen (1981). Ultradian and seasonal rhythms in plasma gonadotropins, prolactin, cortisol and testosterone in pinealectomized rams. Endocrinology 108:639-376.

Kennaway, D.J., L.M. Sanford, B. Godfrey, H.G. Friesen (1983). Patterns of progesterone, melatonin and prolactin secretion in ewes maintained in four different photoperiods. Journal of Endocrinology 97:229-242.

Kennaway, D.J. and T.A. Gilmore (1984). Effects of melatonin implants in ewe lambs. Journal of Reproduction and Fertility 70:39-45.

Kennaway, D.J. and T.A. Gilmore (1985). Effect of melatonin implants in ram lambs. Journal of Reproduction and Fertility 73:85-91.

Kennedy, J.P. (1967). Genetic and phenotypic relationships between fertility and wool production in 2-year old Merino sheep. Australian Journal of Agricultural Research 18:515-522.

Khateeb, A.Al. and E. Johnson (1971). Seasonal changes of pelage in the vole (Microtus agrestis). General and Comparative Endocrinology 16:217-240.

Kilgour, R.J., I.W. Purvis, L.R. Piper and K.D. Atkins (1985). Heritabilities of testis size and sexual behavior in males and their genetic correlations with measures of female reproduction. In:"Genetics of Reproduction in Sheep", editors R.B. Land and D.W. Robinson, pp. 343-345. London, Butterworths.

Kitay, J.I. and M.D. Altschule (1954). "The pineal gland", Harvard University Press, Cambridge, MASS

Koprowski, J.A. and H.A. Tucker (1973). Serum prolactin during various physiological states and its relationship to milk production in the bovine. Endocrinology 92:1480-1493.

Kraeling, R.R., G.B. Rampacek, J.W. Mabry, F.L. Cunningham, J.A. Pinkert (1983). Serum concentrations of pituitary and adrenal hormones in female pigs exposed to two photoperiods. Journal of Animal Science 57:1243-1248.

Kullback, S. (1959). Information theory and statistics. Wiley, New York. 395pp

Labban, F.M. (1957). The effect of growth hormone on wool follicles. Journal of Agricultural Science 49:19-25.

Lambourne, L.J. (1956). A comparison between rotational grazing and set stocking for fat lamb production. New Zealand Journal of Science and Technology A. 37(6):555-567.

Land, R.B. (1973). The expression of female sex-limited characters in the male. Nature, (London), 241:208-209.

Land, R.B. (1974). Physiological studies and genetic selection for sheep fertility. Animal Breeding Abstracts 42:155-158.

Land, R.B. (1977). Genetic variation and improvement. Chapter 22, In: "Reproduction in Domestic Animals", Eds. H.H. Cole, and P.T. Cupps, Butterworths, pp.577-604.

Land, R.B. (1978a). Genetic improvement of mammalian fertility: A review of opportunities. Animal Reproduction Science. 1:109-135.

Land, R.B. (1978b). Reproduction in young sheep: some genetic and environmental sources of variation. Journal of Reproduction and Fertility. 52:437-436.

Land, R.B. and W.R. Carr (1975). Testis growth and plasma LH concentration following hemicastration and its relation with female prolificacy in sheep. Journal of Reproduction and Fertility 45:495-501.

Land, R.B. and W.R. Carr (1979). Reproduction in domestic animals. In: "Genetic variation in hormone systems". Vol. 1. CRC press,J.G.M. Squire (Ed.) FL.p89-112.

Lang, W.R. (1952). Anomalous wool growth in a Merino fleece. Journal of the Australian Institute of Agricultural Science 18:108-109.

Langlands, J.P. and B.A. Hamilton (1969). Efficiency of wool production of grazing sheep.2. Differences between breeds and strains varying in age. Australian Journal of Experimental Agriculture and Animal Husbandry 9:254-257.

Langlands, J.P. and J.L. Wheeler (1968). The dyebanding and tattoo patch procedures for estimating wool production and obtaining samples for the measurement of fibre diameter. Australian Journal of Experimental Agriculture and Animal Husbandry 8:265-269.

Large, R.V. (1970). The biological efficiency of meat production in sheep. Animal Production. 12:393-401.

Larose, P. and A.S. Tweedie (1938). The influence of nutritional and climatic factors on wool growth and quality. II. Laboratory methods used in measurement of wool characters. Canadian Journal of Research 16:166-173.

Lees, J.L. (1979). Factors affecting puberty and mating behavior in sheep. In: "The Management and Diseases of sheep". Edited by the British Council Commonwealth Agricultural Bureaux. p. 124-151.

Legan, S.J. and F.J. Karsch (1979). Neuroendocrine regulation of the estrous cycle and seasonal breeding in the ewe. Biology of Reproduction 20:74-85.

Leining, K.B., H.A. Tucker and J.S. Kesner (1980). Growth hormone, glucocorticoids and thyroxine response to duration, intensity and wavelength of light in prepubertal bulls. Journal of Animal Science 51:932-938.

Lerner, A.B., J.D. Case, Y. Takahashi, T.H. Lee, W. Meri (1958). Isolation of melatonin, the pineal gland factor that lightens melanocytes. Journal of the American Chemistry Society 80:25-87.

Lewer, R.P. (1978). A study of genetic and environmental variation and covariation in productive traits of a flock of Perendale sheep. Thesis, Ph.D. Massey University, Palmerston North.

Lincoln, G. (1983). Melatonin as a seasonal time-cue: a commercial story. Nature 302:755.

Lincoln, G.A. (1984). Central effects of photoperiod on reproduction in the ram revealed by the use of a testosterone clamp. J. Endocr. 103:233-241

Lincoln, G.A., A.S. McNeilly and C.A. Cameron (1978). The effects of a sudden decrease or increase in daylength on prolactin secretion in the ram. Journal of Reproduction and Fertility 52:305-311.

Lincoln, G.A., H. Klandorf and N. Anderson (1980). Photoperiodic control of thyroid function and wool and horn growth in rams and the effect of cranial sympathectomy. Endocrinology 107:1543-1548.

Lincoln, G.A. and R.V. Short (1980). Seasonal breeding: Nature's contraceptive. Recent Progress in Hormone Research 36:1-52.

Lincoln, G.A., O.F.X. Almeida, H. Klandorf and R.A. Cunningham (1982). Hourly fluctuations in the blood levels of melatonin, prolactin, LH, FSH, thyroxine, and cortisol in rams under artificial photoperiods, and the effect of cranial sympathectomy. Journal Edocrinology 92:237-244.

Lincoln, G.A. and F.J.P. Ebling (1985). Effect of constant-release implants of melatonin on seasonal cycles in reproduction, prolactin secretion and moulting in rams. Journal of Reproduction and Fertility 73:241-253.

Lindler, H.R. and K.A. Ferguson (1956). Influence of the adrenal cortex on wool growth and its relation to 'break' and 'tenderness' of the fleece. Nature 177:188-189.

Logan, A. and B. Weatherhead (1980). Post-tyrosinase inhibition of melanogenesis by melatonin in hair follicles in vivo. Journal of Investigative Dermatology 74:47-50.

Lynch, G.R., A.L. Epstein (1976). Melatonin induced changes in gonads, pelage and thermogenic characters in the white-footed mouse (Peromyscus leucopus). Comparative Biochemistry and Physiology Abstracts 53:67-68.

Lyne, A.G. (1964). Effect of adverse nutrition on the skin and wool follicles in Merino sheep. Australian Journal of Agricultural Research 15:788-801.

