

CHAPTER 1

INTRODUCTION

The aim of present day livestock production is to increase productivity of herds and flocks by selecting genetically superior animals for reproduction. Selection objectives differ widely between production systems and between individual breeders. For example, in meat producing enterprises, growth rate is a major determinant of productivity and hence selection for growth forms the basis of most performance recording programmes in the beef industry. The actual measure of growth emphasized depends on the production system for which the selected animals are to be used. In Australia and New Zealand where animals are grown and finished on pasture, the emphasis has been placed on weaning weight (Barlow, 1978).

The sheep industry has a wider range of marketing systems and breeding programmes are intended to enhance the efficient production of one or more products such as wool, meat, and milk. The vast majority of Australia's sheep graze on improved pastures to produce wool and meat. In recent years, emphasis has shifted towards meat as a selection objective, largely because of good markets for sheep meat in the Arab countries (Robertson, 1983). The Australian Merino industry has historically focused on increased wool production with little formal attention paid to increasing growth rates and reproductive performance. The meat production potential of the Merino has generally been overlooked despite the contribution of the sale of surplus lambs to overall flock returns and its role when crossed with the Border Leicester in the prime lamb industry.

It is generally agreed that increasing growth rate increases the efficiency of meat production, and consequently many producers have placed great emphasis on selection for superior rate of growth. However, there are some serious deficiencies in the current state of knowledge regarding correlated responses to selection in other production characters, particularly lactation and reproduction. Direct evidence of the correlation between growth rate and milk production in beef cattle and sheep is scant. Since preweaning growth is largely dependent on the dam's milk production, lactation is an area worthy of further investigation. Concerns have been expressed by both producers and researchers that continued selection for fast growth alone may have detrimental effects on reproductive rate (Barlow, 1978). If present, such effects would offset the economic advantages gained from improvements in the genetic potential for growth. The importance of survival to reproduction and overall productivity is obvious, yet little work has focused on the survival characteristics in high growth rate flocks and herds.

Research into the effects of weight selection in sheep is very limited. The only long-term selection experiment that has established both positive and negative weight selection lines began at the Agricultural Research Station at Trangie, N.S.W., in 1951. Details of this experiment and the selection procedures adopted were reported by Pattie (1965a). Briefly, a base flock of medium Peppin Merino origin was selected solely on weaning weight creating 3 lines: high weaning weight (W+), low weaning weight (W-), and a random bred control (R). These selection lines have been maintained until the present time and have undergone 12 generations

of selection. This thesis deals specifically with animals from the Trangie weight selection lines.

A preliminary report on milk yield and composition of the weight selection ewes after 5 generations of selection was given by Pattie and Trimmer (1964). The main objective of this thesis was to re-examine the lactation performance of the selection ewes after a further 7 generations of selection. Investigations were made into the nature of the lactation curves, the maternal genotype and lamb genotype effects on lactation, and milk composition of the W+, R, and W- lines. A second objective was to study the effects of selection on lamb survival. It is well recognized that early lamb mortality is a major source of reproductive wastage to the Australian sheep industry and thus the opportunity was taken to collect preweaning lamb survival data on the weight selection flocks.

This thesis begins with a review of the relevant literature on lactation and lamb survival, then presents 7 separate experimental studies, and ends with a summary of the main conclusions.

CHAPTER 2

2.1 LACTATION

2.1.1 TECHNIQUES FOR ESTIMATING MILK YIELD

The various methods which have been used to estimate milk production in sheep have been reviewed by Boyazoglu (1963) and the validity and comparability of the methods have been assessed by Doney et al. (1979). The most widely used techniques are the lamb-suckling and test-weighing method and the method of hand- or machine-milking of ewes following the administration of oxytocin. A third and more recent technique, that of the integrated assessment of milk intakes over an extended period by the dilution of injected radioisotopes (Wright et al., 1974; Dove and Freer, 1979), involves the least handling of the animals. However, one of the important disadvantages of this technique is the opportunity to obtain milk samples does not exist. Because it was intended to collect milk samples in the current research, no further consideration was given to the dilution technique in this thesis.

McCance (1959) described three main criteria which he considered the adopted method must satisfy before the results can be accepted as reliable: 1) the udder must be emptied to a comparable degree at the beginning and end of the test, 2) the procedure itself does not affect milk secretion over the test period, and 3) the rate of milk secretion over the test period does not differ from other periods over which the estimate is to be extrapolated.

LAMB-SUCKLING METHOD

The lamb-suckling method estimates the yield of the suckled ewes by measuring the amount of milk consumed by the lamb after a

series of short intervals of separation from the ewes (Doney et al., 1979). The lambs are weighed before and after these intervals and the weight increment is interpreted as the milk produced by the ewe in that interval. Estimations have been made at 5-hour (Coombe et al., 1960) and 6-hour intervals (Davies, 1958) but more commonly at 4-hour intervals over a 24 hour period, repeated weekly (Owen, 1957; Slen et al., 1963; Moore, 1967; and Robinson et al., 1968). The interval must allow time for sufficient accumulation of milk to minimize the considerable errors in measurement of a small weight increment after the sucking (100-500g) relative to the liveweight of the lamb. Therefore, as lactation advances and lamb liveweight increases, accurate measurement of weight gain (i.e. milk intake) becomes increasingly difficult (Coombe et al., 1960).

The lamb-suckling method does not entirely satisfy the three criteria of McCance (1959). Firstly, it is difficult to ensure that the udder has been emptied to a standard extent (Doney et al., 1979). Secondly, the technique may significantly influence the estimate by disrupting the normal grazing and suckling behaviour, possibly resulting in a depression of intake by the ewe (Davies, 1958), which could influence subsequent milk production, as well as a depression in the milk intake in the lamb (Coombe et al., 1960; Moore, 1962). Finally, the duration of the suckling separation interval may affect the estimate. Bawa and Acharya (1971) reported that milk yields estimated from suckling at 4-hour intervals were significantly higher ($P < 0.01$) than 8-hour or 12-hour suckling intervals. The authors suggest the increase in yield recorded in the shortest suckling interval was due to the release of intramammary pressure at each suckling and thereby resulting in more milk secreted in the interim.

Increased intramammary pressure experienced at longer between suckling intervals may have inhibited the secretion of milk.

