COMPARATIVE ASPECTS OF RESISTANCE TO BODY-COOLING IN NEWBORN LAMBS AND KIDS

A thesis presented in partial fulfillment
of the requirements for the degree of
Master of Agricultural Science
in Animal Science
at Massey University.

Sabine Müller

1989

ACKNOWLEDGEMENTS

I want to express my sincere thanks and appreciation to my supervisors, Dr. Stuart McCutcheon and Dr. George Wickham, for their valuable guidance, support and advise during this study.

I also like to thank Dr. Colin Holmes for his assistance with the calorimetric studies.

Special thanks is extended to Mrs. Sonja Hollway, who generously provided me with her pregnant does for Experiment 2.

I want to thank Mr. W.B. Parlane and Mr. Sam Peterson for their help and co-operation given to me during the experimental work.

I also want to thank Mrs. Janice Rumbal for her assistance in the hormone assays and Miss Margaret Scott for proofreading this manuscript.

Special thanks is extended to Mr. T. Inoue for his valuable assistance in the preparation of the figures in this manuscript.

The financial support of the Helen A. Akers, Johannes August Anderson, G.O. Anstiss and the D.J. McGowan Scholarships is gratefully acknowledged.

I want to thank all the post-graduate students and staff in the Department of Animal Science, for their friendship and support.

My sincere gratitude is extended to Dr. Stuart McCutcheon, for his understanding, patience and encouragement throughout this study.

Finally, special thanks are due to my parents for their love, help and encouragement and to my children, Felix and Eva Lena for keeping me sane throughout this exercise.

TABLE OF CONTENTS

Page

CHAPTER II: EXPERIMENTAL

COMPARATIVE ASPECTS OF RESISTANCE TO BODY-COOLING

IN NEWBORN LAMBS AND KIDS

CHAPTER III: GENERAL DISCUSSION

LIST OF TABLES

Page

LIST OF FIGURES

LIST OF ABBREVIATIONS

cm	centimeter
CNS	central nervous system
°C	degree centigrade
dl	decilitre
h	hour
IRT	initial rectal temperature
kg	kilogram
KJ	kilojoule
l	litre
m	meter
mg	milligram
ml	millilitre
mm	millimeter
ng	nanogram
PMI	prematernal interest
RDRT	rate of decline in rectal temperature
RT0	"zero-time" rectal temperature
s.e.	standard error of the mean
S/E	"Starvation-Exposure-Mismothering"-complex
sec	second
STP	standard temperature and pressure
T_3	triiodothyronine
T_4	thyroxine
W	Watt
WT	live weight

Levels of Statistical Significance

NS	not significant
+	$0.05 < p < 0.1$
*	$0.01 < p < 0.05$
**	$0.001 < p < 0.01$
***	$p < 0.001$

CHAPTER I

INTRODUCTION

CHAPTER I

INTRODUCTION

THE PROBLEM OF PERINATAL MORTALITY IN LAMBS AND KIDS

Fibre-producing goats are becoming an increasingly important species on New Zealand farms. There is a considerable lack of information about the physiology of goats, especially as it relates to the development of appropriate management strategies. For instance, goats are reputed to be more susceptible than sheep to cold, wet, windy conditions but comparisons between the species have not been reported. Newborn kids are thought to be very susceptible to cold-stress, but it is not clear whether this is a function of their low birth weight or some particular characteristic of the species (such as a low capacity for heat production) which leads to high mortality.

The problem of kid mortality is important from the viewpoints of both animal welfare and economic loss. The extent of kid losses in New Zealand has not been investigated, but industry sources suggest that kid mortality is high. In particular, deaths occur during inclement weather. It is expected that losses will increase with increasing goat numbers and the consequent reduction in management intensity.

Perinatal lamb mortality, defined as deaths occurring immediately before, at, or within 7 days of, birth has been recognised for many years as contributing to poor reproductive performance in New Zealand sheep flocks (Hight and Jury, 1970). Estimates of losses from birth to weaning range from 5% to 25% of all lambs born in New Zealand (Hight and Jury, 1970) and from 5% to 70% in individual Australian flocks (Alexander, 1985). Not only are the lambs themselves lost for the purposes for which they were intended (meat and/or wool production), but also the ewes produce less wool and require more feed than if they had not been pregnant. The results are lower stocking rates with in-lamb ewes and reduced selection intensity because fewer replacement animals are available (Hight and Jury, 1970).

Perinatal lamb mortality has a multiple causation including environmental, management, behavioural and disease components. There are many interactions between these and more than one factor can often be incriminated in the deaths of individual lambs.

1. Assessment of causes of perinatal lamb mortality

Perinatal mortality is readily assessed in intensive systems by counting living and dead lambs but, in extensive systems, accurate counting of dead lambs can be difficult or impossible (Alexander, 1985). Therefore, most mortality figures are given as estimates.

