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# LANDCORP FARMING LIMITED LECTURE

# A review of *in-utero* environmental effects on sheep production

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## ABSTRACT

There has been recent interest in potential intragenerational and intergenerational effects due to pre-natal programming and the implications these may have on production animals, such as the sheep. Evidence for intergenerational effects has been apparent for a significant period of time. The available data indicate that dam nutrition, age, parity, pregnancy rank, live weight, body condition, genotype and fetal genotype, and environmental conditions can all affect fetal development with potential post natal intra-generational consequences. However it is also clear that many of the observed effects in the fetus and young animal do not translate to productive effects in the adult although some models do exist. It is often difficult to compare studies due to differences in the; timing of the manipulation being investigated, live weight and condition of the dam, nutrition of the dam after the manipulation, and management of the young animal post birth. In the future it is probable that farmers will use this information to manipulate the dam in pregnancy to affect the productive performance of future generation(s). Currently few if any models of intergenerational effects exist. Further studies are required to identify consistent intragenerational and intergenerational models which affect productive performance in the adult and that identify the mechanisms responsible for the observed effects.

**Keywords:** sheep; production; environment; intragenerational; intergenerational; in-utero; fetal programming.

## INTRODUCTION

It is well established that live weight, body condition, nutritional level, environmental conditions and the genotype of an animal affect a range of physical characteristics. However, when all of these factors are taken into account there is still significant unexplained variation in performance. Recent human epidemiological evidence from Barker and his colleagues have shown a link between low birth weight, due to impaired intrauterine growth and development, and increased risk of coronary heart disease, stroke, hypertension and non-insulin-dependant diabetes (Godfrey & Barker, 2000, Symonds *et al*., 2001, Barker, 2004abc, Gluckman & Hanson, 2004, Symonds, 2007). These studies have ignited interest in potential intragenerational and intergenerational/transgenerational effects, which may be due to pre-natal or fetal programming, in production animals. In the present review intragenerational effects are defined as those observed in first generation offspring after exposure to a given in-utero environment or experience, while intergenerational/transgenerational effects are effects observed in the second or later generations. It should also be noted that in the present review so called "long-term" effects are for the most part confined to intragenerational effects.

The sheep has been used as a model for human studies due to it predominantly having one or two offspring and having similarities in; fetal organ growth, metabolic rates, protein turnover rates and maturity of the hypothalamic-pituitary-thyroidal/adrenal axis as well as a relatively long gestation length with a relatively large-sized offspring, in comparison to litter bearing species (Harding, 2001; Greenwood & Bell, 2003; Bell, 2006; Symonds *et al*., 2007). A significant proportion of this human orientated research is focussed on the underlying biology and is not production-based. This can make inference to potential production effects difficult. The magnitude of any affects must have implications for production efficiency if it is to be relevant for sheep farmers and any effects must occur before the animal becomes "aged", as traditional culling based on age may negate any potential affect.

Potential intragenerational effects in sheep production are not new phenomena with Wallace (1948) reporting effects of dam pregnancy nutrition on fetal growth. However, few documented intergenerational models have been reported in sheep production. The difficultly with identifying intragenerational and intergenerational effects are the requirement for relatively long term, controlled experimental conditions, to ensure that potential changes programmed into the developing fetus are not masked by the effects of later environmental influences, or by compensatory changes in physiology (Rhind *et al*., 2001). The costs of such long term experiments are another important consideration (Rhind *et al*., 2001).

Fetal growth and development can potentially be influenced by a number of environmental factors, including; dam nutrition, age, parity, pregnancy rank, live weight, body condition, genotype and fetal genotype, and environmental conditions. The aims of the present review are to firstly, briefly outline some of the reported effects of these environmental factors on the resulting generation(s) productive performance in the areas of: fetal growth, lamb birth weight, post-natal growth, carcass composition, reproduction, lactation and wool production and secondly to briefly outline recent research undertaken at Massey University. Direction is also given, where appropriate, to more detailed reviews. There is a large body of literature in the quantitative genetics field that will have generated values for the effects of dam: age, parity and pregnancy rank. These for the most part have not been reviewed.

The aim of this brief review is not to discuss potential mechanisms for the observed physiological or epigenetic effects, which have previously been reviewed by Harding (2001), Rhind *et al*. (2001, 2004), Greenwood and Bell (2003), Rhind *et al*. (2003), McMillen and Robinson (2005), Schwartz and Morrison (2005), Bell (2006), Wood and Oakey (2006), Wu *et al*. (2006) and Symonds *et al*. (2007) but, are still not fully understood. Further, this review will not discuss potential effects on the offspring's cardiovascular system, organ development, hypertension, metabolism and propensity for obesity which have been reviewed and discussed elsewhere (McMillan & Robinson 2005; Bell 2006; Wu *et al*., 2006; Symonds *et al*., 2007) and may not have direct effects on productive performance.

## Birth rank

Increasing the number of lambs weaned per ewe is a means of increasing farm productive efficiency. In response to this the lambing percentage of the New Zealand flock has increased from approximately 100% to 136% in recent years. Reproductive traits are known to display low to moderate levels of heritability (Safari *et al.,* 2005) with progress in lambing percentages on commercial farms being made through selection of twin born ewe lambs as replacements (Geenty, 1997). However, increases in lambing percentage are associated with increases in the proportion of triplet-born lambs. The long-term impacts of being born a triplet are less well known in comparison to their singleton and twin-born counterparts.

Gootwine *et al*. (2007) stated that litter-size dependant, in-utero, growth restriction effects on sheep health, longevity, reproduction and production are almost unavailable in the literature. Singles are heavier at birth and weaning than twins which are in turn heavier than triplet-born lambs (Trail & Sacker, 1969; Morris & Kenyon, 2004; Afolayan *et al*., 2007; Gardner *et al*., 2007; Gootwine *et al*., 2007; Hopkins *et al*., 2007, Kenyon *et al*., 2007, Safari *et al*., 2007, Kenyon *et al*., 2008a). Gardner *et al*. (2007) offered the explanation that the inverse relationship between litter size and birth weight was due to some, or all of, the physiological capacity for the mother to adequately supply the products of conception with metabolic substrate, the physical capacity of the mother to bear multiple litters, mechanical forces in differing areas of the uterus and fetal genotype effects.