OXYTOCIN METHOD

The hand- or machine-milking technique, which measures the rate of milk secretion by the ewe with the aid of exogenous oxytocin, was developed by McCance (1959). After an intravenous injection of oxytocin, ewes were milked to empty the udder to a standard degree (Corbett, 1968), and then after a known interval of time, the ewes were milked again and the yield recorded. Peart (1982) concluded that a 4-hour test interval would be the most suitable compromise which allows the minimum denial of milk to the lamb whilst providing a reasonably consistent estimate of yield when extrapolated to 24 hours. While Scales (1968) reported a small diurnal variation in milk secretion (8-10%; $P < 0.01$), the majority of authors (e.g. McCance, 1959; Corbett, 1968; Morag, 1969) have found this parameter to be insignificant, implying that the technique satisfies the third of the aforementioned criteria. The second criterion is not entirely met because estimates are somewhat dependent on the interval between milking (McCance, 1959; Morag, 1969). Also, stress imposed by the test procedure may upset the neurohormonal equilibrium of the ewe and hence influence milk secretion. Inhibition of the milk letdown response to endogenous oxytocin induced by administration of adrenalin (Bisset et al., 1967) provides physiological support for this suggestion. The oxytocin method may empty the udder to a greater degree than could be achieved by the offspring, especially single lambs, and hence lead to overestimates of milk production (Coombe et al., 1960).

COMPARABILITY OF TECHNIQUES

Since estimate may be made either on the young's consumption or the dam's yield, it is assumed, when comparing different estimates, that the rates of secretion and consumption are equal (Peart, 1982), although there is evidence that rate of secretion and rate of extraction are not necessarily equal in early lactation (Doney et al., 1979). Several authors have compared the results obtained by the two techniques within a single experiment. Over a 10 week trial, Moore (1962) reported a 6% higher yield estimate ($P < 0.01$) from the oxytocin method. In a subsequent experiment, the same author (1967) also found that the oxytocin method gave a higher yield estimate (by 9%; $P < 0.01$) than the suckling method during the last 6 weeks. The correlation between the two techniques was 0.88. Moore (1962) suggested that a 23% difference in favour of the oxytocin method obtained by Coombe et al. (1960) could be due to a 2-hour interval between hand milkings and a 5-hour interval in the lamb-suckling tests employed by the latter authors. As previously mentioned, the build up of intramammary pressure may inhibit milk secretion over longer intervals. Doney et al. (1979) reported an overall advantage of 0.10kg/day using the oxytocin technique ($P < 0.001$). The oxytocin method gave significantly higher estimates in the first week but from the second to the sixth week of lactation, differences between the two techniques were small. Contrary to other published data, the lamb-suckling method gave significantly higher milk yield estimate in a study by Bawa and Acharya (1971). The authors explained that the comparatively lower yields by the oxytocin method were possibly due to the low frequency of milking. The value of estimates of either technique is not affected by the number of lambs suckled or the

genotype of either the ewe or the lamb (Doney et al., 1979).

Whereas the lamb-suckling and oxytocin techniques are both subject to their own systematic biases, it is evident that valid comparisons for most applied purposes may be obtained by either method. In the experimental sections that follow, both techniques have been used. The oxytocin method was performed when the necessary resources were available and particularly when the aim was to remove possible lamb genotype effects (Experiment 4).

2.1.2 FACTORS AFFECTING MILK YIELD

For both cattle and sheep, the wide range of milk production levels recorded in the literature probably arises from the diversity of the breeds of animals studied, the natural variability of milk production within both individuals and breeds, and differences in such factors as nutritional levels, suckling intensities, and damage. The main factors affecting milk yield are discussed in this section.

GENETIC INFLUENCES

Breed

Many estimates have been made throughout the world to quantify the milk production of mutton breeds of sheep using different measurement techniques under various conditions of nutrition and management (Peart, 1982). These differences must be taken into account when comparisons are made among sources of information. A representative selection of the milk yields of mutton breeds of sheep from Peart (1982) is given below.

Total milk production (kg) of single suckled ewes during a 12 week lactation.

<u>Breed</u>	<u>Milk Production (kg)</u>
Merino	78
Cheviot	91
Suffolk	94
Scottish Blackface	102
Merino Crossbred	108
Romney	115
Finnish Landrace X Blackface	125
East Friesland X Blackface	181

In a comparison of milk production in 5 breeds of sheep, Slen et al. (1963) found that among ewes nursing single lambs, breed differences were evident, but were not entirely consistent during the 2 years of the study. Scales (1968) measured the milk production of Romney, Corriedale and Merino ewes with single lambs and found that interbreed differences were not significant, although large between-animal, within-breed differences existed. The Merino ewes yielded 110kg in 12 weeks, an amount higher than reported by other workers such as Corbett (1968), who obtained a total yield of 90-100kg at 14 weeks. Supporting the general conclusion that breed influences milk production, single suckled Dorset ewes in the study by Geenty (1979) produced 26-63% more milk than Romney ewes in the first 9 weeks of lactation.

The amplitude and timing of peak lactation also varies among breeds. For example, single rearing Merino ewes may peak at 1.1-1.6kg/day in the second or third week of lactation (Corbett, 1968; Zaluska et al., 1978), while Scottish Blackface ewes with a single lamb may peak at or above 2.0kg/day in the third or fourth week of lactation (Peart, 1967; Doney et al., 1979).

Thus, there is considerable evidence to demonstrate differences in milk production among breeds. Both Davies (1958) and Flamant and

Casu (1978) demonstrated the ability of lambs with high growth potentials (and hence increased nutritional requirements and/or appetites) to more completely remove milk from the udder and thus stimulate higher production from the ewe. In 1966, Moore stated that most studies then available in the literature did not distinguish between the potential of the ewe to produce milk and the potential of the lamb to obtain it. This situation still applies, and particular attention was thus paid in the current work to remove possible ewe (Experiment 3) and lamb (Experiment 4) genotype effects on milk production.

Maternal Effects

For 22 species, Linzell (1972) showed milk yield to be closely related to the metabolic body size of the lactating female. Taylor (1973) confirmed earlier reports that peak daily yield is proportional to metabolic body weight ($W^{0.73}$), while total lactational yield was found to be proportional to mature body weight. Applying the genetic size-scaling rules to various species removed 93-95% of the variation in yield. Taylor (1973) also showed that, between breeds, results on peak daily yield were fully consistent with proportionality to metabolic body weight. Using results from 12 dairy breeds tested over 13 consecutive years, the author found that breed differences in body weight accounted for about two-thirds of the variation in daily milk yield.

Significant within-breed relationships between ewe milk production and both ewe liveweight at joining and at parturition have been published by Owen (1957) and Robinson et al. (1968), while Geenty (1979) found no similar significant relationship. Owen (1957) suggested that larger animals may be more efficient at

converting resources available for lactation or that larger animals have better inherent nursing abilities because they are probably daughters of good milkers. In reviewing reports on within-breed associations between milk yield and body weight, Taylor (1973) reported that "by and large, phenotypic correlations have all been positive, some significant, some not" (although the supporting values were not given) and suggested that body size extremes within a breed may be ill-adapted and hence unproductive. However, the latter suggestion was made against the background of the natural variability between animals, within a breed and does not consider the effects of selection for weight within a breed. The only between-strain, within-breed data known to the author is that of Pattie (1965b), who demonstrated a positive correlation (0.325; $P > 0.05$) between ewe weight and milk volume in weaning weight selection lines of Merinos. The significance of possible within-breed genetic selection effects on milk production will be examined in a following section of this review (Genetic Selection, page 13).