Two broad approaches have been used to assess the causes of lamb deaths. The autopsy approach has been used in large scale surveys in which dead lambs are collected and examined for evidence of prenatal death, predation, birth injury, breathing, walking, milk intake,fat depletion and for pathological conditions such as infection, goitre and white muscle disease (Alexander, 1985). During the last decade this approach has included examination of the extremities for evidence of oedema indicative of cold exposure, and of the central nervous system (CNS) for haemorrhages indicative of birth injury (Haughey, 1973 a, b). The autopsy approach provides a basis for classifying lambs according to the stage at which death occurred. Autopsy rarely provides evidence about the causes of starvation and provides little information about deaths from cold exposure (Alexander, 1985).

The other approach depends on direct observations of behaviour at lambing, together with measurements of temperature and weight changes of lambs. This approach is founded on a series of fundamental studies of the physiology of thermoregulation, energy expenditure and mother-young behaviour (Alexander, 1974 a, b, 1979, 1980). In recent years the two approaches have been used together.

2. Causes of perinatal lamb mortality

Most workers agree on the factors that contribute to lamb deaths, but there is still considerable controversy about their relative importance. Estimates show that 28% - 38% of all lamb deaths can be attributed to "starvation - exposure" (McFarlane, 1955; Hight and Jury, 1970), approximately 32% to dystocia, 12% to post-natal infection, 10% to pre-natal deaths and 4% to misadventure (Hight and Jury, 1970).

Both light and heavy lambs have higher mortality rates than lambs of average birthweight (Hight and Jury, 1970), although even lambs in the "optimum birth weight range" (3 - 5 kg) may still have mortality rates in excess of 10% (Hight and Jury, 1970; Dalton *et al.*, 1980).

2.1 Dystocia

Dystocia is one of the single most important causes of lamb mortality in New Zealand and may account for up to 30% of all lamb deaths (McFarlane, 1955; Hight and Jury, 1970). Dystocia may be defined as a parturition considered likely to result in injury to the lamb or ewe and is usually associated with a long and difficult parturition (McSporran, 1975). Deaths from dystocia occur during or immediately after parturition, due to foeto-pelvic disproportion or to malpresentation (McSporran, 1975).

Lambs dying of dystocia commonly exhibit parturient lesions of subcutaneous oedema of the head and neck and internal organ damage (McFarlane, 1965). Furthermore, Haughey (1973 a, b) reported the incidence of central nervous system (CNS) lesions to be almost 100% in these lambs. Haughey (1973 a, b) also claimed that birth injury was a major factor in subsequent neonatal deaths (e.g. those commonly assumed to be due to starvation/exposure). Other workers have disputed this claim and the issue remains controversial (Alexander et al., 1980; Duff et al., 1982). However, the results of Alexander et al. (1980) showed that CNS haemorrhage was associated with reduced cold resistance in lambs. Whether the CNS haemorrhage, or the associated hypoxia and acidaemia, are the direct cause of reduced cold resistance is unclear. Difficult birth often leads to maternal exhaustion and thus can interfere with normal maternal behaviour (Alexander, 1960). This in turn can precipitate death from starvation even in the absence of birth injury.

The incidence of dystocia is highly correlated with the mean birthweight of lambs (McSporran, 1975). Birthweights over 5.5 kg are generally associated with a high incidence of dystocia (Hight and Jury, 1969, 1970),especially in single lambs. Dystocia may increase at low birthweights, presumably because of lamb weakness, poor uterine contractions of the ewes and a slow birth process (Dalton et al., 1980).

Dystocia is generally a more important cause of death in single-born lambs than in twins (Dalton et al., 1980). In a study carried out by Hight and Jury (1970), 45% of single lambs died of dystocia compared to only 16% of twins. Similar differences in the incidence of dystocia between singles and twins have been found in other studies. Much of the birthrank effect on incidence of dystocia can be explained by differences in birth weight, singles being on average 1.0 to 1.5 kg heavier than twins (Hight and Jury, 1970). Birthrank may have an effect independent of birthweight such that twins dying of dystocia were found to be no heavier than average surviving singles. A possible explanation of this may be a higher incidence of malpresentation in twin lambs dying of dystocia (McSporran, 1977).

Male lambs show a higher incidence of dystocia because they tend to be heavier at birth (Dalton et al., 1980; Scales et al., 1986). Female survival rate is estimated to be 1% - 9% higher than that of males (Gunn and Robinson, 1963). However, the difference in birthweight between males and females is not as great as that between singles and twins (Hight and Jury, 1970).

