

Prenatal and pre-weaning growth and nutrition of cattle: long-term consequences for beef production

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Severe, chronic growth retardation of cattle early in life reduces growth potential, resulting in smaller animals at any given age. Capacity for long-term compensatory growth diminishes as the age of onset of nutritional restriction resulting in prolonged growth retardation declines. Hence, more extreme intrauterine growth retardation can result in slower growth throughout postnatal life. However, within the limits of beef production systems, neither severely restricted growth in utero nor from birth to weaning influences efficiency of nutrient utilisation later in life. Retail yield from cattle severely restricted in growth during pregnancy or from birth to weaning is reduced compared with cattle well grown early in life, when compared at the same age later in life. However, retail yield and carcass composition of low- and high-birth-weight calves are similar at the same carcass weight. At equivalent carcass weights, cattle grown slowly from birth to weaning have carcasses of similar or leaner composition than those grown rapidly. However, if high energy, concentrate feed is provided following severe growth restriction from birth to weaning, then at equivalent weights post-weaning the slowly-grown, small weaners may be fatter than their well-grown counterparts. Restricted prenatal and pre-weaning nutrition and growth do not adversely affect measures of beef quality. Similarly, bovine myofibre characteristics are little affected in the long term by growth in utero or from birth to weaning. Interactions were not evident between prenatal and pre-weaning growth for subsequent growth, efficiency, carcass, yield and beef-quality characteristics, within our pasture-based production systems. Furthermore, interactions between genotype and nutrition early in life, studied using offspring of Piedmontese and Wagyu sired cattle, were not evident for any growth, efficiency, carcass, yield and beef-quality parameters. We propose that within pasture-based production systems for beef cattle, the plasticity of the carcass tissues, particularly of muscle, allows animals that are growth-retarded early in life to attain normal composition at equivalent weights in the long term, albeit at older ages. However, the quality of nutrition during recovery from early life growth retardation may be important in determining the subsequent composition of young, light-weight cattle relative to their heavier counterparts. Finally, it should be emphasised that long-term consequences of more specific and/or acute environmental influences during specific stages of embryonic, foetal and neonatal calf development remain to be determined. This need for further research extends to consequences of nutrition and growth early in life for reproductive capacity.

Keywords: birth weight, foetal programming, meat quality, muscle fibres, neonates

Introduction

There are numerous growth path possibilities during early and later life that may influence productive characteristics of cattle. These different growth paths result from factors including climate, soil quality and pasture species, which contribute to variable pasture and nutrient quality and availability. Growth of the bovine foetus has well-studied consequences for survival (Holland and Odde, 1992) and

can be slowed during the latter half of gestation by restricted nutrition and/or inadequate placental development (Bell *et al.*, 2005). Similarly, influences of pre-weaning nutrition, most notably lactational performance of the dam, on growth to market weights of cattle are well characterised (Berge, 1991). However, consequences of foetal calf growth for subsequent growth, and of foetal and neonatal calf growth for efficiency and carcass- and beef-quality characteristics, are less well understood.

Hence, this paper reviews research on consequences of cattle nutrition and growth during foetal and neonatal life

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for subsequent growth and efficiency, and for carcass and beef quality. It includes findings from our recent studies on consequences of maternal nutrition (commencing between days 30 and 90 of gestation) and growth during pregnancy and to weaning of cattle sired by bulls of extreme genotypes for muscle and intramuscular fat development (Cafe *et al.*, 2006a and 2006b; Greenwood *et al.*, 2006). Factors affecting growth and nutrition of the bovine foetus and milk-fed calf are also briefly described. The reader is also referred to reviews on consequences of prenatal development in livestock species by Bell (2006) and Symonds *et al.* (2007), and on consequences of bovine foetal, pre-weaning and early post-weaning growth and nutrition by Berge (1991) and Greenwood *et al.* (2005).

Normal bovine conceptus growth and metabolism

During postnatal growth, energy and nutrient availability directly influence growth and body composition of cattle. However, environmental influences on foetal growth and development and, hence, birth characteristics are regulated via the dam, and by the placenta that functions as a nutritional conduit between the dam and the foetus.