Lyne, A.G., M. Jolly, D.E. Hollis (1970). Effects of experimentally produced local subdermal temperature changes on skin temperature and wool growth in the sheep. Journal of Agricultural Science 74:83-90.

Maddocks, S., Y. Chandrasekhar, B.P. Setchell (1985). Effect on wool growth of thyroxine replacement in throidectomized Merino rams. Australian Journal of Biology Science 38:405-410.

Margolena, L.A. (1960). Season and comparative activity of wool follicles. Anatomical Record 138:368-372.

Marston, H.R. (1928). The chemical composition of wool. Bulletin No. 38., Council of Scientific and Industrial Research , Australia.

Marston, H.R. (1948). Nutritional factors involved in wool production by Merino sheep.I. The influence of fodder intake on the rate of wool growth. Australian Journal of Scientific Research B1:363-375.

Marston, H.R. and A.W. Pierce (1932). The effects following thyroidectomy in Merino sheep. Australian Journal of Experimental Biological and Medical Science 10:203-216.

Martinet, L., J.P. Ravault and M. Meunier (1982). Seasonal variations in mink plasma prolactin measured by heterologous radio-immunoassay. General and Comparative Endocrinology 45:71-75.

Matthews, C.D.,A. le Cornu, D.J. Kennaway and R.F. Seamark (1978). Pineal function in pregnancy. A study of melatonin rhythms in the human and the sheep. The effects of pinealectomy in the sheep. Journal of Neural Transmition, Supplement 13:377-378.

McClelland, L.A., C.M. Clark, H.T. Blair, D.D.S. McKenzie and S.N. McCutcheon (1987). Some physiological changes in sheep selected for high yearling wool production. Proceedings of the 4th Asian-Australasian Association of Animal Production Societies. p.375.

McClelland, L.A., G.A. Wickham and H.T. Blair (1987). Efficiency of Romney hoggets from a fleece weight selected flock. Proceedings of the 4th Asian-Australasian Association of Animal Production Societies. p.329.

McClelland, L.A., H.T. Blair, G.A. Wickham and I.M. Brookes (1986). A comparison of fleeceweight-selected and control Romney rams for intake, liveweight gain, wool growth and feed utilisation. Proceedings of the New Zealand Society of Animal Production 46:215-218.

McCord, C.P. and F.P. Allen (1917). Evidences associating pineal gland function with alterations in pigmentation. Journal of Experimental Zoology 23:207-224.

McCutcheon, S.N., D.D.S. Mackenzie and H.T. Blair (1987). Nitrogen metabolism and plasma urea concentrations in fleeceweight-selected and control Romney rams. Australian Journal of Agricultural Research 38:917-926.

McDonald, B.J. (1984). Photoperiodic control of fibre production in the cashmere- bearing goat. Proceedings of the 10th International Congress of Biometeorology, Tokyo, 1984.

McDonald, B.J. (1985). The cashmere growth cycle. Occassional paper presented at the 1st International Cashmere Seminar, Canberra, 1985.

McFarlane, J.D. (1965). The influence of seasonal pasture production and grazing management on seasonal wool growth. Australian Journal of Experimental Agriculture and Animal Husbandry 5:252-261.

McFarlane, W.V., C.H.S. Dolling and B. Howard (1966). Distribution and turnover of water in Merino sheep selected for high wool production. Australian Journal of Agricultural Research 17:491-502.

McGuirk, B.J. (1976). Relevance for producers of research into the genetic improvement of reproductive performance. Proceedings of the Australian Society of Animal Production 11:93-100.

McGuirk, B.J. (1979). Selection for wool production in Merino sheep. In: "Selection experiments in laboratory and domestic animals". Ed. A. Robertson, Commonwealth Agricultural Bureaux. pp. 176-197.

McGuirk, B.J. (1983). Genetic selection for wool production. In:" Sheep Production", Ed. W. Haresign, Butterworths, London. pp.545-566.

McGuirk, B.J. and K.D. Atkins (1976). In: Sheep Breeding, proceedings of the 1976 International Congress, Muresk, Western Australia, August, 1976. pp.100-104. (Western Australian Institute of Technology, Perth, Western Australia.)

McGuirk, B.J., J.R. Paynter, R.B. Dun (1964). The effect of frequency and time of shearing on the reproduction and wool growth of Bungaree South Australian Merino ewes. Australian Journal of Experimental Agriculture and Animal Husbandry 4:305-310.

McGuirk, B.J. and K.D. Atkins (1976). Response to selection for increased fleece weight in Merino sheep. In: Sheep Breeding. Proceedings of the 1976 International Congress, Muresk and Perth, W.A., Eds. Tomes, G.J., D.E. Robertson and R.J. Lightfoot pp. 100-104.

McManus, W.R., G.W. Arnold and M.L. Dudinski (1966). Studies in wool production of grazing sheep. 4. Variation between sheep in intake, wool production and efficiency. Australian Journal of Experimental Agriculture and Animal Husbandry. 6: 96-100.

McMillan, W.H. (1981). A study of some factors affecting reproduction in one-and two-year old ewes. Thesis, Ph.D., Massey University, Palmerston North.

McMillan, W.H. and McDonald, M.F. (1983). Reproduction in ewe lambs and its effect on two-year-old performance. New Zealand Journal of Agricultural Research. 26:437-442.

Meyer, H.H. and French, R.L. (1979). Hogget live-weight-oestrus relationships among sheep breeds. Proceedings of the New Zealand Society of Animal Production 39:56-62.

Mirachi, R.E., B.E. Howland, P.F. Scanlon, R.L. Kirkpatrick and L.M. Stanford (1978). Seasonal variation in plasma LH, FSH, prolactin, and testosterone concentrations in adult male white-tailed deer. Canadian Journal of Zoology 56:121-129.

Mohn, M.P. (1958). The effects of different hormonal states on the growth of hair in rats.In: "The Biology of hair growth", Academic Press, NY, pp 335-398.

Montgomery, G.W. (1987). Seasonality of oestrus and ovulation rate. Proceedings of the 4th Asian Australasian Association of Animal Production Animal Science Congress, Hamilton, N.Z. p 252.

Montgomery, G.W. and H. Hawker (1987). Seasonal reproduction in ewes selected on seasonal changes in wool growth. Journal of Reproduction and Fertility 79:207-213.

Moore, R.W. and C.H.S. Dolling (1961) Ability to select diet in Merino sheep fed in pens. Australian Journal of Experimental Agriculture and Annimal Husbandry 1:15-17.

Moore, R.W., T.W. Knight and D. Whyman (1978). Influence of hogget oestrus on subsequent ewe fertility. Proceedings of the New Zealand Society of Animal Production, 38:90-93.

Moore, R.W. and D.C. Smeaton (1980). Effects of different growth paths from 4 to 11 months of age on Romney hogget oestrus and subsequent reproduction. Proceedings of the New Zealand Society of Animal Production 40:27-33.

Moore, R.W. and H-U.P. Hockey (1982). The effect of early nutrition and hogget oestrus on subsequent reproduction. Proceedings of the New Zealand Society of Animal Production 42:41-43.

Morley, F.H.W., L.W. Lockart and E.C. Davis (1955). The value of production from a clipped measured area as an index of fleece weight. Austalian Journal of Agricultural Research 6:91-98.

Morris, L.R. (1961). Photoperiodicity of seasonal rhythm of wool growth in sheep. Nature 190:102-103.