2.2 Starvation - Exposure - Mismothering

The second largest single classification of lamb mortality in New Zealand is the "starvation - exposure - mismothering" complex (S/E), which may account for 28% to 38% of all lamb deaths (Hight and Jury, 1970). This is a very broad classification and, as a result, the most difficult to break down into its various components. The elements of starvation, mismothering and exposure can each operate to varying extents in S/E deaths and the influences of each are often superimposed on one another, making interpretation of "cause and effect" relationships difficult (Duff et al., 1982).

The major post-mortem characteristics of lambs dying of S/E are that they die between 1 and 3 days after birth, show evidence of activity (breathed and walked), and have extensive depletion of body reserves and a gut devoid of food (McFarlane, 1965). Alexander (1985) states that no reliable autopsy criterion exists which shows that death of an individual lamb has been due to cold-exposure. The peripheral oedema, or "cold injury" described by Haughey (1973 b) is not seen in the many lambs that die soon after birth in inclement weather (Alexander et al., 1980), although it is seen in lambs dying more slowly in bad weather after having suckled. Prolonged exposure seems to be necessary for the oedema to be severe. Likewise, a fall in body temperature in cold weather is not conclusive evidence that death has been due to cold-exposure, because lambs debilitated for other reasons, such as failure to suckle, show a fall in body temperature and are prone to "chill" during progressive fasting even in mild weather (Alexander, 1985). Consequently, diagnosis of cold-exposure as a cause of death is largely inferential, depending on: the association of increased mortality and declining body temperature with cold, wet, windy weather; the appearance at autopsy of significant numbers of lambs showing evidence of having suckled; and oedema of the extremities (Alexander, 1980).

In large groups of lambs that appear to have died from starvation, a minority of direct causes, such as congenital abnormalities or severe birth injury that prevent suckling, are detectable at autopsy (Alexander, 1985). In the great majority, the causes of starvation can be assessed only by observing the flock. Some starvation deaths are due to shearing injury to the udder, or mastitis, and to delayed lactogenesis associated with ill-health of the ewe or with inadequate nutrition (McCance and Alexander, 1959). Problems with parturition, as mentioned previously, also contribute to starvation by way of maternal exhaustion or inhibition of maternal behaviour (Alexander, 1960), or because suckling behaviour of the lamb is inhibited (Haughey, 1980).

A high incidence of S/E deaths amongst lambs of low birthweight has been reported in a number of studies (Purser and Young, 1964; Hight and Jury, 1970; Dalton et al., 1980). Twin and female lambs have a higher starvation-exposure mortality rate than single or male lambs (Purser and Young, 1964). The reduced survival ability of twins is almost certainly a result of their lower birthweights,since their survival is comparable to that of surviving singles when compared at a common birthweight (Dalton et al., 1980).Also Whatawhata work shows that if twins are born on a steep slope they frequently become separated at birth and only one may be reared. Conversely Eales et al.(1982) have suggested that birthrank may have an effect independent of birth weight.

2.3 Other causes of lamb mortality

Other causes of perinatal mortality include: lethal congenital malformations, which account on average for less than 1% of total losses; specific nutritional deficiencies with sporadic outbreaks, sometimes severe, occuring in fairly well defined geographical areas; a variety of infections (some acquired in utero, others acquired after birth); and predation and misadventure, together responsible for about 4% of all lamb deaths (Haughey, 1975).

These will not be further discussed here as they comprise, with rare exceptions, less than 20% of the total mortality (Hight and Jury, 1970; Haughey, 1975).

3. Possible causes of perinatal kid mortality

Published work on perinatal kid mortality is relatively difficult to obtain. The few established factors known to contribute will be reviewed here and inserted, where appropriate, into the general overview on lamb mortality.

Many scientists have reported that kid losses are highest at parturition and just after birth (Peaker, 1978; Adu et al., 1979; Chawla et al., 1982). In France, more than 50% of total kid losses occur at birth and 75% of all kid mortality occurs within 2 days post-partum (Mohrand-Fehr, 1984).

In goats low birth weight has been reported to be the most frequent cause of mortality in the period from birth to 2 days post-partum, because of a lack of maturity of light kids (Mohrand-Fehr, 1982). It has been suggested that immature animals are deficient in circulating cortisol, triiodothyronine (T_3) and thyroxine (T_4) (Cabello and Levieux, 1981). As will be described later, thyroid hormones play a prominent part in the thermoregulation process. At birth, the thermoregulatory capacity of low weight kids is reduced because fat reserves are more limited. Moreover, the thermal losses per kilogram of liveweight are higher in light kids than in heavy kids. Consequentely, low energy reserves decrease survival time of light kids when they are fasted and mortality rates increase markedly in difficult environmental conditions such as low temperature, wind or draughts (Mohrand-Fehr, 1987).