Offspring Effects

Previous crossfostering studies have demonstrated an effect of lamb genotype on the milk production of the dam. Moore (1966), who crossfostered lambs between Merino and Corriedale ewes, Langlands (1972), who used Merino and Border Leicester ewes, and Doney et al. (1981), who crossfostered to give all combinations of ewe breed (Blackface and East Friesland X Blackface) and lamb breed (Blackface and Suffolk cross), all found a significant effect of lamb breed on milk production which declined after 6-8 weeks of lactation. Beyond that stage, the lactation potential of the ewe replaced the demand by the lamb as the first limiting factor. Similar findings were

reported by Peart, Doney and MacDonald (1975) who, in agreement with Moore (1966), concluded that lamb genotype had a greater influence on milk yield than ewe genotype. The lack of significant lamb sire breed effects on milk production found by Geenty (1979) were probably due to small breed group sizes.

There are inherent differences between lambs in their demand for milk (reflected in the yield of the dam) which appear to be associated with birthweight (Moore, 1966; Doney et al., 1981). A significant ($P < 0.05$) correlation coefficient of milk yield on birthweight for Merino sheep was reported by Scales (1968). However, data from Coombe et al. (1960) revealed no significant correlation between lamb birthweight and milk yield as estimated by both the oxytocin and lamb-suckling techniques. The plane of nutrition during the last third of pregnancy and the size of the ewe influence both the birthweight of the lamb and milk yield (Coombe et al., 1960); therefore, lamb birthweight may only be indirectly correlated with milk production of the ewe. The correlation between lamb birthweight and milk volume in weaning weight selection lines (Pattie, 1965b) was significant (0.44; $P < 0.05$) but not when ewe weight was held constant (0.35; $P > 0.05$).

GENETIC SELECTION

In the dairy cattle literature, estimates of the heritability of milk yield are numerous and in a comprehensive review by Maijala and Hanna (1974), estimates ranged from 0.12 to 0.59 with an average heritability estimate (95% C.I.) of 0.27 (0.25-0.29). Holmes and Wilson (1984) reported a similar range of estimates (0.23-0.59). The average repeatability (95% C.I.) of milk yield given by Maijala and

Hanna (1974) was 0.49 (0.45-0.52).

Owen (1957) estimated values of 0.50 (derived from regression) and 0.61 (derived from correlation) for the heritability of milk production of suckling ewes. For dairy sheep and goats, a lower mean heritability of milk production (0.30 in the first lactation) was reported more recently by Flamant and Morand-Fehr (1982).

In a review of the effects of body size of cows on their biological efficiency, Morris and Wilton (1976) found that genetic and phenotypic correlations of measures of body size with milk yield averaged 0.14 and 0.33, respectively. Since selection for weaning weight or average daily gain will increase liveweight at all other ages from birth to maturity (Barlow, 1978), correlated responses in milk yield with selection for weaning weight should therefore be expected. Barlow (1978) found few estimates of genetic correlations of milk yield with weaning weight in beef cattle, although most estimates in the dairy breeds were small and positive.

Looking at the milk production - body size relationship from the other point of view, Taylor (1973) indicated that selection for milk yield will probably lead to an increase in body size, whereas selection for yield per unit body weight (that is, considering an efficiency aspect) may well reduce body size.

In summary, it may be concluded that both milk yield and growth rate are genetically determined and that the limited available evidence suggests that the two are positively genetically correlated. Within sheep breeds, the only direct evidence known to the author is that of Pattie (1965b) who studied the weaning weight selection lines after 5 generations of selection and observed a quite high correlated response (0.33) in ewe milk yield. The aim of the current thesis was

to expand the knowledge available in sheep by re-examining the lines investigated by Pattie (1965b) after a further 7 generations of selection.

EFFECT OF NUTRITION

Many studies have demonstrated the importance of nutrition, particularly energy and protein, during pregnancy and lactation on milk production of the ewe. The energy level of the diet most directly and rapidly affects milk production (Reid, 1961; Flamant and Morand-Fehr, 1982) and a limited supply of energy, rather than a deficiency of any other nutrient, is most frequently the cause of decreased milk production (Flatt and Moe, 1974; Kilkenny, 1978). Most of the energy intake in the lactating ruminant is used for the synthesis of glucose, a key substrate in lactogenesis (Annison and McDowell, 1980). Milk yield is also responsive to variations in dietary protein, although the efficiency of protein and energy utilization is affected by the level of intake of each (McDonald et al., 1981). There is a diminishing response to increases in the inclusion rate of protein (Broster, 1973; Kilkenny, 1978; Gonzalez et al., 1982) which is typical of the response to protein at a constant energy intake. Responses of the lactating ewe to variations in energy and protein intake and their interrelationships have been reviewed by Robinson (1978).

Nutrition in Late Pregnancy

Udder development and hence the capacity for lactation is governed by nutrition in the later stages of pregnancy. Although a positive relationship of udder size and milk yield occurs on a low plane of nutrition, the reverse occurs on a high plane, where the

size of the udder may not be a true indicator of its secretory capacity due to excess adipose tissue (Thomson and Thomson, 1953; Sejrsen, 1978). Foetal requirements for carbohydrates are high (McDonald et al., 1981) so that in late gestation the metabolizable energy requirement increases to approximately 1.5-2.0 times that for maintenance for ewes carrying singles or twins (Kleemann, 1983).

Undernutrition in the last 6 weeks of gestation has been shown to delay the onset of lactation and significantly affect milk yield (Owen, 1957; McCance and Alexander, 1959; Peart, 1982) and also decrease the persistency of the subsequent lactation (McDonald et al., 1981). Peart (1967) suggested that the principle effect of malnutrition during pregnancy may be to inhibit the growth potential of the lamb, and that the effect on milk production is a result of the inability of a small lamb to exploit the milk potential of the ewe. The reduction in milk yield depends upon the severity of the undernutrition; if the ewes are only moderately underfed, the level of milk production is likely to be directly related to the level of feeding during lactation (Kilkenny, 1978; Peart, 1982).

