Chapter 1 Introduction

Reproductive success is essential to any animal industry and is likely to have been an issue ever since humans first began animal husbandry. Historically, Merino sheep have been selected for wool production with little attention given to reproductive ability. This has resulted in the Merino breed being generally regarded as poor reproductively (Hatcher *et al.* 2010b).

A recent shift the structure of the Australian national sheep flock driven by low financial returns for wool and rising returns for prime lamb has resulted in a decrease in wool only enterprises and an increase in duel fibre and sheep meat production (Hassall & Associates, 2006). This structural shift has resulted in an increase in the number of lambs slaughtered despite the overall sheep population falling significantly. This has focused the industries attention on reproduction rates especially that of Merino ewes which represent 85% of total ewes (Curtis, 2009).

Over the past 40 years there has only been a 5% increase in weaning rates achieved in Australia (Hatcher *et al.* 2010). This increase is poor and lamb mortality to weaning has been identified as the main cause of this disappointing increase (Kleemann and Walker 2005). The causes of lamb mortality have been widely studied and identified (Safford and Hoversland, 1960, Hight and Jury, 1970, Hinch *et al*. 1986, Jordan and le Feuvre, 1989, Haughey, 1991). In 1965 McFarlane first suggested that overall lamb mortality could be reduced by selecting against individual causes of deaths. For effective genetic selection to occur, individuals containing superior genes must first be identified. This identification of genetically superior individuals for lamb survival has proven to be a difficult task.

In Chapter 2, we begin by reviewing published literature on lamb mortality. In Chapter 3, the first of 2 experimental chapters, we present heritabilities for lamb autopsy categories and also for a number of potential survival indicator traits. In Chapter 4, we present genetic correlations between autopsy categories and between autopsy categories and both potential indicator traits and the production traits yearling weight and greasy fleece

weight. Chapter 5 attempts to bring these results together and discuss the implications arising from the results and their usefulness in reducing overall lamb mortality.

Chapter 2 Literature review

2.1 Introduction

In 2009 the size of the Australian national sheep flock had fallen to a low of just 68.1 million animals (ABARES). In addition the structure of the flock had also significantly altered with ewes now representing 70% of the flock of which 85% were pure breed merinos (Curtis 2009) compared to 1990 when ewes represented approximately 50% of the flock and wethers represented 30%. This shift in flock structure to a ewe dominant flock is associated with an increase in prime lamb production. This restructuring of the industry has meant that the number of lambs slaughtered has increased despite the overall sheep population falling significantly (Curtis 2009).

The low number of animals in the national sheep flock has coincided with record high prices achieved for both sheep and sheep meat. These two factors (high value and low numbers) have combined and focused attention on the relatively low reproductive efficiency of the Australian sheep flock, particularly of Merinos (Hatcher *et al.* 2010). The average marking percentage among Australian specialist sheep producer flocks was 76.9 per 100 ewes joined between 1997 and 2009 (Hatcher *et al.* 2010). The marking percentage increase of approximately five percent over the past 40 years is somewhat surprising (Hatcher *et al.* 2010) given the economic importance that increased reproduction success plays within both sheep meat and wool production enterprises. The major identified factor limiting an increase in marking percentage over this period is lamb loss defined as preweaning lamb mortality (Kleemann and Walker 2005).

Lamb loss is a difficult to assess trait as mortality identification usually relies on observed counts of lamb carcasses which are commonly removed or affected by predation. It is generally accepted that loss rates are approximately in the order of between 20 and 30% although published lamb loss rates range from a low of 4% to a high of 72% (Hatcher *et al.* 2010). Based on discrepancies between ultrasound pregnancy scanning and marking percentages it is estimated that in Merino sheep reproductive wastage to weaning commonly exceeds 30% (Kleemann and Walker, 2005).

Another emerging issue associated with lamb loss is that of animal welfare. It has been argued that a high neonatal lamb mortality rate in itself is an indicator of poor animal welfare (Dwyer, 2008) and images of dead or dying lambs would be powerful tools if used negatively by animal welfare groups. Such images would be likely to provoke powerful negative emotional responses among consumers of sheep products and could conceivably result in considerable damage to the sheep industry's public image. Evidence of industry efforts to reduce losses and hence increase animal welfare in this field could then be used as a potential defence against such claims.

2.2 Lamb survival

Lamb survival has been an issue most likely ever since humans began sheep husbandry. There are obvious disadvantages to animal production industries whenever reproduction failure occurs. Lamb losses represent wasted farm resources and are a constraint to efficient production as well as a potential source of animal welfare concern as mentioned. The losses negatively affect farm profits directly through reduced sales but importantly they also negatively affect future production through a reduction in potential selection intensities and subsequent compounding losses in potential genetic gain.

Because of the economic importance of lamb loss to the Australian sheep industry, estimated at $50-100 million dollars annually (Brien *et al.* 2010, King *et al*. 2008) and worlds sheep industries this topic has been expansively studied and reviewed. Australian studies extend back at least to the 1950s (Alexander and Peterson, 1961) and numerous causes of lamb losses have been put forward.

Causes of lamb loss can be broadly categorised as environmental, nutritional and genetic. They relate to the birth process, neonatal adaption to postnatal life and functional disorders, infectious disease or predation (Dwyer, 2008). The ability of a lamb to survive is determined by its own genes and behaviour, its dam's genes, behaviour and experience, its physiology, the environment it experiences and on-farm management practices (Everett-Hinks and Dodds, 2008).

2.3 Management strategies

Many management strategies have been proposed and adopted to reduce lamb losses. Largely these have been effective however even under optimal management it appears that an underlying core loss of lambs still occurs (Alexander 1984).

A 2008 economic analysis of several management strategies to improve reproductive performance (McEachern and Sackett, 2008) concluded that, of the management interventions investigated, only feeding to maintain live weight for increased conception and lamb survival rates was considered to have an economic benefit. Management options that were not cost effective included; supplementary feeding to increase live weight pre joining, feeding in late pregnancy to improve survival and the preferential use of shelter belts for twin lambing ewes. The analyses in this study focused on per hectare and per DSE returns and investigated self-replacing merino, dual purpose sheep and prime lamb enterprises in pastoral, sheep cereal and high rainfall environments. This analysis did not consider other indirect benefits from shelter belt establishment.

Economic benefits from improving reproductive performance are dependent upon stocking rate, the value of products and the timing of lambing in relation to the feed limiting time of the year. Economic increases were larger in flocks where a higher proportion of income was derived from sheep sales than they were in self replacing wool enterprises (McEachern and Sackett, 2008) which are important given the changing nature of sheep production within Australia. Model outcomes implied that an increase in reproductive performance resulted in financial benefits coming from an increased stocking rate in situations where the farm is understocked or from an altered flock structure in cases where the farm was fully stocked.

Management practices that increase the time spent at the birth site by the ewe after parturition and ensure that the appropriate interactions occur between the ewe and her lamb at the birth site can enhance ewe-lamb bonding and also lamb survival (Nowak, 1996). Nowak (1996) observed an increased bonding between twin lambs and their dam when dams were able to spend at least 6 hours at the birth site. It has been observed that

ewes will remain longer at birth sites when provided with adequate pasture quality and shelter (Putu *et al.* 1998).

Ideally, to increase lamb survival, ewes carrying multiple lambs should be identified as early as possible and preferentially fed to ensure that body condition is maintained throughout pregnancy. These ewes should also be moved to locations protected from cold climatic conditions during late pregnancy and parturition. Moving pre-parturition ewes however can also be detrimental to lamb survival as ewes unaccustomed to the presence of humans can become stressed or fearful. Stress and fear or any disturbances during lambing have been shown to cause involuntary suppression of uterine contractions and increase the risk of dystocia (Dwyer, 2008b) although there are other studies which show that ewes more accustomed to human supervision can benefit from this type of human intervention during lambing (Waterhouse, 1996).

Hatcher *et al.* (2010) proposes that there are three options available to commercial sheep breeders that can improve reproductive efficiency. These are; the use of Australian Sheep Breeding Values (ASBVs) to select rams who will breed daughters with the ability to wean more lambs, a combination of identifying and retaining the best performing ewes on a net reproductive rate basis, and management activities that ensure correct nutrition and minimise exposure of newborn lambs to adverse conditions. These three categories can be broadly broken down into, genetic improvement, phenotypic selection and management activities.

 Among the strategies recommended to reduce lamb mortality rates the genetic selection for superior survival rates is particularly desirable. This is because breeding for better survival characteristics offers a permanent low-cost solution when compared with environmental improvements such as enhanced nutrition and the provision of adequate shelter (Slee *et al.* 1991). In addition the genetic selection for increased survival will allow higher selection intensity in selecting replacement ewes, and hence faster genetic improvement over time (McEachern and Sackett 2008).

2.4 Lamb survival and welfare

Animal welfare issues are becoming increasingly important to animal production industries and any action that decreases lamb mortality rates should not only increase productivity returns but also reduce animal welfare issues and result in decreased pressure on sheep breeders from animal welfare lobbyists. Dwyer (2008c) argues that a high neonatal lamb mortality rate is in itself an unambiguous indicator of poor animal welfare (although he does not define exactly what a high neonatal lamb mortality rate is).

It is generally agreed that sentience and consciousness are prerequisites for animal suffering and that consciousness appears for the first time only after birth (Mellor and Diesch, 2006). Mellor and Diesch (2006) contend that stillborn lambs do not represent an animal welfare problem as there are several progesterone metabolites and a placental inhibitor that act to inhibit consciousness in *in-utero* lambs. Mellor and Diesch (2006) conclude that suffering can only occur in the newborn after the onset of breathing that oxygenates an animal's organs to a point sufficient to induce consciousness. Dwyer (2008c) proposes that the birth of a dead lamb may cause anxiety and frustration in the ewe although Hatcher *et al.* (2010) postulate that ewes who do not receive a suckling stimulus quickly lose their maternal drive thereby minimising suffering.

It is assumed that once consciousness has been attained the newborn lamb will be subjected to the same welfare problems as are adult animals (Dwyer, 2008c). These are thought to be breathlessness, hypothermia, hunger, anxiety, sickness and pain (Mellor and Stafford, 2004). Reducing the incidence of these welfare problems would be beneficial from an animal welfare point of view as well as from a production perspective, especially if the reduction also increased lamb survival rates.

2.5 Ewe contribution to lamb survival

Parturition in sheep is characterised by an intensive period of interaction between the ewe and her offspring (Dwyer, 2008b). In general ewes are either indifferent or hostile toward neonatal lambs however this behaviour alters after birth. After parturition ewes generally spend considerable time grooming their newborn while emitting frequent low pitched

vocalisations. Ewes generally also stand still to facilitate access to the udder by the lamb (Dwyer, 2008b). By grooming the newborn lamb the ewe facilitates a bond between the animals while also drying and stimulating activity and respiration in the lamb by helping to clear placental membranes from the nose and mouth of the lamb. Amniotic fluids present in the lamb's coat have been shown to increase the amount of grooming, the frequency of low pitched bleats and ewe acceptance of the lamb to access the udder (Dwyer, 2008b). Classically, during this postpartum period the lamb exhibits behaviours directed toward standing, locating the udder and suckling. Olfactory cues from the nipple region of the udder assist lambs in locating the ewe's udder region (Vince, 1993). Experienced ewes arch their back and stand still with their legs wide apart to facilitate the lamb in finding and accessing the udder (Dwyer, 2008b).

Maternal behaviour can be scored on a 5-point scale based on the distance that the ewe retreats from her lambs during tagging. Maternal behaviour score methods are described in detail by O'Connor *et al.* (1985). This score shows variation within and between breeds and has been shown to be related to both lamb survival rates and weaning weights (O'Connor *et al.* 1985). In general ewes with lower maternal behavioural scores have lower lamb survival percentages. Everett-Hinks *et al.* (2005) found that ewes aged 6 years or older have better maternal behaviour scores than did younger ewes, although after adjustment for the total litter weight at birth it was found that litter survival to 3 days was higher for small litter sizes and younger ewes.

Primiparous ewes tend to have longer labour bouts than older more experienced ewes and also are slower to initiate grooming their lambs (Dwyer and Lawrence, 1998). In addition primiparous ewes, especially Merinos, also tend to be more fearful of the lamb, more aggressive toward the lamb and can completely fail to show maternal behaviour toward their lamb and even abandon it (Dwyer and Lawrence, 1998). A comparison of care-giving behaviour across parities by Dwyer and Lawrence (2000) revealed that ewes are consistent in their grooming, rejection and lamb avoidance behaviours although aggressive behaviours were not repeatable. This result indicates that the behaviour of the ewe during her first parity is indicative of her behaviour in following pregnancies and supports the phenotypic selection strategy advocated by Hatcher *et al.* (2010). Everett-Hinks *et al.*

(2005) also report that ewes with higher body condition scores also had better maternal behaviour scores.

Maternal behaviour scores were found to be lowly heritable 0.13 by Lambe *et al.* (2001) in a population of Scottish Blackface ewes and by Everett-Hinks *et al.* (2005) in a study of a compilation of various breeds. These low heritabilities are possibly a consequence of the trait being based on the behaviour of both the ewe and lamb and the fact that ewe behaviour alters according to parity number and familiarity with human handling.

Selective breeding for ewe rearing performance defined as the ratio of lambs weaned to lambs born has been documented to result in a reduction in lamb mortality, a reduction in the time spent by the lamb between standing and suckling and an increase in the ease and speed of parturition (Knight *et al.* 1988, Everett-Hinks *et al.* 2009). Several studies have shown that survival is enhanced in lambs that stand and suckle quickly (Cloete, 1993, Dwyer *et al.* 2001). Knight *et al.* (1988) suggests that the increase in survival rate in these lambs has arisen through an increased ratio of birth to dam weight.

The repeatability of ewe rearing performance was reported to be affected predominantly by the permanent maternal effect including uterine capacity, pelvic width, lactation capacity and maternal ability assessed as a maternal behaviour score based on how far the ewe retreated from lambs when being tagged (Everett-Hinks *et al.* 2005). In addition, Purser and Young (1963) reported that ewes who successfully reared a lamb in its first parity were 13.5% more likely to successfully rear a lamb in the following parity.

Breed differences in maternal behaviour are also known to exist (Dwyer, 2008b). A study by Dwyer and Lawrence (2005) demonstrated significant and repeatable differences in vocalisation, grooming, acceptance of lamb's suckling attempts, suckling bout lengths, aggressive behaviour toward lambs and distance retreating from lambs between Scottish Blackface ewes and Suffolk ewes. Merino ewes are generally poorer mothers than other breeds of sheep with various reports suggesting that Merino ewes spend less time at birth sites than other breeds and that Merino ewes are more likely to temporarily or permanently abandon their lambs than do other breeds (Alexander *et al.* 1983). A study by Murphy *et al.* (1998, cited by Dwyer, 2008b) reportedly indicates that Merino ewes

selected for temperament and assessed as calm spent more time grooming and vocalising toward their lambs than did ewes assessed as nervous although this study did not indicate if these differences translated into different survival rates for their lambs. Several other measures of temperament have been reported as heritable. For example the heritability of the amount of movement in arena and box tests was estimated to be 0.23 by Martin *et al.* (2004) and the heritability of the frequency of distress calls when separated from other animals was estimated to be 0.48 (Boissy *et al.* 2005). Ewe selection based on temperament has been suggested as a possible route toward improving overall lamb survival (Dwyer, 2008b). Selection for ewe behaviour is however unlikely to be adopted by either commercial producers or ram breeders. Reasons for this include the high level of labour associated with observing behavioural traits and the specific times during which these behaviours can be assessed.

Phenotypic selection against ewes who fail to rear lambs has been practiced in New Zealand (Fisher, 2003). In this system ewes that require assistance in lambing or otherwise fail to rear a lamb have been rigorously culled regardless of how well they might perform in traits other than the ability to survive and to produce live lambs at weaning. This has led to a reduction in mortality rates to around 9% which are comparable to those attained in the intensive labour systems that are practiced in the United Kingdom (Dwyer, 2008b). In the United Kingdom flocks are housed and intensively managed during lambing to reduce the incidence of stillborn deaths by assisting difficult births. This practice minimises lamb deaths caused by abandonment and also by exposure to adverse environmental conditions (Dwyer, 2008b).

The New Zealand 'easy-care lambing system' aims to minimise the detrimental effects associated with carefully supervised lambing in difficult environments, by selecting sheep to suit both that environment and the low labour requirements of modern farm management (Fisher, 2003). These systems aim to optimise the ability of animals within them to care for themselves, through appropriate behavioural responses, resistance and resilience when confronted with health of welfare challenges (Dwyer, 2008b). Ewe flocks that are generally reared under intensive management systems such as those practiced in the United Kingdom, with a high degree of human intervention and assistance during

lambing, are reported to experience higher levels of difficult lambing and poorer maternal care of their offspring (Dwyer and Lawrence, 2005) than do flocks managed under more extensive conditions (Dwyer *et al.* 1996). This suggests that human intervention has exacerbated lambing survival problems through a reduction in natural selection pressure against animals unable to lamb or care for their lambs naturally in these flocks.

2.6 Causes and timing of Lamb mortality

Perinatal lamb mortality has been identified as the major cause of reproductive wastage in Australian sheep flocks (Alexander, 1984). A low level of nutrition during pregnancy and lambing (Alexander 1984), desertion of the lamb by the ewe because of ewe body weight loss and poor body condition, high and low lamb birth weights, damage to the ewe's udder and teats, ewe parity number, central nervous system damage, predators, exposure to cold, wet, windy conditions, birth trauma and infection (Yapi *et al.* 1990) have all been implicated as causes of perinatal mortality in various regions of Australia (Jordan and le Feuvre, 1989). The vast majority of these mortalities occur within the first 3 days of postnatal life (Dwyer, 2008b). The relative prevalence of any of these causes varies between localities and farms depending on both the environment and management practices.

The single biggest factor contributing to lamb mortality is however birth weight (Dwyer, 2008b, Hinch *et al.* 1983, Fogarty *et al.* 2000). Birth weight has a curvilinear relationship with the incidence of lamb mortality where animals with low birth weights frequently die of exposure and starvation (Yapi *et al.* 1990) and animals with high birth weights are more likely to die from difficult birth or classic dystocia (Fogarty *et al.* 2000). Numerous optimal birth weights have been estimated but these are likely to be different for different breeds or even flocks depending upon the mature size of the ewe. Optimal birth weights for survival can even differ within the same flock depending on whether it is perinatal or preweaning survival that is being analysed (Morris *et al.* 2000). In cattle it has been reported (Morris *et al.* 1986) that a difference in the calf to dam weight ratio results in differences in perinatal survival and the actual optimal birth weight in sheep is most likely

dependent upon the ratio between the mature size of the dam and the birth weight of the lamb.

Lambs with lower birth weights have been found to be less vigorous after birth and also to have lower rectal temperatures (Everett-Hinks and Dodds, 2008). Less vigorous, low birth weight animals take longer to stand and seek the udder to suckle when compared to higher birth weight animals (Dwyer and Morgan, 2006). These behavioural deficiencies contribute to the incidence of exposure and starvation in these lambs. In addition these behavioural deficiencies could also contribute to death by predation, infection or misadventure in low birth weight lambs. Yapi *et al.* (1990) reported that low birth weight lambs had the highest likelihood of dying from all causes with the exception of gastrointestinal problems. This is supported by Morris *et al.* (2000) who reported that for all classes of birth, animals with birth weights lower than 1.2 standard deviations from the mean had the highest fatality rates. It is generally accepted that an intermediate birth weight that is within 2 standard deviations of the mean birth weight is optimal for lamb survival (Purser and Young, 1959).