Weak kids first stand later than others. Their chance of being groomed by their dams and of suckling colostrum is reduced, which further decreases their cold-resistance and subsequent resistance to disease. This delay in rising and suckling does not increase linearly with decreasing newborn kid weight, but is reported to appear below a certain weight limit (about 3 kg birth weight for Alpine kids) (Mohrand-Fehr, 1987).

Kid losses are influenced by two additional factors, namely duration of gestation and litter size. In Alpine goats, a 4 day shorter duration of pregnancy increased the frequency of neonatal mortality by about three times and losses were about four times more frequent in triplet births than in twin births (Mohrand-Fehr, 1985).

Increasing litter size is associated with decreased kid viability, for two primary reasons. As litter size increases, birth weight of individual kids decreases. Furthermore, increased litter size strains the capacity of many non-dairy goat breeds to provide adequate colostrum for their offspring (Sherman, 1987).

Many investigators have looked at comparative mortality rates of male and female kids, but results vary to the point that no firm conclusions can be drawn (Sherman, 1987).

Unfortunately, the few studies on kid mortality originate to a large extent from France where the majority of goats are milking or meat types which are kept indoors to kid under close supervision. Accordingly, these results cannot be applied directly to New Zealand conditions, where fibre-producing goats kid outdoors, often with minimal supervision. Given the lower birth weights and the greater litter sizes in goats as compared to sheep, and considering the above-mentioned factors which influence neonatal lamb mortality, it seems reasonable to assume that, under New Zealand conditions, the majority of kid deaths are likely to be due to S/E rather than to difficult births or diseases.

4. Physiology of Starvation - Exposure - Mismothering deaths

4.1 The Starvation - Exposure - Mismothering - Syndrome

Almost all lambs will survive if given adequate obstetrical assistance, warmth and food (Alexander et al., 1959; Alexander and Petersen, 1961). This demonstrates that survival is seldom limited by some major hereditary fault and that failure of the dam to exhibit appropriate behaviour, or failure of the newborn lamb to respond appropriately to conditions of environmental stress, are the main causes of perinatal mortality.

At birth the lamb is delivered in a physiologically advanced state from the warm uterine environment (about 39°C) to a much colder external environment. The environmental temperature may vary from about 15°C down to 0°C or effectively below -10°C, if the cooling effects of wind and rain are taken into consideration. However, wet newborn lambs start losing body heat at "still-air" temperatures below 28°C (Haughey, 1975).

Immediately after birth the lamb is faced with increased energy demands for activities not required to the same degree (or at all) *in utero* (e.g.heat production, walking, suckling), as well as being deprived of the maternal nutrient supply via the placenta. Therefore, the ability to maintain a high metabolic rate, rapid establishment of a bond with the dam and successful suckling are critical for survival.

Initially the rectal temperature of the newborn lamb is higher than that of its dam. This difference is associated with the higher intra-uterine temperature of the ewe (Alexander and McCance, 1958). Immediately after birth a fall in rectal temperature is usually observed. It appears that the lower the environmental temperature at the time of parturition, the greater is the fall in rectal temperature and the greater the time required for rectal temperature to return to normal (Smith, 1961). Many lambs recover their body temperature within a few hours but, in others, the decline continues until their rectal temperature falls below 37°C (Alexander and McCance, 1958).

In order to maintain a stable deep body temperature and to combat the effects of a cold environment, the lamb reduces heat loss (through constricting blood flow to the extremities and through postural changes) and increases its heat production (through shivering and burning brown adipose tissue) (Alexander, 1962 a, b). Immediately after birth the lamb is forced to increase its rate of body heat production by up to fifteen times the foetal level, to compensate for body heat loss to the environment (Alexander 1962 b). However, this increase in heat production causes the lamb to deplete its limited reserves of energy. These are mainly in the form of lipids (60 - 70%) and glycogen (15%), the remainder being derived from protein catabolism (Alexander, 1974). The lamb's energy reserves amount to a mere 4000 KJ (Alexander, 1974 a). Metabolic rates of lambs range from about 72 KJ h^{-1} (20 W) at thermoneutrality to about 360 KJ h^{-1} (100 W), representing the maximum thermogenic effort, or about 180 KJ h^{-1} (50 W) representing the rate sustainable in the cold. Thus energy reserves may be exhausted after about 3 days in thermoneutral conditions and after about 10 hours or less in the cold (Alexander, 1962). Replenishment of energy reserves is therefore imperative if the lamb is to survive for longer periods than these.