Nutrition During Lactation

Lactation is the period of highest nutrient requirement in the ewe's annual production cycle (Peart, 1982) and at peak lactation, the energy requirement is 2-3 times that for dry ewes (Owen, 1957). Milk production is favourably affected by increased nutrition in early lactation (Davies, 1958; Kilkenny, 1978; Flamant and Morand-Fehr, 1982). Cowan et al. (1981) suggested that increased milk production from additional protein in early lactation is due to an increase in the efficiency of energy utilization. In early lactation, when the ewe is commonly in a negative energy balance,

there is evidence that protein intake is important in affecting partitioning of nutrient between milk production and weight loss (Kleemann, 1983). Cowan et al. (1981) and Gonzalez et al. (1982) demonstrated rapid responses to dietary protein concentration in ewes in negative energy balance. However, Gibb and Treacher (1982) found no significant differences in the yield of ewes fed "high" and "low" levels of nutrition in early lactation, and suggested that differences in milk production are likely to be significant only during severe post partum nutritional stress.

The stage of lactation governs the response to increased nutrition, as shown by the study of Peart (1970), in which milk production responded to increased nutrition (ad libitum feeding) at the second week of lactation but not after the fourth. Similar findings were reported by Jagusch et al. (1972). They also showed that restricted nutrition for 1 week delayed peak yield by several days, while restricted nutrition for 4 weeks profoundly depressed milk yield.

The shape of the lactation curve is also influenced by diet. According to Kilkenny (1978), a reduction in milk yield as a result of underfeeding during lactation is usually reflected in a lower peak occurring 2-3 weeks after lambing, as opposed to 3-5 weeks in well fed ewes. In considering energy, Flamant and Morand-Fehr (1982) indicated a relatively flat curve with a late peak would be obtained by a restricted supply, whereas a high energy supply in early lactation results in a earlier and higher peak, but poorer persistency.

Several studies have examined the effect of nutrition on milk yield throughout pregnancy and lactation. For example, Cumlivski

(1978) reported significantly higher milk yields from Merino ewes provided increased protein and energy throughout pregnancy^{and} when the diet was supplemented with protein. Treacher (1971), on the other hand, reported contrasting data in which the level of feeding during pregnancy had no effect on the subsequent milk yield of the ewes. The level of feeding during lactation did not significantly affect milk production, although the yield of the "high" nutrition group was 21% greater than that of the "low" one.

In this thesis, it was not intended to examine, in depth, the nutritional aspects involved in the production of milk. Hence, efforts were made to provide similar nutrition to all the ewes and detailed information on pasture quality and availability and intakes of the ewes was not obtained.

EFFECT OF NUMBER OF LAMBS SUCKLED

Many researchers have shown the milk production of ewes to be significantly influenced by the number of lambs suckled. Among those who have reported higher milk yields in ewes suckling twin rather than single lambs are Davies (1958, 1963), Slen et al. (1963), Robinson et al. (1968), Peart et al. (1979), and Doney et al. (1981). The amount of the increase varies greatly from the non-significant 3% found by Wohlt et al. (1981) to 50-100%, depending on grazing conditions, reported by Doney and Monro (1962). Over 10 weeks of lactation, Davies (1958) recorded 51% more milk produced by twin suckled ewes. According to Treacher (1978), most studies show a 30-50% increase.

While milk production can thus be adjusted to the number of lambs suckled, colostrum production can not and as the number of

lambs (litter size) increases, the amount of colostrum available to each decreases (Halliday, 1981). This could have implications for the survival of multiple lambs (see Chapter 4).

The shape of the lactation curve has also been shown to vary with the number of lambs suckled. The lactation curve for ewes rearing twins has an earlier and more pronounced peak in the second and third weeks (Davies, 1963; Peart, 1967; Geenty, 1979), with a lower persistency after the peak (Peart, Edwards and Donaldson, 1975; Geenty, 1979; Doney et al. 1981) than in ewes suckling singles. Investigating Polish Merinos, Zaluska et al. (1978) found twin suckled ewes peaked in the first week of lactation at a yield which was 33% above the second week peak yield of single suckled ewes.

Alexander and Davies (1959) and Doney and Monro (1962) found ewes bearing twins but rearing singles produced similar amounts of milk as ewes rearing natural singles, which indicated that milk yield is influenced by the number of lambs suckled, not born.

In agreement with Davies (1958), Treacher (1978) suggested that the amount of milk withdrawn in early lactation (i.e. the suckling stimulus) has a profound effect on subsequent yield, as the build up of intramammary pressure may inhibit the secretion of milk. Slen et al. (1963) suggested that the milk drawn by twins is a measure of the potential of the ewe, while that drawn by singles, especially in early lactation, is a measure of the ad libitum consumption of the lamb.

In the following experiments, ewes bearing and rearing single lambs were chosen for the comparison of milk production between weight selection lines. In Experiment 4, possible difficulties associated with variation in the sucking stimuli of lambs of

different genotypes were avoided by removing the lambs completely and machine milking the ewes twice daily.

EFFECT OF AGE

It is widely accepted that milk production of the cow, goat, and sheep is dependent upon parity, or lactation number (e.g. Schmidt, 1971; Flamant and Morand-Fehr, 1982). Since the normal udder commences its second lactation with more secretory tissue than was present for the first lactation (Coop et al., 1972; Schmidt, 1971), a greater production can be anticipated. For instance, a mature cow may produce 25% more milk than a heifer, of which 5% is associated with the increase in body size and the remaining 20% is the result of the increased development of the udder (Foley et al., 1972).

In a study of different age groups of Merino ewes, Corbett (1968) found the milk production of primiparous ewes (2 years old) to be less than that of multiparous ewes, and the effect of ewe age was similar to that reported by Barnicoat et al. (1956) for Romney ewes. In both studies, the highest mean lactation was obtained by ewes 4 years old. Wohlt et al. (1981) reported that significantly higher levels of colostrum were produced by ewes greater than 4 years in age than by younger ewes. However, Treacher (1978) cautioned that studies conducted in a single year indicate little of the trends in yield from lactation to lactation and may be considerably influenced by differing previous management of the different age groups. It is generally concluded that maximum milk production in the ewe is achieved at the third or fourth lactation, decreases slightly to the sixth, and then declines markedly (Barnicoat et al., 1956; Boyazoglu,

1963; Flamant and Morand-Fehr, 1982).

Lactational studies in the current research involve experimental animals of varying ages. Hence, ewe age was incorporated as a covariate in the appropriate statistical analyses.

2.1.3 MILK COMPOSITION

In addition to the quantity of milk produced by the dam, the nutritional adequacy of milk for the young depends upon its chemical composition and biological value, as the offspring is completely dependent on milk to meet its nutritional requirements in early life. Energy intake has a large influence on the growth of the young (Jagusch and Mitchell, 1971) and the sources of energy in milk are the lipids, proteins, and carbohydrates.