Dystocia, or difficult birth, can often be a consequence of a high birth weight (Fogarty and Thompson, 1974) which can be exacerbated by the use of inappropriate sire breeds but can also arise from the dam's pelvic structure (Fogarty and Thompson, 1974), malpresentation, maternal overfeeding or prolonged parturition (Everett-Hinks and Dodds, 2008). Maiden ewes are especially susceptible to dystocia compared to mature ewes that have previously lambed. A selection trial undertaken at Trangie over 15 years for lamb rearing ability resulted in an increase in pelvic dimensions in selected ewes (Kilgour and Haughy, 1993) and an increase in the number of lambs weaned in the high selection line.

Everett-Hinks and Dodds (2008) reported that in high performance New Zealand sheep flocks it was the lighter lambs born in larger litter sizes (3+) who suffered the highest incidence of death by dystocia. Similarly Yapi *et al.* (1990) reported that lighter lambs were at a higher risk of dying from trauma, although this study did not identify if this trauma was birth related it did suggest that difficult births could have been the trauma cause. The high level of dystocia deaths associated with lambs born in larger litter sizes was an unexpected result and Everett-Hinks and Dodds (2008) suggest that it is likely that the incidence of

dystocia is underestimated as a primary source of deaths in highly fecund flocks. They also suggest that dystocia is particularly prevalent in lower birth weight lambs from larger litters possibly resulting from prolonged parturition. This is in direct contrast to findings from Height and Jury (1970) and Smith (1977) who report that death from dystocia is more frequent among high birth weight lambs. In general higher birth weight problems are usually associated with single born lambs although multiples with higher than average birth weights can also have higher fatality rates at birth (Morris *et al.* 2000). Lambs may also die directly through hypoxia or trauma suffered during birth or indirectly through central nervous system damage resulting in an inability to maintain body temperature or exhibit appropriate udder-seeking activity or suckling behaviour (Dwyer, 2008). It is possible that the homeostatic and behavioural failures are due to the lamb suffering sub-lethal hypoxia during the birth process. Birth injury is reported to be present in 80% of the lambs that die up to 3 hours after birth and is also reported to be present in up to 57% of lambs dying from starvation, mismothering or exposure (Haughey, 1991).

Breed differences in lamb mortality rates from dystocia have been reported in published scientific literature (Fogarty and Thompson, 1974, Yapi *et al.* 1990) and are thought to be associated with the size of the pelvic inlet. Fogarty and Thompson (1974) report that external pelvic measurements in Dorset Horn ewes were of no predictive value to their pelvic inlet diameters although forelimb length and body length were both significantly correlated with the pelvic inlet diameter in these animals. Yapi *et al.* (1990) reported that F1 lambs were at a lower risk of death from trauma and gastrointestinal problems than were purebred lambs although the same report indicates that the reasons for these differences were not apparent. A recent paper by Warren *et al.* (2012) indicates that ultrasound imaging of the ewe's pelvic opening may offer an opportunity to detect ewes that are at risk of losing lambs due to dystocia before reproduction events.

Survival rates can also differ among breeds and amongst flocks and years (Fogarty *et al.* 2000, Pope and Atkins, 2007) with cold, windy, wet weather capable of dramatically increasing deaths due to exposure. A 2008 study by Everett-Hinks and Dodds reported that in New Zealand prolonged cold and wet weather conditions had a large negative influence on lamb survival in high performing New Zealand sheep flocks. Similarly Arnold

and Morgan (1975) report that lamb mortality increased significantly in wet winter weather in Western Australia. Somewhat surprisingly the study by Everett-Hinks and Dodds (2008) also revealed that adverse weather conditions resulting in heat loss from the ewes in the period directly before lambing had a greater negative influence on lamb survival than did adverse weather on the day of parturition. The report suggests that during these conditions ewes carrying multiple lambs were unable to meet their daily energy requirements through either feed or the mobilisation of body tissue resulting in the birth of lambs with lower survival viability. Everett-Hinks and Dodds (2008) reported that the detrimental impact of unfavourable cold, wet and windy weather conditions on the day of birth can be mitigated by good maternal care from the ewe. Arnold and Morgan (1975) reported that heat stress was the primary cause of lamb deaths in Western Australia for lambs born during summer months.

Poor maternal condition also contributes to lower lamb vigour through lower birth weights, premature delivery (Mellor and Murray 1981) and a poorer quality of maternal behaviour. In combination these factors result in increased mortality rates among lambs born to these ewes (Dwyer, 2003). The poor maternal behaviour associated with reduced nutrition includes an increased propensity for ewes to desert their lambs and spend less time grooming newly born lambs. In addition, poor ewe condition also causes a reduction in mammary development and weight resulting in a reduction in both colostrum yield and total milk production which further disadvantages the low birth weight lambs born to ewes in poor condition (Mellor and Murray, 1985). Lambs from ewes with poor maternal behaviour suffer an increased risk of death from starvation and exposure (Everett-Hinks and Dodds, 2008).

Mortality is also higher for lambs born to primiparous ewes (Dwyer and Lawrence, 2000). Lambs from primiparous ewes are usually of lower birth weights which is thought to be a contributing factor to their lower survival rates although the survival rate is also thought to be a result of poorer maternal behaviour post parturition (Dwyer and Lawrence, 2000). This contention is however countered in the results of a study of data collected between 1975 and 1981 from a Booroola x Romney flock and a Booroola x Merino flock by Hinch *et al.* (1983). Hinch *et al.* (1983) reported that an apparent ewe age effect on survival was

completely explained in terms of lamb birth weight. A study by Morris *et al.* (2000) based on over 55,000 lambs born in New Zealand research stations reported that lamb survival was lowest from lambs born to 2 year old ewes. It is intuitive that ewe experience would play some part in lowering lamb deaths as is evidenced by the decreased likelihood of lamb abandonment apparent in more experienced Merino ewes and by the results of Safari *et al.* (2005) and Knight *et al.* (1998) who both found lamb survival rates to be highest for lambs from 4 to 6 year old dams.

Lambs also die through an inability to maintain homeothermy and establish regular breathing or to exhibit behavioural competency such as standing or suckling (Dwyer, 2008). Newborn lambs are also extremely susceptible to infectious disease and death through starvation and exposure. Starvation affects lambs born in multiple births differently to those born as singles with almost half of the deaths of lambs born in multiples being attributed to starvation. Conversely deaths in single born lambs are more likely to occur on the day of birth and starvation contributes to only approximately a quarter of these (Dwyer, 2008).

Increased litter size itself also contributes to increased mortality independent of birth weight as does an animal's own behaviour and sex, where male lambs exhibit retarded behavioural progress and have higher mortality rates when compared to female lambs (Dwyer, 2008b). Hinch *et al.* (1983) reported that at any given birth weight lambs born in large litters (≥3) had a lower probability of survival than contemporary lambs born as singles or twins. Many studies indicate that birth rank, or the order of birth in multiples is a significant factor in lamb survival.

Repeated studies (Pope and Atkins, 2007) have reported that the pre-weaning survival rate of single born lambs is higher than for multiple births. This is of concern as, historically, selection efforts to increase the number of lambs weaned have included selection for more fecund ewes (Kilgour and Haughey, 1993). This has resulted in an increased frequency of larger litter sizes and a subsequent increase in lamb mortality (Hatcher *et al.* 2010). The lower survival percentage for lambs born in multiple births is likely to be having an antagonistic effect on efforts aimed at improving ewe net reproduction rates. Atkins (1980)

reported that after 15 years of selection for rearing ability, lamb survival was 8% higher and 15% higher for single and twin born lambs than it was in unselected comparable flocks. This result suggests that selection for rearing ability will reduce mortality especially in flocks that have increased the incidence of multiple births.

The risk of primary predation varies in differing localities and is dependent upon relative predator abundance. It has been reported to account for up to 23% of all mortalities (Lugton, 1993). Known predators of Australian lambs include, feral dogs, foxes and feral pigs (Greentree *et al.* 2000). It is also likely that wedge tailed eagles are also predators of lambs although their impact is likely to be minor when compared to that of feral pigs and dogs.

2.7 Autopsy procedure

McFarlane (1965) suggested that a more successful strategy than direct selection for improved survival might be through selection against the individual causes of death and described a comprehensive autopsy method to definitively determine the cause of lamb deaths in the majority of cases. According to Haughey (1991) the specific cause of death can be determined in about 75% of all deaths by conducting a full autopsy on dead lambs, provided that a history of prenatal nutrition, disease and husbandry, as well as a qualitative estimate of weather conditions over the period of lamb collection is available.

Holst (2004) set out an autopsy procedure that identified 10 categories for causes of lamb death based on work from McFarlane (1965), Haughey, (1973a, 1973b) and Rowley (1970). Holst (2004) recommends that lambs should be tagged at birth and information be recorded on; ewe assistance during parturition, time of birth and death, accidents, birth type and weather, and that flock management records be available.

The procedures advocated by Holst (2004) include a standardised inspection of the lamb to determine if it has been cleaned by the ewe and to check for the presence of meconium staining and subcutaneous oedema. The lamb is also inspected for congenital abnormalities, signs of predation and the hooves are inspected for signs of wear on their membranes indicating that the lamb has stood or walked. In addition the dead lamb is

opened for internal examination and is inspected for: infection, the presence of blood, oedema colour, loss of organs, the presence of a milk clot or other substances indicating that the lamb has fed, the size and firmness of the liver and indications of metabolized fat around the kidneys. The heart and lungs are also checked for evidence of petechiation and pericardial fat or inflation, respectively. Finally, the brain is inspected for signs of vascular abnormalities. This procedure identifies 9 causes of death which are: 3 types of dystocia based on oedema severity, starvation, exposure, animals that have died *in utero*-pre-birth, predation, infection and animals that have died from misadventure.

2.8 Genetic selection for Survival

For effective genetic selection to occur, individuals containing superior genes must first be identified. This identification of genetically superior individuals for lamb survival has proven to be a difficult task. Reproductive traits in general pose difficulties for selection because often they relate to a single sex and only expressed during later stages in life. In addition, the accurate estimation of genetic parameters and correlations for any trait requires large inter-generational data sets. Most reproductive traits are labour intensive and expensive to monitor and record. Heritability estimates of the majority of reproductive associated traits are commonly low and lamb survival has proven to be no exception (Hatcher *et al.* 2010).

Complicating efforts to estimate genetic variation in lamb survival are the multiple components that influence this trait genetically. Whether or not a lamb survives is not entirely dependent upon its own genes (the individual or direct effect). For example a lamb with superior genes for survival may not survive as it is born to a poor mother or conversely an animal with poor survival genes may survive if it is born to an excellent mother. It is therefore necessary to consider both the direct genetic effect of the lamb's own genes and the maternal effect of the dam which has both genetic and environmental components (Bradford 1972).

Survival can be analysed as a trait of the ewe or as a trait of the lamb but in general heritability estimates resulting from both types of analysis are extremely low. Early genetic studies (Matos *et al.* 2000) generally analysed lamb survival as a trait of the dam although

exceptions existed. Eventually an effective argument was raised contending that the genetic makeup of the offspring was more important to survival than that of its dam (Cundiff *et al.* 1982). The advent of faster computers (Barwick *et al.* 1990) and better programs now allow genetic models to include random effects for both direct and maternal components. It is now a relatively simple process to analyse the trait as either a trait of the lamb or of its dam or as a trait affected by both the dam and the lamb and to simultaneously fit direct and maternal effects – for both the lamb and ewe traits.

Morris *et al.* (2000) analysed their lamb survival data as a trait of the ewe opposed to one of the lamb. This analysis also resulted in a very low heritability for survival (0.02) and concluded that genetic parameters for lamb survival offered very limited opportunities within breed to increase survival rates.

Survival is by nature a binary (0-1) trait and survival analysis results can be affected by transforming this trait on a logit scale. Transformation of the data can result in slightly higher heritability estimates on the underlying scale (Matos *et al.* 2000). For example Morris *et al.* (2000) found that logit transformation of the data resulted in heritabilities in the order of 1/3 higher than heritability estimates from untransformed (binary) data.

A threshold model proposed by Wright (1934) has also been used to estimate direct and maternal effects (Matos *et al.* 2000). These threshold models assume that a survival response is related to an unobserved continuous variable with a fixed threshold. A goodness of fit comparison conducted by Matos *et al.* (2000) between threshold and linear models used for survival found only a very slight advantage for the threshold model over the linear model. Other studies in cattle (Weller *et al.* 1988, Ron *et al.* 1990) have reported that estimated breeding values generated via threshold models correlate very highly (above 0.9) with those generated from linear models using the same data.

Reported heritability estimates are also affected by the way that the lamb survival trait is defined. In general the heritability estimates for survival increase as the length of the time period defined for survival declines. As animals age the number of factors that could result in that animal's death also increase and this has been hypothesised as part of the reason

why the heritability of survival to three days is higher than the heritability of survival to weaning.

Numerous papers have estimated the direct heritability of lamb survival in various sheep breeds to be low or very low (Hatcher *et al.* 2010). A review of 16 independent estimates for the direct heritability of lamb survival was conducted by Safari *et al.* (2005) (Table 2.1). Safari *et al.* (2005) presented weighted means for direct and maternal heritability estimates, based on these 16 studies. Unfortunately due to insufficient records weighted means of estimates for common environmental effects and the correlation between direct and maternal effects were not available for lamb survival. This review reported a weighted mean direct heritability and standard error for survival of 0.03 ± 0.01. In a similar review based on 24 earlier studies Fogarty (1995) reported a direct heritability of 0.04 for survival. In more recent studies Everett-Hinks *et al.* (2005) estimated the direct heritability of lamb survival at birth and to 3 days at 0.00 ± 0.00 in a New Zealand study based on 9,815 animals of various breeds and Brien *et al.* (2010) estimated a direct heritability of 0.014 ± 0.010 for survival to three days age and 0.010 ± 0.010 for survival to weaning.

The genetic correlation between direct genetic effects for birth weight and survival was estimated to be strongly negative (-0.7) by Barwick *et al.* 1990. Hatcher *et al.* (2010) report this correlation to be low (0.06) and not significantly different from zero. This suggests that selection for birth weight to increase survival would be of limited use. Given the nature of the phenotypic relationship between birth weight and survival the result of Barwick *et al.* (1990) would be expected in flocks with a large number of high birth weight singles although this could well alter in flocks with higher incidences of death associated with dystocia in larger litter sizes as discussed by Everett-Hinks and Dodds (2008) and serves as a possible explanation of the results of Hatcher *et al.* (2010).

A large part of estimating additive genetic variance for any individual trait is accounting for effects that are understood to cause phenotypic variance for that trait. In general fixed effects and covariates included in survival models include a term for a contemporary group, age of dam, birth rank, sex and birth weight plus a birth weight quadratic. A study by Morris *et al.* (2000) reported that heritability estimates of survival were similar regardless

of which covariates were included in their models indicating that these effects accounted for only minimal variation in the observed data.

Survival of lambs to three days is a biologically complex trait that is affected by numerous factors. It is unlikely that the different causes of death in lambs are controlled by the same genes. For example it is unlikely that the genes that affect death by dystocia are the same genes that affect death by infection. It may be that the mixing of different causes of death within lamb survival genetic analysis is a contributor to the extremely low heritability estimates for lamb survival and to the poor level of increase in marking percentages.

In what appears to be almost a consensus among published literature, the direct genetic component for lamb survival indicates that direct selection for this trait would be of limited use in improving lamb survival percentages and that if this trait was included in selection indices it would be very unlikely to achieve the desired outcome.

2.9 Maternal Effects

Reproduction success is known to be affected by a large range of factors and is also complicated by interactions between the dam and her offspring. When maternal effects are included into genetic estimation models, direct heritability estimates that were low to start with can be further diminished. This is not totally unexpected given the large and important role that ewe behaviour and the uterine environment play in lamb survival. A failure to include maternal effects in variance estimation models however would lead to misleading heritabilities and could result in suboptimal selection decisions (Maniatis and Pollott, 2002). It is also possible that in limited data sets, both genetic and non-genetic maternal effects could mask direct lamb effects and vice versa.

Barwick *et al.* (1990) estimated the maternal genetic heritability of survival (0.017) to be similar in size to the direct genetic heritability (0.025) in a population of U.S. Suffolk ewes. The same study did however find that the maternal environment component was in the order of 4 times larger (0.095) than the direct or maternal heritabilities for survival. Similarly, Morris *et al.* (2000) also found that the largest variance component in their study came from the maternal environment as did Cloete *et al.* (2009) and Brien *et al.* (2010).

Morris *et al.* (2000) estimated maternal environment effects to consistently account for approximately 14% of the phenotypic variation for perinatal survival and reported that genetic variance for the maternal environment was in the order of 1.5 to 5 times larger for perinatal and preweaning survival than the size of the lambs own additive genetic variance using a logit model. Similarly, Safari *et al.* (2005) calculated weighted means from published studies for maternal heritability to be 0.05 ± 0.01 and reported that maternal environmental variance and a litter component accounted for 10% and 5% of total variance respectively.

Of concern is the fact that Morris *et al.* (2000) consistently estimated negative genetic correlations between direct and maternal genetic effects on survival although in all cases estimates were exceeded by their standard errors. Similarly Cloete *et al.* (2009) estimated the correlation between direct and maternal effects to be -0.60 and Everett- Hincks *et al.* (2005) reported an unfavourable direct-maternal correlation of -0.74. Conversely Barwick *et al.* (1990) reported a positive correlation between maternal genetic effects and survival although the estimate by Barwick *et al.* (1990) exceeded the parameter space (1.24). Barwick *et al.* (1990) postulated that it is possible that genes of the dam influencing lamb survival might closely resemble those which nourish the foetus and that the correlation might approach unity. However, given the large number of factors influencing survival and the contrary results of other studies this hypothesis is unlikely. The negative correlations reported by Morris *et al.* (2000), Everett-Hinks *et al.* (2005) and by Cloete *et al.* (2009) suggest that efforts to improve survival by selection on a lambs direct genetic effects would have an antagonising effect on the genetic maternal survival component. Given that the size of the maternal genetic component invariably exceeds the size of the direct genetic component such a selection strategy could conceivably result in a reduced overall survival rate.

These results add weight to suggestions that phenotypic selection focus for survival should be applied to the dam and go some way toward explaining why phenotypic selection for ewe rearing success has been an effective selection strategy to improve reproductive performance. It appears unquestionable that models used to estimate genetic variance for survival should include maternal effects.

Table 2.1, Reproductive direct heritability (h^2), maternal heritability (m^2), permanent environmental effect (c^2), genetic correlation between direct and maternal effects (ram), numbers of records and years of records, mean, coefficient of variation (CV%), breed and reference reported in literature (adapted from Safari and Fogarty, 2003).