The lamb is completely dependent on maternal milk supply for provision of metabolic substrates. However, its ability to establish and maintain successful suckling may be compromised by environmental stresses which lead to a decline in deep body temperature. Alexander and Williams (1966 a) demonstrated that the lamb's suckling reflex is markedly depressed when deep body temperature falls below 37°C so that even mild hypothermia, while in itself non-lethal, may predispose to death by starvation. In addition, Alexander and Williams (1966 a) demonstrated a possible effect of "discomfort" due to cold-exposure which, while apparently independent of the hypothermia effect, also decreases the vigour of the suckling drive. These effects are compatible with field observations that the average time from birth to first suckling is prolonged in lambs born in cold, windy conditions compared with those born in less severe environments (McBride, Arnold, Alexander and Lynch, 1967). Thus cold-exposure can accelerate death by starvation as well as cause acute hypothermia.

Alexander and Williams (1966 a) also found that early success in teat-seaking activity was important since the drive to suckle declines with age. If successful suckling is not established, and the lamb's body reserves are thus not replenished, the capacity for heat production declines and rectal temperature falls. This in turn accelerates the lamb's susceptibility to cold-stress, deep body temperature falls even further, and the lamb may die at body temperatures below 30°C (Alexander and McCance, 1958).

According to Eales et al. (1982) there are two ages at which hypothermia is most likely to occur. In the first period, from birth to five hours post-partum, the major cause of hypothermia is excessive heat loss, presumably related to exposure of the wet newborn lamb to inclement climatic conditions. Some lambs become hypothermic because of depressed heat production related either to severe hypoxia during birth or to immaturity. Depletion of energy reserves is not a characteristic of lambs becoming hypothermic during this period. Hypothermia in the second period, from 12 to 36 hours post-partum, is associated with starvation, depleted energy reserves and a low rate of heat production.

4.2 Factors affecting the lamb's ability to suckle

There are many reasons for failure of the lamb to suckle successfully, including failure of the ewe to bond with her lamb(s), accidental separations after bonding (Alexander, 1980), udder defects such as shearing injury or mastitis (Quinlivan, 1968), delayed lactogenesis usually of nutritional origin (McCance and Alexander, 1959), competition with litter mates, birth problems that affect behaviour of the ewe and/or the lamb, congenital abnormalities, severe birth injury and cold-stress (Alexander,1974).

4.2.1 Maternal behaviour

The essential feature of maternal behaviour is the rapid development by the mother of a bond with her young, to the exclusion of other young. Various aberrant behaviour patterns of ewes can hinder this and so negatively affect lamb survival. These include: limited grooming ability, failure to co-operate with suckling attempts (butting and rotating away from the approach of the lamb, as often occurs in young and inexperienced ewes), preferences towards litter-members, rejection of offspring, desertion and premature maternal interest (PMI) (Holmes, 1975).

Of these desertion is associated with prolonged parturition, high birth weight of lambs and excessive body condition of the ewe, these three factors being interrelated. Undernourished ewes are frequently exhausted by parturition and remain recumbent for some time; the lamb sometimes wanders away and becomes lost before the ewe can get to her feet (Alexander, 1964). Exhaustion and injury can prolong the establishment of the essential ewe-lamb relationship and adversely affect the lamb's teat-seaking activity. Bonding of ewe and lamb(s) is assisted by grooming(e.g.licking of the lamb by the ewe) and through co-operation with suckling attempts of lamb(s) (Alexander et al., 1983 a).

Pre-lambing maternal interest often leads to mismothering of lambs born to other ewes (Welch and Kilgour, 1970). Because the newborn lamb is a source of attraction to ewes nearing or just completing parturition, and the ewe and her lamb(s) are unable to discriminate each other from other ewes and their offspring, problems of lamb-stealing and desertion arise.

Aberrant behaviour which leads to delays in establishing the vital ewe-lamb bond and delays or prevents successful suckling, will increase the susceptibility of the lamb to the influences of cold and starvation. This may in turn have an adverse effect on lamb behaviour, thus creating a vicious circle (Duff, 1981).

4.2.2 Central nervous system injury

Haughey (1973 b ; 1978) has suggested that the starvation - exposure syndrome is merely a secondary cause of lamb mortality, the primary cause being damage to the lamb's central nervous system (CNS) sustained during the birth process. In lambs which survive the birth process, the primary effect of CNS damage is apparently a depression of the suckling drive. Haughey (1975) states that this effect is more pronounced under conditions of cold-stress.

Other workers (Alexander et al., 1980; Duff et al., 1982) have disputed the finding of Haughey (1973 a, 1975) that approximately 60% of lambs assigned to the starvation-exposure mortality class have CNS lesions. Duff et al. (1982), in a New Zealand study, found that only 34% of lambs assigned to the starvation-exposure classification exhibited CNS lesions and that severe lesions were rarely seen in this group. The extent to which CNS injury is an important determinant of starvation-exposure mortality therefore remains controversial and warrants further investigation.