Most growth of the bovine foetus occurs during the final 100 days or so of a gestation averaging approximately 280 days (Winters *et al.*, 1942; Lyne, 1960; Ferrell *et al.*, 1976; Prior and Laster, 1979). Foetal nutrient uptake becomes a quantitatively important contributor to maternal nutrient requirements only after mid-gestation (Ferrell *et al.*, 1983). Unlike the sheep, in which the placenta attains most of its mass of dry tissue, protein and DNA by mid-gestation (Ehrhardt and Bell, 1995), the bovine placenta normally continues to increase in weight until near term (Prior and Laster, 1979; Ferrell, 1989). As a result, it has been suggested that placental growth may be less sensitive to nutritional deficiencies in cattle than in sheep. Placental weight and birth weight are highly correlated in cattle (Anthony *et al.*, 1986b; Echternkamp, 1993; Zhang *et al.*, 1999); however, the functional capacity of the placenta is closely related to placental perfusion. Bovine uterine and umbilical blood flow increases exponentially during the second half of gestation, which equates to relatively constant rates of umbilical blood flow on a foetal weight-specific basis during this period (Reynolds *et al.*, 1986). A more detailed account of placental function and metabolism in cattle is provided by Ferrell (1989), and of foetal macronutrient requirements and metabolism in cattle and sheep, and of placental function and metabolism, by Bell *et al.* (2005).

Intrauterine growth retardation

Maternal nutrition

Severe nutritional restriction for at least the last half to one-third of pregnancy is usually required to reduce bovine foetal growth. Significant reductions in birth weight were

caused by prolonged underfeeding of heifers from weaning until parturition (Wiltbank *et al.*, 1965), and underfeeding of heifers and cows for the second and third trimesters (Ryley and Gartner, 1962; Hodge and Rowan, 1970; Freetly *et al.*, 2000; Cafe *et al.*, 2006b) or late pregnancy only (Hight, 1966; Tudor, 1972; Bellows and Short, 1978; Kroker and Cummins, 1979). The effect of nutritional restriction on birth weight was more pronounced in calves from heifers than those from cows when the period of restriction encompassed mid- and late gestation (Hennessy *et al.*, 2002) rather than late gestation only (Tudor, 1972). However, birth weight was not significantly affected by nutritional restriction of heifers from mating to 140 days gestation (Cooper *et al.*, 1998) or during the final 12 weeks of pregnancy (Hodge *et al.*, 1976), or of mature cows for the second trimester (Freetly *et al.*, 2000).

During the final one-half to one-third of pregnancy, feed energy available to the dam appears to have more influence on birth weight than the availability of protein, although results are variable (Holland and Odde, 1992). Variation in feed energy available to the dam during this period resulted in differences in birth weight, ranging from 0 to 8.2 kg (Dunn *et al.*, 1969; Tudor, 1972; Laster, 1974; Corah *et al.*, 1975; Bellows and Short, 1978; Kroker and Cummins, 1979; Bellows *et al.*, 1982). Similarly, variable protein supply of the diet during the third trimester may (Bellows *et al.*, 1978) or may not (Anthony *et al.*, 1986a; Holland and Odde, 1992) alter birth weight of calves, while restricted or supplemental dietary protein during early or mid-pregnancy had little effect on birth weights (Perry *et al.*, 1999 and 2002). Furthermore, supplementation of grazing cows for 3 months *pre-partum* with 0.45 kg/day of 42% crude protein supplement did not affect calf birth weights (Stalker *et al.*, 2006). However, more chronic nutritional restriction of energy and/or protein of heifers from weaning until parturition resulted in birth weight differences of up to 10 kg due to energy supply and up to 7.3 kg due to protein supply (Wiltbank *et al.*, 1965).

As described above, placental weight and birth weight are highly correlated in cattle. However, because the bovine placenta may continue to increase in mass until near term, it is less clear whether the placenta regulates bovine foetal growth to the same extent as it does in sheep (Ferrell, 1989). Placental characteristics may be altered by nutrition during early and mid-pregnancy without significantly affecting foetal size (Rasby *et al.*, 1990), and protein supplementation of cows during early or mid-pregnancy may also alter placental characteristics without necessarily affecting birth weight (Perry *et al.*, 1999 and 2002).

Development and growth of vital organs precede development of bone, muscle and fat (Palsson, 1955), respectively; hence the mass of the relatively late maturing carcass tissues are generally considered more susceptible to the effects of nutrition during later pregnancy when nutrition impacts most on foetal growth. However, more subtle effects on organ and tissue development due to nutrition during early pregnancy may occur, with the potential for

long-term consequences for health, as shown in sheep (Greenwood and Bell, 2003; Bell *et al.*, 2005; Symonds *et al.*, 2007).

Thermal environment

Foetal growth in cattle was restricted (18% lower foetal weight) by chronic heat stress of pregnant cows, while provision of shade resulted in a 3.1 kg increase in birth weight (Collier *et al.*, 1982). In sheep, chronic heat stress in early to mid-gestation restricts placental development, thus imposing a limitation on subsequent foetal growth irrespective of nutrition later in pregnancy (Bell *et al.*, 1987). This suggests that restricted foetal calf growth due to heat stress is probably a consequence of reduced placental development. Severe cold stress of cattle may also reduce foetal growth if inadequate nutrition is provided to meet the additional metabolic requirements of cows in addition to foetal requirements for growth and development (Andreoli *et al.*, 1988), although in sheep, more moderate cold stress of ewes in late gestation increased birth weight by 15% (Thompson *et al.*, 1982). It is believed that temperature regulates blood flow to the periphery and lungs in order to preserve or dissipate body heat, resulting in increased or decreased blood flow and nutrient supply to the gravid uterus (Reynolds *et al.*, 1985).