CONSTITUENTS OF MILK

Lipids

The lipids, or milk fats, are mainly a wide variety of triacylglycerols in small globules, although phospholipids and cholesterol are also present in small amounts. Fat provides the greater part of the energy of the milk (38.12 MJ/kg ^{DM of} gross energy; McDonald et al., 1981). Of the constituents in milk, fat is the most variable in both percent composition of fat and the fatty acid composition of the triacylglycerols (Schmidt, 1971). In agreement with the literature in dairy cows, Ashton et al. (1964) found great variability in the fat content of ewe's milk, much of this associated with differences in the amount secreted and with incomplete evacuation of the udder.

Protein

The milk proteins contain more essential amino acids than any other natural food (Foley et al., 1972); hence, the biological value, as defined by the completeness with which essential amino acids are supplied, is very high. Proteins also provide 24.52 MJ/kg ^{DM of} gross energy (McDonald et al., 1981). The protein fraction is represented by casein (76.6-78.7% of total crude protein; Bouchard and Brisson, 1969; Poulton and Ashton, 1970), with β -lactoglobulin present in the next greatest amount, and small amounts of α -lactalbumin. These proteins are specific to milk and comprise greater than 90% of total proteins (Foley et al., 1972). The remainder of the fraction is made up of non-specific milk proteins which include blood serum albumin and immunoglobulins.

Carbohydrates

The principle carbohydrate of milk is a disaccharide, lactose, which is composed of a molecule of glucose and a molecule of galactose. The synthesis of this sugar is unique to the mammary gland of mammals. The average energy value for carbohydrate given by McDonald et al. (1981) is 16.54 MJ/kg ^{DM of} gross energy. Lactose accounts for approximately one-third of the osmotic pressure of milk (Schmidt, 1971) and is thus involved in the maintenance of the osmotic equilibrium with blood (Foley et al., 1972). Therefore, within a species, the concentration of lactose is generally constant and the variation among individuals is usually small, while the concentration varies greatly among milks of different species (Jenness and Sloan, 1970). Several studies have demonstrated the low variability of lactose in ewe's milk (e.g. Ashton et al., 1964; Jagusch and Mitchell, 1971; Poulton and Ashton, 1972).

On the basis of these findings, it was concluded that the percentage of lactose would be unlikely to vary significantly between the current experimental animals and hence analysis for lactose was not included in the compositional analysis of milk in Experiment 5.

Total Solids and Ash

The dry matter of milk is known as the total solids, and this value varies widely, particularly as a reflection of variations in the fat percentage. Data from a number of sources reviewed by Ashton et al. (1964) indicates that ewe's milk contains 16.3-21.8% total solids. The minor constituents of total solids include minerals, vitamins, enzymes, phospholipids, sterols, pigments, and various non-protein nitrogen compounds.

The amount of non-combustible matter, known as ash, gives an approximation of the total mineral content of milk. Unlike the other constituents, the variability of ash is low and the typical range in ewe's milk is 0.83-0.97% (Ashton et al., 1964).

COMPARISON OF COLOSTRUM WITH NORMAL MILK

The composition of colostrum, the first secretion from the mammary gland, differs considerably from later secretions. A comparison of the composition of colostrum with that of normal milk for the cow and ewe is given below.

<u>Percent</u>	Holstein Cow ^a		Finnish Landrace X Blackface Ewe ^b	
	<u>Colostrum</u>	<u>Milk</u>	<u>Colostrum</u>	<u>Milk</u>
Fat	6.7	4.0	12.9	8.8
Protein	14.0	3.1	6.5	5.3
Lactose	2.7	5.0	4.1	4.7
Total Solids	23.9	12.9	23.4	19.7
Ash	1.11	0.74	-	-

a. Parrish et al. (1950)

b. Peart, Edwards and Donaldson (1975)

Fat

The fat content of colostrum can be variable (Schmidt, 1971), although several authors agree that colostrum contains higher levels of fat than normal milk (e.g. Parrish et al., 1950; Noble et al., 1970). The higher levels found by Peart, Edwards and Donaldson (1975) were statistically significant ($P < 0.001$), whereas Wohlt et al. (1981) found lower levels of fat in colostrum than in normal milk. The composition of colostrum changes very rapidly. For example, Corbin and Whittier (1965) reported the total solids content in cow's milk decreased by more than half within 24 hours post partum.

Protein

The most striking difference between the two types of secretions is the high protein content of colostrum (Bouchard and Brisson, 1969; Schmidt, 1971; Peart, Edwards and Donaldson, 1975), which may exceed twice the level in normal milk (Parrish et al. (1950); Wohlt et al., 1981). In ewe's milk, Bouchard and Brisson (1969) recorded a drop in the protein level from 8% at the beginning of lactation to 4.5% after 7 days. The high protein content of colostrum reflects the difference in its protein distribution, particularly the globulin content. Immunoglobulins account for 50-60% of the protein in colostrum (Wohlt, et al., 1981). Bouchard and Brisson (1969) reported immunoglobulins were 13.2% of total nitrogen on Day 1 of lactation and dropped sharply to 2.4% on Day 7. Halliday (1981) also reported a sharp decline in immunoglobulin levels, from 85mg/ml to 18mg/ml in 48 hours.

As the antibody titre of the newborn lamb or calf is very low, absorption of the immunoglobulins in colostrum builds up the titre, which provides passive immunity and enhances the mechanisms of active

resistance. Colostrum production in the first 24 hours is crucial, as the permeability of the newborn gut to immunoglobulins decreases rapidly after that time (Tizard, 1982).

Lactose

The lactose content of colostrum milk is lower than that of ordinary milk (Parrish et al., 1950; Peart, Edwards and Donaldson, 1975; $P < 0.01$). High lactose levels may cause scouring in the young; therefore, low level of lactose in colostrum may be a built-in mechanism to reduce the incidence of scours in the newborn while it consumes colostrum (Schmidt, 1971).

Total Solids and Ash

Colostrum has a higher percentage of total solids (principally due to the increased levels of protein), as well as ash (Parrish et al., 1950; Wohlt et al., 1981). In the milk of Finnish Landrace X Blackface ewes, Peart, Edwards and Donaldson (1975) found higher percentages ($P < 0.001$) of total solids in colostrum samples (see table page 23).

The composition of colostrum and of normal milk throughout lactation were investigated in the following work (Experiment 5).

2.1.4 FACTORS AFFECTING MILK COMPOSITION

Many of the factors known to affect milk yield similarly affect milk composition. The main factors will now be considered in detail.

SPECIES AND BREED

The composition of the milk of each species is designed to provide for the inherent rate of growth of its young. Between species, the faster the rate of growth, the more concentrated are the milk constituents needed in order to provide nutrients for that growth (Corbin and Whittier, 1965; McDonald, 1969). Comprehensive tables of the composition of milk of various species are available in the literature (e.g. Jenness and Sloan, 1970; Schmidt, 1971). Some representative values for the major domestic species are given below.