Morrison, D.F. (1976). Multivariate statistical methods. 2nd Edition, McGraw-Hill Inc.

Moule, G.R. (1965). Field investigations with sheep: A manual of techniques. C.S.I.R.O.

Munro, C.J., K.P. McNatty and L. Renshaw (1980). Circa-annual rhythms of prolactin secretion in ewes and the effect of pinealectomy. Journal of Endocrinology 84:83-87.

Nagorcka, B.N. (1977). The description and analysis of wool growth. Australian Journal of Agricultural Research 28:737-746.

Nagorcka, B.N. (1979). The effect of photoperiod on wool growth. In: "Physiological and Environmental Limitations to Wool Growth",Eds. J.L. Black and P.J. Reis, U.N.E. Publishing Unit, Armidale, N.S.W. pp.

Nett, T.M. and G.D. Niswender (1982). Influence of exogenous melatonin on seasonality of reproduction in sheep. Theriogenology 17:645-653.

Neyman, J. and E.S. Pearson (1928). On the use and interpretation of certain test criteria for purpose of statistical inference. Biometrika 20 A,pp175-240;263-294.

Nir, I. (1978). Non-reproductive systems and the pineal gland. Journal of Neural Transmition, Supplement 13:225-244.

Nir,I., R.J. Reiter, R.J. Wurtman (1978). The pineal gland. Journal of Neuralogical Transmition, Supplement 13:245-256.

Nitter, G. (1978). Breed utilization for meat production in sheep. Animal Breeding Abstracts 46:131-143.

Norriss, M.H. and C.C. Claasens (1931). Crimp in wool as a periodic function of time. Journal of the Textile Institute 22:T224-240.

Nowak, R. and Rodway, R.G. (1985). Effect of intravaginal implants of melatonin on the onset of ovarian activity in adult and prepubertal ewes. Journal of Reproduction and Fertility, 74:287-293.

Orwin, D.F.G., J.L. Woods and K.H. Elliot (1980). Composition of the cortex of sound and tender wools. Proceedings of the 6th International Wool Textile Research Conference, Pretoria. Vol II, pp.193-206.

Orwin, D.F.G., J.L. Woods and R.G. Gourdie (1985). Cortical cell type and wool strength. Proceedings of the 7th International Wool Textiles Research Conference, Tokyo, Vol 1, pp.194-203.

Orwin, D.F.G., K.G. Geenty and J.N. Clarke (1986). Breeding for improved staple strength. W.R.O.N.Z. Proceedings of the Wool Production Seminar 5:34-38.

Panaretto, B.A. (1979). Effects of light on cyclic activity of wool follicles and possible relationships to changes in the pelage of other mammals. In: 'Physiological and Environmental Limitations to wool growth', Eds. J.L. Black and P.J. Reis, U.N.E. Publishing Unit, Armidale, N.S.W. pp.

Panaretto, B.A., R.E. Chapman, A.M. Downes, P.J. Reis, A.L.C. Wallace (1975). Some effects of three glucocorticoid analogues on wool growth and their efficacy as defleecing agents in sheep. Australian Journal of Experimental Agriculture and Animal Husbandry 15:193-202

Panaretto, B.A. and A.L.C. Wallace (1978a). The administration of fluomethasone by three different routes, its measurement in the plasma and some effects on wool growth in Merino wethers. Australian Journal of

Biological Science 31:601-620.

Panaretto, B.A. and A.L.C. Wallace (1978b). Dexamethasone concentrations in ovine plasma during its intravenous infusion, its relation to the production of some endogenous hormones and some of the effects on wool growth. Australian Journal of Biological Science 31:247-256.

Panaretto, B.A. and A.L.C. Wallace (1979). Synergistic effects of thiocynate with fluomethasone in inhibiting wool growth in Merino wethers. Australian Journal of Biological Science 32:77-90.

Pang, S.F. and A.E. Allen (1986). Extra-pineal melatonin in the retina: Its regulation and physiological function. Pineal Research Reviews 4:55-95.

Pattie, W.A. and R. Barlow (1974) Selection for clean fleece weight in Merino sheep. I. Direct response to selection. Australian Journal of Agricultural Research 25:643-655.

Pattie, W.A. and A.J. Williams (1967). Selection for weaning weight in Merino sheep. III. Maintenance requirements and the efficiency of conversion of feed to wool in mature ewes. Australian Journal of Experimental Agriculture and animal Husbandry 7:117-125.

Pelletier, J. (1973). Evidence for photoperiodic control of prolactin release in rams. Journal of Reproduction and Fertility 35:143-147.

Pelletier, J., S. Carrez-Camous and J.C. Thiery (1981). Basic neuroendocrine events before puberty in cattle, sheep and pigs. Journal of Reproduction and Fertility, Supplement 30:91-102.

Peters, R.R. and H.A. Tucker (1978). Prolactin and growth hormone responses to photoperiod in heifers. Endocrinology 103:329-336.

Peterson, A.J.,L. Bodin, J.F. Smith and J.N. Clarke (1986). Physiology of sheep selected for prolificacy. New Zealand Ministry of Agriculture and Fisheries, Research Division Annual Report 85/86. p 32-33.

Petterborg, L.J. (1986). Photoperiod, pineal and reproduction in the white-footed mouse, (Peromyscus leucopus). Advances in Pineal Research, Vol. 1. R.J. Reiter and M. Karasek, eds., John Libbey & Co. Ltd., pp.179-183, London.

Piper, L.R. and B.M. Bindon (1982) The Booroola Merino and the performance of medium non-Peppin crosses at Armidale. In: "The Booroola Merino", Proceedings of a workshop held in Armidale, August, 1980. C.S.I.R.O. Division of Animal Production. pp. 9-20.

Piper, L.R. and C.H.S. Dolling (1966). Variation in the sulphur content of wool of Merino sheep associated with genetic differences in wool-producing capacity. Australian Journal of Biological Science 19:1179-1182.

Piper, L.R. and C.H.S. Dolling (1969) Efficiency of conversion of food into wool. V. Comparison of the apparent digestive ability of sheep selected for high clean wool weight with that of sheep from a random control group. Australian Journal of Agricultural Research 20:579-587.

Purvis, I.W. (1987). Genetic improvement of reproductive efficiency in Merino sheep - selection criteria. Proceedings of the 6th Australian Association of Anima Breeding and Genetics Conference, Perth, WA., Feb 9-11. pp.242-244.

Quirke, J.F. (1978). Onset of puberty and oestrus activity in Galway, Finnish Landrace and Finn-cross ewe lambs during their first breeding season. Irish Journal of Agricultural Research 17:15-23.

Quirke, J.F. (1979). Effect of body weight on the attainment of puberty and reproductive performance of Galway and Fingalway female lambs. Animal Production 28:297-307.

Quirke, J.F. (1981). Regulation of puberty and reproduction in ewe lambs: A review. Livestock Production Science 8:37-53.

Quirke, J.F. and J.P. Hanrahan (1985). Breed differences in the breeding season in sheep. In:" Endocrine causes of seasonal and lactational anoestrus in Farm Animals". Eds. F. Ellendorff and F. Elsaesser, Martinus-Nijhoff, Publishers.

Quirke, J.F., G.H. Stabenfeldt and G.E. Bradford (1985). Onset of puberty and duration of the breeding season in Suffolk, Ramboillet, Finnish Landrace, Dorset and Finn-Dorset ewe lambs. Journal of Animal Science 60:1463-1471.