Trail and Sacker (1969) and Butler (1982) reported that twins were lighter than singletons at 11 and 14 months of age respectively. Hopkins *et al*. (2007) found differences in live weights of single and twin and triplet lambs to 657 days of age. Similarly, Safari *et al*. (2007) found that multiple-born and reared lambs were lighter than singles at 17 months of age. Conversely, Kenyon *et al*. (2008a) reported that twins were lighter than their single born counterparts to 9 months of age but that there was no difference after this time point. At two years of age, Corner *et al*. (2006) reported no difference in live weight between twin- and triplet-born ewes. These combined results indicate that birth rank can affect live weight however this affect is not always still apparent as the animal ages. It is probable that in good growth environments, the difference in mature live weight between birth ranks are small, if present at all, while in poorer environments multiples may "struggle to catch up".

There are few data describing the effect of birth rank on carcass composition. Kenyon *et al*. (2007) reported that triplet fetuses had a lighter semitendinous muscle than twins but no differences in peri-renal fat levels. No comparison was made between muscle and fat measures post-birth. Afolayan *et al*. (2007) found that birth- and rearing-rank affected; carcass weight, dressing yield, and eye muscle depth and area although no effect was reported on GR fat depth or muscle ultimate pH levels. The carcass weight differences are likely explained by differences in live weight. Interestingly when adjusted to the same carcass weight, triple-born lambs had the highest dressing out percentage.

Twin-born ewe lambs have been reported to reach puberty at a lighter weight, but slighter older age, than their singleton-born counterparts although the percentage that achieved puberty in their first breeding season did not differ (van der Linden *et al*., 2007). In contrast Kenyon *et al*. (2008a) reported no difference between singleton- and twin-born ewes in any of the puberty onset measures. No reports were identified which examined puberty onset in triplet-born lambs.

Twin-born ewes were reported to have a higher lifetime lambing percentage compared to their single-born counterparts (Gonzalez *et al*., 1986).

Gonzalez *et al*. (1986) stated that Turner (1968) also observed twin-born ewes produced 2 to 10% more lambs than their single-born counterparts. Similarly, Safari *et al*. (2007) found that reproductive performance of multiple-born and -reared ewes was greater than that observed in single-born ewes. In contrast, Baharin and Beilharz (1977) reported that as two year olds, twin-born ewes gave birth to fewer lambs than single-born ewes although at three years of age the relationship had swapped and in the following years there was no difference. Overall in that study there was no a difference in twinning rates between single- and twin-born ewes. Kenyon *et al*. (2008a) also reported no difference in pregnancy percentage at 20 months of age between single and twin-born ewes. In small numbers, Corner *et al*. (2006) reported no difference in lambing percentage between twin- and triplet-born ewes at two years of age, although the data tended to suggest that triplet born ewes may display higher lambing percentages. Interestingly, Corner *et al*. (2006) reported that triplet-born ewes gave birth to lighter singletons but not twins, compared to twin-born ewes. Further triplet-born ewes displayed poorer maternal behaviour that twin-born ewes at their first lambing (Corner *et al*., 2005). These combined data suggest that survival of lambs born to triplet-born ewes may be deceased, although further studies with larger numbers of animals is required to confirm this hypothesis. Interestingly Gonzalez *et al*. (1986) reported that progeny born to twin-born two-year-old ewes had a lower survival rate than those born to single-born ewes although this difference was not apparent in later years

Twin- and multiple-born animals have been reported to produce less wool than their singleton-born counterparts but this difference decreased with age (Turner, 1961; Gonzalez *et al*., 1986; Behrendt, 2006; Safari *et al*., 2007). Turner (1961) and Butler (1992) reported lighter fleeces at 16 and 14 months of age respectively in twin-born animals compared to their singleton-born counterparts, although twin-born animals also displayed lighter live weights in the study of Butler (1992). Multiple-born animals have tended to produce finer wool than their single-born counterparts (Butler 1992; Behrendt, 2006; Safari *et al*., 2007). Sherlock *et al*. (2005) reported that at five months of age triplet-born lambs had lighter fleeces and slightly finer fleeces than twins. In a previous study using these same animals at 3 months of age, triplets displayed lighter live weights than their twin counterparts (Morris & Kenyon, 2004) therefore it is possible that the lighter fleece weights were due to reduced body size.

## Age and parity of the dam

Breeding ewes at a younger age has the potential to increase lifetime performance and improve the production efficiency of the ewe. Further if progeny are selected from young dams, increased genetic gain can be made through reducing the generation interval. In response to these potential benefits an increasing proportion of New Zealand farmers have chosen to breed from young females to lamb at 12 months of age rather than the normal practice of lambing at 24 months of age. The long term impact on a sheep production system of breeding ewes at a younger age is thus of commercial interest.

Care must be taken when interpreting data from studies comparing the effects of dam parity as these are often confounded with dam age. Few studies have specifically examined the effect of dam parity in dams of the same age. Gluckman and Hanson (2004) stated that the physiological limitations of fetal growth are greater in primiparous pregnancies. This leads to smaller birth size which may be related to a lesser capacity for vasodilation in primiparous uterine vasculature. Gardner *et al*. (2007) stated that the first pregnancy leaves a permanent uterine physiological imprint that influences the second parity. Young maternal age has also been suggested to affect fetal growth, as young mothers tend to give birth to smaller fetuses (Gluckman & Hanson, 2004). This may in turn be compounded by maternal size and parity. These same authors hypothesised that the younger mother has priority for utilising nutrients for her own anabolism and growth as an evolutionary survival adaption.