Trait	h^2	m^2	c^2	r$_{am}$	Record	Yrs	Mean	CV	Breed	Reference
Lamb survival – Lamb										
	0.05 ± 0.05	0.05 ± 0.04	0.47 ± 0.08	na	2,844	3	0.81	46	Crossbreed	Hall *et al.* 1995
	0.11 ± 0.09	**0.04 ± 0.07**	**0.19 ± 0.08**	**na**	**2844**	**3**	**na**	**na**	**Crossbreed**	**Hall *et al.* 1995**
Mortality21	0.07	na	0.04	na	2032	8	0.19	na	Canadian	Hansen & Shrestha, 1997
	0.04	na	0.03	na	2844	8	0.18	na	Outaouais	Hansen & Shrestha, 1997
	0.04	na	0.04	na	2977	8	0.18	na	Rideau	Hansen & Shrestha, 1997
	0.00	**na**	**na**	**na**	**10210**	**28**	**0.83**	**na**	**Merino**	**Oliver *et al.* 1998**
	0.00	**na**	**na**	**na**	**9174**	**19**	**0.86**	**na**	**Merino**	**Oliver *et al.* 1998**
	0.02	**na**	**na**	**na**	**4816**	**26**	**na**	**na**	**Afrino**	**Snyman *et al.* 1998**
	0.01 ± 0.01	**0.04 ± 0.02**	**na**	**-0.26 ± 0.04**	**25874**	**7**	**0.87**	**na**	**Romney**	**LopezVillalobos & Garrick 1999**
	0.03	0.03	na	0.44	2554	10	0.82	47	Rambouillet	Matos *et al.* 2000
	0.09	0.19	na	0.14	3306	13	0.75	57	Finsheep	Matos *et al.* 2000
Perinatal	0.01 ± 0.02	0.03 ± 0.02	na	0.92 ± 1.68	26147	26	0.92	na	Romney	Morris *et al.* 2000
	0.03 ± 0.01	0.01 ± 0.01	na	-0.23 ± 0.03	26147	26	0.92	29	Romney	Morris *et al.* 2000
	0.02 ± 0.02	**0.11 ± 0.05**	**na**	**-0.52 ± 0.60**	**16424**	**7**	**0.92**	**na**	**Romney**	**Morris *et al.* 2000**
	0.04 ± 0.01	0.05 ± 0.02	na	-0.38 ± 0.30	16424	7	0.92	28	Romney	Morris *et al.* 2000
Preweaning	**0.01 ± 0.01**	**0.03 ± 0.01**	**na**	**0.00**	**20568**	**26**	**0.78**	**na**	**Romney**	**Morris *et al.* 2000**
	0.01 ± 0.02	0.02 ± 0.02	na	-0.03 ± 0.40	20568	26	0.78	52	Romney	Morris *et al.* 2000
	0.02 ± 0.01	**0.10 ± 0.03**	**na**	**-0.34 ± 0.40**	**13065**	**7**	**0.8**	**na**	**Romney**	**Morris *et al.* 2000**
	0.04 ± 0.01	0.07 ± 0.02	na	-0.33 ± 0.20	13065	7	0.8	0.48	Romney	Morris *et al.* 2000
	0.09 ± 0.02	na	0.04 ± 0.02	na	12932	12	0.86	na	Merino	Cloete *et al.* 2001

Bold text represents estimates generated with a threshold model, normal text are estimates generated with an animal model

2.10 Genetic selection for individual death categories

Slee *et al.* (1991) proposed that progress on reducing lamb loss might be advanced through the genetic selection for other traits as opposed to the direct genetic selection for survival provided that the trait under contemplation exhibited a higher heritability than does lamb survival. For example genetic variation in a lamb's ability to withstand cold is known to exist (Slee, *et al.* 1991). Slee *et al.* (1991) estimated the heritability of this trait to be 0.55. This trait was measured however by immersing lambs in a water bath and measuring their resistance to cooling and the time that they took to recover from this induced hypothermia. This type of measurement technique is very unlikely to be adopted in field situations however as labour costs due to the time taken for such measurements would be prohibitive.

It is known that neonatal lambs warm themselves almost entirely through the metabolism of brown adipose tissue which is regulated via thyroid hormones (Dwyer, 2008). Forrest *et al.* (2006) reported that variation in the ovine beta3-adrenergic receptor gene is associated with lamb survival. Forrest *et al.* (2006), using univariate and multivariate odds ratios for each beta3-adrenergic receptor gene allele, revealed a significant association of one allele (E) with cold survival and of another (D allele) with mortality. This variation at the beta3-adrenergic receptor locus may assist in the genetic selection for increasing survival due to exposure in Merino sheep although a cost efficient methodology of detecting variation in this gene is not yet available. In addition it is likely that natural selection has reduced the incidence of the beta3-adrenergic receptor gene D allele in sheep populations commonly exposed to hypothermic conditions.

Positive correlations exist between birth weight and both hogget weight and growth rate (Safari and Fogarty, 2003). This is of concern as selection for increased growth rates or hogget weights should to lead to corresponding increases in birth weights and a possible increase in dystocia-related lamb deaths. Morris *et al.* (1986) report that a positive correlation exists between increased hogget weight and dam weight which may counteract the effect of increasing birth weight. These positive correlations however make selection for intermediate birth weights more difficult. When these factors are considered together

selection for growth rate and hogget weight is likely to have an effect on dystocia rates in both single and multiple bearing ewes however it is unclear if this will result in an overall benefit through a decrease in dystocia related deaths in light weight multiple lambs or an increase in dystocia in heavier multiple and single born lambs.

2.11 Conclusions

Lamb survival is a complex trait and this complexity and the associated low heritability has contributed to the lack of success in improving this important economic trait over time. Intense management of ewes during parturition has been shown to successfully reduce mortality rates although this practice is labour intensive and appears to contribute to an increasing requirement for assistance in subsequent generations. Obviously any practice that leads to an increase in the amount of labour over time is not commercially sustainable and for this reason alone this potential solution should be avoided.

The numerous factors that combine to influence lamb survival and the numerous different causes of lamb mortality are together likely contributors to the low heritability estimates for lamb survival. The combination of different causes of death into one single trait, survival, would contribute to low heritability estimates for this trait if all mortality causes have low heritabilities and the traits are in general uncorrelated (absolute value of correlation estimates not significantly different from zero).

Birth weight is an obvious contributor to lamb survival and has a reasonable heritability. There is however a danger that selection for higher or lower birth weights would have a negative influence on different death causes and that selection for an intermediate birth weight would be advisable.

Studies seem to concur that the magnitude of the maternal component of survival variance exceeds that of the direct component. This maternal variance is made up of both maternal environment and a maternal genetic component. Of these the maternal genetic component can be passed onto future generations. The successful separation of the maternal environment and genetic components however requires large data sets with multiple

records for ewes over multiple generations. The cost of generating such data sets would be significant.

Phenotypic selection against ewes that fail to rear a lamb or for the ability to rear multiple lambs appears to be successful at reducing overall mortality. The success of this strategy implies that there is a genetic component to lamb survival and the most obvious candidate is the maternal genetic variation given it has been found to be consistently larger than the direct effect. This implies that the maternal effect of the ewe is consistently larger than the direct effect of the ewe and the direct effect of the lamb. The obvious drawback to this strategy is that such selection can only be practised after the ewe has failed reproductively. Therefore any success can only come after the ewe has matured and comes at the cost of reproductive failure.

It is possible that some of the individual causes of lamb mortality have a higher heritability than overall survival. If identified it may be possible to include the trait or traits into selection indexes. The advantages of such a strategy would be that selection could be practiced on younger animals and that genetic progress would therefore be quicker than phenotypic selection.

Chapter 3 Variance Components

3.1 Introduction

Lamb survival is a complex trait affected by numerous factors and is dependent upon the successful establishment of a relationship between the dam and its offspring. Management of lambing ewes to minimise losses, although often successful, is a time consuming and costly option for producers which may ultimately be counterproductive and lead to an increased requirement for management and labour over time (Dwyer and Lawrence, 2005).

Genetic selection for improved lamb survival is perceived to be a low cost and permanent solution to the lamb survival problem. However, all literature estimates show that the trait is lowly heritable with an average estimated direct heritability of approximately 0.03 based on 12 separate studies (Safari and Fogarty, 2003). In addition, the identification of easily field measured traits that are strongly correlated with survival has not yet been successful. Thus, the selection of superior animals for lamb survival has not been achieved despite its desirability in industry (Hatcher *et al.* 2010).

It is well understood that there are numerous causes of lamb deaths and it is suggested that this is a major factor contributing to the low heritability of overall survival (Hatcher *et al.* 2010). In some cases it appears that factors affecting survival are antagonistic, for example higher birth weight lambs that would be expected to be more resilient against death from exposure or starvation are likely to be the same animals that are prone to death from classic dystocia because of their size. McFarlane (1965) first described a comprehensive autopsy method to determine the cause of lamb deaths for the majority of fatalities and suggested that selection against individual death causes as a possible path to improving lamb survival rates. For such selection to be successful reliable estimates of genetic parameters for individual death categories are essential. The objective this study is to estimate genetic parameters for each of the 10 death categories recorded between 2008 and 2011 by the Sheep Co-operative Research Centre (CRC) in 8 Information Nucleus Flocks distributed in divergent sheep producing regions of Australia.

3.2 Materials and Methods

3.2.1 Data

Data were obtained for all lambs born from 2008 to 2011 to dams belonging to the Sheep CRC's Information Nucleus. The Information Nucleus (IN) is a population of approximately 4250 ewes and their progeny bred from key young industry sires selected for high performance, likely to be used by industry and having genetic variation for a range of production traits. The INF consists of eight linked flocks at research sites in differing environments around Australia (Fogarty *et al.* 2007). The New South Wales INF sites were Armidale (1000 ewes), Trangie (500 ewes) and Cowra (500 ewes). Victoria sites were Rutherglen and Hamilton (500 ewes each) and the 2 South Australian sites were located near Naracoorte and Gawler (500 ewes each). There was also 1 site in Western Australia at Katanning (1000 ewes). Of the total number of foundation ewes, 80% were Merino and 20% were first cross Border Leicester - Merinos. All sites except Trangie first mated ewes in 2007. Each year approximately 100 key industry linked young sires were mated with IN ewes by artificial insemination, and most sires were represented at all sites. Further details regarding the IN including foundation sire and dam genotypes used in the IN are provided by Fogarty *et al.* (2007).

Information nucleus flock animals were routinely assessed for numerous traits at birth including: birth type (litter size at birth, 1 to 5), status (alive or dead), assistance given during parturition, scored 1 to 5 where 1 was no assistance and 5 was veterinary assistance (Lamb ease), birth weight, circumference of the thorax at the last rib (Thorax circumference) and length between the crown and rump (Crown-rump length) of the lamb. Dead lambs were collected several times daily and autopsied directly or frozen for later autopsy inspection. Autopsy procedures included a standardised inspection of the lamb to determine if it had been cleaned by the ewe and to check for the presence of meconium staining and subcutaneous oedema. The lamb was also inspected for congenital abnormalities, signs of predation and the hooves were inspected for signs of wear on their membranes. In addition the lamb was opened for internal examination and inspected for: infection, the presence of blood, oedema colour, loss of organs, the presence of a milk clot

or other substances indicating that the lamb had fed, the size and firmness of the liver and indicators of metabolized fat around the kidneys. The heart and lungs were also checked for evidence of petechiation and pericardial fat or inflation, respectively. Finally the brain was inspected for signs of vascular abnormalities (Holst, 2004).

There were 3,224 lambs that died to 5 days age and were autopsied of the 26,630 lambs born. Using the autopsy results dead lambs were placed into only one of 9 death categories which were: Dystocia A (most severe oedema, n=276), Dystocia B (mild oedema, n=664), Dystocia C (no oedema, n=588), Starvation-mismothering complex (n=825), Predation (n=216), animals that had Died *in utero*-pre-birth (DIUPB) (n=300), Exposure (n=159), Infection (n=44), animals that died from Misadventure (n=29) and animals whose cause of death could not be determined (n=123). Death category allocations for all animals were reviewed by G. Refshaugie of the Cowara Department of Primary Industries and standardised according to Holst's recommendations (2004) so that death classifications were consistent with autopsy results across all years and sites.

The 3 classes of dystocia in Table 3.1 were based on the level of oedema observed on autopsied carcasses. Dystocia A was associated with severe oedema or swelling, Dystocia B had mild oedema and central nervous system damage and Dystocia C had no oedema but severe central nervous system damage.

Table 3.1, Autopsy category numbers (Positive = 1, Negative = 0)

Trait	Positive	Negative	Percent of deaths
Dystocia A	276	26,364	0.09
Dystocia B	664	25,976	0.21
Dystocia C	588	26,052	0.18
Starvation-mismothering	825	25,815	0.26
Predation	216	26,424	0.07
Died *in-utero* pre-birth	300	26,340	0.09
Exposure	159	26,481	0.05
Infection	44	26,596	0.01
Undiagnosed	123	26,517	0.04
Misadventure	29	26,611	0.01

After data editing to remove records containing typographical errors and records without a pedigree structure 26640 birth records for INF lambs born between 2008 and 2011 representing a total of 445 sires and 11487 dams were analysed. There were 4 dam breeds represented in the data and 18 sire breeds (Table 3.2). The dam breeds, the number of lambs from each breed and the average birth weights of their lambs were; INF composite dams, 2103 and 4.96 kg, Merino dams, 18510 and 4.71 kg, Poll Merino dams, 729 and 4.66 kg and Cross-bred dams, 5298 and 4.98 kg.

The average birth weight of lambs across breeds was 4.78 kg. The mean Thorax circumference was 39 cm and the mean Crown-rump length was 46 cm. Lamb Surface area (SA) and lamb Volume (LV) traits were created by using the formula for the volume (V) and surface area (SA) of a cylinder ($V = \pi r^2 h$), ($SA = 2\pi r^2 + 2\pi rh$) and where r was derived from Thorax circumference measurements and h was the Crown-rump length. Greasy-fleece weight (n = 4601, mean = 3.53) and Yearling weight (n = 8377, mean = 42.3) measurements on lambs representing all sire types were also analysed so that correlations between these traits and autopsy or survival predictor traits could be estimated.

Table 3.2, Sire breed frequencies and birth weight means for all lambs

Sire breed	Frequency	Mean Birth weight (kg)
Border Leicester	1,986	4.74
Corriedale	815	4.72
Bond	61	4.79
Hampshire Down	51	5.25
Southdown	63	5.20
Coopworth	846	4.81
Poll Dorset	4,700	4.96
Texel,	780	4.88
Suffolk	909	4.94
White Suffolk	3,641	4.98
INF composite	998	4.99
Booroola	195	4.61
Prime Samm	766	4.58
Merino	5,924	4.59
Dohne Merino	956	4.60
Poll Merino	3,649	4.63
Ile De France	60	5.03
Cross Breed	240	5.13

In addition to the individual death category traits identified composite traits were developed. These composite traits were based on combined individual Dystocia and Starvation-mismothering (SMM) records. This was done so that variance component estimates and fixed effect solutions between these composite and individual autopsy traits could be assessed and to increase the number of animals in each category. The individual traits chosen to form composite traits were based on similarities in biological causes or similarities in solution results from individual traits. In addition an All Dystocia Ordered composite trait was created in an attempt to force binary data to be a continuous trait. The composite traits were: All Dystocia Binary (ADB), All Dystocia Binary plus Starvation-mismothering (ADB+), All Dystocia Ordered (ADO), All Dystocia Ordered plus Starvation-mismothering (ADO+), Dystocia A plus Dystocia B (Dystocia AB), Dystocia B plus Dystocia C (Dystocia BC) and Dystocia C plus Starvation-mismothering (DCS). Finally a survival trait to 3 days age consisting of all lambs that died was included so that variance components for lamb survival could be compared against those for individual death categories.

The ADB trait was created by allocating a 1 to animals classified as dying of Dystocia A, B and C, the ADB+ trait allocated a 1 to positive Starvation-mismothering records and to positive ADB records. All Dystocia Ordered records were created by ordering the 3 classes of Dystocia records by oedema severity so that positive Dystocia A records received 3, positive Dystocia B records received 2 and positive Dystocia C records received 1, ADO+ records were created by adding 1 to the value of all ADO records and a value of 1 for positive Starvation-mismothering records. The Dystocia AB trait allocated a 1 to positive Dystocia A and Dystocia B records and the Dystocia BC trait allocated a 1 to positive Dystocia B and Dystocia C records. The DCS trait allocated a 1 to positive Dystocia C and Starvation-mismothering records. In all composite traits negative records (animals that did not die in the individual or composite category) were allocated 0. The numbers of animals in each composite death category are shown in Table 3.3.

Table 3.3, Composite death category numbers (Positive = 1, Negative = 0)

Trait	Categories	Positive	Negative
All Dystocia Binary	0 or 1	1,528	25,112
All Dystocia Binary plus Starvation-mismothering	0 or 1	2,353	24,287
All Dystocia Ordered	0,1,2 or 3	1,528	25,112
All Dystocia Ordered plus Starvation-mismothering	0,1,2,3 or 4	2,353	24,287
Dystocia A plus Dystocia B	0 or 1	940	25,700
Dystocia B plus Dystocia C	0 or 1	1,252	25,388
Dystocia C plus Starvation-mismothering	0 or 1	1,413	25,227
Survival	0 or 1	3,224	23,416

3.2.2 Statistical Models

Fixed effect models for all traits analysed were developed using mixed models in the SAS statistical software (SAS, 2002). The main effects reported in literature as impacting on lamb survival (contemporary group, birth type, age of dam, sex, birth weight and birth type by birth weight interactions) were all significant for 1 or more traits in these data (Table 3.4) as were sire breed and dam breed. Contemporary group (CG) was created by concatenating flock and birth year together. Only significant effects and covariables ($P <$ 0.05) were retained in the final models with the exception of birth weight, birth weight squared, and sire and dam breeds which were included regardless of significance. Birth weight, the quadratic effect of birth weight and breed effects were included, to allow factors independent of these components to be identified. Birth weight and its polynomial were not fitted to the overall survival model. Birth weight and its polynomial were included in all models. The inclusion of birth weight squared allows the quadratic nature of this trait to be modelled.

Table 3.4, Effects fitted to autopsy trait models and their significance

Effect Trait	SB	DB	BT	CG	AoD	Sex	BWL	BWQ
Dystocia A	ns	***	***	****	**	****	**	***
Dystocia B	****	****	****	****	X	***	****	****
Dystocia C	**	****	****	****	*	X	****	****
Starvation mismothering	***	****	****	****	X	**	****	****
Predation	*	ns	*	****	X	****	****	****
DIUPB	ns	ns	****	****	X	****	****	****
Exposure	****	ns	X	****	*	****	****	****
Infection	ns	ns	X	***	*	X	*	*
Undiagnosed	***	ns	X	****	X	X	**	ns
Misadventure	ns	ns	X	**	X	****	ns	ns

BWL (birth weight linear) and BWQ (birth weight quadratic) were fitted within Birth type (BT) wherever BT was significant, DIUPB = Died *in-utero* pre-birth, SB = Sire Breed, DB = Dam Breed, CG = contemporary group, AoD = Age of Dam
**** = <0.0001, *** = <0.001, ** = < 0.01, * = <0.05, ns = not significant, X = not fitted

Variance components for all traits were estimated using ASReml software (Gilmour, *et al.* 2008). All effects were fitted as class variables with the exception of birth weight linear and quadratic which were centred (deviations from a mean that was set to zero) before variance estimation. Potential survival or autopsy indicator traits, thorax circumference, crown-rump length, lamb surface area and lamb volume were not used as fixed effects in final models to allow the estimation of genetic correlations between these traits. All autopsy traits were analysed using four models; 1, an animal model only, 2, an animal model including the permanent environment of the dam, 3, a sire model only and 4, a sire model including the permanent environment of the dam. Maternal genetic effects could not be modelled in these data as the animals originated from a discreet generation on the maternal side. Maternal grand-sires were not known for all animals in these data. This reduced the number of animals within autopsy category and for this reason maternal grand-sire models were not included. The INF is a progeny test with most information coming through sires and half sibs. As a result both animal and sire models were tested so the results could be compared between models. A comprehensive pedigree was available for all animals consisting of 47,041 identities. Foundation animals without a conclusive

pedigree were assigned one of 84 genetic groups as defined by the sheep CRC to account for differences in breed, selection strategy, selection lines and flocks in these foundation animals.