Rae, A.L. (1958) Genetic variation and covariation in productive characters of New Zealand Romney Marsh sheep. New Zealand Journal of Agricultural Research 1:104-123.

Rae, A.L. (1982). Objectives in sheep breeding. Proc. 1st World Congress of Sheep and Beef Cattle Breeding, Vol II:29-37.

Ralph, C.L. (1984). Pineal bodies and thermoregulation. In:

"The pineal gland". Ed. R.J. Reiter, Raven Press,N.Y., pp. 193-220.

Rattray, P.V. (1977). Nutrition and reproductive efficiency. Chapter 21, In:" Reproduction in domestic animals". Eds. H.H. Cole and P.T. Cupps, pp.557-576.

Ravault, J.P. (1976). Prolactin in the ram: seasonal variations in the concentration of blood plasma from birth until 3 years old. Acta Endocrinologica 83:720-725.

Ravault, J.P. and R. Ortavant (1977). Light control of prolactin secretion in sheep. Evidence for a photoinducible phase during a diurnal rhythm. Annales de Biologie et Animales Biochemistrie, Biophysique. 17:459-471.

Ravault,J.P., F. Martinat-Botte, R. Mauget, N. Martinat, A. Locatelli and F. Bariteau (1982). Influence of the duration of daylight on prolactin secretion in the pig: hourly rhythm in ovariectomized females, monthly variation in domestic males and females and wild strains during the year. Biology of Reproduction 27:1084-1097.

Reeve, E.C.R. and F.W. Robertson (1953). Factors affecting multiple births in sheep. Animal Breeding Abstracts, 21:211-224.

Reis, P.J. (1965). Variations in the sulphur content of wool. In: 'Biology of the skin and hair growth'. Eds. A.G. Lyne and B.F. Short, Angus and Robertson, Sydney, pp. 365-376.

Reis, P.J. (1965). The growth and composition of wool. III. Variations in sulphur content of wool. Australian Journal of Biological Science 18:671-687.

Reis, P.J. (1967). The growth and composition of wool IV. The differential response of growth and of sulphur content of wool to the level of sulphur-containing amino acids given abomasally. Australian Journal of Biological Science 20:809-825.

Reis, P.J. (1969). The growth and composition of wool V. Stimulation of wool growth by the abomasal administration of varying amounts of casein. Australian Journal of Biological Science 22:745-749.

Reis, P.J. (1979). Effects of amino acids on the growth and properties of wool. In:" Physiological and Environmental Limitations to Wool Growth", Eds. J.L. Black and P.J. Reis, U.N.E. Publishing Unit, Armidale, N.S.W., pp. 223-242.

Reis, P.J. and P.G. Schinckel (1961a). Some effects of sulphur-containing amino acids on the growth and composition of wool. Australian Journal of Biological Science 16:218-230.

Reis, P.J. and P.G. Schinckel (1961b). Nitrogen utilization and wool production by sheep. Australian Journal of Agricultural Research 12:335-352.

Reis, P.J and P.G. Schinckel (1964). The growth and composition of wool II. The effect of casein, gelatin, and sulphur containing amino acids given per abomasum. Australian Journal of Biological Science 17:532-547.

Reis, P.J. and D.A. Tunks (1968). Reproducability of individual differences in the sulphur content of wool grown by Merino sheep. Proceedings of the Australian Society of Animal Production 7:402-406.

Reis, P.J., D.A. Tunks and L.F. Sharry (1973). Plasma amino acid patterns in sheep recieving abomasal infustions of methionine and cystine. Australian Journal of Biological Science 26:635-644.

Reis, P.J. and O.B. Williams (1965). Variations in the sulphur content of wool from Merino sheep on two semi-arid grasslands. Australian Journal of Agricultural Research 16:1011-1020.

Reklewska, B. (1974). A note on the effect of bovine somatotrophic hormone on wool production in growing lambs. Animal Production 19:253-255.

Relkin, R. (1983). Pineal-hormone interactions. In 'The Pineal gland'. Eds. R. Relkin, Elsevier Biomedical NY, pp. 225-246.

Ricourdeau, G., M.R. Blanc and L. Bodin. (1984). Teneurs plasmatiques en FSH et LH des agneaux males et femelles issus de beliers Lacaune prolifiques et non-prolifiques. Genetique, Selection, Evolution, 16:195-210.

Riveire,J.E., F.R. Engelhardt and J.Solomon (1977). The relationship of thyroxine and cortisol to the moult of the harbour seal (Phoca vitulina). General and Comparative Endocrinolgy 31:398-408.

Robards, G.E. and K.D. Atkins (1976) Efficiency of wool production of hogget ewes from a Merino flock selected for fertility. Proceedings of the Australian Society of Animal Production 11:29-32.

Robards, G.E. and W.A. Pattie (1967) Selection for crimp frequency in wool of Merino sheep. I. Direct response to selection. Australian Journal of Experimental Agriculture and Animal Husbandry 7:552-558.

Robards, G.E., C.H. Davis and D.G. Saville (1976) Skin folds and Merino breeding.9. Efficiency of conversion of food to wool. Australian Journal of Experimental Agriculture and Animal Husbandry 16:361-366.

Robards, G.E., A.J. Williams and M.H.R. Hunt (1974). Selection for crimp frequency in the wool of Merino sheep II. Efficiency of conversion of food to wool. Australian Journal of Experimental Agriculture and Animal Husbandry 14:441-448.

Roberts, N.F., J.F.P. James and V.D. Burgmann (1960). Tenderness in fleece wool. Journal of the Textile Institute 51:T935-952.

Robinson, J.E., N.L. Wayne and F.J. Karsch (1985). Refractoriness to inhibitory daylengths initiates the breeding season of the Suffolk ewe. Biology of Reproduction 32:1024-1030.

Rodway, R.G.; Swift, A.D.; Nowak, R.; Smith, J.A. and Padwick, J.A. (1985). Plasma concentrations of melatonin and the onset of puberty in the female lamb. Animal Reproduction Science 8:241-246.

Roe, R., W.H. Southcott, H.N. Turner (1959). Grazing management of native pasture in the New England region of N.S.W. 1. Pasture and sheep production with special reference to grazing and internal parasites. Australian Journal of Agricultural Research 10:530-554.

Rollag, M.D. and G.D. Niswender (1976). Radioimmunoassay of serum concentrations of melatonin in sheep exposed to different lighting regimes. Endocrinology 98:482-489.

Rose J., F. Stormshak, J. Oldfield, J. Adair (1984). Induction of winter fur growth in mink (Mustela vison) with melatonin. Journal of Animal Science 58:57-61.

Ross, D.A. (1960). Staple strength I. The measurement of staple strength. New Zealand Journal of Agricultura Research 3:503-525.

Ross, D.A. (1961a). Staple strength II. Some factors affecting the measurement of staple strength. New Zealand Journal of Agricultural Research 4:57-71.

Ross, D.A. (1961b). Staple strength III. Variations through the wool selling season. New Zealand Journal of Agricultural Research 4:523-537.

Ross, D.A. (1961c). Biological aspects of the sulphur content of Romney wool. Proceedings of the New Zealand Society of Animal Production 21:153-165.

Ross, D.A. (1962). Follicle productivity and wool production in Romney ewes. Australian Journal of Agricultural Research 13:924-942.