4.2.3 Cold - stress

As mentioned above, cold-stress affects the lamb in two ways. First, it forces the lamb to increase its metabolic rate and thus to more rapidly utilise its limited energy reserves. If these reserves are not replenished deep body temperature falls. Second, cold-stress may then prevent the replenishment of these reserves by reducing the lamb's mobility and inhibiting the suckling drive, which in turn can cause an adverse effect on maternal behaviour. Thus, as a result of cold-stress, the lamb may enter a vicious circle of falling heat production, falling deep body temperature, supressed suckling drive, starvation and/or mismothering. The ability of the newborn lamb to maintain deep body temperature above 37°C is therefore critical for its survival.

5. Factors affecting the lamb's susceptibility to hypothermia

5.1 Heat production

Since newborn lambs have a low capacity for body heat storage (Alexander, 1961), one of the main ways in which the lamb can combat the effects of cold is to increase its heat production or metabolic rate. Metabolic rate may be classified into two categories: "Basal" metabolic rate (the rate of metabolism recorded at rest under thermoneutral conditions) and "Summit" metabolic rate (maximum sustainable metabolic rate achieved in response to acute cold-exposure).

Thermoneutrality of the dry newborn lamb is in the region of 25°-30°C, where metabolic heat production is about 60-70 W m^{-2} (Alexander, 1979).

5.1.1 Level of summit metabolism

The level of summit metabolism attained by the newborn lamb is an important determinant of neonatal survival since it provides the limit to which body heat loss (per unit body weight) may increase before hypothermia occurs.

The maximum level of metabolism which lambs can achieve in response to cold within the first days of life is given by Alexander(1974) as 20 W kg^{-1} (28 W $kg^{-0.75}$) irrespective of the weight of the lamb. In normal lambs from adequately fed ewes, summit metabolism, which is about five times the basal rate, may be achieved within minutes of birth (Alexander, 1974).

Exposure of newborn lambs to extreme cold causes an increase in metabolic rate to three or four times the minimum resting level of metabolism (Alexander, 1962). This increase results from both shivering thermogenesis in skeletal muscle and non-shivering thermogenesis, apparently in brown adipose tissue. Shivering and non-shivering thermogenesis together contribute to the summit metabolic response of lambs less than one week old (Alexander and Williams, 1968).

In newborn lambs all of the adipose tissue appears to be of the brown variety but it is gradually replaced by white adipose tissue in the first weeks of life (Gemmel et al., 1972). This change is accompanied by, and may be responsible for, a decline in the level of summit metabolism per unit bodyweight attained by the lamb as it ages (Alexander, 1962 b). Dissection of newborn lambs of several breeds has shown that brown adipose tissue constitutes about 1.5% of the body weight, with the largest amount being in the abdominal and cervical regions. These are the principal sites of the non-shivering thermogenesis that has been estimated to contribute about 33% of the maximum metabolic response to cold (Alexander and Bell, 1975).

The balance of the maximum metabolic response to cold is due to the effects of shivering. Shivering thermogenesis occurs in the striated muscles of the body (Alexander and Williams, 1968). Normally shivering becomes obvious only under conditions of extreme cold, which has lead Alexander (1975) to suggest that, in the lamb, shivering may not be employed until non-shivering thermogenesis is approaching its full potential. However, since striated muscle may respond to increased requirements for body heat production simply by increasing muscle tone, "shivering" thermogenesis may occur even when shivering is not observed.

Subjecting lambs to environmental conditions which evoke a summit response to heat production results in a number of metabolic changes. These include the elevation of plasma concentrations of glucose, free fatty acids, glycerol and lactate (Alexander, 1962 b; Alexander, Mills and Scott, 1968; Alexander, Bell and Hayes, 1972). Similar effects are observed in lambs exposed to less extreme cold (Alexander and Mills, 1968). The increases in the plasma levels of glucose, free fatty acids and lactate caused by cold stress are mimicked by the infusion of catecholamines into lambs under thermoneutral conditions and may be prevented in lambs exposed to cold stress by the use of adrenergic blocking drugs (Alexander et al., 1968).

Other changes which accompany induction of a summit response in metabolism include the elevation of cardiac output, depth of respiration and blood pressure; disturbance of the blood acid-base status and a redistribution of blood flow in favour of the thermogenic tissues (Alexander and Williams, 1970; Alexander, Bell and Hales, 1972 , 1973).