Parity

Heifers give birth to smaller calves, on average, than cows (reviewed by Holland and Odde, 1992) due at least in part to size and nutritional requirements for growth of heifers, limiting nutrient availability for placental and foetal growth. Severe maternal nutritional restriction may impact more on birth weights of calves of heifers than of cows, particularly among male calves and those of sires with inherently high birth weight of offspring (Hennessy *et al.*, 2002), presumably due to their greater requirements for nutrients compared with female calves and those of sires with inherently low birth weight of offspring. In adolescent sheep fed to attain excessive fatness prior to and during gestation, placental and foetal growth and birth weight are reduced (Wallace *et al.*, 1996 and 1999), although the extent to which over-nutrition of adolescent heifers influences birth weight is not clear.

Litter size

Twin calves and higher multiples are rare in cattle unless exogenous regulation of ovarian function or embryo transfer is practised. Individuals within litters have reduced foetal growth compared with singletons due to a reduced number of placentomes and mass of placenta per foetus (Hafez and Rajakoski, 1964; Greenwood *et al.*, 2000b) and because of greater total nutrient requirements of the litter. On average, twin calves range from 7.4 to 9.8 kg lighter than singletons (Gregory *et al.*, 1990 and 1996; De Rose and Wilton, 1991; Cummins, 1994; Wilkins *et al.*, 1994).

Restricted nutrition limits foetal growth earlier and more severely in twins or higher multiples than in singletons, although stocking rates of pregnant cows fed on pasture did not significantly influence the birth weight of twins (Wilkins *et al.*, 1994).

Foetal and maternal genotype

Foetal genotype is most important in determining foetal growth during early and mid-pregnancy, whereas maternal genotype is more important in determining foetal growth during late pregnancy when most foetal growth normally occurs and foetal growth is increasingly subject to external influences mediated via the dam. The effect of foetal and maternal genotype on foetal growth has been most convincingly demonstrated in cattle by Ferrell (1991) who implanted Charolais (heavier birth weight) or Brahman (lighter birth weight) embryos into Charolais and Brahman cows. At 232 days of pregnancy, each foetal genotype was similar in size, irrespective of dam breed. However, by 274 days of gestation Charolais foetuses in Brahman cows were 7 kg lighter than those in Charolais cows. In contrast, Brahman foetuses in Charolais cows were only 2 kg heavier than those in Brahman cows. Similar results were obtained by Joubert and Hammond (1958) for birth weights for South Devon and Dexter cattle and their reciprocal crosses. In this regard, foetal growth capacity as influenced by sex and sire-genotype may also influence the nutritional status of the pregnant cow during late gestation (Greenwood *et al.*, 2002b), probably due to differences in foetal nutrient uptake, contributing to maternal nutrient requirements.

Growth and development from birth to weaning

Calves undergo a transition at birth from a diet comprising primarily glucose and amino acids to one that is quantitatively greater and is proportionately higher in fat. This is associated with maturation of the digestive, metabolic and endocrine systems. Evidence in sheep suggests severely growth-retarded newborns are immature with respect to energy metabolism and have more foetal-like metabolism than their well-grown counterparts (Greenwood *et al.*, 2002a; Rhoads *et al.*, 2000a and 2000b).

The major nutritional factors affecting pre-weaning calf growth and composition at weaning are the lactational performance of the dam and the quality and availability of nutrients from pasture and/or supplementation prior to and following parturition. Most notably, maternal genotype, age and parity, nutrient availability and body condition and live weight of the dam, and capacity of the calf to grow and consume milk, interact to influence lactational output. Calves become increasingly dependent on forage-based diets that result in the production of volatile fatty acids that stimulate development and maturation of the rumen (Warner and Flatt, 1965) until weaning, when this dependence becomes complete.

Long-term consequences of altered growth during the early life of cattle

In this section, the long-term consequences of altered growth early in life for growth, feed efficiency, and carcass, yield, beef quality and myofibre characteristics are discussed first for altered foetal growth, and then for altered pre-weaning growth. Interactions between prenatal and pre-weaning growth are then discussed.