Models for the potential predictor traits; Lamb ease, Thorax circumference, Crown-rump length, Lamb surface area and Lamb volume as well as the production traits Greasy-fleece weight and Yearling weight included; birth type, sire and dam breeds, contemporary group, age of dam and birth weight (linear and quadratic) within birth type. In addition models for Lamb ease, Thorax circumference, and Crown-rump length included sex and models for Greasy-fleece weight and Yearling weight included rear type.

All fixed effects in the composite trait models were significant with the single exception of age of dam (AoD) in the Dystocia BC, composite trait which was not fitted (Table 3.5). This was expected and was the result of adding data for individual traits together. Age of Dam was only significant to the 0.05 level in the Dystocia C model and was not significant in the Dystocia B model.

Table 3.5, Effects fitted to composite trait models and their significance

Effect Trait	SB	DB	BT	CG	AoD	Sex	BWL	BWQ
ADB	****	****	****	****	**	***	****	****
ADB+	****	****	****	****	***	****	****	****
ADO	****	****	****	****	***	****	****	****
ADO+	****	****	****	****	***	****	****	****
Dystocia AB	****	****	****	****	**	***	****	****
Dystocia BC	****	****	****	****	X	**	****	****
DCS	****	****	****	****	*	***	****	****
Survival	****	****	****	****	***	****	****	****

BWL (birth weight linear) and BWQ (birth weight quadratic) were fitted within Birth type
ADB = All dystocia binary, ADB+ = ADB plus Starvation-mismothering, ADO = All dystocia ordered, ADO+ = ADO plus Starvation-mismothering, Dystocia AB = Dystocia A and B combined, Dystocia BC = Dystocia B and C combined, DCS = Dystocia C plus Starvation-mismothering, SB = Sire Breed, DB = Dam Breed, BT = Birth type, CG = contemporary group, AoD = Age of Dam, BW = Birth weight and BW^2=Birth weight squared
Significance, **** = <0.0001, *** = <0.001, **= < 0.01, * = <0.05, X = not fitted

3.3 Results and Discussion

3.3.1 Fixed effects

Contemporary group

The contemporary group fixed effect (CG) was highly significant for all traits highlighting the importance that the physical environment and management at birth has on lamb survival. This was expected, given that different flocks in different years are likely to be impacted by differing climatic events. Animals within contemporary groups share managerial decisions that could affect numerous factors ranging from feed quality to the incidence and appetite of various predators. Although contemporary group was highly significant it is not the intention of this thesis to discuss this environmental effect further.

Birth weight within Birth type

It is well understood that both birth type and birth weight are associated with lamb mortality and that the 2 effects are correlated, where lambs born in larger litter sizes are predominantly smaller. Much published literature reports that the single largest known factor contributing to lamb mortality is birth weight (Dwyer, 2008, Hinch *et al.* 1983, Fogarty *et al.* 2000) and that birth weight has a curvilinear, positive quadratic, relationship with the incidence of lamb mortality (Yapi *et al.* 1990, Fogarty *et al.* 2000) as shown in Figure 1. This relationship appears because larger lambs are more prone to death from classic dystocia and smaller lambs have insufficient body reserves to resist various challenges. In this study birth weight (linear and quadratic, fitted within birth type) was a significant effect for all autopsy categories with the exception of those lambs dying from Misadventure and those whose cause of death was Undiagnosed (Table 3.4). Model solutions for all autopsy categories (Table 3.6) indicate that the curvilinear relationship between birth weight and causes of death was observed although the magnitude differed between death causes.
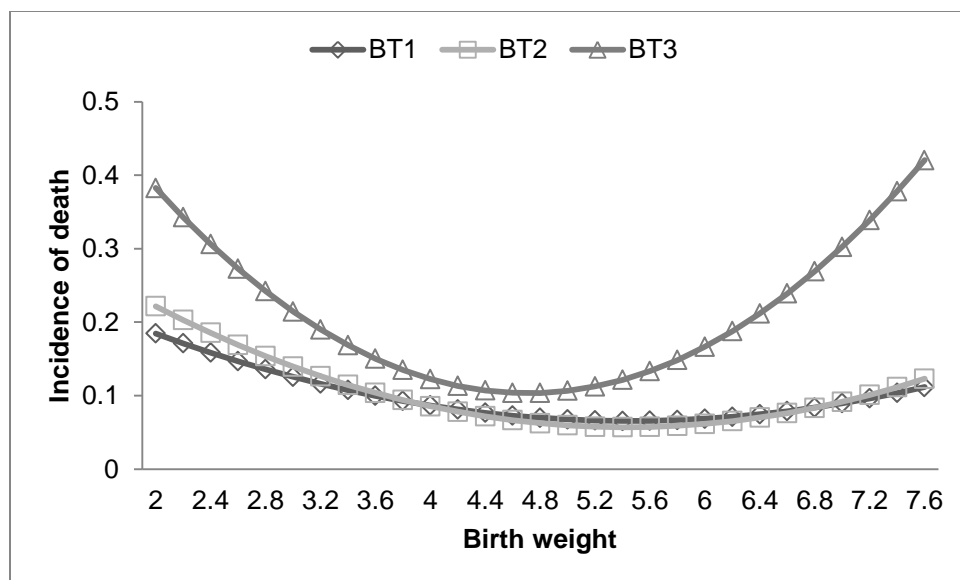
Figure 1, Predicted incidence of a lamb dying from All Dystocia by birth type at various birth weights adjusted for fixed effects
BT1 = Birth type single, BT2 = Birth type twin, BT3 = Birth type triplet
*Birth types 4 and 5 not shown due to a low number of animals contributing to solutions

In this study the risk of death increased as litter size increased. It is well documented that twin and triplet born lambs have higher mortality rates than singles (Hall *et al.* 1988). Studies of medium and highly prolific sheep flocks (Maund *et al.* 1980, Hinch *et al.* 1986) report that a large proportion of losses within 24 hours of parturition were associated with stillbirths and lamb weakness caused by prolonged births for lambs born in larger litter sizes. Birth rank of the lamb (Dutra *et al.* 2007) and lighter birth weights (Schreurs *et al.* 2009) have both been identified as major factors contributing to the brain and spinal meningeal haemorrhages associated with deaths in larger litter sizes (Haughey, 1973a). Unfortunately birth order is not know in these data but it is expected that mechanisms similar to those reported by Haughey, (1973a) Hinch *et al.* (1986), Dutra *et al.* 2007 and Schreurs (*et al.* 2009) are also influencing deaths associated with larger litter sizes in these data.

Investigation of the effect of birth type on the incidence of Dystocia A in these data revealed that this death category was primarily associated with single (n = 105) and twin born lambs (n = 102) of high birth weights. Dystocia A was thought to primarily be associated with lambs of a high body weight having difficulty fitting through the dams' pelvic opening.

The solution arising from ASReml for birth weight (Table 3.6) indicated that heavier weights are positively associated with increased incidences of death, as expected, and that this association is curvilinear as reported by Yapi *et al.* (1990) and Fogarty *et al.* (2000).

Table 3.6, Solutions for birth weight linear (L) and quadratic (Q) fitted within birth type[*]

	BT2	BT 3	BT1 L	BT1 Q	BT2 L	BT2 Q	BT3 L	BT3 Q
Dystocia A	-0.044	-0.053	-0.025	0.003	-0.008	0.001	-0.002	0.001
Dystocia B	0.132	0.475	-0.050	0.005	-0.106	0.010	-0.270	0.030
Dystocia C	0.020	0.161	-0.034	0.002	-0.038	0.003	-0.086	0.007
SMM	0.140	0.101	-0.049	0.004	-0.099	0.008	-0.063	0.004
Predation	0.035	0.046	-0.008	0.001	-0.019	0.002	-0.021	0.002
DIUPB	0.072	0.187	-0.045	0.003	-0.083	0.008	-0.142	0.015
All Dystocia	0.107	0.584	-0.109	0.010	-0.152	0.014	-0.358	0.038
Dystocia+	0.247	0.685	-0.159	0.013	-0.251	0.022	-0.421	0.042
Dystocia AB	0.087	0.422	-0.076	0.007	-0.114	0.011	-0.272	0.031

BT1 = single birth, BT2 = twin birth, BT3 = Triplet birth
SMM = Starvation-mismothering, DIUPB = Died *in-utero* pre-birth, Dystocia+ = All Dystocia Binary plus Starvation-mismothering, Dystocia AB = Dystocia A plus Dystocia B
*Solutions for birth types 4 and 5 are not presented due to a low number of animals contributing to each solution within autopsy class

Birth type and birth weight, linear and quadratic, were highly significant for animals dying from Dystocia B (Table 3.4). This was expected although the mean birth weight for live animals (4.79 kg) surprisingly was higher than the mean birth weight for lambs that died in this category (4.36 kg). This suggests that a high birth weight is not solely responsible for these types of deaths. It was found that single birth type lambs dying in this category were 0.4 kg heavier than their living contemporaries but that lambs dying in twin and triplet births were respectively 0.3 and 0.4 kg lighter. The death of the heavier singles and associated problems with lambs born in twin and multiples births is similar to results presented by Smith (1977) for cross breed lambs.

It was expected that the model for Dystocia B would be the same as that for Dystocia A although significant effects at or below 0.05 indicated that dam age was not significant for this trait and that sire breed effects were. These differences imply that the causes of Dystocia B are different to those that cause Dystocia A.

Raw means for birth weight for surviving lambs (4.8 kg) versus raw means for lambs that were classified as dying from Dystocia C (4.0 kg) indicate that in this data set it is the lighter birth weight lambs that are most susceptible to death from this category. Again deaths in this category primarily occur in twin (n = 321) and triplet births (n = 172) with singles (n = 65) accounting for a considerably lower proportion of the total. Several experiments (Marumo *et al.* 2001, Loeliger *et al.* 2003) have confirmed that repetitive umbilical cord occlusion, mimicking the type of umbilical cord compression that occurs during parturition, can induce various types of brain damage in foetal lambs. Taken together these results would appear to indicate that lamb deaths due to Dystocia C are likely to be associated with extended periods of hypoxia that are related to birth duration and that this and affects smaller, lower birth rank lighter lambs most severely. In these data incidences of Dystocia B and C as well as Starvation-mismothering were all markedly higher in twin and triplet birth types and it is likely that these deaths causes were influenced by the extended parturition times that are associated with multiple births.

This implies that breeding for increased birth weight would be advisable in flocks with high proportions of multiple litters. Figure 1 shows that the incidence of death from dystocia rises as birth weight deviations from the mean of 4.8 kg increases. Figure 1 also shows that the likelihood of dying from dystocia is markedly increased for lambs born in triplet litters. This suggests that overall survival can be improved by breeders targeting optimal birth weights. Birth type solutions (Table 3.6) for all other autopsy categories imply that the incidence of death increases as birth litter size increases. This result indicates that breeding for an increase in multiple births will only be successful in increasing the ewe to lamb weaning ratio if birth weight can be maintained.

Raw birth weight means showed that that lambs that died of Starvation-mismothering (3.9kg) had lower than average (4.8kg) birth weights. Birth type was also highly significant for Starvation-mismothering deaths and ASReml solutions (Table 3.6) again indicated that lambs from larger litters were more susceptible than were single birth type lambs. Haughey, (1991) reported that meningeal haemorrhages contributed to incidences of Starvation-mismothering and Darwish and Ashmawy (2011) noted that ewes that had prolonged and difficult births did not show competent maternal behaviour post

parturition. Hinch *et al.* (1986) and Darwish and Ashmawy (2011) both noted that lambs from prolonged and difficult births were significantly less vigorous after birth. Taken together this information would appear to suggest that a component of Starvation-mismothering is associated with smaller lambs who have suffered sub-lethal hypoxia during birth.

Lambs with lower birth weights were also more prone to death from Predation and this possibly arises as these smaller animals would most likely be slower, weaker and less able to fend off or run away from predators. Birth type solutions showed that Predation generally increased with increasing litter size.

Sire breed

Sire breed had a significant effect on incidences of; Dystocia B, Dystocia C, Starvation-mismothering, Predation, Exposure and Undiagnosed autopsy traits. Surprisingly sire breed was not significant for incidences of Dystocia A. Fixed effects models removed variance due to difference in birth weight and birth type and the results here suggest that sire breed is not an important factor for death from classic dystocia.

Sire breed solutions (not shown) for individual autopsy traits showed no clear trend in rankings although the Texel sire breed ranked worst for every death category where sire breed was significant. Combined these categories (Dystocia B, Dystocia C, Starvation-mismothering, Predation, Exposure and Undiagnosed) account for approximately 80% of all deaths recorded and the poor performance of Texel sires in these categories imply that lambs from these sires are different from other lambs. Numerous possible reasons for these differences exist, including; lamb shape, maturity at birth and lamb post parturition behavioural patterns. Dwyer and Morgan (2006) showed that breed differences do exist between Scottish Blackface and Suffolk lambs in neonatal behaviour. Dwyer and Lawrence (2000) showed that breed differences also exist between Scottish Blackface and Suffolk lambs for gestation length and crown-rump length and that these are both negatively influenced by increasing litter size. Dwyer and Lawrence (2000) speculated that gestation length and crown-rump length may be indicators of maturity at birth. In this study the

Crown-rump length of lambs from Texel sires (mean 45.1 cm, s.d. 4.5) were not noticeably different to the overall mean (45.8 cm, s.d. 4.9) of all sire breeds.

Several studies (Leymaster and Jenkins 1993, Fogarty *et al.* 2000, Freking and Leymaster 2004, Dutra and Banchero, 2011, Leeds *et al.* 2012) have looked at the viability of lambs sire by Texel breed and the results are equivocal. Leymaster and Jenkins (1993) reported that Texel sired lambs survived better than Suffolk sired lambs while Fogarty *et al.* (2000) found no significant Texel effect on survival, Freking and Leymaster (2004) reported that Texel sired lambs were below both Romanov and Finn sired lambs but above Dorset and Montadale sired lambs for survival to weaning and Leeds *et al.* (2012) also reported higher death losses for Texel sired lambs. Dutra and Banchero (2011) however reported that Texel sired lambs appeared to be more immature at birth than Polwarth lambs and had a number of physiological differences including a lower bone density, smaller brains and shorter forelimbs. Lambs that are more immature at birth would be expected to suffer higher levels of death through Starvation-mismothering, predation, and exposure although Dutra and Banchero (2011) suggested that this immaturity at birth resulted in less lambs dying from dystocia.

Dam Breed

The dam breed fixed effect was significant for all types of Dystocia and also for Starvation-mismothering but was not significant in models for the other autopsy categories. The significance of dam breed in Table 3.4 implies that even after adjustment for birth weight and birth type the dam breed does impact on survival. It is not clear what the causes of these results are although published literature does report differences in maternal behaviour (Dwyer and Lawrence, 1998) and also in pelvic opening dimensions (Knight *et al.* 1988) between dam breeds. Knight *et al.* (1988) also reports that there are genetically based differences in lamb shape and it is likely that these differences affect parturition ease. Knight *et al.* (1988) reported that the pelvic opening of Marshall Romney ewes was 8% larger than for Romney ewes and that the Marshall Romney ewes exhibited better maternal behaviour compared to the Romney ewes. Lamb survival was also better for lambs born to the Marshall Romney ewes in Knight *et al.'s* (1988) study and this was

attributed to a lower incidence in both dystocia and starvation in these lambs. It does not appear to be unreasonable to expect that there would be conformational differences between the ewe breeds used in this study for dam pelvic openings or differences in breed maternal behaviour. These differences could explain why dam breed is a significant effect for Dystocia A, B and C and also for Starvation-mismothering. Smaller pelvic openings would inhibit the passage of lambs which would lead directly to incidences of Dystocia A where lambs exhibit obvious oedema. Similarly this would also account for incidences of Dystocia B which and would also prolong parturition increasing incidences of Dystocia C. This would also be expected to contribute to sub-lethal hypoxia which is implicated in cases of Starvation-mismothering (Haughey, 1973a, Haughey, 1991, Dutra *et al.* 2007 and Dutra and Banchero 2011) especially in low birth rank and low birth weight lambs. In support of this contention Hinch *et al.* (1985) reported that difficult births at low birth weights were prolonged and Cloete *et al.* (1998) reported that parturition duration was also significantly longer in litters that contained 1 or more lambs that had died of birth stress when compared to litters where all lambs survived birth.

Dam breed solutions (Table 3.7) show that lambs from cross breed ewes were less likely to die from any form of Dystocia or Starvation-mismothering than were lambs from other dam breeds. It is known that cross breed ewes contained some genetics from maternal lines. The superiority of cross bred ewes found here reinforces the value of including reproductive traits in selection indices. Merino dams had the highest proportion of deaths due to all forms of dystocia and Starvation-mismothering.

Table 3.7, Dam breed solutions (relative to cross bred animals)

Breed	Merino	INF composite	Poll Merino
Trait			
Dystocia A	0.012	0.004	0.014
Dystocia B	0.020	0.008	0.032
Dystocia C	0.007	-0.001	0.025
Starvation-mismothering	0.015	0.004	0.033
Predation	-0.001	-0.005	0.001
ADB	0.035	0.010	0.065
ADB+	0.048	0.016	0.096
ADO	0.124	0.042	0.217
ADO+	0.076	0.026	0.121
Dystocia AB	0.029	0.011	0.042
Dystocia BC	0.027	0.007	0.057
DCS	0.020	0.005	0.056

ADB = All dystocia binary, ADB+ = ADB plus Starvation-mismothering, ADO = All dystocia ordered, ADO+ = ADO plus Starvation-mismothering, Dystocia AB = Dystocia A and B combined, Dystocia BC = Dystocia B and C combined, DCS = Dystocia C plus Starvation-mismothering

Age of Dam

The age of the dam was a significant effect for Dystocia A, Dystocia C, Exposure and Infection as well as any composite traits that included these individual traits with the exception of Dystocia BC combined. It is well understood that Dam age has an effect on birth weight where younger ewes have lighter lambs (Hight and Jury, 1970) and Everett-Hinks (2009) also reports that age of dam also impacts on dam behaviour.

Age of dam solutions for Dystocia A (Table 3.8) indicated that ewes aged 8 years and older were the worst performers for lambs dying from this cause. This supports the general industry practice of culling animals before they reach this age. Age of dam solutions also indicated that primiparous ewes perform poorly once other effects included in variance estimation models had been accounted for. This was expected given that these ewes often have lower body weights and are also unfamiliar with the birthing process. Solutions for dams of other ages generally indicate that as ewe's age up to 7 years they become more able to handle the demands of parturition, possibly as a result of experience and mildly decreasing birth weights.