Feeding is of immediate survival benefit to the newborn lamb. Eales and Small (1981) found an increase of nearly 20% in summit metabolic rate in fed lambs as opposed to unfed lambs, which would result in a reduction of the lower temperature survival limit of the lambs by approximately 10°C (Alexander, 1962 a). However, there is little published information on substrate utilization in newborn lambs. Protein does not seem to be a significant energy substrate (Alexander, 1962; Eales and Small, 1981). It appears that lipid utilization is quantitatively more important than carbohydrate utilization (Eales and Small, 1985). However, Eales and Small (1985) suggest that the newborn lamb has a greater dependence on carbohydrate as a substrate for heat production than does the adult sheep which can depend almost entirely on lipid (Bennett, 1972). A restricted ability to utilize relatively abundant lipid reserves (2-3% of body weight; Alexander and Bell, 1975) and a dependency on relatively sparse body carbohydrate reserves (1% of body weight; Shelley, 1960) would appear to severely limit the newborn lamb's ability to maintain its body temperature.

The increase in metabolic rate from basal to summit metabolism is positively correlated with the associated increases in plasma concentrations of glucose, glycerol, free fatty acids and the blood concentrations of lactate (Eales and Small, 1980). This suggests not only that plasma catecholamine concentrations increase during summit metabolism but also that the increase in metabolic rate is related to the increase in plasma catecholamine concentration and thus to the level of sympathetic nervous activity (Eales and Small, 1980).

Other studies have suggested that summit metabolism may be limited by the supply of oxygen to the thermogenic tissues, since summit metabolic rate has been shown to be significantly correlated with such parameters as cardiac output, heart rate and respiratory frequency (Alexander and Bell, 1975 a). Alexander and Williams (1970 b) demonstrated that increasing the oxygen content of air inspired by lambs resulted in an increased level of summit metabolism in some lambs and an improved ability to maintain summit metabolism in others. These effects tended to be reversed under conditions of hypoxia. Severe hypoxia may result in depressed heat production by up to 66% (Eales and Small, 1980, 1985) and immaturity is commonly associated with depressed heat production capacity (Dawes and Pary, 1965).

The thyroid gland is highly significant in influencing metabolic rate (Slee, 1978), but little attention has been given to the role of thyroid hormones in the response of newborn lambs to cold stress (Alexander, 1970). It is generally assumed that thyroid function plays a greater part in adaption to a prolonged cold exposure than in short term thermoregulation. However, it has been shown that triiodothyronine (T_3) administration is able to increase heat production significantly in the newborn lamb within one hour of administration (Andrews, Lynch and Moore, 1979). Cabello (1983) suggested that the thyroid hormones influence short-term thermogenesis in the newborn lamb. He found positive relationships between rectal temperature and plasma T_3 concentrations at 30 minutes post-partum (spontaneous neonatal cooling) and during neonatal exposure to cold. In the latter instance lambs dying of hypothermia did not show any evidence of the thyroid hyperactivity observed in all other animals. Klein, Reviczki and Padbury (1984) have reported that T_3 administration to the ovine foetus enhances the norephinephrine stimulation of oxygen consumption by adipose tissue. Therefore, the thyroid hormones could affect neonatal non-shivering thermogenesis by altering the lipolytic responsiveness to catecholamines. Caple and Nugent (1982) subjected newborn lambs to cold stress in a progressively cooled waterbath and observed a significant positive relationship between plasma T_4 concentration and the time taken for the rectal temperature of lambs to decrease to 35°C.

Newborn lambs have higher plasma thyroxine concentrations than their mothers, if the ewes have adequate iodine nutrition. Lambs born with goitre, due to iodine deficiency, may have plasma thyroxine (T_4) levels lower than those of their mothers and are particularly susceptible to cold stress (Caple and Nugent, 1982).

5.1.2 Rate of attainment and maintenance of summit metabolism

Rapid attainment of a high level of summit metabolism immediately after birth greatly enhances the lamb's chances of survival. Little is known about the factors affecting the rate at which summit metabolism is attained although Alexander (1962 b) has commented that poor pre-natal nutrition of the lamb appears to lead to a slow attainment of high metabolic rates immediately after birth. The final level of summit metabolism achieved is, however, independent of pre-natal nutrition.

Many of the factors which influence the lamb's ability to maintain a high level of summit metabolism have already been mentioned above. To summarize, Alexander (1962 b) has reported that declining summit metabolism (per unit body weight) may be associated with: falling deep body temperature (below 36°C), increasing lamb age, and with prolonged starvation.

5.2 Heat loss

5.2.1 Birthcoat characteristics

The heat loss from a lamb depends on its thermal insulation as well as on the environment. Differences in the thermal insulation provided by different types of birthcoat have been observed. Lambs with long hairy coats can withstand cold temperatures better than lambs with short coats. Resistance to cold stress increases with coat depth (McCutcheon et al., 1983 b). Wetting of the coat reduces this advantage considerably (Alexander, 1958). McCutcheon (1983 a) stated that wetness was the single most important factor determining whether or not lambs became hypothermic. Wet lambs suffered a reduction in coat insulation, principally as a result of reduced coat depth, but this was a small effect compared with the increase in evaporative heat loss which occured as a result of wetting.