In studies where dam parity and age were confounded, primiparous dams have been reported to give birth to either lighter lambs (Annet & Carson, 2006; Gardner *et al*., 2007) or lambs which did not differ in birth weight to those born to multiparous dams (Trail & Sacker, 1969; Marcedo & Hummel, 2006). Gootwine *et al*. (2007) reported that primiparous ewes gave birth to lighter lambs up until a dam age of 21 months, after which the birth weight of lambs born to primiparous ewes did not differ from multiparous ewes. Somewhat in support of this finding, Wu *et al*. (2006) stated that it was maturity of the dam and not parity that affected intrauterine growth.

In studies where parity and age are confounded, or where these factors are not clearly defined, lambs born to first parity or two-year-old ewes have either not differed in weaning weight (Marcedo & Hummel, 2006) or were lighter (Hazel & Terrill, 1945, 1946; Sidwell *et al*., 1949; Versly & Slen, 1961; Trail & Sacker, 1969; Gbangoche *et al*., 2006) than those born to older multiparous dams. Versly and Slen (1961) also reported that offspring born to young dams were lighter at one year of age.

Turner (1961) reported that offspring born to two-year old ewes, parity not clearly defined, had lower fleece weights compared to those born to mature ewes. This difference was most likely due to the observed decrease in secondary follicle numbers. Similarly, offspring born to two-year-old ewes, parity not clearly defined, were reported to produce a lighter fleece with a shorter staple length at one year of age compared to those born from older ewes (Hazel & Terrill, 1945, 1946; Vesely & Slen, 1961).

In humans the first-born child is at greater risk of obesity (Gluckman & Hanson 2004) and therefore it might be expected that progeny born to primiparous ewes have greater levels of fat than counterparts born to multiparous dams. Little work has examined the effect of dam parity on carcass composition in sheep. Symonds *et al*. (2004) reported that young animals born to adult primiparous ewes had a greater level of adiposity compared to multiparious ewes.

Recently the potential long term impact of breeding ewe lambs and effects of parity in ewes of a constant age have been studied at Massey University. Three types of 18-month-old ewes currently exist on New Zealand sheep farms: those not presented for breeding as a ewe lamb, those presented for breeding and that lambed as a ewe lamb and those presented for breeding but did not lamb as a ewe lamb. Kenyon *et al*. (2008a; 2008c) reported no effect of dam parity on birth weight, weaning weight, live weight at 18 months of age or body condition of offspring born to two-year-old ewes. Ewes born to either first or second parity two-year old dams did not differ in the percentage that reached puberty, weight at puberty or age at puberty in their first breeding season or two-year-old pregnancy rate the following year (Kenyon *et al*., 2008a). Interestingly, offspring born to two-year old ewes which had failed to lamb at one year of age were less likely to display puberty in their first breeding season. Grand-dam parity had no effect on lamb birth weight or live weight at weaning (P.R. Kenyon, Unpublished data). These later combined findings suggest that parity of two-year-old dams may have few long-term impacts in a pastoral-based New Zealand sheep production system.

High liveweight gains of pregnant housed ewe lambs, fed a concentrate diet, have been reported to result in lighter lamb birth weights and increased risk of spontaneous abortion (Wallace, 2000). Ewe lamb pregnancies in these studies involved embryo transfer. Potential mechanisms for this unexpected inverse relationship between fetal growth/lamb birth weight and maternal nutrition have been reviewed by Wallace (2000). In these studies altered fetal ovarian follicular development has occurred (Da Silva *et al*., 2002) although no affect was observed on time of onset of puberty, ovulation rate or ovarian function in female offspring (Da Silva *et al*., 2001). In addition reduced male testosterone concentration and testicular volume was recorded to 35 weeks of age and lighter live weight at 25 weeks of age (Da Silva *et al*., 2001) but no productive data appears to be available at an older age.

A series of five studies have been conducted at Massey University to determine if high levels of ewe lamb nutrition, resulting in high liveweight gains, under pastoral grazing conditions with naturally-mated ewe lambs, could cause the reported negative effects on fetal growth and pregnancy outcome. To date high levels of maternal nutrition have tended to increase birth weight, as would be expected in mature ewes. Only on one occasion has a high level of ewe lamb nutrition been associated with increased rates of fetal loss (Morris *et al*., 2005; Kenyon *et al*., 2008b; F.J. Mulvaney, Unpublished data). There has been a positive relationship between maternal ewe lamb nutrition and lamb weaning weights (Morris *et al*., 2005; Kenyon *et al*., 2008b; F.J. Mulvaney, Unpublished data). To date there have been no long-term intragenerational or intergenerational studies examining the effects of ewe lamb nutrition during pregnancy on the resulting progeny's live weight, carcass and wool characteristics and reproductive performance post-weaning.

## Maternal nutrition

A ewe's pregnancy can be divided into three approximately equal periods or trimesters, from a nutritional point of view. During the first trimester, energy requirement for the developing embryo and conceptus is relatively small but fetal metabolic activity and specific growth rate are high (Robinson *et al*., 1999). The second trimester is the period of placental development, peaking around day 90, with fetal size and growth being relatively small at this stage. The last trimester is the period of rapid fetal growth and is associated with the highest nutritional demand (Kenyon & Webby, 2007).

Tables 1, 2 and 3 briefly outline maternal nutritional studies which have examined impact on the progeny. The studies presented are not a complete list but represent a range of nutritional studies commencing prior to conception (peri-conceptional) through to late pregnancy. Only brief descriptions of the nutritional manipulations are given in the tables. It should also be noted that in some studies it is difficult to accurately interpret the nutritional regimens used.