Ross, D.A. (1964). Wool production and sulphur content. New Zealand Journal of Agricultural Research 7:663-665.

Ross, D.A. (1965). Wool growth of the New Zealand Romney. New Zealand Journal of Agricultural Research 8:585-601.

Ross, D.A. (1982). Staple strength, staple length, fibre length and processing. Wool 7(4):12-15.

Ross, D.A. (1984). Measurement of staple strength in New Zealand. Lincoln College Wool Bull. No.1. Report of a seminar on staple strength. Eds. D.A. Ross and L.F. Story, pp. 15-28.

Ross, D.A., R.L. Bratt and L.F. Story (1961). The effect of staple strength on carding and combing. Journal of the Textile Institute 51:T907-921.

Ross, D.A., G.A. Wickham and K.H. Elliot (1982). Breeding objectives to improve wool used in carpets. Proceedings of the 1st World Congress of Sheep and Beef Cattle Breeding Vol I:37-45.

Ross, D.A. and H.E. Meikle (1985). The processing significance of variation in staple strength within and between fleeces. Proceedings of the 7th International Wool Textiles Research Conference Tokyo. Vol II:45-54.

Rottenbury, R.A. (1979). Staple strength - Appraisal and measurement. C.S.I.R.O. Division of Textile Physics., Proceedings of a seminar on staple length and staple strength of greasy wool. pp39-61.

Rougeot, J. (1957). (The action of the seasonal variation in daylength on the shedding of certain fibres of the fleece of the Limousine breed. C. R. Society of Biology 151:834-837.

Rougeot, J. (1961). (Comparative actions of the annual and semestrial periodic variations of the daylight on the follicle cycles of the short kemps of the fleece of the Limousine ewes and its relationship to reproductive cycles. Annales de Biologie de Animales 1:385-402.

Rougeot, J., D.Allain, L. Martinet (1984). Photoperiodic and hormonal control of seasonal coat changes in mammals with special reference to sheep and mink. Acta Zoologica Fennica 171:13-18.

Rudall, K.M. (1933). Effect of shearing on hairiness in the fleece of the Romney lamb. New Zealand Journal of Agriculture 47:1-9.

Rust, C.C. and R.K. Meyer (1969). Hair colour, moult, and testis size in male, short-tailed weasels treated with melatonin. Science 165:921-922.

Rust, C.C., R.M. Shackelford and R.K. Meyer (1965). Hormonal control of pelage cycles in the mink. Journal of Mammalogy 46:549-565.

Ryder, M.L. (1956). Observations on nutritional and seasonal changes in the fleece of some Masham sheep. Journal of Agricultural Science,Cambridge 47:129-144.

Ryder, M.L. (1956). Seasonal and nutritional variations in fleece growth. W.I.R.A. Bulletin 18,2:1-2.

Ryder, M.L. (1957). A survey of the follicle population in a range of British breeds of sheep. Journal of Agricultural Science, Cambridge 49:275-282.

Ryder, M.L. (1958). The moulting of wool fibres. W.I.R.A. Bulletin 20,4:138-141.

Ryder, M.L. (1960). A study of the coat of the mouflon (Ovis musimon) with special reference to seasonal change. Proceedings of the Zoological Society, London 135:387-498.

Ryder, M.L. (1962). Preliminary observations on seasonal changes in the fleeces of unshorn Merino sheep. Proceedings of the Australian Society of Animal Production 4:46-48.

Ryder, M.L. (1969). The development and structure of, and seasonal change in, the coat of some Wiltshire sheep. Animal Production 11:467-477.

Ryder, M.L. (1971). Wool growth cycles in Soay sheep. Journal of Agricultural Science 76:183-194.

Ryder, M.L. (1973). A note on the failure of thyroxine to restore wool growth to inactive follicles. Animal Production 16:319-321.

Ryder, M.L. (1978). Growth cycles in the coat of ruminants. International Journal of Chronobiology 5:369-394.

Ryder, M.L. (1979). Thyroxine and wool follicle activity. Animal Production 28:109-114.

Ryder, M.L. and S.K. Stephenson (1968). 'Wool Growth', Academic Press, London.

Ryder, M.L. and G.A. Lincoln (1976). A note on the effect of changes in daylength on the seasonal wool growth cycle in Soay sheep. Animal Production 23:257-260.

Sackville, J.P. and J.E. Bowstead (1938). The influence of nutritional and climatic factors on wool growth and quality. 1. Statement of problem and experimental procedure. Canadian Journal of Research and Development 16:153-165.

Saville, D.G. and G. E. Robards (1972). Efficiency of conversion of food to wool in selected and unselected Merino types. Australian Journal of Agricultural Research 23:117-130.

Schanbacher, B.D. and D. Crouse (1981). Photoperiodic regulation of growth: a photosensitive phase during light-dark cycle. American Journal of Physiology 241:El.

Schinckel, P.G. (1956). Body-weight-fleece-weight relationships in a strain of Merino sheep. Australian Journal of Agricultural Research 7:57-75.

Schinckel, P.G. (1960). Variation in feed intake as a cause of variation in wool production of grazing sheep. Australian Journal of Agricultural Research 11:585-594.

Sharkey, M.J., I.F. Davis and P.A. Kenny (1962). The effect of previous and current nutrition on wool production in Southern Victoria. Australian Journal of Experimental Agricultural Animal Husbandry 2:160-169.

Short, B.F. (1958). A dominant felting lustre mutant fleece-type in the Australian Merino sheep. Nature, Lond. 181:1414-1415.

Simpson, S. (1924). Effects of thyroidectomy on the cutaneous system in the sheep and goat. Quarterly Journal of Experimental Physiology 14:185-192.

Slee, J. (1963). Birthcoat shedding in Wiltshire horn lambs. Animal Production 5:301-316.

Slee, J. (1965). The genetics of hair growth. In:'The Complete physiology and pathology of the skin',Blackwell Scientific Publications, Oxford. pp. 103-118.

Slee, J. (1965). Seasonal patterns of moulting in Wiltshire horn sheep. In:'Biology of the skin and hair growth', Eds. A.G. Lyne and B.F. Short, Angus and Robertson, Sydney, pp. 543-563.

Slee, J. and H.B. Carter (1961). A comparative study of fleece growth in Tasmanian fine Merino and Wiltshire Horn ewes. Journal of Agricultural Science 57:11-19.

Slen, S.B. and F. Whiting (1956). Wool growth in mature range ewes as affected by stage and type of pregnancy and type of rearing. Canadian Journal of Animal Science 36:8-13.

Slen, S.B. and R. Connell (1958). Wool growth in sheep as affected by the administration of certain sex hormones. Canadian Journal of Animal Science 38:38-47.

Smith, J.F., P.V. Rattray, K.T. Jagusch, N.R. Cox and H.R. Tervit (1979). Ovulation-liveweight relationships in ewes. Proceedings of the New Zealand Society of Animal Production 39:50-55.

Smith, J.F., L. Bodin, J.N. Clarke, D.L. Johnson and L.T. McGowan (1987). Effect of genotype on ovulatory response of pre-pubertal lambs to PMSG. Proceedings of the 4th Asian Australasian Association of Animal Production Animal Science Congress, Hamilton, N.Z. p. 224.

Smith, V.G., R.R. Hacker and R.G. Brown (1977). Effect of alterations in ambient temperature on serum prolactin concentration in steers. Journal of Animal Science 44:645-649.

Sokal, R.R. and F.J. Rohlf (1969). Biometry. W.H. Freeman and Co. San Francisco, 776 pp.