Consequences of foetal growth and nutrition

Postnatal growth. In our recent studies of consequences of foetal growth, which compared performance of calves differing by 10.2 kg or by 35% in birth weight (Table 1), capacity of low-birth-weight cattle to exhibit compensatory growth was limited. Cattle significantly growth retarded during foetal life due to severely restricted maternal nutrition from early pregnancy (commencing between day 30 and 90 of pregnancy) to parturition remained smaller during rearing on their dams and at any given postnatal age after weaning compared with their well-grown or better-nourished counterparts (Table 1). However, it remains speculative whether this represents a permanent stunting or simply a delay of attainment of mature size of cattle. Growth of low-birth-weight cattle was significantly slower than those of high birth weight at all stages of postnatal growth, although about half the difference in average daily gain (ADG) during feedlotting was explained by differences in weight at feedlot entry between the low- and high-birth-weight cattle (Table 1). However, when differences in birth weights were less-pronounced, post weaning and feedlot growth were not significantly affected by birth weight (Cafe

et al., 2006a). These findings are consistent with those of Swali and Wathes (2006) who found that small size at birth resulted in smaller cattle compared with high-birth-weight cattle at 15 months of age, while average-birth-weight cattle did not differ significantly in weight during postnatal growth compared with the low- or high-birth-weight groups.

In contrast to the above findings, artificially reared low-birth-weight male calves grew more rapidly to weaning than their high-birth-weight counterparts, although the opposite occurred for female calves (Tudor and O'Rourke, 1980). Hence, it is important to recognise that an assessment of influences of foetal development on postnatal performance requires consideration of the consequences of nutrition during pregnancy on subsequent maternal performance when offspring remain on their dams to weaning, due to carry-over effects on the dam. In this regard, readers are referred to Greenwood *et al.* (1998) for an example of a rearing system designed to uncouple prenatal and postnatal influences in ruminants varying in birth weight. The net effects of maternal nutrition during pregnancy on the calf remain of practical significance to livestock producers, and influences of nutrition during mid- and late pregnancy or late pregnancy only on calf weaning weight have been consistently shown (e.g. Hight, 1966 and 1968a; Cafe *et al.*, 2006b; Stalker *et al.*, 2006), irrespective of effects on foetal growth.

In relation to potential interactions between prenatal and postnatal nutrition and growth, differences in weight of calves at birth following three levels of maternal nutrition during late pregnancy disappeared by weaning when postnatal nutrition was of high quality and availability

Table 1 Consequences of growth in utero for growth and live-weight characteristics of beef cattle to 30 months of age (adapted from Greenwood *et al.*, 2005 and 2006)[†]

	Prenatal growth/birth weight		Significance of difference (<i>P</i>)
	Low (<i>n</i> = 120)	High (<i>n</i> = 120)	
Birth weight (kg)	28.6	38.8	
Pre-weaning ADG (g)	670	759	<0.001
Weaning (7 months) weight (kg)	174	198	<0.001
Backgrounding ADG (g)	571	603	<0.001
At equivalent age (26 to 30 months)			
Feedlot entry (26 months) weight (kg)	481	520	<0.001
Feedlot ADG (g)	1480	1617	<0.001
Feedlot exit (30 months) weight (kg)	647	703	<0.001
At equivalent feedlot entry live weight (500 kg)			
Age at feedlot entry (day) [‡]	797	715	<0.001
Feedlot ADG (g)	1515	1583	0.019
Feedlot exit weight (kg)	671	679	0.017
Age at feedlot exit (day) [§]	914	833	<0.001

Abbreviation is: ADG = average daily gain.

Values are predicted means from residual maximum likelihood (REML) analyses including effects of birth weight, pre-weaning nutrition, sex/year cohort, sire-genotype and their interactions.

[†] Maternal nutritional treatments commenced between days 30 and 90 of pregnancy (refer to Cafe *et al.* (2006b) and Greenwood *et al.* (2006) for details of pasture-based nutritional treatments and selection criteria for calves used to study long-term consequences of growth early in life).

[‡] Predicted from mean ADG during backgrounding.

[§] Predicted from mean ADG during background and mean feedlotting period.

Table 2 Consequences of growth in utero for feed intake and efficiency of beef cattle during feedlotting from 26 to 30 months of age (L. M. Cafe and P. L. Greenwood, unpublished results)

	Prenatal growth/birth weight		Significance of difference (<i>P</i>)
	Low (<i>n</i> = 77)	High (<i>n</i> = 77)	
Birth weight (kg)	28.1	38.4	
At equivalent age (26 to 30 months)			
Feedlot entry (26 months) weight (kg)	466	513	<0.001
Feedlot ADG (g) [†]	1279	1396	0.004
Feed intake (kg/day) [†]	13.21	14.63	<0.001
Feed efficiency (kg DM intake/kg LW gain)	10.00	10.38	0.26
Residual feed intake (kg) [‡]	-0.005	0.003	0.99
At equivalent feedlot entry LW (490 kg)			
Feedlot ADG (g) [†]	1317	1361	0.46
Feed intake (kg/day) [†]	13.86	14.01	0.55
Feed efficiency (kg DM intake/kg LW gain)	10.25	10.15	0.89

Abbreviations are: ADG = average daily gain, DM=dry matter; LW=live weight.