## Fetal growth and lamb birth weight

Effects of pregnancy nutrition on fetal growth and lamb birth weight have been reviewed previously to varying degrees by Mellor (1983), Robinson *et al*. (1999), Harding (2001) and Symonds *et al*. (2007). It can be observed in Table 1 that maternal under-nutrition from the peri-

**TABLE 1**: The effect of maternal nutritional regimen and timing of nutritional regimen on fetal growth, lamb birth weight and growth to weaning.

| Reference | Timing of nutritional regimens | Nutritional regimens | Fetal growth and birth weight | Growth to weaning |
|---|---|---|---|---|
| Edwards & McMillan 2002a | 60 days pre-mating (d -60) to day 7 of pregnancy (d7) then d8 to d147 | Maintenance (M) vs. 70% M. in each period. Four treatments | No effect nutrition on singleton fetal growth. In twins restricted feeding after M feeding reduced fetal growth | |
| Gopalakrishnan *et al*. 2004 | d0 to d95 | 0.5 M vs. 1.0 M | No effect on birth weight (B/W) | |
| Schinckel & Short 1961 | d0 to parturition | Low vs. high | Low light B/W | |
| Krausgrill *et al*. 1999 | d1 to d70 | Control vs. restricted | No effect on B/W | No effect |
| Parr *et al*. 1986 | d1 to d 35 | 0.5 M vs. 1.5 M | No effect on B/W | No effect |
| Rae *et al*. 2002a | d1 to d95 | 0.5 M vs. 1.0 M | No effect on B/W | No effect |
| Everitt (1967a) | d1 to d90, d91 to parturition | Loss or gain of 25% body weight. Four treatments | Loss in each period reduced B/W | Loss in each period reduced weaning weight |
| Gopalakrishnan *et al*. 2005 | d28 to d80 | 0.5 M vs. 1.0 to 1.5 M | No effect | No effect |
| Vonnahme *et al*. 2003 | d28 to d78 | 0.5 M vs, 1.0 M | 0.5 M fetuses lighter | |
| Ford *et al*. 2007 | d28 to d78 | 0.5 M vs, 1.0 M | No effect on B/W | |
| Daniel *et al*. 2007 | d30 to d70 | 0.5 M vs. 1.0 M | No effect on B/W | |
| | d30 to d85 | 0.5 M vs. 1.0 M | | |
| Deligeorgis *et al*. 1996 | d30 to parturition | 0.9 M vs. 1.1 M | No effect on B/W | 0.9 M lighter |
| Gardner *et al*. 2007 | d1 to d30, d31 to d80, d110 to d147 | Varying models | Only d110 to d147 nutrition affected B/W | |
| Bielli *et al*. 2001 | Mid to late pregnancy | 1.0 M vs. above M | Above M increase B/W | Above M increased growth |
| Gunn *et al*. 1995 | d47 to parturition | Under nutrition vs. high nutrition | Under nutrition reduced B/W | |
| Kelly *et al*. 1996 | d50 to d140 | sub M vs. M | Sub M lighter B/W | Sub M lighter at weaning |
| Kelly *et al*. 2006 | d50 to d140 | sub M vs. M | Sub M lighter B/W | Sub M lighter at weaning |
| | d50 to 12 weeks post birth | | | |
| Bielli *et al*. 2005 | d70 until parturition | 0.7 M vs. 1.1 M | 0.7 M lighter B/W | |
| Morris & Kenyon 2004 | d64 until parturition | 2, 4, 6, 8 cm swards | 2cm lighter B/W | No effect |
| Corner *et al*. 2005 | d64 until parturition | 2 vs. 6 cm swards | | |
| Corner *et al*. 2008 | d70 to d107 to d147 | 2-2, 2-4, 4-2, 4-4 cm swards | 2-2 and 4-2 lighter B/W than 4-4 | 2-2 lighter at weaning than 4-4 |
| Borwick *et al*. 2003 | d100 until parturition | 0.7 M vs. 1.0 M | 0.7 M lighter B/W | 0.7 M lighter at weaning |
| Wallace 1948 | Last 6 weeks of gestation | Sub M vs. 1.0 M vs. Ad-lib | Sub M lighter than M, M lighter than Ad-lib | Sub M lighter at weaning |
| Tygesen *et al*. 2007 | Last 6 weeks of gestation | 0.6 M vs. H | 0.6 M lighter | No effect |

conceptional period through to late pregnancy can reduce lamb birth weight. However, it is apparent that under-nutrition in early pregnancy is less likely to negatively affect birth weight than under-nutrition in the later stages of pregnancy. Relatively few studies have examined the effects of above maintenance levels of maternal nutrition, including the requirements of the conceptus. It is well established that light lamb birth weight is associated with an increased risk of lamb death. These combined studies clearly indicate that maternal under-nutrition can have negative impacts for newborn survival.

At Massey University, Morris and Kenyon (2004) reported that sward height in mid- to late-pregnancy affected lamb birth weight. A cohort of the ewe lamb offspring from that study was kept for two years. No intergenerational effects of grand-dam pregnancy nutrition on birth weight were observed in lambs born to these young ewes (Corner *et al*., 2006). While, Gardner *et al*. (2007) reported that every 1 kg increase in the birth weight of the dam resulted in her offspring being 0.15 kg heavier at birth, a response they attributed to an intergenerational effect, it is likely that much of this observed effect was genetic.