<u>Species</u>	<u>Fat</u>	<u>Protein</u>	<u>Total Solids</u>	<u>Ash</u>	<u>Reference</u>
Bovine	3.8	3.8	12.9	0.7	McDonald (1969)
	3.7	3.4	12.7	0.7	Jenness and Sloan (1970)
	3.5	3.9	14.7	0.8	Schmidt (1971)
	3.5-4.0	3.2-3.6	12.5-13.0	0.90-0.95	Flamant and Morand-Fehr (1980)
Caprine	4.25	3.52	13.0	0.86	cited in Corbin and Whittier (1965)
	4.5	2.9	13.2	0.8	Jenness and Sloan (1970)
	2.5-4.5	2.8-3.6	11.5-13.5	0.7-0.9	Flamant and Morand-Fehr (1980)
Ovine	5.1-10.0	4.6-6.8	16.3-21.8	0.83-0.97	Ling et al. (1961)
	7.9	5.23	19.3	0.9	cited in Corbin and Whittier (1965)
	7.4	5.5	19.3	1.0	Jenness and Sloan (1970)
	5.5-7.0	5.3-6.0	17.0-18.5	0.90-1.0	Flamant and Morand-Fehr (1980)

The one indisputable fact regarding the composition of milk can be stated with one word: variation. The large variation shown within a species is, in part, due to differences between breeds. Representative values from the numerous compositional analyses of several breeds of ewes which have been reported in the literature are summarized below.

<u>Breed</u>	<u>Fat</u>	<u>Protein</u>	<u>Total Solids</u>	<u>Ash</u>	<u>Reference</u>
Merino	8.0	4.6	18.9	0.90	cited in Ashton et al. (1964)
	8.19-8.53	5.21-5.34	-	-	Corbett (1968)
	6.47	5.84	17.80	0.92	Zaluska et al. (1978)
Clun Forest	6.2	5.3	16.9	0.87	Ashton et al. (1964)
	5.8	5.9	-	-	Poulton and Ashton (1970)
Dorset	12.6	5.2	23.4	0.79	Wohlt et al. (1981)
Finnish Landrace X Blackface	8.81	5.51	19.67	0.96	Peart, Edwards and Donaldson (1975)
N.Z. Romney	5.5	5.5	16.3	0.87	cited in Ashton et al. (1964)

These data illustrate the great variability between breeds in milk constituents, particularly fat, which is also reflected in the amount of total solids. Referring to cattle, Taylor (1973) reported that body weight accounted for an insignificant amount of variation in the milk fat percentages between breeds. Using crossfostering techniques with Merino (M) and Border Leicester (BL) ewes and lambs, Langlands (1972) demonstrated that milk fat content in early lactation was significantly influenced ($P < 0.01$) by the breed of the ewe as well as by the genotype of the suckling lambs. Milk fat content was lowest in BL ewes suckling BL lambs (8.8%) and greatest in BL suckling M lambs (9.7%).

Individual animals within a breed also exhibit wide differences in composition of milk and interbreed standard deviations for fat content have been reported higher than for the other constituents in both dairy cattle (Foley et al., 1972; Jenness, 1974) and sheep (Ashton et al., 1964).

EFFECTS OF NUTRITION

The influence of nutrition on the composition of milk in ruminants has been extensively investigated, particularly in dairy cattle. Lower percentages of milk fat are found in animals fed diets in which the ratio of digestible carbohydrates to roughage is high (Storry, 1970; Annison and McDowell, 1980). These diets change the rumen fermentation pattern, decreasing the proportion of acetic acid production and also increasing propionic acid production, which increases gluconeogenesis. The resulting raised blood glucose levels stimulate insulin release, which promotes lipogenesis in adipose tissue at the expense of milk fat production (Annison and McDowell, 1980). Increased propionic acid levels also promote milk protein synthesis (Storry, 1970).

The milk from ewes fed on a high plane of nutrition during lactation has been shown to contain increased levels of protein and reduced levels of fat compared to ewes on a moderate plane of nutrition. For instance, when Ashton et al. (1964) gave ewes supplementary concentrates (750g/ewe/day) and hay ad libitum and Treacher (1971) fed an extra 7.5gDM/kg/day throughout lactation, higher fat and lower protein percentages were recorded, although significant only in the latter study. Similar results were reported by Poulton and Ashton (1972) when ewes were given a barley-rich diet. The immediate response to the introduction of the high-concentrate low-fibre diet was a marked decrease (e.g. from 4.2 to 3.2%) in the milk fat percentage. Within a week, however, milk fat content had increased to beyond its initial level (e.g. to 5.9%). It has been confirmed many times in the dairy cattle literature that feeding rations low in fibre depresses milk fat percentage (e.g. Foley et

al., 1972; McDonald et al., 1981).

The influence of dietary protein on the composition of ewe's milk has also been investigated. Both Cowan et al. (1981) and Flamant and Morand-Fehr (1982) found that crude protein levels in the diet affected neither fat nor protein content of the milk, while Whiting et al. (1952) and Gonzalez et al. (1982) found the percentage protein in milk to significantly increase with the inclusion of extra protein in the diet. Whiting et al. (1952) showed that ewes maintained on a ration containing 10.5% protein gave milk which, on a fat-free basis, was higher ($P < 0.01$) in protein than milk from ewes on a ration containing 7.3% protein.

Milk composition is also influenced by the dietary energy intake. For example, Annison and McDowell (1980) reported that increased energy intake in the cow, above the level required to maintain minimum solids-not-fat levels, usually raised the protein content of the milk.

As mentioned previously, detailed investigations of nutritional effects on milk production or composition were not considered within the scope of this thesis hence this aspect of the literature will not be considered in greater detail in this review.

EFFECT OF AGE

Few authors have considered the possible effects of ewe age on milk composition. Torres-Hernandez and Hohenboken (1979) reported no significant differences in milk composition between 3 and 4 year old ewes. Corbett (1968) found the milk fat content of 6 year old Merino ewes to be higher ($P < 0.05$) than that of 2 year old ewes, yet he concluded that there were insufficient data to determine the effect of

ewe age on milk composition. Working with Dorset ewes ranging in age from 1.5 to 8 years, Wohlt et al. (1981) showed ewe age had no effect on the nutrient composition of the milk. Halliday (1981) suggested that ewe age may influence the levels of immunoglobulins in the milk.

While the available data are not conclusive, there is strong evidence to suggest that ewe age may influence milk composition. Therefore, in the relevant statistical analyses that follow, ewe age was used as a covariate.