Values are predicted means from residual maximum likelihood (REML) analyses including effects of birth weight, pre-weaning nutrition, sex/year cohort, sire-genotype and their interactions, with feedlot entry weight as a covariate (linear and, where significant, quadratic) to predict means at equivalent feedlot entry weight. Difference in significance of feedlot ADG between Tables 1 and 2 is due to the number of cohorts studied (three cohorts in Table 1 v. two cohorts in Table 2) and the duration of the measurement period (average of 117 days in Table 1 v. 70 days in Table 2).

[†] During 70-day period in feed intake pens.

[‡] At mean metabolic live weight.

(Hight, 1968b). In this study, however, residual effects of the previous year's nutrition influenced calf growth, with cows previously well nourished producing heavier calves, and vice versa (Hight, 1968b). Similarly, effects of variable nutrition during mid- and/or late pregnancy on weight at birth were overcome by adequate nutrition *post partum*, resulting in no difference in body weight at 58 days of age (Freetly *et al.*, 2000). While twin cattle are lighter at birth and grow more slowly on their dams to weaning (Hennessy and Wilkins, 1997), they may grow more slowly (Gregory *et al.*, 1996), at a similar rate (De Rose and Wilton, 1991) or more rapidly (Wilkins *et al.*, 1994; Clarke *et al.*, 1994; Hennessy and Wilkins, 1997) post-weaning than singletons, depending on the rearing system and subsequent nutritional regimen.

Feed intake and efficiency. Slower feedlot growth by low-birth-weight calves was associated with the consumption of fewer nutrients in the feedlot but no difference in feed efficiency or residual feed intake compared with high-birth-weight calves at an equivalent age from 26 to 30 months (Table 2). When compared at equivalent feedlot entry live weights, differences in feed intake due to birth weight were no longer apparent, consistent with findings in twin cattle, which tended to consume less feed in feedlot than singletons, due primarily to their lower live weight (De Rose and Wilton, 1991). Similarly, provision of supplement to cows for 3 months *pre-partum* had no significant post-weaning effects on ADG, feed intake and feed efficiency in steers (Stalker *et al.*, 2006) or heifers (Martin *et al.*, 2007) that were individually fed following weaning, although the heifers of supplemented cows tended to have greater absolute and residual feed intakes during individual feeding for 84 days post-weaning.

Body and carcass composition. Few studies have examined long-term consequences of foetal nutrition and growth for body and carcass characteristics in cattle (Tudor *et al.*, 1980) prior to our more recent studies (Greenwood *et al.*, 2006). Our research has shown that a significant reduction in birth weight following severe maternal nutritional restriction did not influence indices of fatness, apart from P8 (rump) fat, in carcasses of Wagyu- or Piedmontese-sired steers and heifers at 30 months of age, beyond that normally attributable to differences in live or carcass weight (Table 3). Low-birth-weight cattle had a similar intramuscular fat content, retail yield, fat trim and bone content at equivalent carcass weight, suggesting little overall difference in carcass composition from their high-birth-weight counterparts. However, ossification score was higher in low- compared with high-birth-weight calves (Table 3), suggesting an impact of prenatal growth on calcification of bone and relative maturity. Similar to our findings, gross compositional differences were not evident in the whole body or in the carcass of Hereford steers or heifers grown to 370 to 400 kg live weight following restricted or adequate nutrition of their dams from 180 days of pregnancy to parturition with a resultant 22% or 6.8 kg difference in calf birth weight (Tudor *et al.*, 1980). Furthermore, *pre-partum* supplementation of cows had no effects on the carcass composition of offspring following feedlotting for 222 days post weaning (Stalker *et al.*, 2006).

Research on twin cattle has also demonstrated that, despite significantly lower birth weights and reduced pre-weaning growth, compositional differences at equivalent slaughter weights or ages are small and not significant, with twins generally having similar or leaner carcasses than singletons (De Rose and Wilton, 1991; Wilkins *et al.*, 1994; Clarke *et al.*, 1994; Gregory *et al.*, 1996).