**Growth after birth**

The effects of maternal nutrition on the growth of offspring post-birth either reared by their dam or artificially, have been reviewed by Greenwood and Thompson (2007). Care must be taken when interpreting the effects of maternal nutrition on postnatal growth as there can be carry-over effects of the nutritional regimen on the dam’s subsequent

**TABLE 2:** The effect of maternal nutritional regimen and timing of nutritional regimen on live weight post weaning and carcass characteristics of offspring.

| Reference | Timing of nutritional regimens | Nutritional regimens | Livewight post weaning | Carcass characteristics |
|---|---|---|---|---|
| Nordby *at al*. 1987 | 30 days pre-mating (d-30) to day 100 of pregnancy (d100) | 0.7 M vs. 1.0 M | | No effect on muscle and fat % |
| Gopalakrishnan *et al*. 2004 | d0 to d95 | 0.5 M vs. 1.0 M | No effect at 3 years of age | No effect on fat levels at 3 years of age |
| Schinckel & Short 1961 | d0 to parturition | Low vs. high | Low lighter as adults by approx. 4 – 5kg | |
| Gardner *et al*. 2005 | d0 to parturition, d0 to d30, d110 to parturition | 0.5 M vs. 1.0 M | No different at 1 year of age | Late pregnancy 0.5 M had increased fat levels at 1 year of age |
| Krausgrill *et al*. 1999 | d1 to d70 | Restricted vs. control | | No muscle weight difference<br>Restricted group meat more tender at 35 kg |
| Parr *et al*. 1986 | d1 to d 35 | 0.5 M vs. 1.5 M | No effect to 2 years of age | |
| Everitt (1967a) | d1 to d90, d91 to parturition | Loss or gain of 25% body weight. Four treatments | Ewe loss in early pregnancy reduced liveweight to 7 months, ewe loss in liveweight in late pregnancy reduced liveweight to at least 3 years by approx. 2 - 3 kg | |
| Rae *et al*. 2002a | d1 to d95 | 0.5 M vs. 1.0 M | No effect on liveweight or body condition at 20 months of age | |
| Gopalakrishnan *et al*. 2005 | d28 to d80 | 0.5 M vs. 1.0 to 1.5 M | No effect at 6 months of age | |
| Gnanalingham *et al*. 2005 | d28 to d80, d110 to d147 | 0.6 M vs. 1.5 M, 0.6 M vs. 1.0 M | | No effect on adipose tissue level to 6 months of age |
| Ford *et al*. 2007 | d28 to d78 | 0.5 M vs, 1.0 M | 0.5 heavier at 280 days of age | 0.5 M higher backfat levels at 280 days of age |
| Daniel *et al*. 2007 | d30 to d70<br>d30 to d85 | 0.5 M vs. 1.0 M<br>0.5 M vs. 1.0 M | | No effect on carcass composition to 24 weeks of age |
| Gunn *et al*. 1995 | d47 to parturition | Under nutrition vs. high nutrition | No effect liveweight or body condition as an adult | |
| Kelly *et al*. 1996 | d50 to d140 | sub M vs. M | No effect to 1.4 years of age | |
| Kelly *et al*. 2006 | d50 to d140,<br>d50 to 12 weeks post birth | sub M vs. M | As an adult sub M lighter when low feeding in lactation also | |
| Corner *et al*. 2005 | d64 until parturition | 2 vs. 6 cm swards | No effect to 2 years of age | |
| Borwick *et al*. 2003 | d100 until parturition | 0.7 M vs. 1.0 M | No effect to 18 months | |
| Oliver *et al*. 2001 | d105 to d125 | Restricted vs. ad libitum | | At 30 months of age those from restricted for 20 days less backfat but not for those restricted 10 days |
| Tygesen *et al*. 2007 | Last 6 weeks of gestation | 0.6 M vs. High | | No effect meat quality or tenderness at 5 months |

milk production which may either mask or exacerbate any potential effects. Further, the level of nutrition in the lactation period and/or in late pregnancy, if the nutritional insult was in early- and/or mid-pregnancy, may overshadow any potential effects. The effects of maternal nutrition during pregnancy should ideally be examined in artificially reared lambs. The information in Table 1 indicates that under-nutrition in late pregnancy tends to negatively affect lamb growth rate to weaning, while under-nutrition in early pregnancy is less likely to affect weaning weight.

The literature reviewed suggests that maternal nutrition in all stages of pregnancy are less likely to affect live weight after weaning than prior to weaning (Table 2).

Greenwood and Thompson (2007) stated that short term nutritional insults in pregnancy have no long-term effect. Further they concluded that in artificially-reared lambs, while prolonged severe fetal growth retardation achieved through poor maternal nutrition may adversely influence post-natal growth, less severe conditions are unlikely to have long term effects. They also suggested that any potential effects of early- and mid-gestation maternal nutrition could be overcome by adequate maternal nutrition in late pregnancy.

In summary, the previously mentioned results suggest that longer –term intragenerational liveweight consequences for the offspring may be unlikely or relatively minor although the data does imply that undernutrition in late-pregnancy will

**TABLE 3**: The effect of maternal nutritional regimen and timing of nutritional regimen on reproductive traits and wool characteristics of offspring.