EFFECT OF STAGE OF LACTATION

It is widely accepted that the composition of milk varies over the course of lactation (e.g. Schmidt, 1971; Jenness, 1974; McDonald et al., 1981). In the ewe, fat, protein, and total solids show a similar pattern of change, all declining in early lactation, then gradually recovering to the approximate levels of early lactation (Barnicoat et al., 1949b; Corbett, 1968; Peart, Edwards and Donaldson, 1975). However, the minimum level of each constituent is reached at different stages of lactation. Peart et al. (1972) found that fat content reached a minimum at 4-5 weeks of lactation, whereas the minimum protein content was recorded at 2-3 weeks of lactation. Gardner and Hogue (1964) showed that percentage fat, protein and total solids were high at the beginning of lactation, declined to their lowest levels after 2-4 weeks, remained constant for a time, then rose with each successive week of lactation. Significant increases in these constituents after minimum levels were reached have also been reported by Ashton et al. (1964), Poulton and Ashton (1970), and Torres-Hernandez and Hohenboken (1970). In a study by

Wilson et al. (1971), the percentage fat^{had} increased by the tenth week of lactation; however, the percentage protein remained relatively constant, over lactation, a finding in agreement with that of Bouchard and Brisson (1969). Major differences between the similar studies of Poulton and Ashton (1970) and Bouchard and Brisson (1969) may be attributable to different dietary regimes of the ewes. In the former study, the ewes grazed "good spring pasture" supplemented with concentrates, while Bouchard and Brisson (1969) fed hay ad libitum plus concentrates. Based on the previous review of the effects of nutrition on milk composition (page 28), it is feasible that these differences in dietary protein and energy could produce the different results in protein concentration and lactation trends.

The percentage of ash also varies and significant increases in ash content as lactation advances have been reported (Ashton et al., 1964; Corbin and Whittier, 1965). Peart et al. (1972) showed ash levels to decline in early lactation, then rise for the remainder of lactation. In a later study, Peart, Edwards and Donaldson (1975) established no significant stage of lactation effect on ash.

The foregoing review has established that significant differences occur in milk yield and composition with such factors as genotype, nutrition, number of lambs suckled, and ewe age. The major aim of the experimental work which follows was to examine genetic (weight selection line) effects on lactation performance and thus every effort was made to equalize nutritional and litter size influences in the various experimental designs adopted. To further minimize the effects of variations in ewe age, age was adopted as a covariate in the statistical analyses whenever possible.

Fat, protein, total solids, and ash have been shown to be the major constituents determining the nutritional value of milk. These parameters were thus examined in Experiment 5 where genetic effects on milk composition were under study.

2.2 LAMB SURVIVAL

Early lamb survival has been the subject of substantial research in both Australia and New Zealand. Although reports of lamb mortality vary widely under certain conditions, 15-20% is accepted as an average (e.g. McFarlane, 1955; Dennis, 1974a; Dalton et al., 1980; McCutcheon^{et al.}, 1981). Heavy lamb losses occur at or within 7 days of birth (Moule, 1954; McFarlane, 1955; Hughes et al., 1964; Haughey, 1973a; Dennis, 1974a).

The following section briefly reviews the most frequently reported causes of lamb death and factors affecting survival.

2.2.1 CAUSES OF LAMB DEATH

Numerous field and laboratory investigations over the last 30 years have incriminated a number of specific causes of lamb death, acting singly or in combination. These causes may be separated into two categories: infectious and non-infectious. A variety of bacterial, protozoal, and viral agents responsible for pre- and post natal infections have been reported (Hughes et al., 1964; Watt, 1965; Plant et al., 1972). Total infectious causes accounted for 18% of lamb deaths in a large survey of flocks in Western Australia (Dennis, 1974a), but less than 8% in other surveys

(Alexander, 1984). The vast majority of lamb deaths are due to non-infectious causes. Researchers generally agree that dystocia, starvation, and exposure are the predominant non-infectious causes, although there is debate as to their relative importance. These topics have been adequately reviewed by Alexander (1984), McCutcheon et al. (1981), and Slee (1981).

DYSTOCIA

Dystocia, due to foeto-pelvic disproportion or malpresentation, has been well recognized as a cause of lamb death. Results from two investigations of large numbers of lambs found 19% (Dennis, 1974b) and 24% (McFarlane, 1955) of lamb deaths were due to dystocia. Breed differences in susceptibility to dystocia have also been documented. For example, under similar conditions, 10% of lamb mortality in Merinos and 36% in Dorsets was attributed to dystocia (George, 1975; 1976).

Haughey (1973a, 1973b, 1982) believes that birth injury is implicated in up to 70% of all lamb deaths, based on the hypothesis that vascular abnormalities in the central nervous system were the result of trauma and/or anoxia during a difficult or prolonged birth (Haughey, 1973a). With damage to the CNS, lambs had a poorer suckling drive and increased susceptibility to hypothermia, thus reducing their ability to cope with cold weather (Haughey, 1980; 1982). Therefore, it was suggested that "starvation-exposure complex" is merely a secondary cause of lamb mortality, the primary cause being damage to the CNS during birth (Haughey, 1973a; McCutcheon et al., 1981). However, Duff et al. (1982) found that CNS injury was a minor cause of starvation-exposure deaths, because

the injury was usually slight. Regardless of the controversy, problems of birth are clearly an important cause of mortality.

STARVATION

The reasons for failure to obtain adequate nutrition, apart from birth injury, include poor mothering ability (see page 36), competition with littermates, delayed onset of lactation due to undernutrition of the ewe (see page 16), and "accidental" separations of ewe and lamb (Alexander, 1980). Reports of lamb deaths due to starvation vary from 19% (McFarlane, 1955) to 46% (Dennis, 1974b). On post mortem, starvation is indicated by the depletion of brown fat.

EXPOSURE

Exposure as a primary cause of lamb death is difficult to assess because factors such as birth injury, starvation, low birthweight (see page 37), and fine hair coat (see page 35) may increase susceptibility of lambs to chilling. Exposure may become apparent when a number of lambs are found dead during or shortly after a period of inclement weather. On post mortem, lambs that have died of cold exposure show peripheral subcutaneous oedema, with minimal depletion of body reserves (Haughey, 1973c: et al., McCutcheon / 1981).

MINOR CAUSES

Other reported causes of lamb mortality are considered to be minor on a large scale, but some may be devastating to the individual producer. These include congenital malformations,

deficiencies of trace elements such as selenium, iodine and copper, Vitamin A deficiency, ingestion of poisonous plants, and predation (Hughes et al., 1964; Dennis, 1974b; Alexander, 1984).

2.2.2 FACTORS AFFECTING SURVIVAL

Factors influencing lamb survival may be divided into two broad categories, according to Moule (1954): intrinsic factors, such as birthcoat, birthweight, neonatal nutrition and mothering ability; and extrinsic factors, such as climatic conditions. Although many of these factors are interrelated, they are reviewed separately in this section.