Southan, E.R., C.V. Hulet and M.P. Botkin (1971). Factors influencing reproduction in ewe lambs. Journal of Animal Science, 33:1282-1287.

Southcott, W.H. and W.M. Royal (1971). Effect of implanted testosterone proprionate on the growth and wool production of Merino wethers. Australian Journal of Agricultural Research 22:271-282.

Squires, V.R. (1964). Field evaluation of dye-banding as a technique for measuring the seasonal variation in wool growth. Australian Journal of Experimental Agriculture and Animal Husbandry 4:92-94.

Stapleton, D.L. (1978). Mohair production and seasonal variability in the fleece of the Australian Angora goat. Thesis, Ph.D., University of N.England, Armidale, NSW.

Steele, R.G.D. and J.H. Torrie (1980). Principles and Procedures of statistics - A biometrical approach. McGraw-Hill Book Company, New York.

Stephenson, S.K., D.C. Dalton and A.H. Kirton (1980). The relationship of growth, body shape and body composition to the initiation of oestrous activity in different sheep breeds. Proceedings of the New Zealand Society of Animal Production 40:258-267.

Stevens, P.G. and G.M. Wright (1951). Some variations in the fleece of Romney Marsh stud ewes. Proceedings of the New Zealand Society of Animal Production 11:18-21.

Stewart, A.M., R.J. Moir and P.G. Schinckel (1961). Seasonal fluctuations in wool growth in south Western Australia. Australian Journal of Experimental Agriculture Animal Husbandry 1:85-91.

Story, L.F. and Ross, D.A. (1959). Effect of shearing time on wool iv. Effect on the fleeces. New Zealand Journal of Agricultural Research 2:1096-1103.

Story, L.F. and D.A. Ross (1960). Effect of shearing time on wool VI. The rate of growth of wool and its relation to the time of shearing. New Zealand Journal of Agricultural Research 3:113-124.

Sumner, R.M.W. (1969). A comparative study of the effect of two stocking levels on wool follicle development and wool production of the New Zealand Romney sheep. Thesis, M.Sc., Massey University, Palmerston North, New Zealand.

Sumner, R.M.W. (1977). Nutritional factors affecting production in Border Leicester and super-fine Merino sheep: with emphasis on protein nutrition. Thesis, Ph.D., Univ. New England, Australia.

Sumner, R.M.W. (1979). Efficiency of wool and body growth in pen-fed Romney, Coopworth, Perendale and Corriedale sheep. New Zealand Journal of Agricultural Research 22:251-257.

Sumner, R.M.W. (1983). Effect of feeding and season on fleece characteristics of Cheviot, Drysdale and Romney hogget wool. Proceedings of the New Zealand Society of Animal Production 43:79-82.

Sumner, R.M.W. (1984). Effects of shearing on flock productivity. In:" Coloured sheep and their products", Proceedings of the 2nd World Congress on coloured sheep, N.Z. pp. 289-29.

Sumner, R.M.W. (1986). Time of shearing and its production implications. W.R.O.N.Z Special Publication #5. Proceedings of the Wool Production Seminar, 1986, Christchurch, N.Z. pp. 23-33.

Sumner, R.M.W. and G.A. Wickham (1969). Some effects of an increased stocking level on wool growth. Proceedings of the New Zealand Society of Animal Production 29:208-217.

Sumner, R.M.W. and G.A. Wickham (1970). A comparison of wool follicle development of New Zealand Romney lambs at two stocking rates. New Zealand Journal of Agricultural Research 13:395-400.

Sumner, R.M.W.; During, C. and Webby, R.W. (1981). Effect of grazing management on hogget fleece characteristics. Proceedings of the New Zealand Society of Animal Production 41:128-132.

Tamarkin, L., W.K. Westrom, A.L. Hamill and B.D. Goldman (1976). Effect of melatonin on the reproductive systems of male and female Syrian hamsters: A diurnal rhythm in sensitivity to melatonin. Endocrinology 99:1534-1541.

Tamarkin, L.,C.W. Hollister, N.G. Lefebvre and B.D. Goldman (1977). Melatonin induction of gonadal quiescence in pinealectomized Syrian hamsters. Science 198:953-955.

TEAM final report (1985). Report to the wool measurement research advisory committee of the Australian wool corporation.

Tergui, M., C. Delouis and R. Ortavant (1984). Photoperiodism and hormones in sheep and goats. In: 'Manipulation of growth in farm animals'. Eds. J.F. Roche, D. O'Callaghan, Martinus Nijhoff, pp. 246-257.

Ternouth, J.H. and A.W. Beattie (1970). A note on the voluntary food consumption and the sodium- potassium ratio of sheep after shearing. Animal Production 12:343-346.

Theriez, C. and J. Rougeot (1962). Influence of thyroid hormones on the growth in length of wool fibres. Annales de Biologie, Animales, Biochemique 2:5-11.

Thimonier, J., J.P. Ravault, R.Ortavant (1978). Plasma prolactin variations and cyclic ovarian activity in ewes submitted to different light regimes. Annales de Biologie, Animales, Biochemique, Biophysique 18:1229.

Thun, R.,E. Eggenberger, K.Zerobin, T.Luscher and W. Vetter (1981). Twenty-four hour secretory pattern of cortisol in the bull: Evidence of episodic secretion and circadian rhythm. Endocrinology 109:2208-2216.

Tierney, M.L. (1976). Genetic aspects of puberty in Merino ewes. In:' Sheep breeding '. Proceedings of the 1976 International congress, Muresk and Perth, W.A., Eds. G.J. Tomes, D.E. Robertson and R.J. Lightfoot, pp.322-329.

Tucker, H.A. (1982). Seasonality in cattle. Theriogenology 17:53-71.

Turner, H.N. (1962). Breeding Merino sheep for multiple births. Wool Technology and Sheep Breeding, 9:19-24.

Turner, H.N. (1968). The effect of selection on lambing rates. Proceedings of a Symposium on the Physiology of Reproduction in Sheep, Oklahoma State University, Stillwater, OK., July 26-27,1968. pp.67-93.

Turner, H.N. (1969). Genetic improvement of reproductive rate in sheep. Animal Breeding Abstracts 37:545-563.

Turner, H.N. (1972). Genetic interactions between wool, meat and milk production in sheep. Animal Breeding Abstracts 4:621-634.

Turner, H.N., M.G. Brokker and C.H.S. Dolling (1970). Response to selection in Australian Merino sheep. III. Single character selection for high and low values of wool weight and its components. Australian Journal of Agricultural Research 21:955-984.

Turner, H.N. C.H.S. Dolling and J.F. Kennedy (1968) Response to selection in Australian Merino sheep. I. Selection for high clean wool weight with a ceiling on fibre diameter and degree of skin wrinkle. Response in wool and body characteristics. Australian Journal of Agricultural Research 19:79-112.

Turner, H.N. and N. Jackson (1978). Response to selection in Australian Merino sheep. VIII. Further results on selection for high clean wool weight with attention to quality. Australian Journal of Agricultural Research 29:615-629.

Underwood, H. (1984). The pineal and circadian rhythms. In: "The pineal gland", Ed. R.J. Reiter, Raven Press,N.Y. pp. 221-251.

Vesely, J.A. and Swierstra, E.E. (1986). Reproductive parameters of crossbred ewe lambs sired by Romanov, Finn, Dorset and Western Range rams. Journal of Animal Science 62:1555-1562.