| Reference | Timing of nutritional regimens | Nutritional regimens | Reproductive traits | Wool characteristics |
|---|---|---|---|---|
| Schinckel & Short 1961 | day 0 of pregnancy to parturition | Low vs. high | | Low fewer wool follicles and lower fleece weight at maturity |
| Lea *et al*. 2006 | d1 to d30, d31 to d50, d31 to d35, d31 to d110 | 0.5 M vs. 1.0 M | 0.5 M negatively affected fetal ovary development | |
| Rae *et al*. 2001 | d1 to d30, d31 to d50, d31 to d35, d31 to d110 | 0.5 M vs. 1.0 M | 0.5 M delayed fetal follicle development | |
| Rae *et al*. 2002b | d1 to d30, d31 to d50, d31 to d35, d31 to d110 | 0.5 M vs. 1.0 M | No effect on fetal testis mass although, some effects observed in fetal steroidogenic capacity in early pregnancy | |
| Parr *et al*. 1986 | d1 to d 35 | 0.5 M vs. 1.5 M | No effect on ovulation rate to 2 years of age | No effect on wool production or quality to 2 years of age |
| Everitt (1967a) | d1 to d90, d91 to parturition | Loss or gain of 25% body weight. Four treatments | | No effect of early pregnancy liveweight loss<br>Loss liveweight in late pregnancy reduced secondary follicle number, secondary to primary follicle ratio and clean fleece weight to 18 months. |
| Rae *et al*. 2002a | d1 to d95 | 0.5 M vs. 1.0 M | No effect on semen quality or scrotal size<br>Ovulation rate lower in 0.5 M at 20 months | |
| Deligeorgis *et al*. 1996 | d30 to parturition | 0.9 M vs. 1.1 M | 0.9 M reduced response to GnRH<br>No effect on female or male gonad weight at 55 days of age | |
| Bielli *et al*. 2002 | Week 10 until parturition | 0.7 M vs. 1.1 M | 0.7 M tended to have lower testis weight and had lower stertoli number at 2 days of age | |
| Bielli *et al*. 2001 | Mid to late pregnancy | 1.0 M vs. above M | 1.0 M lower testis weight and tendency for lower stertoli cell numbers at 99 days of age | |
| Gunn *et al*. 1995 | d47 to parturition and in lactation | Under nutrition vs. high nutrition | Undernourished less likely to have multiple births to 4 years of age. No difference in ovulation rate | |
| Kelly *et al*. 1996 | d50 to d140 | sub M vs. M | | Sub M less 1.4 yr wool and slightly broader |
| Kelly *et al*. 2006 | d50 to d140<br>d50 to 12 weeks post birth | sub M vs. M | | Sub M less adult wool and combined across studies it was broader |
| Sherlock *et al*. 2005 | d64 until parturition | 2, 4, 6, 8cm swards | | Slight increase in micron with increased sward height in twins only. No effect on fleece weight at 5 months |
| Borwick *et al*. 2003 | d100 until parturition | 0.7 M vs. 1.0 M | No difference on ewe hypothalamic-pituitary function to 18 months of age | |

negatively impact on lamb weaning weight. In production systems where the aim is to achieve lamb slaughter weights at a young age as a means of increasing productive efficiency, the data indicate ewes should be adequately fed in mid- to late-pregnancy period. The potential negative impact of undernutrition will be further exacerbated if the ewes' lactational performance is affected.

**Carcass composition and meat quality**

The potential effects of maternal nutrition on the carcass composition and obesity of the resulting progeny has beenreviewed by Bell (2006), Wu *et al.* (2006), Greenwood and Thomson (2007), and Taylor and Poston (2007). Inconsistent effects of maternal nutrition on the level of adipose tissue in the offspring have been reported. Gardner *et al.* (2005) and Ford *et al.* (2007) observed increased levels of fatness in offspring born to nutritionally restricted dams while Oliver *et al*. (2001) observed the opposite effect and Nordby *et al*. (1987), Gopalakrishnan *et al*. (2004), Gnanalingham *et al.* (2005) and Daniel *et al*. (2007) reported no effect. There is no apparent explanation for these varying results. Greenwood *et al*. (1998) reported that relatively low birth weight lambs, in a study where lambs were selected on birth weight, were associated with greater levels of fatness at 20 kg live weight compared to their heavier born counterparts.

Maternal nutrition appears to have little effect on muscle and meat quality (Table 2). Greenwood and Cafe (2007) suggested that for beef cattle raised in pasture-based production system, the plasticity of the carcass tissues, particularly of muscle, allowed animals that are growth-retarded in early life to attain normal composition at equivalent weights in the long term at an older age.

## Fetal reproductive development and adult reproductive performance

The effects of maternal nutrition on the reproductive development and performance of offspring have previously been reviewed by Rhind *et al*. (2001), Rhind (2004) and Bell (2006). In both the male and female fetuses there are critical windows of development with germ cell migration, steroidogenesis, gonad development, folliculogenesis, and sertoli cell replication occurring in distinct periods of development (Rhind *et al*., 2001; Rhind, 2004). Table 3 indicates that maternal nutrition can affect the fetal reproductive system at differing stages of development, although the relative importance of each time period is not well understood. Rhind (2004) stated that whilst some effects on the fetus are exerted at one particular stage of development, in some cases these effects are not expressed until a later stage. Further he suggested that knowledge of the processes though which maternal nutrition affects reproductive function in the offspring is limited.

If the effects of maternal nutrition are to be of significance to New Zealand farmers they must manifest as changes in the adult reproductive performance. However, relatively few studies have shown effects in adult ewe reproductive performance. Rae *et al*. (2002a) found, in a relatively small number of ewes, decreased ovulation rates in offspring born to undernourished dams. While Gunn *et al*. (1995) reported that ewes born to dams undernourished in mid- to late-pregnancy and lactation gave birth to less multiple-born lambs. They attributed this effect to decreased embryo and/or fetal loss rather than increased ovulation rates.

No studies were identified that reported effects of maternal nutrition on the reproductive performance of the adult ram. Rae *et al*. (2002a) reported no effect on scrotal circumference or semen characteristics. Bielli *et al*. (2001, 2002) found that nutrition of the dam affected sertoli cell number in the young male and suggested that sertoli cell number is highly correlated with adult testicular size and maximum rate of sperm production and hence potential fertility in later life. Detecting differences in fertility and mating performance of the male in the field requires large numbers of ewes which may have limited the numbers of studies directly examining these parameters.

Interestingly, early pregnancy nutrition has been shown to impair cognitive flexibility and increase emotional reactivity in 18-month old rams (Erhard *et al*., 2004). Whether these changes would also manifest in altered reproductive performance is unknown (Rhind, 2004). Corner *et al*. (2005) reported no effect of maternal nutrition on the resulting young ewe's maternal behaviour at her first lambing. Although those born to well-fed ewes appeared to be less at ease in an arena behaviour test.