Table 3 Consequences of growth in utero for carcass and yield characteristics of beef cattle at 30 months of age (adapted from Greenwood et al., 2006)

	Prenatal growth/birth weight		Significance of difference (<i>P</i>)
	Low (<i>n</i> = 120)	High (<i>n</i> = 120)	
At equivalent age (30 months)			
Carcass weight (kg)	364	396	<0.001
Retail yield (kg)	239	257	<0.001
At equivalent carcass weight (380 kg)			
Eye muscle area (cm ²)	90.4	88.9	0.25
P8 fat depth (mm)	21.3	19.6	0.048
Rib fat depth (mm)	10.9	10.5	0.35
Aus-Meat marble score	1.83	1.86	0.56
USDA marble score	447	444	0.98
<i>Longissimus</i> IMF (%)	6.8	7.0	0.62
Ossification score	206	195	0.009
Retail yield (kg)	249	247	0.20
Bone (kg)	66.9	67.6	0.10
Fat trim (kg)	54.6	56.0	0.58

Abbreviation is: IMF = intramuscular fat.

Values are predicted means from residual maximum likelihood (REML) analyses including effects of birth weight, pre-weaning nutrition, sex/year cohort, sire-genotype and their interactions, with carcass weight as a covariate (linear and, where significant, quadratic) to predict means at equivalent carcass weight. Refer to Table 1 for growth characteristics of the cattle.

Table 4 Consequences of growth in utero for objective measurements of *m. longissimus* (striploin) and *m. semitendinosus* (eye round) quality in beef cattle at 30 months of age (adapted from Greenwood et al., 2006)

	Prenatal growth/birth weight		Significance of difference (<i>P</i>)
	Low (<i>n</i> = 120)	High (<i>n</i> = 120)	
<i>Longissimus</i>			
Peak force (N) [†]	39.2	40.5	0.26
Compression (N) [†]	13.9	14.4	0.19
Cooking loss (%)	21.6	21.7	0.57
Ultimate pH	5.47	5.48	0.50
Colour L (lightness)	39.5	40.0	0.21
Colour a (red/green)	26.3	26.7	0.20
Colour b (yellow/blue)	13.6	13.8	0.15
<i>Semitendinosus</i>			
Peak force (N) [†]	46.2	46.4	0.81
Compression (N) [†]	22.6	22.7	0.97
Cooking loss (%)	21.5	21.3	0.52

Values are predicted means from residual maximum likelihood (REML) analyses including effects of birth weight, pre-weaning nutrition, sex, sire-genotype and their interactions. Refer to Tables 1 and 3 for growth and carcass characteristics of the cattle.

[†] Objective measures of texture, as defined by Perry et al. (2001).

Beef quality and myofibre characteristics. There were no adverse effects on objective measurements of beef quality including peak force, compression, cooking loss and colour in the *longissimus* (striploin) and *semitendinosus* (eye round) muscles at 30 months of age due to restricted growth *in utero* (Table 4).

Myofibre characteristics including number and size of myofibres, and percentages and relative areas of myofibres in the *m. longissimus lumborum* (Table 5) and *semitendinosus* (results not shown) muscles at 30 months of age, were also unaffected by calf growth *in utero* (Table 5).

In this regard, nutrition during pregnancy resulting in divergent foetal calf growth resulted in differences at birth in the percentages of type 1 (low 17.2 v. high 23.3%) and type 2A (28.2 v. 23.5%) myofibres, the ratio of fast to slow (4.8 v. 3.4) myofibres and the cross-sectional area of type 2X (673 v. 831 μm²) myofibres (Greenwood et al., 2004). However, differences in myofibre characteristics due to foetal growth were no longer evident by weaning (P. L. Greenwood, unpublished results). Within the present study, as with newborn lambs restricted in growth during mid- to late pregnancy (Greenwood et al., 1999 and 2000a),

Table 5 Consequences of growth in utero for longissimus lumborum myofibre characteristics of heifer beef cattle at 30 months of age (P. L. Greenwood and L. M. Café, unpublished results)

	Prenatal growth/birth weight		Significance of difference (<i>P</i>)
	Low (<i>n</i> = 38)	High (<i>n</i> = 40)	
Birth weight (kg)	27.3	35.9	
Live weight at 30 months (kg)	594	655	<0.001
Carcass weight (kg)	335	370	<0.001
Muscle weight (g)	4097	4453	0.002
Muscle CSA (cm ²)	85.3	90.4	0.029
Myofibres per mm ²	130.5	126.8	0.62
Apparent myofibre number ($\times 10^{-6}$)	1.112	1.137	0.78
Average myofibre CSA (μm^2)	5708	5731	0.86
Total myofibre area (%)			
Type 1	22.5	22.5	0.99
Type 2C	0.55	0.71	0.52
Type 2A	21.9	23.4	0.43
Type 2AX	5.61	6.27	0.53
Type 2X	49.5	47.2	0.44

Abbreviation is: CSA = cross-sectional area.