Wallace, A.L.C. (1979). The effect of hormones on wool growth. In:" Physiological and Environmental Limitations to Wool Growth", Eds. J.L. Black and P.J. Reis, U.N.E. Publishing Unit, Armidale, N.S.W., pp. 257-268.

Wallace, L.R. (1958). Breeding Romneys for better lambing precentages. New Zealand Journal of Agriculture 97:545-550.

Wallace, L.R. (1964). The effect of selection for fertility on lamb and wool production. Proceedings of the Ruakura farmer's conference p.25-26.

Ward, K.A. and S.E. Kasmarik (1979). Studies on the in vitro metabolism of 3H-cortisol and 3H- Oestradial by sheep skin and wool roots. Australian Journal of Biological Science 32:197-204.

Watson-Whitmyre, M. and M.H. Stetson (1983). Simulation of peak pineal melatonin release restores sensitivity to evening melatonin injections in pinealectomized hamsters. Endocrinology 112:763-765.

Weston, R.H. (1959) The efficiency of wool production of grazing Merino sheep. Australian Journal of Agricultural Research 10:865-885.

Weston, R.H. (1970). Voluntary consumption of low quality roughage by sheep during cold exposure. Australian Journal of Experimental Agriculture Animal Husbandry 10:679-684.

Wettemann, R.P. and H.A. Tucker (1974). Relationship of ambient temperature to serum prolactin in heifers. Proceedings of the Society of Experimental Biology and Medicine 146:908.

Wheatley, I.S., A.L.C. Wallace, J.M. Bassett (1966). Metabolic effects of ovine growth hormone in sheep. Journal of Endocrinology 35:341-353.

Wheeler, J.L., T.F. Reardon and L.J. Lambourne (1963). The effect of pasture availability and shearing stress on herbage intake of grazing sheep. Australian Journal of Agricultural Research 14:364-372.

Wheeler, J.L., D.A. Hedges and C. Mulcahy (1977). The use of dyebanding for measuring wool production and fleece tip wear in rugged and unrugged sheep. Australian Journal of Agricultural Research 28:721-735.

Whitely, K.J. and Jackson, N. (1982). Breeding for apparel wool. Proceedings of the 1st World congress on Sheep and Beef Cattle Breeding, Vol I:47-55.

Wickham, G.A. (1968). Break and tenderness in wool. Sheep Farming Annual 68:73-78.

Wickham, G.A. (1970). Wool growth in relation to sulphur-containing amino acid administration to sheep. Proceedings of the New Zealand Society of Animal Production 30:209-215.

Wickham, G.A. and MacPherson, A.W. (1985). A review of the importance of wool traits as genetic improvement objectives and selection criteria for New Zealand Romney sheep. Proceedings of the New Zealand Society of Animal Production 45:203-208.

Wildman, A.B. (1957). Photoperiodicity and wool growth in Romney rams and wethers. Nature 180:296-297.

Wilks, S.S. (1946). Sample criteria for testing equality of means, equality of variances, and equality of covariance in a normal multivariate distribution. Annals of Math. Stat. 17:257-281.

Williams, A.J. (1964). The effect of daily photoperiod on wool growth of Merino rams subjected to unrestricted and restricted feeding regimes. Australian Journal of Experimental Agriculture and Animal Husbabdry 4:124-128.

Williams, A.J. (1966) The efficiency of conversion of feed to wool during limited and unlimited feeding of flocks selected on clean fleeceweight. Australian Journal of Experimental Agriculture and Animal Husbandry 6:90-95.

Williams, A.J. (1973) Metabolism of Cystine by Merino sheep Genetically Different in Wool Production. III. The incorporation of radioactivity into wool fibres during and after intravenous infusions of l-[^{35}S] cystine and its relationship to wool growth and efficiency of conversion of food into wool. Australian Journal of Biological Science 26: 465-476.

Williams, A.J. (1973) Metabolism of Cystine by Merino sheep Genetically Different in Wool Production. IV. Rates of entry of cystine into plasma, measured with a single intravenous injection of L-[^{35}S] cystine, and the subsequent incorporation of ^{35}S into wool fibres. Australian Journal of Biological Science 29:513-524.

Williams, A.J. (1976). The efficiency of wool production. Report to the Australian Wool Corporation. 53pp.

Williams, A.J. (1979). Speculation on the biological mechanisms responsible for genetic variation in the rate of wool growth. In:" Physiological and Environmental Limitations to Wool Growth", Eds. J.L. Black and P.J. Reis, U.N.E. Publishing Unit, Armidale, N.S.W., pp. 337-354.

Williams, A.J. (1984). Early evidence of a difference in wool producing ability. Proceedings of the Australian Society of Animal Production 15:770.

Williams, A.J. (1987). Physiological consequences of selection for increased fleece weight. Proc. of the Australian Wool Board conference on "The application of sheep breeding and genetics to the sheep and wool enterprises in Australia".

Williams, A.J., R.A. Leng and S.K. Stephenson (1972) Metabolism of cystine by Merino sheep genetically different in wool production. I. Comparison of the entry rates of cystine in sheep from flocks selectively bred for high and low fleeceweight. Australian Journal of Biological Science. 25:1259-1268.

Williams, A.J. and H.P. Miller (1965). The voluntary feed intake of sheep genetically different in wool production. Australian Journal of Experimental Agriculture and animal Husbandry 5: 385-389.

Williams, A.J., G.E. Robards and D.G. Saville (1972) Metabolism of cystine by Merino sheep genetically different in wool production II. Responses in wool growth to abomasal infusions of L-cystine or DL-methionine. Australian Journal of Biological Science 25:1269-1276.

Williams, A.J. and R.J. Winston (1965). Relative efficiencies of conversion of feed to wool at three levels of nutrition in flocks genetically different in wool production. Australian Journal of Experimental Agriculture and Animal Husbandry 5:390-395.

Williams, A.J. and R.J. Winston (1987) A study of the characteristics of wool follicle and fibre in Merino sheep genetically different in wool production. Australian Journal of Agricultural Research 38:743-756.

Williams, O.B (1964). A relationship between forage availability and wool growth rate for high and low producing sheep. Proceedings of the Australian Society of Animal Production 5:280-283.

Williams, O.B. and P.G. Schinckel (1962). Seasonal variations in wool growth and liveweight in several environments. Proceedings of the Australian Society of animal Production 4:38-45.

Williams, O.B. and H. Suijdendorp (1968). Wool growth of wethers grazing Acacia aneura-Triodia pungens savanna and ewes grazing triodia pungens hummoda grass steppe in the Pilbara district. W.A.. Australian Journal of Experimental Agriculture and Animal Husbandry 8:653-660.

Wilson, A.D. and N.L. Hihdley (1968) Comparison of the voluntary water intakes of some Australian Merinos. Field Station Research, Division of Plant Industry, CSIRO 7:25-36.

Wilson, T.F. (1931). The influence of the plane of nutrition upon various factors related to wool growth. National Wool Grower 21:23-28.

Winklmaier, M.A. (1983). The seasonal production of mohair from Angora goats in Canterbury. Theses, M.Agr.Sci., Lincoln College, Canterbury, N.Z.

Wodzicka, M. (1960). Seasonal variations in wool growth and heat tolerance of sheep. 1. Wool growth. Australian Journal of Agricultural Research 11:75-84.