Table 3.8, Age of dam solutions

Age of dam	Dyst A	Dyst C	Inf	Exp	ADB	ADB+	ADO	ADO+	Dyst AB	DCS
1	0.007	0.003	0.000	-0.002	0.014	0.014	0.046	0.031	0.010	0.003
2	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
3	0.000	-0.006	0.001	0.003	-0.010	-0.017	-0.031	-0.013	-0.003	-0.013
4	-0.005	-0.003	0.000	0.000	-0.005	-0.019	-0.030	-0.011	-0.001	-0.017
5	-0.008	0.005	0.000	-0.002	0.000	-0.010	-0.022	-0.012	-0.004	-0.005
6	-0.001	0.002	0.001	0.000	0.010	0.002	0.019	0.018	0.008	-0.005
7	-0.001	0.003	0.005	-0.001	0.001	-0.005	-0.007	-0.002	-0.002	-0.002
8	0.013	0.004	0.004	0.006	0.033	0.048	0.124	0.077	0.030	0.020
9	0.016	-0.002	-0.001	-0.003	0.012	0.027	0.069	0.043	0.015	0.014

Dyst A = Dystocia A, Dyst C = Dystocia C, Inf = Infection, Exp = Exposure, ADB = All Dystocia Binary, ADB+ = ADB plus Starvation-mismothering, ADO = All Dystocia Ordered, ADO+ = ADO plus Starvation-mismothering, Dystocia AB = Dystocia A and B combined, DCS = Dyst C plus Starvation-mismothering

For Dystocia C the solutions however not indicate any clear pattern for the age of dam effects. It is understood that death from this type of dystocia is associated with lighter birth weight lambs that have died from hypoxic related brain injury. Solutions indicate that the better ewes were those aged 3 and 4 years although there was no clear association between age and incidence.

Sex

Sex was a significant fixed effect for all individual autopsy classifications with the exception of Dystocia C, Infection, and lambs whose cause of death was Undiagnosed (Table 3.4). Solutions for lamb gender (not shown) indicated that female lambs were less likely to die from all death classifications than were their male contemporaries. This was not unexpected and is similar to results from numerous other studies that have found that female offspring from most mammalian species tend to survive better than do males.

3.3.2 Variance components

In general the heritabilities for individual autopsy traits were low and ranged between 0.01 and 0.04 (Table 3.9) from the maternal effects models that were the best fit according to log-likelihood ratio tests. These heritability results are disappointing although not overly surprising and imply that direct selection against any individual death category is unlikely

to result in rapid genetic gain against any individual mortality causes or survival itself. The maternal effect ranged between 0.00 and 0.12 for the autopsy traits. Maternal effect variance is composed of both maternal genetic and maternal permanent environmental components and the successful separation these components require a data structure that contains records for ewes with multiple generations of multiple births which was not possible with these data. The maternal permanent environment includes the full-sib environmental covariance between lambs of the same litter. Litter effects on important components such as birth weight could result in littermates dying from the same cause and could easily translate into litter effects affecting lamb survival traits. The separation of litter effects from maternal genetic and across-year permanent environmental effects is not possible in these data but the potential for a temporary litter effect to affect the maternal permanent environment and the complexity of the measured permanent environment should be acknowledged.

Results here imply that phenotypic selection against animals that fail reproductively would result in some genetic gain, assuming that there is a maternal genetic component, although this gain would be relatively slow given that ewes must be of reproductive age and have failed before this type of selection could be implemented. A reduction in this maternal genetic component could help explain why the phenotypic culling practice used in the 'easy-care lambing system' in New Zealand (Fisher, 2003) has successfully reduced lamb mortality to around 9%. This level of mortality is similar to that achieved under the intensive animal husbandry systems regularly practiced in the United Kingdom (Dwyer, 2008) but does not increase the incidences of difficult lambing and poor maternal care that are reported to occur in intensively managed United Kingdom flocks (Dwyer and Lawrence, 2005). Although mortality rates to 5 days age in these data were approximately 11 % of all births, this does include lambs from dams who were assisted during parturition. This implies that death rates would have been higher in these data if dams were not assisted during parturition.

Table 3.9, Phenotypic variance, heritabilities (in bold) and standard errors from a variety of variance estimation from animals and sire models for autopsy traits, with and without maternal effects (ME)

Model	Animal			Sire		
	Pvar	h^2	ME	Pvar	h^2	ME
Dystocia A	0.010	**0.07**(0.01)	-	0.010	**0.02**(0.01)	-
plus ME	0.010	**0.02**(0.01)	**0.08**(0.01)	0.010	**0.02**(0.01)	**0.08**(0.01)
Dystocia B	0.023	**0.08**(0.01)	-	0.023	**0.02**(0.01)	-
plus ME	0.025	**0.02**(0.01)	**0.06**(0.01)	0.023	**0.02**(0.01)	**0.07**(0.01)
Dystocia C	0.021	**0.17**(0.02)	-	0.021	**0.04**(0.01)	-
plus ME	0.021	**0.03**(0.01)	**0.09**(0.01)	0.021	**0.03**(0.01)	**0.09**(0.01)
Starv/mm	0.029	**0.06**(0.01)	-	0.029	**0.02**(0.01)	-
plus ME	0.029	**0.01**(0.01)	**0.06**(0.01)	0.029	**0.02**(0.01)	**0.06**(0.01)
Predation	0.008	**0.03**(0.01)	-	0.008	**0.03**(0.01)	-
plus ME	0.008	**0.02**(0.01)	**0.03**(0.01)	0.008	**0.02**(0.01)	**0.04**(0.01)
DIUPB	0.010	**0.32**(0.02)	-	0.010	**0.06**(0.01)	-
plus ME	0.010	**0.04**(0.01)	**0.11**(0.01)	0.010	**0.04**(0.01)	**0.12**(0.01)
Exposure	0.006	**0.06**(0.01)	-	0.006	**0.04**(0.01)	-
plus ME	0.006	**0.03**(0.01)	**0.04**(0.01)	0.006	**0.04**(0.01)	**0.05**(0.01)
Infection	0.002	**0.02**(0.01)	-	0.002	**0.02**(0.01)	-
plus ME	0.002	**0.02**(0.01)	**0.01**(0.01)	0.002	**0.02**(0.01)	**0.01**(0.01)
Undiagnosed	0.005	**0.01**(0.01)	-	0.005	**0.01**(0.01)	-
plus ME	0.005	**0.01**(0.01)	**0.00**(0.01)	0.005	**0.01**(0.01)	**0.00**(0.01)
Misadventure	0.001	**0.03**(0.01)	-	0.001	**0.01**(0.01)	-
plus ME	0.001	**0.01**(0.01)	**0.06**(0.01)	0.001	**0.01**(0.01)	**0.06**(0.01)

Pvar = Phenotypic variation, h^2 = heritability, Starv/mm = Starvation-mismothering, DIUPB = Died *in-utero* pre-birth

3.3.3 Death categories

Dystocia A

Dystocia A or classic dystocia is characterised by the presence of subcutaneous oedema or swelling in regions of the autopsied lamb. Dystocia A resulted in 276 total deaths and represented approximately 9% of total lamb fatalities. The direct heritability estimate for Dystocia A (0.02 ± 0.01) was considerably lower than the heritability estimate of 0.13 ± 0.03 for dystocia presented by Smith (1977). Smith's model did not include maternal effects and his result is more comparable with the estimate from the animal only model (0.07 ± 0.01) used here. In addition Smith's (1977) study also used a completely different measure of dystocia where animals were scored according to the amount of assistance

required during birth which is likely to have affected his results. A review of published literature did not uncover heritability estimates for other autopsy categories.

Dystocia B

Dystocia B represented an intermediate form of dystocia, with lambs exhibiting a mild oedema that was only noticeable after dissection. Animals dying from Dystocia B like those from Dystocia A also had evidence of central nervous system damage once autopsied. Dystocia B accounted for a total of 664 dead lambs and was the second leading cause of death, representing approximately 21% of all deaths in these data. Dystocia B was also thought to be caused by lambs of a high body weight having difficulty fitting through the dams' pelvic opening.

Dystocia C

Dystocia C was found to cause 588 deaths in this data set and accounted for approximately 18% of all mortalities. Dystocia C is a relatively new classification of dystocia that has arisen from observations that often lighter, later born animals, with no evidence of oedema are stillborn. Autopsy results however show that these animals have suffered central nervous system damage that is thought to result from an extended period of hypoxia (Haughey, 1973b). Lambs with low body mass and resulting low blood volume decreases the lamb's ability to withstand periods of oxygen depletion. This raises the possibility of reducing the incidence of death from this category by increasing the speed of birth for lambs born in multiples. Studies of pigs have shown that piglets with lower haemoglobin levels are more prone to death from hypoxia during birth especially in low birth order animals (Rootwelt *et al.* 2012). Unfortunately blood samples were not taken from the dead lambs in this study however it may be worthwhile to sample blood haemoglobin levels and to run a trial where the iron status of ewes carrying multiple foetuses is assessed. Perhaps an iron supplement or injection prior to parturition may increase the haemoglobin content of lambs and thus mitigate the incidences of death from this category.

Starvation-mismothering

Death from the Starvation-mismothering complex was the leading single death cause as determined by autopsy in this data set and accounted for 825 animals or almost 26% of all death lambs. The Starvation-mismothering complex occurs for several reasons. The cause of death is starvation however exactly why the lamb starves can be the result of abandonment, a failure of the lamb to stand and drink, a failure of the lamb or ewe to recognise or find each other in mobs or an infection or other fault in the ewe's udder.

It would also appear that small and weak lambs suffering sub-lethal meningeal haemorrhages from extended parturition durations are further disadvantaged by sub-optimal maternal behaviour exhibited by their dams. The heritability estimations for Starvation-mismothering were extremely low (0.01, 0.02) in both models that included Maternal effects (Table 3.9). This trait is also strongly affected by the behaviour and interaction of both the lamb and ewe and this in conjunction with the multiple mechanisms that causes starvation may help explain why the heritability estimates for this trait is so low.

Died in-utero pre-birth

There were 300 lambs in this data set that were classified as Died *in-utero* pre-birth. This represents just over 9% of all deaths. It is unclear as to the reason why these animals die pre-birth however it may be caused by a chromosomal abnormality similar to trisomy making the lamb unviable or possibly by a stressor or form of trauma or infection encountered by the ewe during latter stages of gestation. All lambs recorded as dying in this category were carried full term or near full term and there is therefore a high probability that other embryos died in this fashion earlier during gestation and were not accounted for during autopsy analysis. If this is true then this death category would be a higher contributor to reproductive failure than the raw numbers here suggest and addressing this cause of mortality would be beneficial in increasing the number of viable lambs born into flocks each year. Possible causes for these deaths are disease, placental insufficiency especially in multiples and inactive genes caused by DNA transcription errors or chromosomal abnormalities. In humans it is well known that increasing maternal age

increases the risk of most chromosomal abnormalities and the non-significance of age of dam for this trait suggests either that the trait is not associated with genetic abnormalities or that in sheep dam age is not associated with genetic abnormalities to the same degree that human mothers are.

The Died *in-utero* pre-birth category was the most highly heritable of all death categories in this data set with direct heritability estimates of 0.04 from both animal and sire models that included maternal effects. The Died *in-utero* pre-birth category also had the highest maternal component estimate for any autopsy trait. This again suggests that phenotypic selection against ewes with lambs in this category should reduce the incidence of this type of death in future generations although incidences of Died *in-utero* pre-birth most often occur in multiple bearing ewes. Given that the number of lambs dying in this category is likely to be underestimated action to reduced its incidence could significantly increase overall reproductive performance over generations.

Predation

Predators such as feral pigs, foxes and dogs are known to take lambs as do wedge tailed eagles on rare occasions. The incidence of these strikes is most often related to environmental factors that allow predator numbers to build up. Management activity, such as baiting, and shooting the mammalian predators can assist mitigating deaths from predation however this is not always successful or possible. Death from Predation accounted for approximately 7% of all deaths in this data set. Given the large environmental influence on this trait it was not surprising that direct heritability estimates for death by Predation were very low, 0.02, as were the estimated maternal effect components (Table 3.9). Unlike other traits so far discussed there would be little advantage in phenotypic selection against this trait. It is likely that predators target lambs that have already been weakened from some other cause and correlations between this trait and other death categories may be useful in illuminating potential underlying causes for predation.

Exposure

Death from Exposure occurs when environmental conditions exceed the lambs' capacity to offset adverse conditions metabolically. Usually this occurs in cold conditions where a lamb lacks the sufficient body reserves to maintain a sufficiently high temperature and the lamb then dies of hypothermia. Less frequently lambs can die of hyperthermia where the lamb's core body temperature becomes too high to sustain life, this can happen during high temperature extremes and although this is unlikely to occur presently in most lamb producing areas of Australia this could become a more important factor in the future as the incidence of heat wave events is predicted to rise. Death from Exposure in this data set accounted for almost 5% of all deaths with 159 animals falling into this category. Body weight and prevailing weather conditions are known to be strongly associated with this trait and unsurprisingly contemporary group, which accounts for environment, and birth weight fitted within birth type were highly significant for death from Exposure (Table 3.4). Body reserves of lipids are the primary source of energy in new born lambs and increased body weight is expected and reported (Holst *et al.* 2002) to have a positive association with increased lipid deposits. In addition lipid deposits or fat are insulators that would further protect lambs from extremes of both hot and cold temperatures. Numerous managerial options are available to limit death from exposure including timing of birth events by joining rams at earlier or later dates, sheering ewes prior to lambing to increase their propensity to seek shelter, establishing shelter belts and moving ewes into more protected paddocks prior to parturition.

Direct heritability estimates for death from Exposure were low, 0.03 and 0.04 from animal and sire models that included a maternal effects component. The maternal effects component (consisting of a combination of genetic and non-genetic maternal effects) was also low, estimated at 0.04 and 0.05 from the animal and sire models respectively. Again this low direct heritability indicates that direct selection against Exposure would result in minimal gain for this trait. The maternal effects estimate also suggests that phenotypic selection against ewes with lambs suffering this cause of death would not be as rapid in reducing the maternal genetic component that associated this trait as phenotypic selection against death causes with higher maternal components.

Infection

Death from infection only accounted for 44 animals in this data set which represented only 1% of the total number of animals that died. Perhaps this low number is a reflection of the high managerial standards or the dryer conditions experienced by the IN flocks. In flocks less well managed or in wetter environment this death category is likely to account for a larger proportion of deaths. Such low numbers are difficult to base a genetic analysis on however significant effects for this death category included both birth weight and dam age. Model solutions for birth weight (Table 3.6) indicated that lower birth weight animals were more prone to death from infection and perhaps this was a result of lower available body reserves to fight off the pathogens or lower colostrum intake arising perhaps from a lower suckling drive. Heritability estimates for infections were all very low regardless of the model used and did not exceed double their standard errors on any occasion. If infection is a problem in flocks it is highly likely that management techniques to address the source would be a quicker and more successful strategy than would genetic selection.

Undiagnosed

The cause of death for these animals was not able to be determined by autopsy analysis of their carcasses. This occurred on 123 occasions and represented fewer than 4% of the total deaths in these data. Heritability estimates from all models (Table 3.9) were very low and did not exceed their standard errors on any occasion. This can give some confidence that there is no genetic component to this death category and from these results it cannot be successfully selected against.

Misadventure

Lambs can die from numerous form of misadventure including falling into water points and drowning or getting caught in fences. Lambs classified into this category died as a result of these types of mishaps. Fortunately there were only 29 such animals which is possibly representative of superior management of these research flocks. Again this is too low a number to base a reliable genetic analysis on. Flock management is a contributing factor to these type of deaths and managerial considerations can do much to mitigate deaths from misadventure. Direct heritability estimates were low (Table 3.9) although there was a

relatively high maternal component estimate 0.06 from both models. This suggests that the dam plays a role in the death of her lamb from misadventure. Given that these lambs were born viable it is likely that this results from dam behaviour and could perhaps be explained by the dam partaking in dangerous activities like drinking from a dangerous watering point or attempting to cross fence lines. Phenotypic selection against dams who fail to rear a lamb would reduce any maternal genetic component that contributes to these types of deaths and would also reduce the opportunity for animals to learn from ewes who exhibit potentially dangerous behaviours.

3.3.4 Composite traits

Composite traits were developed in order to increase the number of records available for analysis and so that some traits could be assessed as a block for genetic correlation estimation. Ordered Dystocia was created to compare the results of a more normally distributed trait with the otherwise binary traits. Starvation-mismothering records were included with the Ordered and Binary Dystocia traits and the Dystocia C trait on the basis of published scientific literature that suggests that the 2 traits are related. Effects that were significant for any of the individual traits models (Table 3.4) were usually significant in composite trait models (Table 3.5) and their significance was a function of the proportion of records that any individual trait contributed to the composite trait. Direct heritability results from the composite traits (Table 3.10) were again very low, ranging from 0.02 to 0.04. Results indicated that there was no benefit derived in terms of the size of the heritability from splitting dystocia into the 3 different categories although this separation of dystocia traits did give some insight into the biological mechanisms associated with deaths in each category.

Table 3.10, Heritabilities and standard errors from a variety of variance estimation models for composite dystocia traits

Model	Animal			Sire		
	Pvar	h^2	PE	Pvar	h^2	PE
ADB	0.051	**0.19**(0.02)	-	0.050	**0.04**(0.01)	-
plus ME	0.050	**0.04**(0.01)	**0.09**(0.01)	0.050	**0.04**(0.01)	**0.10**(0.01)
ADB+	0.075	**0.22**(0.01)	-	0.073	**0.05**(0.01)	-
plus ME	0.073	**0.04**(0.01)	**0.10**(0.01)	0.073	**0.04**(0.01)	**0.11**(0.01)
ADO	0.447	**0.18**(0.02)	-	0.439	**0.04**(0.01)	-
plus ME	0.436	**0.03**(0.01)	**0.09**(0.01)	0.438	**0.03**(0.01)	**0.10**(0.01)
ADO+	0.199	**0.14**(0.01)	-	0.193	**0.03**(0.01)	-
plus ME	0.193	**0.03**(0.01)	**0.09**(0.01)	0.193	**0.03**(0.01)	**0.10**(0.01)
Dystocia AB	0.033	**0.10**(0.01)	-	0.033	**0.02**(0.01)	-
plus ME	0.033	**0.02**(0.01)	**0.08**(0.01)	0.033	**0.02**(0.01)	**0.09**(0.01)
Dystocia BC	0.042	**0.18**(0.02)	-	0.042	**0.04**(0.01)	-
plus ME	0.041	**0.03**(0.01)	**0.09**(0.01)	0.042	**0.04**(0.01)	**0.10**(0.01)
DCS	0.048	**0.21**(0.01)	-	0.047	**0.04**(0.01)	-
plus ME	0.047	**0.03**(0.01)	**0.09**(0.01)	0.047	**0.03**(0.01)	**0.10**(0.01)
Survival	0.098	**0.25**(0.02)	-	0.094	**0.05**(0.01)	-
plus ME	0.094	**0.04**(0.01)	**0.10**(0.01)	0.095	**0.05**(0.01)	**0.11**(0.01)

h^2 = heritability, PE = Maternal effect, ADB = All Dystocia Binary, ADB+ = ADB plus Starvation-mismothering (SMM), ADO = All dystocia ordered, ADO+ = ADO plus SMM, Dystocia AB = Dystocia A and B combined, Dystocia BC = Dystocia B and C combined, DCS = Dystocia C plus SMM

All Dystocia Binary (ADB)

Deaths from the 3 Dystocia classes combined accounted for 1519 animals which represented almost half of all mortalities in this data set. This is less than that reported by Holst *et al.* (2002) who reported that two thirds of the dead lambs in their study based on lambs from Merino and Border Leicester × Merino ewes died from dystocia related causes but is comparable to the results presented by Scales *et al.* (1985) and Hinch *et al.* (1986). The total number of deaths from combined Dystocia categories in this data set would have been higher without the intervention and assistance that was given to ewes enduring difficult births.