Values are predicted means from residual maximum likelihood (REML) analyses including effects of birth weight, pre-weaning nutrition, sex, sire-genotype and their interactions.

Refer to Lehnert *et al.* (2006) for myofibre classification and measurement methodology. Type 1, type 1 myosin heavy chain (MHC) \equiv slow oxidative; type 2C, intermediate between type 1 and type 2A; type 2A, type 2A MHC \equiv fast oxidative-glycolytic; type 2AX, intermediate between type 2A and type 2X; type 2X, type 2X MHC \equiv fast glycolytic.

apparent myofibre number was not affected by divergent growth *in utero* (Table 5).

Consequences of pre-weaning growth and nutrition

Postnatal growth. Consequences of nutritional restriction from birth to weaning for subsequent growth of cattle were reviewed by Alden (1970), Berge (1991) and Hearnshaw (1997). It is generally recognised that severe pre-weaning nutritional restriction limits the capacity of cattle to exhibit compensatory growth and achieve equivalent weight for age in later life. In reviewing a series of Australian studies on consequences of pre-weaning nutritional systems, Hearnshaw (1997) concluded that compensatory gain following pre-weaning growth restriction occurred most frequently when overall post-weaning growth rates were less than 0.6 kg/day, whereas at higher post-weaning growth rates compensation was less evident. However, in feedlot the differences in growth were in the opposite direction to differences in growth post-weaning, and when compensation did occur among cattle restricted prior to weaning, the gains were only small. In more recent studies, calves reared slowly (464 g/day) compared with those reared rapidly (872 g/day) from birth to weaning were 37 kg lighter at weaning, but 48 kg lighter following backgrounding due to a trend towards slower backgrounding growth among the previously restricted cattle, and remained 46 kg lighter at slaughter at 17 months of age (Hennessy and Morris, 2003; Hennessy and Arthur, 2004).

In our recent studies, a difference in weaning weight of 73 kg resulted in a 40 kg difference in live weight and 24 kg in carcass weight at 30 months of age (Greenwood *et al.*,

2005 and 2006; Table 6). The low weaning weight cattle grew more rapidly during backgrounding and at a similar rate in the feedlot, resulting in more rapid growth overall from weaning to 30 months of age. However, compensation in live weight remained incomplete by the conclusion of the study. Similarly, in steers restricted in growth from birth to weaning, then backgrounded to the same feedlot entry weight as cattle grown rapidly to weaning, some compensatory growth was observed during backgrounding but not in the feedlot (Café *et al.*, 2006a). These studies have confirmed earlier findings that severe, chronic nutritional restriction to weaning limits compensatory growth, which only occurred prior to feedlot entry and not in the feedlot, resulting in smaller cattle and carcasses and less retail yield of beef at an equivalent age.

Feed intake and efficiency. During feedlotting from 26 to 30 months of age, feed intake was lower among cattle grown slowly to weaning than those grown rapidly; however, this effect of pre-weaning growth rate was not evident when assessed at the same feedlot entry weight (Table 7). Differences in feed efficiency or residual feed intake were not apparent on an age- or live-weight equivalent basis. Consistent with these findings, when variation in live weight that contributed to differences in energy requirements for maintenance and growth were accounted for, low pre-weaning growth rates did not influence measures of efficiency in the feedlot of cattle of equivalent age compared with those grown more rapidly prior to weaning (Hennessy and Arthur, 2004). Furthermore, effects of early *post partum* nutrition on growth, intake and efficiency of

Table 6 Consequences of growth from birth to weaning for growth and live weight characteristics of beef cattle to 30 months of age (adapted from Greenwood *et al.*, 2005 and 2006)[†]

	Pre-weaning growth		Significance of difference (<i>P</i>)
	Low (<i>n</i> = 119)	High (<i>n</i> = 121)	
Birth weight (kg)	33.1	34.2	
Pre-weaning ADG (g)	554	875	
Weaning (7 months) weight (kg)	151	221	
Backgrounding ADG (g)	615	558	<0.001
At equivalent age (26 to 30 months)			
Feedlot entry (26 months) weight (kg)	483	517	<0.001
Feedlot ADG (g)	1527	1570	0.15
Feedlot exit (30 months) weight (kg)	655	695	<0.001
At equivalent feedlot entry live weight (500 kg)			
Age at feedlot entry (day) [‡]	789	724	<0.001
Feedlot ADG (g)	1558	1540	0.49
Feedlot exit weight (kg)	674	676	0.52
Age at feedlot exit (day) [§]	907	841	<0.001

Abbreviation is: ADG = average daily gain.

Values are predicted means from residual maximum likelihood (REML) analyses including effects of birth weight, pre-weaning nutrition, sex/year cohort, sire-genotype and their interactions, with feedlot entry weight as a covariate (linear and, where significant, quadratic) to predict means at equivalent feedlot entry weight.