Wodzicka-Tomaszewska, M. (1963). The effect of shearing on the appetite of sheep. New Zealand Journal of Agricultural Research 6:440-447.

Wodzicka-Tomaszewska, M. (1966). Efficiency of wool growth. 1. Comparison of differences between high- and low-producing sheep under restricted and under ad libitum feeding. New Zealand Journal of Agricultural Research 9:909-915.

Wodzicka-Tomaszewska, M., M.L. Bigham (1968). The tattooed patch technique for measurement of wool growth. New Zealand Journal of Agricultural Research 11:943-947.

Wood, E. (1984). Fibre breakage in carding. Lincoln College Wool Bulletin No.1. Report of a seminar on staple strength , Australia. p.pp. 95-104.

Woolaston, R.R. and Butler, L.G. (1987). Genetic improvement of reproductive efficiency in Merino sheep - economic considerations. Proceedings of the 6th Australian Association of Animal Breeding and Genetics Conference, Perth, WA., Feb 9-11. p.247-252.

Wurtman, R.J. (1978). Physiological effects of melatonin. Journal of Neural Transmition, Supplement 13:205-208.

Wurtman, R.J. and J. Alexrod (1965). The pineal gland. Scientific American 213:50-60.

Wynn, P.C., A.L.C. Wallace and E.F. Annison (1979). Effects of growth hormone on wool growth and nitrogen balance in ewes. Proceedings of the Nutrition Society of Australia 4:133.

Yeates, N.T.M. (1954a). Environmental control of coat changes in cattle. Nature 174:609-610.

Yeates, N.T.M. (1954b). Daylight changes. In "Progress in the physiology of farm animals", Ed. J. Hammond, Butterworths. Chapter 8.

Yeates, N.T.M. (1955). Photoperiodicity in cattle. 1. Seasonal changes in coat character and their importance in heat regulation. Australian Journal of Agricultural Research 6:891-902.

Yeates, N.T.M. (1957). Photoperiodicity in cattle. 2. The equatorial light environment and its effect on the coat of European cattle. Australian Journal of Agricultural

Research 8:733-739.

Yellon, S.M. and D.L. Foster (1982). Long days are required to initiate and sustain ovulatory cycles under short days in the lamb. Endocrinology 110(Supplement 1) Abstr. 178.

Yellon, S.M. and D.L. Foster (1985). Alternate photoperiods time puberty in the ewe lamb. Endocrinology 116:2090-2097.

Young, S.S.Y., H.N. Turner and C.H.S. Dolling (1963). Selection for fertility in Australian Merino sheep. Australian Journal of Agricultural Research 14:460-482.

Young, S.S.Y. and H.N. Turner (1965). Selection schemes for improving both reproductive rate and clean wool weight in the Australian Merino under field conditions. Australian Journal of Agricultural Research 16:863-880.

Allison, A.J., R.W. Kelly, J.S. Lewis and D.B. Binnie (1975). Preliminary studies on the efficiency of mating ewe hoggets. Proceedings of the New Zealand Society of Animal Production 35:83-90.

Anderson, S.L. (1954). The Airflow method of measuring wool fibre diameter. Journal of the Textile Institute 45:312-316.

Arnold, G.W. (1962). Estimating quality and quantity of intake of pasture by grazing animals. Australian Society of Animal Production. Proceedings of a seminar on "Aspects of utilisation of pasture by sheep". Melbourne. Federal Council Bulletin No.3.

Atkins, K.D. and G.E. Robards (1976). The efficiency of growth and wool production of young Merino ewes from a flock selected for fertility. Australian Journal of Experimental Agriculture and Animal Husbandry 16:315-324.

Baker, R.L., T.A. Steine, A.W. Vabeno, A.Bekken and T. Gjedrem (1978). Effect of mating ewe lambs on lifetime productive performance. Acta Agriculturae Scandinavica 28:203-217.

Bigham, M.L. and F.R.M. Cockrem (1984). Observations on wool growth and other characteristics of feral sheep. In: "Coloured sheep and their products." Proceedings of a World Congress on Coloured Sheep. Ed. H.T. Blair, New Zealand. pp 302-305.

Ch'ang, T.S. and A.L. Rae (1970). The genetic basis of growth, reproduction and maternal environment in Romney ewes. I. Genetic variation in hogget characters and fertility of the ewe. Australian Journal of Agricultural Research 21:115-129.

Chapman, R.E. and J.L. Wheeler (1963). Dye-banding: a technique for fleece growth studies. Australian Journal of Science 26:53-54.

Clark, V.R., K.R. Keshary, I.E. Coop and A.E. Henderson (1965). The relationship between fleece weight and efficiency in Romney and Corriedale sheep. New Zealand Journal of Agricultural Research 8:511-522.

Dalton, D.C. (1981). Hogget lambing: Achieving good performance. New Zealand Ministry of Agriculture and Fisheries. AGLINK FPP552.

Downes, A.M., P.J. Reis, L.F. Sharry and D.A. Tunks (1970). Metabolic fate of parenterally administered sulphur-containing amino acids in sheep and effects on growth and composition of wool. Australian Journal of Biological Science 23:1077-1088.

McGuirk, B.J. (1980). The effects of selection for increased fleece weight. Proceedings of the Australian Society of Animal Production 13:171-174.

McGuirk, B.J., J.R. Paynter and R.B. Dun (1966). The effect of frequency and time of shearing on the reproduction and wool growth of Bungaree South Australian Merino ewes. Australian Journal of Experimental Agriculture and Animal Husbandry 6:305-313.

Moore, R.W. and W.H. McMillan (1984). Hogget mating and subsequent performance. Proceedings of the Ruakura Farmer's Conference 36:107.

Orwin, D.F.G., J.L. Woods and S.L. Ranford (1984). Cortical cell types and their distribution in wool fibres. Australian Journal of Biological Science 37:237-255.

Rudge, M.R. (1984). Distribution, status and preservation of feral sheep in New Zealand. In: "Coloured sheep and their products." Proceedings of a World Congress on Coloured Sheep. Ed. H.T. Blair, New Zealand. pp 295-301.

Ryder, M.L. (1984). The historical development of fleece type and loss of colour. In: "Coloured sheep and their products." Proceedings of a World Congress on Coloured Sheep. Ed. H.T. Blair, New Zealand. pp 212-221.

Scoffield, J.E. (1970). Some aspects of grazing ecosystems. Thesis, M.Sc., Massey University, Palmerston North, New Zealand.

Setchell, B.P. and G.M.H. Waites (1965). Variations in blood flow to the skin. In: "Biology of the Skin and Hair Growth." Eds. A.G. Lyne and B.F. Short. Angus and Roberston, Sydney, Australia. pp 617-624.

Stuart, A.M., R.J. Moir and P.G. Schinckel (1961). Seasonal fluctuations in wool growth in Southwestern Australia. Australian Journal of Experimental Agriculture and Animal Husbandry 1:85-92.

Vercoe, J.E. and J.E. Frisch (1982). Animal breeding for improved productivity. In: "Nutritional limits to animal production from pasture." Ed. J.B. Hacker. Proceedings of an International Symposium, St. Lucia, Queensland. August 24-28,1981.

Wodzicka, M. (1960). Seasonal variations in wool growth and heat tolerance of sheep. 1. Wool growth. Australian Journal of Agricultural Research 2:75-84.

Woods, J.L. and D.F.G. Orwin (1987). Wool proteins of New Zealand Romney sheep. Australian Journal of Biological Science 40:1-14.