Results from the individual Dystocia categories indicate that although all deaths are related to difficult births there are different mechanisms involved especially between Dystocia A and C. When the individual death categories are combined twin births have the highest solution indicating the lowest incidence (Figure 1). Birth weights for twin lambs are

generally lower than that of singles and it is possible that this reduces incidents of classic dystocia in twin lambs births. Similarly the interval between the onset of labour and delivery of the final lamb is expected to be shorter for twins than for higher multiple births thereby reducing the duration of birth-associated hypoxia in twins compared to higher order multiple births. This seems to suggest that breeding for ewes that bear twin lambs of approximately mean birth weights could be an effective strategy in reducing all dystocia related lamb fatalities and increasing weaning rates. The heritability of ADB was estimated at 0.04 from the models that included the maternal effect. This indicates that there is no advantage from a variance estimation perspective in separating animals that have died as a result of difficult births into distinct categories.

All Dystocia Binary plus Starvation-mismothering (ADB+)

This category was created with the reasoning that a genetic element of Starvation-mismothering is related to birth difficulties. Numerous scientific papers (Haughey, 1973a, Dutra *et al.* 2007, Dutra and Banchero 2011, Hinch *et al.* 1986, Schreurs *et al.* 2009, Maund *et al.* 1980 and Woolliams *et al.* 1983) have demonstrated that a relationship exists between parturition duration and neonatal viability and behavior, where longer parturition times decrease viability and results in impaired lamb behavior.

The direct heritability for this trait was the same as that estimated for the ADB trait and suggests that from a genetic analysis perspective there is no gain or loss obtained by including Starvation-mismothering records with ADB records although direct genetic selection against would result in little gain.

All Dystocia Ordered (ADO)

Ordered Dystocia was created to compare the results of a more normally distributed trait with the otherwise binary traits. Solution results from this trait similar to those from the All Dystocia Binary trait. The direct heritability estimate was higher than those for the individual categories and lower but not significantly different from the ADB heritability estimate.

All Dystocia Ordered plus Starvation-mismothering (ADO+)

This trait was similar to the ADB+ trait and as for ADO heritability estimates were again lower but not significantly different to those for the binary trait. This is the same result as seen for ADB and ADB+ where the inclusion of the Starvation-mismothering data did not alter the direct heritability estimate. This suggests that the ordering of this data does impact on variance estimates and perhaps assessing it as a binary trait is more reliable.

Dystocia AB and Dystocia BC

These traits were created to determine if combining Dystocia B with either of the other dystocia categories resulted in higher heritability estimates. Birth weight solutions from the individual autopsy traits suggested that Dystocia B was more related to Dystocia A than to Dystocia C. Solution rankings for other significant effects for these traits are not as informative as solutions from individual autopsy traits and are representative of the weightings of the number of animals represented by each category. Somewhat surprisingly direct heritability results (Table 3.10) for Dystocia AB were lower than those for Dystocia BC.

Dystocia CSM

Again this composite trait was created so that heritability estimates of the combined trait could be compared between this trait and other composite and individual estimates. Published literature indicates that longer parturition times are associated with lambs that are slower to suckle and it was thought that animals that had died from this composite category had mostly suffered from extended parturition times. Interestingly this trait had a higher direct heritability than either component trait in the basic animal model however when maternal effects were included the majority of the variation was shifted in this effect. Again this implies that the maternal component of the dam (both genetic and environmental) is the factor that is most responsible for death from either Dystocia C or from Starvation-mismothering.

3.4.5 Indicator traits

A number of potential indicator traits for lamb survival were also available in these data. These included measurements on Lamb ease, Crown-rump lengths and Thorax circumference at the last rib. Crown-rump lengths and Thorax circumference were also used as proxies for height and circumference in formulas for the surface area and volume of a cylinder to test whether these traits were of more value than their individual component traits.

Thorax circumference, Crown-rump length, Lamb surface area and Lamb volume were not fitted in final variance estimation models. This was again done so that correlations between these potential predictor traits could be estimated. Trial models were run using the SAS software where these traits were fitted to individual autopsy traits. These models revealed that these traits were generally significant for many autopsy traits indicating that they have potential as indicator traits.

Heritabilities for the potential predictor traits ranged from 0.08 for Lamb ease to 0.21 for Crown-Rump length (Table 3.11). Heritability estimates for Lamb Surface area (0.18) and Lamb volume (0.16) were intermediate between their constituent traits Crown-rump length and Thorax circumference. Maternal effect estimates ranged between 0.18 and 0.30. Both direct heritability and maternal effect estimates were considerably higher than estimates for individual death categories indicating that selection based on these traits would result in more rapid genetic gain than selection for individual or composite autopsy traits would achieve, should they be correlated with lamb survival.

Table 3.11, Heritabilities (in bold) and standard errors from a variety of variance estimation models for potential indicator traits

Model	Animal			Sire		
	Pvar	h^2	PE	Pvar	h^2	PE
Lamb ease	0.271	**0.64**(0.02)		0.237	**0.09**(0.01)	
plus ME	0.239	**0.08**(0.01)	**0.30**(0.01)	0.239	**0.09**(0.01)	**0.32**(0.01)
CR Length	12.83	**0.59**(0.02)		11.72	**0.21**(0.02)	
plus ME	11.84	**0.21**(0.02)	**0.17**(0.01)	11.83	**0.20**(0.02)	**0.22**(0.01)
Thorax	5.93	**0.51**(0.04)		5.40	**0.11**(0.02)	
plus ME	5.47	**0.12**(0.02)	**0.18**(0.02)	4.46	**0.10**(0.02)	**0.21**(0.01)
Lamb SA	44333	**0.70**(0.04)		38374	**0.17**(0.01)	
plus ME	39248	**0.18**(0.03)	**0.22**(0.02)	39012	**0.16**(0.03)	**0.26**(0.01)
Lamb Volume	739700	**0.65**(0.04)		648010	**0.15**(0.01)	
plus ME	663600	**0.16**(0.03)	**0.21**(0.02)	0.000	**0.15**(0.02)	**0.25**(0.01)

CR Length = Crown-rump length, Lamb SA= Lamb Surface area, h^2 = heritability, PE = Maternal effect

3.3.6 Production traits

Heritability estimates for the production traits Greasy-fleece weight and Yearling weight were estimated. This was done so that these traits could be used for genetic correlation estimation with the autopsy traits. Heritability estimates for Greasy-fleece weight and Yearling weight (Table 3.12) were moderately high at 0.50 ± 0.06 and 0.37 ± 0.06 and these are similar to published estimates for these traits (Safari *et al.* 2005).

Table 3.12, The number of records (n), mean values, phenotypic variance (σ_P^2), heritabilities (h^2) and maternal permanent environment (pe) for Greasy-fleece weight and Yearling weight

	n	mean	σ_P^2	h^2	pe
Greasy-fleece weight (kg)	4601	3.53	0.36	0.50(0.06)	0.08(0.03)
Yearling weight (kg)	8377	42.3	30.17	0.37(0.04)	0.08(0.02)

3.3.7 Logit link models

All traits analysed thus far with the exception of ADO and ADO+ had binary distributions and were analysed in ASReml using the assumption of a normal distribution. Results from the ADO and ADO+ analysis indicated that heritability estimates might alter if these traits were more normally distributed. The ASReml program can analyse traits using a logit link

function. This is accomplished by randomly allocating a value to all values above and below a threshold (in this case 1) so that a more normal distribution can be approximated. The variance on the underlying scale is $\pi^2/3 \sim 3.3$ (underlying logistic distribution) for the logit link (Gilmour *et al.* 2008). Literature also indicates that transformation of the data in this manner results in higher heritability estimates on the underlying scale (Matos *et al.* 2000, Morris *et al.* 2000). Sire models are more robust than animal models when estimating variance components in this way (pers comm. David Johnson).

The use of the logit link function in these data did result in noticeably higher direct and maternal affect estimates although corresponding standard errors were also increased (Table 3.13). Models converged faster and appeared to be more in line with expectation when record numbers were higher. Heritability and maternal effect estimates from individual autopsy and composite traits (Table 3.14) were all higher when modelled as binary traits suggesting that survival may be improved genetically by the incorporation of these traits into selection indices. Direct heritability estimates imply that All Dystocia Binary and Died *in-utero* pre-birth category may be useful in genetically reducing lamb losses through their inclusion in selection indices. The results here again suggest that there is no advantage in splitting dystocia into its different sub categories. Results also suggest that phenotypic selection against ewes that fail reproductively would also assist in reducing lamb losses through the removal of the genetic component of the maternal effect in breeding flocks.

Table 3.13, Underlying heritabilities (in bold) and standard errors from animal and sire models with and without maternal effects (PE) for autopsy traits using the logit link function

Model	Sire		
	Pvar	**h²**	**PE**
Dystocia A	3.53	**0.28**(0.12)	-
plus ME	4.52	**0.08**(0.10)	**0.25**(0.05)
Dystocia B	3.46	**0.20**(0.06)	-
plus ME	4.24	**0.10**(0.05)	**0.20**(0.03)
Dystocia C	3.49	**0.23**(0.07)	-
plus ME	4.38	**0.09**(0.06)	**0.23**(0.03)
Starvation-mismothering	3.39	**0.12**(0.05)	-
plus ME	4.04	**0.05**(0.04)	**0.17**(0.03)
Predation	3.69	**0.44**(0.15)	-
plus ME	4.07	**0.32**(0.16)	**0.11**(0.07)
DIUPB	3.88	**0.61**(0.14)	-
plus ME	5.07	**0.19**(0.12)	**0.30**(0.04)
Exposure	3.60	**0.35**(0.18)	-
plus ME	4.11	**0.22**(0.17)	**0.14**(0.08)
Infection	4.11	**0.80**(0.42)	-
plus ME	4.37	**0.72**(0.49)	**0.07**(0.24)
Undiagnosed	3.42	**0.14**(0.25)	-
plus ME	3.64	**0.11**(0.24)	**0.07**(0.17)
Misadventure	3.92	**0.64**(0.60)	-
plus ME	5.09	0.00	**0.35**(0.13)

Pvar = Phenotypic variation, h^2 = heritability, PE = Maternal effect**,** DIUPB = Died *in-utero* pre-birth

Table 3.14, Heritabilities (in bold) and standard errors from animal and sire models with and without maternal effects (PE) for composite autopsy traits using the logit link function

Model	Sire		
	Pvar	h^2	PE
ADB	3.46	**0.20**(0.04)	-
Plus ME	4.21	**0.13**(0.04)	**0.19**(0.02)
ADB+	3.45	**0.18**(0.03)	-
Plus ME	4.11	**0.13**(0.13)	**0.17**(0.01)
Dystocia AB	3.44	**0.17**(0.05)	-
Plus ME	4.24	**0.09**(0.04)	**0.20**(0.02)
Dystocia BC	3.46	**0.20**(0.04)	-
Plus ME	4.20	**0.12**(0.04)	**0.19**(0.02)
DCS	3.42	**0.16**(0.04)	-
Plus ME	4.23	**0.08**(0.03)	**0.20**(0.02)

h^2 = heritability, PE = Maternal effect**,** ADB = All dystocia binary, ADB+ = ADB plus Starvation-mismothering (SMM), Dystocia AB = Dystocia A and B combined, Dystocia BC = Dystocia B and C combined, DCS = Dystocia C plus SMM

3.4 Conclusions

The major causes of death in these data are some form of Dystocia and Starvation-mismothering. Results imply that there are 2 different mechanisms involved with death by dystocia, the first being large lambs and the second being smaller birth weight lambs in larger litters. It appears that higher birth weights are involved with deaths from Dystocia A and B and lower birth weights are associated with death from Dystocia C and Starvation-mismothering. Heritability estimates indicate that there will be little to no advantage achieved by genetically selecting against individual traits over the more easily observed survival trait. Survival was estimated to have a direct heritability of 0.04 plus a maternal component of 0.10. Both traits could be included in BLUP (Best Linear Unbiased Prediction) models to generate estimated breeding values for survival that could be included into selection indices.

Heritability estimates derived using the logit link function, do indicate that the selection against the combined dystocia category (ADB) and the Died *in-utero* pre-birth traits could prove effective in reducing mortalities. Also, assuming there is a maternal genetic component phenotypic selection against ewes whose lambs die from these causes should

result in an overall decrease in lamb mortality over time. In addition results imply that twin lambs are less likely to die from dystocia associated deaths and that there is most likely an optimum weight for these lambs. Management is probably the key to reducing death from other less heritable causes including Exposure, Predation and Infection.

Chapter 4 Genetic Correlations

4.1 Introduction

Genetic correlations are an indication of how related one trait is to another genetically or how one trait will vary in line with variations in the other. A high genetic correlation indicates that the two traits are genetically similar and that the causal genes are shared (pleiotropism) or linked through gametic phase disequilibrium while a low genetic correlation indicates that the two traits have few shared or linked genes. In addition, understanding the size and direction of genetic correlations between traits of economic importance like cause of death and greasy-fleece weight or yearling weight indicate how the autopsy trait is expected to vary due to selection pressure being placed on the production trait.

Repeated studies have shown that lamb survival is a very lowly heritable trait (Safari *et al.* 2005). This could be the result of the numerous different biological causes of lamb death and the many different genes that control these causes. Therefore direct genetic selection for increased survival, although highly desirable because of its permanence, is unlikely to be a successful option. The identification of easily measured field traits that are correlated with survival has not yet been achieved.

The objective of this chapter is to estimate and discuss genetic correlations between autopsy traits, between autopsy traits and the potential survival indicator traits Lamb ease, Thoracic circumference, Crown-rump length, Lamb Surface area and Lamb volume as well as between autopsy traits and the production traits Greasy-fleece weight and Yearling weight.

4.2 Materials and methods

Genetic correlations were estimated using the same data as used for Chapter 4 for all traits with the exception of survival. To estimate genetic correlations with lamb survival to 3 days age, additional data from the Sheep Co-operative Research Centre (CRC) Information Nucleus Flocks for the 2007 drop were included so that an element of the lamb survival

trait was independent of the autopsy results. This resulted in the addition of 5,582 birth records bringing the total number of records to 32,222. Of these 3,755 lambs died and 3224 had autopsy records. The total number of sires represented for survival was 529 and the total number of dams was 12,775. Genetic correlations were not estimated for the traits: Exposure, Infection, Undiagnosed and Misadventure due to the low number of animals in these categories and the very low heritability estimates for these traits (Chapter 3, Table 3.9). Similarly correlations were not estimated for the composite traits Ordered Dystocia and Ordered Dystocia + Starvation-mismothering as the traits were very similar to the All Dystocia Binary and All Dystocia Binary plus Starvation-mismothering traits which had higher heritabilities.

4.2.1 Models

All correlations were estimated using sire models which included maternal permanent environment effects using ASReml software (Gilmour, *et al.*, 2008). Sire models were used as they are much more stable in ASReml software when estimating genetic correlations than animal models (pers. comm. D. Johnson) as they require fewer equations to be solved than do animal models. In addition, not all animals have all records as the INF is designed to record traits among half sibs. Correlations were also estimated using animal models however fewer of these models converged compared to sire models. All models used the same fixed and random effects as the individual and composite trait models outlined in Chapter 4 (Tables 3.4 and 3.5). Residual co-variances could not be estimated between all trait combinations and for this reason were ignored for those traits where both traits were recorded on the same animal.

4.3 Results and Discussion

The large standard errors associated with the majority of correlation estimates are a function of the low heritability estimates for the traits, the low number of autopsy records available for analysis and the binary nature of the autopsy category data. Given these large standard errors, the estimates presented here would be likely to change if more data became available for analysis and this should be taken into consideration and all results presented in this chapter should be viewed as preliminary only. Even with additional data

the standard errors associated with correlation estimates would be likely to remain high as heritability estimates would not be expected to significantly rise and autopsy records are segregated into individual death causes.

4.3.1 Correlations between autopsy traits

Individual autopsy traits

The genetic correlation between Dystocia A and Dystocia B (Table 4.1) was very low and not significant (0.02 ± 0.22). The lack of a significant genetic correlation between the 2 traits implies that the traits are controlled by different genes which was surprising given that both traits are the result of difficult parturitions and share evidence of oedema. Another surprising result was the stronger genetic correlation estimate between Dystocia A and Dystocia C (0.41 ± 0.22). Results in Chapter 4 indicated that these two death categories were likely to be caused by different mechanisms and a moderate positive correlation between these 2 traits was not expected. The moderately high correlation implies that selection against either death category is likely to impact favourably on the incidence of the other while not acting in a detrimental manner on instances of Dystocia B.

Table 4.1, Genetic correlations between individual autopsy traits

	Dystocia A	Dystocia B	Dystocia C	Starvation-mismothering
Dystocia B	0.02 (0.26)	-	-	-
Dystocia C	0.41 (0.22)	0.40 (0.21)	-	-
Starvation-mismothering	-0.34 (0.27)	0.48 (0.27)	0.36 (0.22)	-
Died *in-utero* pre-birth	0.24 (0.19)	0.02 (0.18)	-0.16 (0.15)	-0.05 (0.19)

Dystocia A was negatively genetically correlated with Starvation-mismothering (-0.34 ± 0.27). The correlation implies that both traits are associated with difficult births independent of birth weight. Unfortunately this correlation implies that selection against either Dystocia A or Starvation-mismothering would lead to a rise in the incidence of the other trait. Overall incidences of death from Starvation-mismothering outnumber incidences of Dystocia A by approximately 3 to 1. These correlations create some doubt over the previously stated hypothesis (Chapter 3, page 52) that these traits could be combined for variance estimation purposes. This hypothesis was based on the heritability

results for the combined All Dystocia trait and All Dystocia plus Starvation-mismothering reported in Chapter 3, Table 3.10.

Dystocia A was positively genetically correlated with the Died in-*utero* pre-birth autopsy category (0.24 ± 0.19). This association is favourable in that selection against either should lead to a reduction in the incidence of both. The genetic correlation between Starvation-mismothering and Dystocia A was negative (-0.34) while the genetic correlations between Starvation-mismothering and both Dystocia B (0.48) and Dystocia C (0.36) were positive.

Dystocia B correlations with Dystocia C (0.40 ± 0.21) and with Starvation-mismothering (0.48 ± 0.27) exceeded their standard errors. This suggests that genetic selection against any of these categories would lead to a reduction in deaths from the other. In addition the correlation estimate between Dystocia B and Dystocia A was very low (0.02 ± 0.26) suggesting that selection against Dystocia B would have little impact on the incidence of Dystocia A. However, direct selection against any of these categories would be difficult as the traits all have low heritabilities (Chapter 3, Table 3.9) and the individual dystocia category can only be determined after the carcass has been autopsied. Overall the moderate positive correlations between the different classes of Dystocia imply that categorising events of Dystocia into different classes imparts little additional benefit over the combined Dystocia category although it does show that reducing the incidence of Dystocia A would adversely impact on the incidence of Starvation-mismothering. Given that the number of animals impacted by Dystocia B, C and Starvation-mismothering (2077) far outweigh the number of animals impacted by Dystocia A (276) this result is of minor consequence to the overall goal of reducing lamb mortality.