## Wool follicle and fibre characteristics

Primary wool follicle density peaks around day 80 of gestation while secondary follicle development begins after this period with its density peaking around day 120 (Hocking-Edwards, 1996). Therefore it is expected that maternal under-nutrition in early pregnancy does not alter the wool characteristics of wool production of their offspring (Table 3). Maternal nutritional restriction during the mid- and late-pregnancy period has generally resulted in fewer wool follicles, lighter fleece weights and slightly increased fibre diameters in the resulting offspring (Table 3). Behrendt (2006), Behrendt *et al*. (2006) and Curnow (2006) have all reported that improved nutrition during pregnancy in the Australian Lifetime wool project has resulted in increased fleece weight and a tendency for a finer fleece in offspring 2 to 5 years of age. These combined results indicate that improved nutrition, especially in the mid- to late-pregnancy period, can be used as a means to manipulate wool production characteristics in the resulting offspring.

Interestingly, Everitt (1967b) stated that adequate nutrition in the early post natal period may compensate for observed pre-natal penalties observed. However more recent evidence suggests that as both primary and secondary follicle development is complete by birth it may be difficult to alter wool follicle development after this period (Hocking-Edwards *et al*., 1996; Hocking Edwards, 1999).

In many of the studies examining the effects of maternal nutrition on fleece weight of the offspring, little attempt has been made to adjust for body weight. Thus it is possible that some of the reduction in fleece weight from maternal undernutrition could be attributed to reduced body weight.

## Recent nutritional models developed at Massey University

Clear conclusions regarding the effects of maternal nutrition on all of the above mentioned production traits are difficult to formulate due to differences in: the magnitude and length of the nutritional regimens utilised, the nutrition of the dam prior to and after the period being investigated, pregnancy/birth rank and the live weight and/or body condition of the dam, which may affect her ability to buffer against any nutritional insult. It is also apparent that the potential effects of maternal nutrition on the resulting female offspring's lactational performance have not been addressed. Jenkinson (2006) reported that maternal nutrition beginning on day 21 of gestation affected fetal mammary gland development. Unfortunately all pregnancies in that study were terminated.

A long-term study is currently underway at Massey University which investigates the potential intragenerational and intergenerational effects of maternal nutrition beginning at day 21 of pregnancy, involving two ewe body sizes and two pregnancy ranks. Ewes in this long term study were either offered a maintenance level of herbage or *ad-libitum* level from day 21 of pregnancy (van der Linden *et al*., 2007). The birth weight and weaning weights of twin lambs born to maintenance fed ewes were lighter than those born to *ad-libitum* ewes (P.R. Kenyon, Unpublished data). This relationship was not observed in single born lambs. Dam nutritional regimen had no effect on body composition in a group of male lambs from this study that were slaughtered (Johnson *et al*., 2007). Interestingly, examination of muscle and bone in a cohort of fetuses indicated that the bone mineral content/lean mass ratio was highest in singleton fetuses from *ad-libitum* fed ewes, irrespective of dam size, and lowest in singleton and twin fetuses from small maintenance-fed dams (E.C. Firth, Unpublished data). These data suggest that the bone mineral content/lean mass ratio is affected by the degree of constraint placed on the developing fetus(es).

Female progeny from the above trial have been retained and have undergone intensive monitoring. No effect of dam pregnancy nutrition has been observed on live weights of the female progeny at 13 months of age (van der Linden *et al*., 2007) or at two years of age (D.S. van der Linden, Unpublished data). Neither nutrition of the dam during pregnancy nor dam size affected the percentage of ewe lamb progeny achieving puberty in their first potential breeding season (van der Linden *et al*., 2007). Grand-dam nutrition tended to affect the birth weight of twin lambs born to the young ewes at two-years of age, a potential transgenerational effect such that lambs born to young ewes whose dam had been offered a maintenance level of nutrition in pregnancy tended to be heavier than those born to ewes whose dam had been offered *ad-libitum* feeding conditions (D.S. van der Linden, Unpublished data). Grand dam size had no effect on lamb birth weight. The accumulated milk yield of young ewes born to small *ad-libitum* fed dams was less than that from ewes born to large maintenance fed dams, while those born to small maintenance fed dams did not differ from either (D.S. van der Linden, Unpublished data). The growth rates to weaning of lambs born to these young ewes matched their lactational performance (D.S. van der Linden, Unpublished data). The young ewes are being re-bred in 2008 to obtain a further year's productive performance. The second generation ewe lambs are being retained and male lambs will be slaughtered and examined for carcass differences.

Bloomfield *et al*. (2003) and Edwards and McMillan (2002) reported that peri-conceptional nutrition affects fetal growth and the probability of preterm birth. Further, Kenyon *et al*. (2004) and Gardner *et al*. (2007) have shown that live weight and body condition of the ewe just prior to breeding can affect lamb birth weight. A study lead by the Liggins Institute, University of Auckland with assistance from AgResearch, Landcorp Farming and Massey University utilising about 1,700 ewes was undertaken in 2007 to examine the potential impact of ewe live weight 60 days prior to conception on the resulting offspring growth. Preliminary results suggest that dams fed at a lower level post weaning gave birth to heavier singleton-born ewe lambs compared to ram lambs (H.T. Blair, Unpublished data). Further analysis is underway.