In a study by Samson and Slee (1981) it was found that the cold resistance of lambs chilled in a water bath was related not to the coat depth but to the weight of wool per unit area of skin. Presumably coat insulation affected cold resistance by trapping air between the water and the skin surface, or by preserving a warmer layer of water next to the skin, during the early stages of cooling. The effectiveness of this type of insulation was apparently reflected more by coat weight than by coat depth.

Small lambs tend to have shorter and sparser coats than large lambs, owing largely to failure of 'secondary' skin follicles to mature and produce wool fibres. The thermal insulation of the coat of small lambs is therefore low so that, per unit of surface area, small lambs tend to exchange heat more rapidly with the environment than large lambs. In a study by McCutcheon et al. (1983 b) twins exhibited lower coat depths (by 1.1mm at each measurement site) than singles.

Observations by Alexander (1982 a) suggest that the birth coats of lambs which have dried, but are then re-wetted, tend to trap air better than the coats of lambs still wet with amniotic fluid. The drying of the coat immediately after birth may therefore have important consequences for its insulative value.

5.2.2 Peripheral vasomotor control

The rate of blood flow from the deep body to the peripheral tissues influences the rate of heat loss because blood flow results in convective heat transfer. The thermal effects of changes in cutaneous blood flow are seen most readily in the extremities of the body. Sophisticated techniques have been used to measure the rates of blood flow through different parts of the body (Alexander et al., 1973). The most significant results in animals exposed to cold conditions were: large increases in rates of heat production, total cardiac output and heart rate; large decreases in cutaneous blood flow over the whole body, large increases in blood flow to brown fat depots (in newborn lambs); and a general decrease in blood flow to visceral organs.

Peripheral vasoconstriction is widely regarded as being an "all-or-none" phenomenon which is activated prior to the onset of cold-induced thermogenesis in environments just cooler than the lower critical temperature (Alexander, 1961, 1962 a). However, Webster and Johnson (1968) reported that cold-stressed sheep may show increased respiration rates (presumably associated with increased thermogenesis) before vasoconstriction has been fully employed. Open faced sheep have been shown to be more productive than sheep with woolly faces, especially in characters concerned with growth and reproduction (Cockrem and Rae, 1966). These differences may be associated with poorer ability of woolly-faced sheep to control peripheral blood flow and therefore body temperature (Cockrem, 1967). Cockrem and Rae (1966) also found that the mortality of lambs born to open-faced ewes was lower than among the progeny of woolly-faced ewes.

In a study with Romney and Drysdale-cross lambs, McCutcheon et al. (1983 a) showed that wetness and air-speed were major determinants of variation in hind-limb skin temperature. Whereas wet lambs were able to minimize the skin temperature - air temperature gradient, dry Romney-type lambs generally failed to do so. As a result their skin temperatures were higher than those of Merino lambs examined under the same conditions (McCutcheon et al., 1983 a). This suggests that an effect of breed type was partially involved (ie. that the ability to reduce vasoconstriction in response to cold may have a genetic basis).

5.3 Surface area to volume considerations

As mentioned before, the maximum heat production of a lamb depends on a number of variables, but particularly on birth weight. As shown by Alexander (1985) summit metabolism (per kilogramm body weight) tends to be constant over a wide range of birth weights. Total summit heat production is therefore directly related to birth weight. However, surface area, which determines total heat loss, is proportional to metabolic body weight (ie.body weight raised to a power of about 0.75). It follows that summit metabolism per unit of surface area is lower in small than in large lambs. This explains the extreme susceptibility of small lambs to inclement weather.

6. Purpose and scope of the investigation

The New Zealand goat industry is expanding and neonatal kid deaths have been identified as a major problem, but little is known about their causes. By contrast, the causes of lamb losses have been well studied. One third of all lamb deaths are due to dystocia (in particular large and/or single lambs are affected) and one third can be attributed to the starvation-exposure-classification (especially small and/or twin lambs). Starvation-exposure deaths, in the absence of poor maternal behaviour, are primarily a result of the inability of some lambs to maintain their deep body temperature in a cold environment. This may in turn reflect a poor ability to achieve and maintain a high summit metabolic rate and limited body insulation (via the birth coat and through control of peripheral vasoconstriction).

Given the higher litter sizes and low birth weights of goats, it is likely that starvation-exposure is a major contributor to neonatal mortality in this species. The objective of this study was therefore to compare responses to cold in newborn lambs and kids with a view to determining similarities and differences in factors affecting their ability to maintain deep body temperature. The study was concerned primarily with the effects of metabolic rate, birth coat characters and body size as determinants of resistance to hypothermia in the two species.