As well as being positively correlated with both other dystocia categories Dystocia C was genetically positively correlated with Starvation-mismothering (0.36 ± 0.22) and negatively correlated with the Died *in-utero* pre-birth category (-0.16 ± 0.15). The positive correlation between Dystocia C and Starvation-mismothering is favourable but the negative correlation with the Died *in-utero* pre-birth category is not. The positive correlation between Dystocia C and Starvation-mismothering indicates that similar genes are involved in deaths from both categories and is expected given the negative effects that

low birth weight and increasing litter size has on both traits (Chapter 3, Table 3.6). This adds further weight to the argument that the causal mechanisms are similar between the two traits as discussed in Chapter 1 and suggests that a portion of the lambs dying from Starvation-mismothering may have suffered some form of birth trauma as suggested by Haughey (1973a); the most likely cause being sub-lethal hypoxia.

Composite autopsy traits

Genetic correlation estimates between the composite autopsy trait Survival and individual and composite autopsy traits ranged between 0.39 (Dystocia A) and 0.88 (All Dystocia Binary plus Starvation-mismothering) (Table 4.2). Unfortunately in these data all animals with an autopsy record appeared in the survival trait as dead animals and all genetic correlation estimates were a function of the proportion of animals that contributed to the dead category in the Survival trait. For example the lowest correlation estimate (0.39) for Dystocia A had the lowest number of records (276) and the highest genetic correlation estimate (0.88) was for All Dystocia Binary plus Starvation-mismothering, which was the trait with the largest number of records (2353). Unbiased correlation estimation requires the 2 traits under examination to be independent (not a component) of each other and in these data information on Autopsy traits and Survival were not independent. This lack of independence between traits and the resulting bias in correlation estimates severely restricts the value of all correlation estimates between survival and all individual and composite autopsy traits in these data.

The genetic correlation between Dystocia A and the combined Dystocia BC category was positive which was expected given the moderate correlation found between Dystocia A and Dystocia C. There was also a strong correlation between Dystocia C and the combined Dystocia AB category. Interestingly there was also a moderately strong correlation (0.54) found between Dystocia B and the combined Dystocia C and Starvation-mismothering category (DCS). This implies that all 3 causes of death share similar genes. This result reinforces Haughey's (1973b) contention that a large element of Starvation-mismothering is related to sub-lethal hypoxia suffered as a result of difficult parturitions.

Table 4.2, Genetic correlations between and individual and composite autopsy traits

	DystA	DystB	DystC	Smm	Diupb	ADB	ADB+	DAB	DBC
ADB	0.61	0.75	0.91	0.37	-0.03				
	(0.14)	(0.09)	(0.06)	(0.21)	(0.14)				
ADB+	0.38	0.80	0.88	0.71	-0.03	0.94			
	(0.17)	(0.10)	(0.08)	(0.11)	(0.14)	(0.03)			
DAB	0.61	0.88	0.56	0.27	0.14	0.90	0.85		
	(0.16)	(0.05)	(0.22)	(0.27)	(0.19)	(0.06)	(0.09)		
DBC	0.30	0.83	0.90	0.49	-0.09	0.97	0.96	0.87	
	(0.20)	(0.07)	(0.05)	(0.21)	(0.14)	(0.02)	(0.04)	(0.09)	
DCS	0.09	0.54	0.89	0.81	-0.13	0.84	0.94	0.53	0.90
	(0.22)	(0.21)	(0.06)	(0.07)	(0.15)	(0.10)	(0.04)	(0.22)	(0.09)
Surv	0.39	0.76	0.66	0.69	0.41	0.81	0.88	0.81	0.82
	(0.17)	(0.11)	(0.10)	(0.12)	(0.11)	(0.06)	(0.03)	(0.10)	(0.06)

DystA = Dystocia A, DystB = Dystocia B, DystC = Dystocia C, Smm = Starvation-mismothering, Diupb = Died *in-utero* pre-birth, ADB = All dystocia binary, ADB+ = All dystocia binary plus Starvation-mismothering, DAB = Dystocia A plus B, DBC = Dystocia B plus C, DCS = Dystocia C plus Starvation-mismothering, Surv = Survival

4.3.2 Correlations with indicator traits

With the exception of Lamb ease the genetic correlations between individual autopsy traits and potential indicator traits (Table 4.3) only exceeded their stand errors for a minority of traits. These were: Thorax circumference and Dystocia B (0.38 ± 0.22), Crown-rump length and Dystocia A (-0.15 ± 0.14) and Lamb surface area and Died *in-utero* pre-birth (0.18 ± 0.16). However, Lamb ease was positively correlated with Dystocia A (0.45 ± 0.16), Dystocia C, (0.18 ± 0.13), Died *in-utero* pre-birth (0.25 ± 0.11) and overall Survival (0.38 ± 0.11).

Table 4.3, Genetic correlations and their standard errors between potential predictor traits and individual and composite autopsy traits

	Lamb ease	Thorax	Crown-rump	Lamb surface area	Lamb volume
Dystocia A	0.45 (0.16)	0.24 (0.26)	-0.15 (0.14)	0.01 (0.23)	0.07 (0.24)
Dystocia B	0.09 (0.15)	0.38 (0.22)	-0.02 (0.14)	0.03 (0.20)	0.13 (0.20)
Dystocia C	0.18 (0.13)	-0.03 (0.19)	0.07 (0.11)	0.01 (0.18)	0.03 (0.18)
Starvation-mismothering	0.14 (0.17)	0.25 (0.23)	-0.02 (0.15)	-0.08 (0.22)	-0.02 (0.22)
Died *in-utero* pre-birth	0.25 (0.11)	-0.05 (0.17)	-0.02 (0.10)	0.18 (0.16)	0.13 (0.16)
All Dystocia Binary	0.26 (0.12)	0.26 (0.18)	-0.01 (0.11)	0.02 (0.16)	0.10 (0.17)
All Dystocia Binary+	0.26 (0.12)	0.27 (0.17)	-0.01 (0.10)	-0.03 (0.16)	0.05 (0.16)
Dystocia AB	0.29 (0.15)	0.44 (0.23)	-0.10 (0.14)	0.03 (0.21)	0.15 (0.21)
Dystocia BC	0.16 (0.12)	0.23 (0.18)	0.04 (0.11)	0.01 (0.16)	0.09 (0.17)
DCS	0.20 (0.13)	0.16 (0.19)	0.04 (0.11)	-0.04 (0.18)	0.02 (0.18)
Survival	-0.38 (0.11)	0.18 (0.20)	-0.03 (0.13)	0.11 (0.19)	0.13 (0.19)

All Dystocia Binary + = All Dystocia plus Starvation-mismothering, Dystocia AB = Dystocia A plus Dystocia B, Dystocia BC = Dystocia B plus Dystocia C, DCS = Dystocia C plus Starvation-mismothering

Lamb ease

Results in Table 4.3 show that Lamb ease, or the amount of difficulty experienced by the ewe during parturition has the highest genetic correlation of all the potential indicator traits with the various autopsy categories and also a moderately favourable correlation with the Survival trait.

Thorax circumference

Thoracic circumference was positively correlated with Dystocia B (0.38 ± 0.22) and Starvation-mismothering (0.25 ± 0.23) as well as all composite categories that included Dystocia B. Together, Dystocia B and Starvation-mismothering account for almost half of all deaths in these data. The positive correlation estimates indicate that animals with larger Thoracic circumferences, independent of birth weight, are genetically associated with increased incidences of mortality. This implies that selection against larger thoraxes should lead to a reduction in death incidences from these death causes. In addition, the positive correlation estimated between Thoracic circumference and All Dystocia plus Starvation-mismothering implies that selection based on Thoracic circumference should also reduce deaths in this combined category that encompasses over 70% of all deaths in these data. It would be expected that selection for decreased Thoracic circumference at fixed birth

weights would result in lambs that were longer and thinner provided that birth weight was maintained. This would be expected to facilitate easier births for these lambs especially in instances where the dam's pelvic opening is a limiting factor to ease of birth.

Surprisingly Thoracic circumference was not correlated with Dystocia A. It would be expected that selection for decreased Thoracic circumference would decrease Crown-rump length given the positive genetic correlation estimate between the 2 traits of 0.17 ± 0.11. Lambs that have smaller thoracic circumferences and shorter crown-rump lengths would also be likely to have lower birth weights. This implies that selection on Thoracic circumference would only be advisable when attention was given to maintaining birth weight at acceptable levels.

Results in Chapter 3 of this thesis suggested that different mechanisms may be involved in deaths arising from Dystocia C opposed to the other two dystocia classes. The negative non-significant genetic correlation estimate between Dystocia C and Thoracic circumference reported here appears to support that interpretation. This negative genetic correlation although non-significant does imply that selection for smaller Thoraxes could increase instances of Dystocia C.

Crown-rump length

The negative genetic correlation estimate between Crown-rump length and incidences of Dystocia A (-0.15 ± 0.14) was the only correlation estimate with Crown-rump length that exceeded its standard error (Table 4.3). This suggests that animals with longer bodies at given birth weights will be likely to breed lambs that are less likely to die from this classic form of dystocia. This also suggests that Crown-rump length may be a useful indirect selection criterion for reducing the incidence of Dystocia A without adversely affecting other autopsy categories. It is expected that selection for increased Crown-rump length while maintaining birth weight would change the shape of lambs so that they would become longer and thinner. Longer and thinner lambs would be expected to less prone to trauma caused by feto-pelvic disproportion and would be expected to suffer less oedema and reduced hypoxia as a result. Measurements on Crown-rump length could be easily undertaken in the field and Crown-rump length was the most heritable (0.21 ± 0.02)

(Chapter 3, Table 3.9) of all the potential survival indicator traits. The negative genetic correlation between Crown-rump length and Dystocia A however did have a large standard error and this correlation should be confirmed before any selection of this type is implemented.

Lamb Surface area and Lamb volume

The only genetic correlation between Lamb Surface area and Lamb volume that exceeded its standard error was the correlation between Lamb surface area and the Died *in-utero* pre-birth category (0.18 ± 0.16) (Table 4.3). This correlation indicates that genetically, death in this category is associated with lambs that have larger surface areas. Lambs that have died *in-utero* are generally small for their gestational age (pers. comm. G. Hinch) and would therefore be expected to have large surface areas per unit weight.

The only genetic correlation between Survival and the potential survival indicator traits that exceeded its standard error was with Lamb ease (-0.38 ± 0.11). The negative genetic correlation between Lamb ease and Survival indicates that the more difficult the birth and the more assistance required during birth the more likely the lamb would be to breed animals that are likely to die. However, Lamb ease is an easy to score trait in seed-stock flocks which are generally used to human contact. Ewes within these flocks would be unlikely to exhibit the negative effects that are reported to occur in flocks unused to human contact.

Lambing ease as a trait is already available in Sheep Genetics (The national genetic information and evaluation service for the meat and wool sectors of the Australian sheep industry) and is already being used by early adopting breeders to reduce lambing difficulty. Genetic gain in lambing ease and associated lamb survival from selection based on Lamb ease by seed-stock breeders has the potential to be widely disseminated and should be encouraged. Unfortunately Survival was not significantly correlated with other potential indicator traits (Table 4.3). This is disappointing given that it was hoped that these potential indicator traits could be used during selection to reduce overall mortality.

4.3.3 Correlations with production traits

Greasy fleece weight

Greasy fleece weight genetic correlations exceeded their standard errors with Dystocia C and Starvation-mismothering and all of the composite traits that included either Dystocia C or Starvation-mismothering (Table 4.4). The genetic correlation between Greasy-fleece weight and yearling weight was positive as expected giving some reassurance that the models were correctly modelling these traits. The correlation estimate of 0.36 ± 0.09 is comparable with the correlation estimate presented by Brown (2001) of 0.39 ± 0.02 between the same 2 traits and also the 0.35 weighted mean estimates of 8 studies reported by Safari *et al.* (2005). The unfavourable positive correlations between Greasy fleece weight and both Dystocia C and Starvation-mismothering may be a reason for concern given that some wool producers are selecting for genetic gain in fleece weight. The present results imply that selection for increased greasy fleece weight is likely to be negatively impacting on deaths from Dystocia C and Starvation-mismothering and that selection against these autopsy traits may have a negative impact on fleece weight in future generations.

Yearling weight

The positive genetic correlation between yearling weight and Lamb ease 0.20 ± 0.10 (Table 4.4) is also of concern given the moderately high and unfavourable correlations between Lamb ease and individual autopsy traits (Table 4.3). The result implies that selection for animals of higher yearling weights could increase the incidences of more difficult lambing which in turn would be expected to increase incidences of related birth trauma and death from Dystocia A, Dystocia C and Starvation-mismothering (Table 4.3).

Table 4.4, Genetic correlations and their standard errors () between production parameters Greasy-fleece weight and Yearling weight and individual and composite autopsy traits

	Greasy-fleece weight	Yearling weight
Survival	-0.10 (0.15)	-0.12 (0.12)
Lamb ease	0.12 (0.13)	0.20 (0.10)
Thorax	0.02 (0.15)	0.10 (0.12)
Crown-rump length	0.00 (0.10)	0.10 (0.09)
Dystocia A	0.18 (0.23)	0.13 (0.18)
Dystocia B	0.05 (0.20)	ne
Dystocia C	0.22 (0.15)	0.12 (0.12)
Starvation-mismothering	0.24 (0.21)	ne
Died *in-utero* pre-birth	-0.01 (0.01)	ne
All Dystocia Binary	0.22 (0.15)	0.02 (0.13)
All Dystocia Binary plus Starvation-mismothering	0.27 (0.15)	0.10 (0.12)
Dystocia A plus Dystocia B	0.13 (0.21)	ne
Dystocia B plus Dystocia C	0.19 (0.15)	0.01 (0.13)
Dystocia C plus Starvation-mismothering	0.28 (0.16)	0.17 (0.13)
Greasy-fleece weight	-	0.36 (0.09)
Yearling weight	0.36 (0.09)	-

4.4 Conclusions

These results indicate that the most useful trait in reducing lamb mortality rates is probably Lamb ease. Selection against difficult lambing is possible given that this trait is easily observed and heritable, albeit potentially disruptive for extensively reared animals. This is not likely to be an issue for seed-stock producers who routinely monitor and tag lambs at birth. Selection against difficult lambing should reduce the incidence of deaths arising from Dystocia A, Dystocia C and Starvation-mismothering. This would be especially beneficial if such selection was practiced by seed-stock producers where any gains in reduced mortality would be expected to be multiplied in production flocks. Selection for a reduced Thoracic circumference should be beneficial in reducing the incidence of Dystocia B and is also likely to increase Crown-rump length provided that lamb birth weight is held constant. The current selection practice of increasing yearling weight and greasy fleece are likely to be having detrimental effects on ease of lambing and incidences of Dystocia C and Starvation-mismothering.

Chapter 5 General Discussion

This study was undertaken with the aim of determining whether breaking lamb death into one or more autopsy categories, or a possible indicator trait(s) comprising individual categories and/or other traits of the lamb or ewe, could be included in selection indices and used to reduce overall lamb mortality. Unfortunately heritability estimates for all autopsy categories (individual and composite) were very low ranging from 0.01 to 0.04. This suggests that selection based on lamb autopsy results would provide little if any advantage over the more easily observed lamb survival trait itself in improving lamb survival.

An unresolved challenge when analysing autopsy data is the unwitting removal of potential additive genetic variance for a survival trait by fitting a related trait such as birth weight. The association between birth weight and survival is not linear and thus cannot be adequately accounted for by knowing the correlations, whereas fitting birth weight as a fixed effect allows for non-linear adjustment of its effect. Some carcase traits currently genetically analysed by Sheep Genetics use pre adjustment however exactly how to deal with non linear associations is an area that requires further work.

In all autopsy categories with the exception of lambs who died of Infection or whose cause of death could not be diagnosed, a higher proportion of the variance was partitioned into the maternal permanent environment compared to the direct effects (range 0.03 - 0.12). Maternal effect variance is most likely composed of both maternal genetic and maternal environmental components and the successful separation these components require a data structure that contains records for ewes with multiple generations of multiple births which was not possible with these data. These results imply that phenotypic selection against animals that fail reproductively would result in some genetic gain, assuming that there is a maternal genetic component, although this gain would be relatively slow given that ewes must be of reproductive age before this type of selection can be implemented. But they would accumulate records in their life, and with data on female relatives, young rams and ewes would get mid-parent EBVs of modest but useful accuracy.

In this study autopsy results revealed that the Dystocia categories combined accounted for almost 50% of all lamb deaths and that Starvation-mismothering accounted for a further 26%. This is similar to results presented in numerous studies of lamb mortality (Hinch *et al.* 1986, Jordan and Le Feuvre, 1989, Kerslake *et al.* 2005, Everett-Hincks and Dodds, 2008). Combined the remaining autopsy categories, Predation, Died *in-utero* pre-birth, Exposure, Infection, Undiagnosed and Misadventure, only accounted for 24% of total deaths. Although the proportion of deaths attributable to these causes would be likely to vary under different environmental conditions it is likely that deaths from these causes, with the possible exception of the Died *in-utero* pre-birth category, could be best dealt with by management techniques that reduce exposure to the causes of these death categories.

Dystocia can result from numerous different causes but it appears that in general there are 2 main mechanisms that cause mortality in lambs. The classic form of dystocia arises when the lamb is too large for the dam's pelvic opening. This occurs as a result of a foeto-pelvic disproportion primarily in single or twin born lambs of high birth weight although this can also be the result of malpresentation by smaller lambs born in larger litters. In these data this was primarily represented by the Dystocia A autopsy category which accounted for 8.5% of all deaths and was a minor cause of death when compared to Dystocia B, Dystocia C and Starvation-mismothering. Incidences of Dystocia A can be reduced through genetic selection against high birth weight. Birth weight is a heritable trait, estimated between 0.15 and 0.21 (Safari *et al.* 2005) and incidences of Dystocia A are already being controlled by selection against excessively high birth weights and for lambing ease in ewes (Sheep Genetics). This strategy is likely to be more successful than direct selection against Dystocia A given its extremely low heritability estimate of 0.02 ± 0.01.

Selection for improved lamb-rearing ability in one selection line of Merino ewes has resulted in an increase in ewe pelvic size (Kilgour and Haughey, 1993) and it is likely that pelvic size is a trait that could be measured and used in selection indices to improve lamb survival. However, measuring the pelvic dimensions of a mature ewe is likely to be costly given that it would be time consuming and thus labour expensive and would also involve the use of specialist equipment and trained personnel. In addition selection based on this

strategy would give little advantage over phenotypic selection against ewes who fail to rear a lamb. For these reasons this is a strategy that is unlikely to be adopted by breeders.