**Environmental conditions**

The effects of heat stress (hyperthermia) on fetal growth and weight have been reviewed by Anthony *et al*. (2003). Chronic heat stress in mid- and late-pregnancy has been associated with reduced fetal growth and lamb birth weight (Yeates, 1958; Shelton, 1964; Shelton & Huston, 1968; Alexander & Williams, 1971; Hopkins *et al*., 1980). Heat stress is unlikely to occur under New Zealand's environmental conditions. However, it could be argued that a degree of cold stress may occur in winter-shorn pregnant ewes. Cold stress has been associated with increased lamb birth weights (Thompson *et al*., 1982). Shearing pregnant ewes in winter at the time of housing or during the housing period has long been known to increase lamb birth weight (Dyrmundsson, 1991; Kenyon *et al*., 2003). A series of studies examining the use of pregnancy shearing to increase lamb birth weight and survival under outdoor pastoral winter conditions has been undertaken at Massey University. Shearing ewes in mid-pregnancy between day 50 to day 100 of pregnancy has consistently been shown to increase lamb birth weight (Morris & McCutcheon, 1997; Kenyon *et al*., 2003; Corner *et al*., 2007) and to increase lamb survival (Kenyon *et al*., 2006a). Inconsistent birth weight effects has been reported from early- and late-pregnancy shearing (Morris &

McCutcheon 1997; Kenyon *et al*., 2003, 2005a). Kenyon *et al*. (2002) suggested that to achieve a birth weight response from mid-pregnancy shearing the ewe must have been destined to give birth to an otherwise light weight lamb(s) and secondly have the means to respond through an adequate level of maternal reserves and/or level of nutrition to partition towards fetal growth. Mid-pregnancy shearing has inconsistently affected newborn lamb thermoregulatory capability (Kenyon *et al*., 2003). Kenyon *et al*. (2004) reported that shearing in mid-pregnancy increased lamb growth to weaning although this was explained by increased lamb birth weight.

Mid-pregnancy shearing has had inconsistent effects on the resulting progeny's fibre follicle and wool characteristics. Revell *et al*. (2002) reported that single fetuses from mid-pregnancy shorn ewes had higher secondary follicle densities and secondary-to-primary-follicle ratios than those from unshorn dams. While, Kenyon *et al*. (2005b, 2006b) and van Reenen (E.H. van Reenan, Unpublished data) using Merinos, reported that mid- and late-pregnancy shearing had no effect on the progeny's fibre diameter. Sherlock *et al*. (2002) reported higher mean fibre diameter in offspring born to mid-pregnancy shorn Romney dams.

Although mid-pregnancy shearing has consistently been shown to increase lamb birth weight under pastoral conditions in more than 15 studies, few studies have examined the long-term effects in terms of live weight post weaning, carcass characteristics or reproductive performance. Van Reenen (E.H. van Reenan, Unpublished data) reported no effect of dam pregnancy shearing on the live weight of progeny at 12 months of age.

## Maternal and fetal genotype

When Walton and Hammond (1938) used artificial insemination to cross Shetland ponies with Shire horses they concluded that foal birth weight was approximately proportional to maternal size and that fetal genotype had little influence. In reciprocal crosses of Dexter, a small cattle breed, and South Devon, a larger breed, Joubert and Hammond (1958) reported similar findings. Allen *et al*. (2002) using embryo transfer between Thoroughbred horses and ponies suggested that both maternal environment and fetal genotype effected birth weight. While with sheep, Hunter (1956) using embryo transfer of Border Leicesters, a relatively large breed, and Welsh Mountain, a relatively small breed, suggested that it was the lamb's genotype which had the greatest influence on birth weight. Although it was still apparent in the study of Hunter (1956) that the growth restriction of a large genotype fetus in a small dam was greater than the enhancement of growth of a small genotype fetus in a larger breed dam. Dickinson *et al*. (1962) using embryo transfer with Lincoln, Welsh Mountain and Blackface ewes reported effects of both maternal environment and fetal genotype on birth weight. It also appeared that the large breed genotype (Lincoln) was much more affected by maternal environment than the smaller genotype (Welsh Mountain). There appears to be little information available on intragenerational long-term impacts of both fetal genotype and maternal environment in sheep. Allen *et al*. (2004) using their horse model showed that at 36 months of age, live weight of the Thoroughbred horses did not differ irrespective of their in-utero environment. In contrast, pony foals born to Thoroughbred mares were still heavier than foals born to pony mares (Allen *et al*., 2004).

To examine to role of maternal and fetal genotype a series of studies have been undertaken at Massey University, using reciprocal crosses and embryo transfer experiments with Cheviot (small) and Suffolk (large) breeds of sheep. Jenkinson *et al*. (2007) reported that crossbred lamb birth weights were lighter when the dam was the Cheviot compared to the Suffolk suggesting that the size of the ewe affects intrauterine development. Similarly, Earl (2007) reported that crossbred fetuses at Day 100 in Cheviot ewes were constrained to a similar weight to those of straightbred Cheviot fetuses while crossbred fetuses in Suffolk ewes were intermediate to straightbred Cheviot and Suffolk fetuses.

R.K. Sharma (Unpublished data) using embryo transfer found that straightbred Suffolk lambs born to Cheviot dams were lighter at birth than straightbred Suffolk lambs born to Suffolk ewes indicative of the Cheviot ewe restricting fetal growth. However, straightbred Cheviot lambs born to Suffolk ewes did not differ in birth weight from those born to Cheviot ewes suggestive of no enhancement of fetal growth or alternatively no genetic capacity to grow. At weaning and at 6 months of age Suffolk lambs born to Cheviot ewes did not differ in live weight compared to Suffolk lambs born to Suffolk ewes demonstrating that catch up growth must have occurred. The ewe and ram lamb progeny are currently being monitored.

## Conclusion

Research to date indicates that dam nutrition, age, parity, pregnancy rank, live weight, body condition and genotype and fetal genotype and environmental conditions all affect fetal development and potentially have post natal consequences. These effects are often term "fetal programming" effects. If these are to be of importance to pastoral based sheep farming systems they must affect productive performance in some manner and most likely need to manifest before the animal becomes "aged".

Todate most effects are intragenerational in nature with few intergenerational models being identified in sheep. It is also apparent that there is variation in results between studies and that many effects are observed in the fetus and young animal only, and are no longer apparent in the adult. Rhind *et al.* (2001) stated that additional work is required to elucidate further the critical windows in development and the mechanisms by which environmental factors affect the reproductive organs of developing offspring. This suggestion should be expanded to cover all production parameters. Understanding of these environmental effects would enable appropriate management systems to be put in place to either avoid adverse effects or to capitalise on potential positive effects.

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