BIRTHCOAT

Field studies with both Australian Merino (Obst and Evans, 1970) and Welsh Mountain lambs (Purser, 1967) have demonstrated an effect of birthcoat type on survival. Some lambs are born with a thick, heavy coat while others have a fine, curly coat. Fine coated Merino lambs had higher mortality than those with hairy coats when exposed to very cold weather, although these differences were minimized when the lambs were born in less severe environments. Among the Welsh Mountain lambs, those of the intermediate birthcoat type had lower mortality than lambs at either extreme of the range. Increased survival with increased thickness of birthcoat has also been shown by Alexander (1962a) and Slee (1981). Heritability of birthcoat is reportedly high (Purser, 1967), so selection for specific birthcoat types may be a simple method of improving the newborn lamb's resistance to cold stress.

NEONATAL NUTRITION

The type of placentation in sheep prevents the passage of maternal immunoglobulins across the placenta, and the newborn lamb is thus dependent on the antibodies passively received through the colostrum (Tizard, 1982). These immunoglobulins assist the newborn in combating infection until the immunological system of the newborn is established.

Early ingestion of colostrum is also important as a source of energy to maintain body temperature which is quickly dissipated due to the poor thermodynamic properties of the lamb (Peart, 1982). Studies have shown that the majority of lambs dying in the first few days failed to obtain milk (Alexander et al., 1959; Alexander and Peterson, 1961). In a cold environment, the importance of early postnatal nutrition is self evident, since the cold depletes the energy reserves by inducing an elevated metabolic rate which may exceed five times the resting level (Slee, 1981). However, Alexander and Williams (1966) showed that the sucking drive may be depressed in cold exposed lambs. A vicious cycle is thus set up where the lamb requires more energy to maintain body temperature but does not consume it due to the effects of the cold. Colostrum deprivation may therefore result in reduced performance and higher mortality.

MOTHERING ABILITY

The mothering ability of a ewe may be defined as the combination of the establishment of a postnatal maternal bond with her lamb and her ability to provide milk to her young. The state of the ewe's udder is thus an intrinsic factor affecting neonatal

survival (Moule, 1954). Shearer's cuts, blind teats, and mastitis are such factors that can reduce the lactation potential of the ewe sufficiently to jeopardize lamb survival. Compared to other breeds, Slee (1981) showed that post natal maternal bonding in Merinos was low and consequently lamb mortality was high. Maternal bonding is very important in twin bearing ewes. In a study of Merinos, Stevens et al. (1982) found that one half of twin bearing ewes became permanently separated from one twin due to the ewe moving on and leaving one lamb behind. Low vigor of one twin usually results in early separation from the ewe. The ewes appeared unconcerned if only followed by one lamb. The study concluded that the inability to keep twins together contributed to higher mortality in twins than singles in the same birthweight ranges. Mothering ability may also be influenced by parity of the ewe, as maternal behaviour has been reported extremely variable in maiden Merinos (Alexander and Peterson, 1961).

Although several workers have described neonatal maternal bonding, few have attempted to quantify it. In the research that follows, maternal bonding is quantitatively assessed and examined in relation to lamb survival.

BIRTHWEIGHT

Considerable importance has been attached to the role of birthweight as a factor in lamb survival because of the susceptibility of small lambs to starvation and exposure (Hight and Jury, 1970; Dalton et al., 1980). This is considered to be due to their higher ratio of surface area to volume (Alexander, 1974) and consequently, their rate of heat loss per unit body weight is

higher than for larger lambs. Smaller lambs may also be disadvantaged by lower levels of body reserves. The higher mortality in twin-born lambs reported by Purser and Young (1964) and Dalton et al. (1980) was attributed to lower birthweights of twin lambs compared to single lambs. Death from dystocia was rare in twins. Therefore, high mortality at low birthweight is mainly due to stillbirths and deaths within 14 days.

The chances of survival in single lambs have been shown to increase with birthweight (Smith, 1977) but only to a point, so there appears to be a range of birthweights over which lamb survival is maximal. McMillan (1983) reported an optimum range of 3.3-4.1kg for Romney lambs. In the larger lambs (>4.1 kg), there was high mortality at birth due to dystocia. These findings support earlier work by Fogarty (1971) with Dorset and Border Leicester sheep which revealed increased incidence of dystocia and higher lamb mortality as birthweight increased. In cases of high birthweight, dystocia results from foeto-pelvic disproportion. Simply stated, the lamb is too big for the size of the ewe's pelvis. Hence, the incidence of dystocia may be more closely associated with the dimensions of the lamb than with its weight, albeit the two are interrelated. The two widest parts of the lamb as it passes through the birth canal are the head and chest. In the experimental work that follows, head and chest circumference, as well as birthweight, are examined in relation to lamb survival.

The various factors influencing the birthweight of lambs have been reviewed by Alexander (1974), including sex of the lamb and nutrition of the ewe during pregnancy. On average, males tend to be heavier than females at birth. Birthweight is particularly

sensitive to variations in the supply of nutrients to the foetus, particularly in the last 6 weeks of gestation when foetal growth is the most rapid. Undernutrition during that period has been shown to decrease birthweight (Peart, 1967; Alexander, 1974). Thus, nutrition in late pregnancy can be manipulated to alter birthweight. Preferential feeding of ewes carrying multiple lambs may increase the birthweight of their lambs and hence reduce mortality. At the same time, restrictive feeding of single bearing ewes may decrease birthweight and reduce the risk of dystocia (Hinch et al., 1983).

CLIMATIC CONDITIONS

Climate may influence the survival of lambs directly, or indirectly through its effect on the plane of nutrition of the ewe during pregnancy. The lamb is most susceptible to environmental stresses during the neonatal period, and poor weather conditions at that time may result in heavy losses. In a study by Alexander et al. (1959), inclement weather was implicated in 22 of 25 deaths within 3 days of birth.

The three main climatic components directly affecting lamb survival are temperature, wind, and rain. In cold conditions, body heat is rapidly lost to the environment. To compensate, the lamb increases its rate of body heat production which results in rapid utilization and, unless the lamb suckles, rapid depletion of its limited body reserves (Alexander, 1962b). Thus, while the energy derived from the breakdown of body reserves may be sufficient to sustain the lamb for 3-5 days in a warm environment, survival time is markedly reduced in severe cold (McCutcheon, et al. 1981). Rain

can thoroughly wet a lamb's coat, thereby reducing its total insulative value and increasing the rate of body heat loss by surface evaporation (McCutcheon et al., 1981). Hence, lamb mortality has been found to increase in wet weather (Arnold and Morgan, 1975). Wind also affects lamb mortality by influencing the rate of heat loss by surface evaporation. Egan et al. (1972) concluded that the reduction of windspeed was important in reducing lamb losses.

The preceding section was not intended to exhaustively review the current literature, but rather to briefly establish the main constraints to lamb survival. Examination of the genetic (weight selection line) effects on lamb survival was a secondary aim of the experimental work which follows.