The second primary mechanism identified to be associated with lamb mortality arising from difficult birth involves lambs of low birth weights born into larger litter sizes. Death from this type of Dystocia is always associated with central nervous system damage that is the result of an extended period of hypoxia suffered during the birth process (Holst, 2004). The hypoxia occurs as a result of either a separation of the placenta before birth or through extended periods of umbilical cord occlusion during birth (Marumo *et al.* 2001, Loeliger *et al.* 2003). In this dataset deaths of this type were categorised as Dystocia C which was the third most frequent cause of mortality. Deaths from Dystocia C were primarily associated with low birth weight lambs born in larger litters. This should be a major issue of concern to the industry as selection of multiple bearing ewes is effectively a major part of the standard industry selection to increase ewe lambing rates. The raw mean birth weight of lambs dying from Dystocia C was 4.0 kg compared to a raw mean overall birth weight of 4.75 kg. This suggests that a strategy to reduce the incidence of this mortality type should attempt to increase the weight of the lightest lamb. One possible method of achieving this may be to analyse variation in lamb weight within litters and select for minimal variation.

The Dystocia B category, characterised by mild oedema and central nervous system damage appears to be an intermediate form that has elements of both Dystocia A (oedema) and Dystocia C (central nervous system damage). Dystocia C was present in all birth types though as a proportion of the number of lambs born Dystocia C incidences increased with increasing litter size. When the average birth weight of live animals was compared with the birth weight of animals that died in this category it was found that dead single born lambs were 0.4 kg heavier than their living contemporaries but lambs born in twin and triplet births were 0.3 and 0.4 kg lighter respectively. This suggests that single birth animals are experiencing birth difficulties primarily as a result of heavier weights and that twins and triplets are dying due to an inability to withstand periods of parturition associated hypoxia associated with lower weight and possibly birth order. These birth weight by birth type results and the lack of a mechanism that explains Dystocia B suggests that this category could be abolished and that lambs with both oedema and central nervous system damage

be categorised into the other 2 Dystocia categories based on their birth weights and types. Birth order was not known in these data but lower birth order has been widely implicated in increased death from hypoxia related brain injury.

Starvation-mismothering was the largest autopsy category in these data. It is a complex trait as it depends on the successful establishment of a bond between both ewe and lambs. Losses can be due to aberrant ewe or lamb behaviour, deficient milk supply or through teat and udder abnormalities. In addition sub-lethal hypoxia during parturition has also been implicated in Starvation mismothering deaths (Haughey, 1973a, Haughey, 1991, Dutra *et al.* 2007 and Dutra and Banchero 2011). It is likely that the numerous mechanisms responsible for Starvation-mismothering are controlled by completely different sets of genes and this is contributing to the low heritability estimate for this trait (0.01 ± 0.01).

Published literature indicates that low birth weight lambs born in lower birth ranks are often weak Knight *et al.* (1988) and Hinch *et al.* (1983) reported that autopsied lambs dying from Starvation-mismothering often exhibited spinal haemorrhages. Such lambs are also at an increased risk of dying from Dystocia C and therefore there is the likelihood that Starvation-mismothering is in some way related to sub-lethal hypoxia suffered during parturition as first suggested by Haughey (1973). In these data lambs categorised as dying from Starvation-mismothering were on average lighter at birth (3.9 kg) compared to the mean birth weight (4.78 kg) and were more often from twin and triplet litters confirming the observations of Knight *et al.* 1988 and Hinch *et al.* 1986. The inclusion of Starvation-mismothering records with combined dystocia records did not alter the heritability estimate for the combined Dystocia trait (Chapter 3, Table 3.10). This result is surprising given the negative genetic correlation estimated between Starvation-mismothering and Dystocia A.

It is assumed that losses classified as Died *in-utero* pre-birth are higher than the raw numbers of autopsied lambs reported here would indicate. This assumption is based on the fact that autopsied lambs were carried full term by the ewe and it is likely that earlier losses of this type were either reabsorbed into the ewe's body or lost to the environment. Kleeman and Walker (2005) reported that losses between ovulation and parturition

accounted for 20.4% of total loses which is considerably higher than the 9% found in this study and provides further support for this hypothesis, although ovulation and conception rate data were not analysed in this study. Losses from this category were largest in twin and triplet litters and surprisingly models indicated that this was not associated with dam age. Of all individual autopsy categories analysed in this study this trait had the highest heritability (0.04) and maternal effect (0.11) estimates. Edwards *et al.* (1989) showed that losses of this type can be associated with disease and in this data set the proportion of lambs classified as Died *in-utero* ranged from a high of 5.08% to a low of 0.13% between flocks and years. This wide variation may be related to disease in certain flocks and years. More investigation of this trait could prove to be highly beneficial in raising weaning rates especially as the trait is phenotypically associated with larger litters.

The survival indicator trait with the most potential to be used to decrease lamb mortality found in this study was lambing ease. Lambing ease is a relatively easily observed trait in seed-stock flocks although it does have the potential to disrupt ewes unfamiliar with human contact (Dwyer and Lawrence, 2005). Increasing lambing difficulty was positively genetically correlated with incidences of Dystocia A and C and also with the Died *in-utero* pre-birth autopsy category. This is in accord with published literature (Cloete *et al.* 1998) which reports that ease of birth clearly influences lamb survival. The 3 autopsy traits Dystocia A, Dystocia C and Died *in-utero* pre-birth, combined account for just over one third of all lamb deaths in these data and selection against ewes suffering from difficult births would be expected to reduce lamb mortality in all 3 categories. The heritability of Lamb ease was estimated at 0.08 in this study (Chapter 3, Table 3.11) which is similar to the 0.06 heritability reported by Brown (2007) and 0.09 reported by Brien *et al.* (2010) for the same trait. Lamb ease was found to have a relatively large maternal component of 0.30 in this study and 0.24 in Brown's study (2007), which can also be selected on and implies that overall genetic gain in lambing ease could be greater than the direct heritability alone would suggest.

Lambing ease was not significantly genetically correlated with Starvation-mismothering. The non-significant correlation with Starvation-mismothering was surprising given the evidence that difficult parturitions are associated with sub-lethal hypoxia (Haughey, 1973,

Hinch *et al.* 1986) which has been associated with Starvation-mismothering these studies. Starvation-mismothering is strongly affected by the behaviour and interaction of both the lamb and ewe and this in conjunction with the multiple mechanisms that can cause starvation may help explain why the correlation estimates between it and Lambing ease was not significant. Lambing ease genetic correlation estimates with All dystocia and All Dystocia plus Starvation-mismothering were not different (Chapter 4, Table4.3). In addition, the genetic correlation between lambing ease and the combined Dystocia C and Starvation-mismothering trait (0.20) was higher than the correlation estimate between Lambing ease and Dystocia C (0.18). In general Lamb ease had an unfavourable correlation with all individual autopsy categories even when not significant. This implies that selection for easy lambing ewes would be of benefit to improving lamb survival in all of the highest causes of lamb mortality. Given the potential that human observation has to disrupt ewes that are not used to human presence and the labour necessary to monitor lambing ewes, recording Lamb ease is not recommended for commercial producers. For seed-stock breeders however, the recording of lambing ease and subsequent selection for animals that lamb easily is expected to result in a lowering of overall mortality from leading death causes. This could have a significant effect on weaning rates as the effects of such selection decisions would be multiplied in producer flocks. Lambing ease as a trait is already available in Sheep Genetics and is already being used by early adopting breeders to reduce lambing difficulty.

The significant genetic correlation between larger thorax circumferences and both Dystocia B and Starvation-mismothering plus the significant genetic correlation between thorax circumference and the All Dystocia plus Starvation-mismothering composite traits imply that this easily field measured trait may be useful in reducing the incidences of these leading death causes. Thoracic circumference was estimated to have a heritability of 0.11 implying that genetic selection against large thoracic circumferences is achievable.

Of concern were the genetic correlation estimates between greasy fleece weight and the composite All Dystocia plus Starvation-mismothering trait (0.27 ± 0.17) and between yearling weight and lambing ease (0.20 ± 0.10). The genetic correlation estimate between greasy fleece weight and the composite All Dystocia plus Starvation-mismothering trait

was primarily driven by significant unfavourable correlations with Dystocia C (0.22 ± 0.15) and with Starvation-mismothering (0.24 ± 0.21). This result is in accord with the review by Safari and Fogarty (2003) who reported that wool production is genetically negatively correlated (-0.49 to -0.10) with reproduction rate. Herselman *et al.* (1998) and Cloete *et al.* (2002) both reported that sheep breeds with high wool production may have low lamb production. These results imply that selection for increased greasy fleece weight is likely to be negatively impacting on deaths and these are likely to be from Dystocia and Starvation-mismothering. Selection against these autopsy traits might have a negative effect on fleece weight in future generations. Similarly selection practices that aim to increase yearling weight are likely to be increasing lambing difficulty which, given its positive genetic correlations with important death causes is likely to also having a detrimental impact on overall survival. These results support the need to use multiple trait selection indexes that take all traits of economic importance into account.

5.1 Including Survival, Lamb ease and Thorax circumference in selection indexes

The variance component for lamb survival estimated in this study indicate that survival has genetic additive and maternal (genetic and permanent environment) components that could be used to improve lamb survival. Similarly, both Lamb ease and Thorax circumference both have direct and maternal components and appear to have the potential to be used as indirect selection criteria to reduce lamb mortality. However including these traits into selection index calculations is not entirely straightforward when compared to normal production traits.

Models developed to partition variance components for Survival, Lamb ease and Thorax circumference included birth weight (both linear and quadratic) as a fixed effect. The results both in this thesis (Chapter 3, Table 3.6) and in published literature (Yapi *et. al* 1990) show that birth weight has a curvilinear phenotypic relationship with survival, where deviations from the optimum decrease the likelihood of a lamb surviving. Furthermore there are interactions of this relationship with litter size. This curvilinear relationship poses a problem for index selection models especially when calculating the

response in correlated traits. Generally index calculation methodology relies on a linear response in correlated traits and the methodology used to calculate correlated response would need to account for this non-linearity.

In addition, genetic correlations between all important production traits and Lamb survival, Lamb ease and Thorax circumference are not known and would have to be estimated. This would require additional records on all traits to reduce standard errors associated with correlation estimates so that both phenotypic and genetic correlations estimates could be used with confidence that they were accurate. Both direct and maternal genetic effects are significant for all these traits and to maximise possible progress both traits should be utilised. To accommodate this, genetic and phenotypic correlations between and within all direct and maternal traits are required.

Furthermore, records for direct and maternal effects for both Survival and Lamb ease would become available at different times. Records for lambs would become available shortly after birth but records for the animals own maternal component would not be available until after the ewe had completed her first parturition. In addition the chance of a ewe receiving its own maternal record is influenced by its own performance for lamb survival as a lamb. This creates computational difficulties in index prediction models.

Conducting full selection index calculations was outside the scope of this project, but we can summarise anticipated results, based on the genetic parameters estimated and reported here (Chapter 3, Table 11, Chapter 4, Tables 4.3 and 4.4) and elsewhere (Safari *et al.* 2005, Huisman and Brown 2008).

For a simple terminal sire selection index aimed at high growth and improved carcase traits, Sheep Genetics uses the traits; weaning weight, post weaning weight, fat depth and eye muscle depth and places an emphasis of 30%, 35%, 5% and 30% on these traits respectively. It predicts that economic gain will come from changes in weaning weight (15%), post weaning weight (38%) and eye muscle depth (45%) and that increases in fat depth will contribute a 2% loss in economic gains.

To include Lamb ease into this simple index, genetic correlations are required between Lamb ease and; weaning weight, post weaning weight, fat depth and eye muscle depth. The only correlation estimate currently available is between Lamb ease and Yearling weight estimated at 0.20 in this study (Chapter 4, Table 4.4).

Safari *et al.* (2005) reports no weighted mean genetic correlation estimates for yearling weight, however, the review does report a weighted mean genetic correlation estimate of 0.85 between post weaning weight and weaning weight. Correlation estimates between yearling weight and both fat depth (0.29) and eye muscle depth (0.18) were obtained from Huisman and Brown (2008).

If it is assumed that the correlation between post weaning weight and yearling weight approaches 1 and that the correlations between other weight and fat measures are a function of the 0.20 genetic correlation estimate between Lamb ease and post weaning weight, multiplied by the correlation estimate between post weaning weight and the other measures of weight, fat depth and eye muscle depth, then all correlations would be positive or unfavourable for all terminal sire index traits except fat depth. Correlation estimates with Lamb ease would be approximately; 0.17 with weaning weight, 0.06 with fat depth and 0.04 with eye muscle depth.

Given the relative weights placed on weaning weight, post weaning weight, fat depth and eye muscle depth, their relative contributions to expected economic gain and their assumed genetic correlations with Lamb ease, it would be expected that the inclusion of Lamb ease into this index would result in slower gain in all traits. This would be detrimental to all traits except fat depth. The main trait impacted would be post weaning weight which contributes 38% of expected gains whereas eye muscle depth, the trait that contributes most (45%) to expected economic gains, would only be minimally effected. This predicted decrease in expected gain would however, be offset by an increase in the number of sale lambs and also a decrease in the amount of labour and veterinary assistance required in current lambing flocks.

The estimated genetic correlations between Lamb ease; and the All Dystocia Binary plus Starvation mismothering (ADB+) composite trait (0.26 ± 0.12) and the Died *in-utero* pre-

birth trait (0.25± 0.11) imply that selection against difficult lambing would reduce these causes of mortality that together account for approximately 83% of lamb deaths in these data. If this was done in seed-stock flocks reductions in lamb mortality are expected to be considerable when multiplied through production flocks.

Some seed-stock breeders are already using Lamb ease as a selection criterion within their selection indices to reduce lamb mortality. This is reported to have reduced the incidences of death from difficult births in these flocks although lamb mortality from other causes appears to have become more prevalent (pers. comm. D. Brown). This implies that research into death causes should be an ongoing issue.

The value of including Survival, Lamb ease or Thorax circumference into wool focused indexes was not considered, however, it is likely that this would come at some cost to wool production given the unfavourable non-significant genetic correlation found in this study between Lamb ease and greasy fleece weight. If this resulted in a reduction in mortality rates some of this lost wool production could be offset in future generations by the increase in selection intensity that more surviving lambs would enable. In addition, financial returns to producers would also be boosted through an increase in the number of market lambs above replacement requirements.

The antagonistic relationship involved between lamb survival traits and production traits highlight the importance of using properly formulated indexes to efficiently select for breeding objectives which include lamb survival.

5.2, Death mechanisms by Autopsy category

A table of possible mechanisms for lamb mortality by autopsy category was created to compare possible death causes or biological mechanisms within autopsy categories with those for other autopsy categories (Table 5.1). While the table is not comprehensive and indeed some allocations are arbitrary the results do however reveal an interesting association regarding mechanisms and heritabilities. Firstly any individual death can be caused by a number of different mechanisms or indeed interactions between mechanisms. The factors affecting survival can be broadly categorised as environmental, traits of the

ewe and traits of the lamb which can interact with each other as well as interact with the various mechanism that are implicated in lamb deaths. Using these categorisations, shown below in Table 5.2, there are 2 x 8 x 3 = 48 possible combinations of death mechanisms. This implies that modelling autopsy categories is unlikely to capture all variation in individual deaths as these interactions can differ even within Autopsy categories. The second observation that can be made is that as the number of possible biological mechanisms increases within an autopsy category the heritability estimate for those traits tend to decrease (r= 0.64). These results suggest that the more clearly a biological cause of death can be defined and assessed the more potential there is to identify the underlying genetic variation.

Table 5.1, Death mechanisms by Autopsy category

	Traits of Lamb			Traits of Ewe						Environmental				
	Hbw	Lbw	Mal	PC	LB	EB	LIM	IU	IN	Ch	Dis	PP	W	Total	h^2
Dyst A	1	0	1	1	0	0	0	0	0	0	0	0	0	3	0.02
Dyst B	1	1	1	1	0	0	0	0	0	0	0	0	0	4	0.02
Dyst C	0	1	1	1	0	0	0	0	0	0	0	0	0	3	0.03
SMM	0	1	0	0	1	1	1	1	1	0	1	0	1	8	0.01
Pred	0	1	0	0	1	1	1	0	0	0	0	1	0	6	0.02
DIUPB	0	0	0	0	0	0	0	0	0	1	1	0	0	2	0.04
Exp	0	1	0	0	1	1	1	0	1	0	0	0	1	6	0.03
Inf	0	1	0	0	1	1	0	1	0	0	1	0	1	6	0.02
Miss	0	0	0	0	1	1	1	1	0	0	0	0	1	5	0.01

Hbw = High birth weight, Lbw = Low birth weight, Mal = Mal presentation, PC = Pelvic conformation, LB = Lamb behavior, EB = Ewe behavior, LIM = Lost in mobs, IU = Infected udder, IN = inverted nipples, Ch = Chromosomal disorder, Dis = Disease, PP = Predator presence, W = Weather conditions
Dyst A = Dystocia A, Dyst B = Dystocia B, Dyst C = Dystocia C, SMM = Starvation-mismothering, Pred = predation, DIUPB = Died in-utero pre-birth, Exp = Exposure, Inf = Infection, Miss = Misadventure

The many factors indentified here as traits of the lamb, traits of the ewe and environmental can all interact with flock management decisions and affect lamb survival. This highlights just how complicated a trait lamb survival is. This complexity and the negative association found here between complexity and heritability can assist in explaining why survival heritability estimates are consistently low and also why lamb mortality has remained an issue in the national flock despite considerable efforts aimed at reducing it.

5.3 Conclusions

Estimated heritabilities for all autopsy categories were low and suggest that there would be no advantage in using lamb autopsy results for direct selection to improve lamb survival rates over the lamb survival trait itself. The separation of the causes of death into discrete categories did provide some further insight into the different biological mechanisms that cause lamb mortality. The separation of dystocia into 3 distinct categories did not improve heritability estimates above those for the combined category. In all individual and composite autopsy traits the ewe's maternal effect accounted for a greater proportion of the phenotypic variance. The maternal effect contains both genetic and environmental components and phenotypic selection against ewes who fail to rear lambs should, over time, slowly improve lamb survival by improving the maternal genetic contribution to survival in these flocks. The successful separation of maternal genetic and environmental components would require autopsy records to extend over multiple generations and it is unlikely to be achieved given the effort required to assemble such a data structure.

Autopsy trait correlations were strongest between Dystocia A and Dystocia C which was surprising given that these 2 traits appear to share different phenotypic relationships with birth weight. This relatively strong correlation provides some evidence that selection against either category will be favourable to the other.

 It would seem that Lambing ease, which is easily recorded in seed-stock flocks, is the most appropriate selection criteria for use by seed-stock producers to improve overall lamb survival. This should reduce the incidence of death from all types of dystocia and starvation-mismothering which together account for the majority of deaths in well managed flocks. Any gains from this would be multiplied in producer flocks and although it has the potential to slow desired gains in both terminal sire and wool breeds this is likely to be more than offset by an increase in the number of marketable lambs from both enterprises and by a reduction in labour costs, ewe attrition and veterinary bills that are now associated with difficult lambing.

Results from this study suggest that selection for increased yearling weight, greasy fleece weight and number of lambs born are all likely to be having an unfavourable impact on

lamb survival. The difficulty is and is likely to remain the identification of animals that break these correlations for selection purposes.

Further research into methods to reduce birth weight variation in multiple litters and into the impact of animals that have died *in-utero* pre-birth could significantly alter lamb weaning rates and is advised.

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