[†] Refer to Cafe *et al.* (2006b) and Greenwood *et al.* (2006) for details of pasture-based nutritional treatments and selection criteria for calves used to study long-term consequences of growth early in life.

[‡] Predicted from mean ADG during backgrounding.

[§] Predicted from mean ADG during background and mean feedlotting period.

Table 7 Consequences of growth from birth to weaning for feed intake and efficiency of beef cattle during feedlotting from 26 to 30 months of age (L. M. Cafe and P. L. Greenwood, unpublished results)

	Pre-weaning growth		Significance of difference (<i>P</i>)
	Low (<i>n</i> = 75)	High (<i>n</i> = 79)	
Weaning weight (kg)	149	215	
At equivalent age (26–30 months)			
Feedlot entry (26 months) weight (kg)	477	502	<0.001
Feedlot ADG (g) [†]	1319	1356	0.36
Feed intake (kg/day) [†]	13.59	14.24	0.002
Feed efficiency (kg DM intake/kg LW gain)	10.02	10.36	0.33
Residual feed intake (kg) [‡]	−0.042	0.040	0.51
At equivalent feedlot entry LW (490 kg)			
Feedlot ADG (g) [†]	1317	1361	0.94
Feed intake (kg/day) [†]	13.89	13.98	0.55
Feed efficiency (kg DM intake/kg LW gain)	10.13	10.27	0.66

Abbreviations are: ADG = average daily gain, DM = dry matter, LW = live weight.

Values are predicted means from residual maximum likelihood (REML) analyses including effects of birth weight, pre-weaning nutrition, sex/year cohort, sire-genotype and their interactions, with feedlot entry weight as a covariate (linear and, where significant, quadratic) to predict means at equivalent feedlot entry weight. Difference in significance of feedlot ADG between Tables 6 and 7 is due to the number of cohorts studied (three in Table 6 *v.* two in Table 7) and the duration of the measurement period (average of 117 days in Table 6 *v.* 70 days in Table 7).

[†] During 70-day period in feed intake pens.

[‡] At mean metabolic live weight.

steers (Stalker *et al.*, 2006) and heifers (Martin *et al.*, 2007) in the feedlot soon after weaning were not evident. These results are consistent with earlier findings, reviewed by Berge (1991), that feed conversion efficiency is little affected in the long term by nutrition prior to weaning. However, following extremely severe postnatal nutritional restriction where calves were held near their birth weights for 200 days, compared with cattle well grown to weaning,

feed efficiency was adversely affected in males during growth from 200 kg to about 400 kg live weight, whereas during the same period females were more efficient (Tudor and O'Rourke, 1980).

Body and carcass composition. At equivalent carcass weight, there was more fat trim, less retail yield and there

Table 8 Consequences of growth from birth to weaning for carcass characteristics of beef cattle at 30 months of age (adapted from Greenwood *et al.*, 2006)

	Pre-weaning growth		Significance of difference (<i>P</i>)
	Low (<i>n</i> = 119)	High (<i>n</i> = 121)	
At equivalent age (30 months)			
Carcass weight (kg)	368	393	<0.001
Retail yield (kg)	242	254	<0.001
At equivalent carcass weight (380 kg)			
Eye muscle area (cm ²)	90.1	89.2	0.55
P8 fat depth (mm)	20.1	20.8	0.41
Rib fat depth (mm)	10.4	11.0	0.33
Aus-Meat marble score	1.92	1.77	0.15
USDA marble score	450	441	0.49
<i>Longissimus</i> IMF (%)	6.88	6.98	0.80
Ossification score	202	199	0.53
Retail yield (kg)	251	246	<0.001
Bone (kg)	67.8	66.7	0.053
Fat trim (kg)	52.8	57.8	<0.001

Abbreviation is: IMF = intramuscular fat.

Values are predicted means from residual maximum likelihood (REML) analyses including effects of birth weight, pre-weaning nutrition, sex/year cohort, sire-genotype and their interactions, with carcass weight as a covariate (linear and, where significant, quadratic) to predict means at equivalent carcass weight. Refer to Table 6 for growth characteristics of the cattle.

tended to be less bone in the carcass among the cattle grown rapidly compared with those grown slowly to weaning (Greenwood *et al.*, 2006; Table 8). This suggests the greater fatness at weaning of the rapidly reared cattle persisted to 30 months of age. However, because of failure to compensate fully in weight, the carcasses from light weaners remained smaller and weight of retail beef was lower compared with the heavy weaners at the same age. When cattle grown rapidly or slowly to weaning were backgrounded to the same feedlot entry weight and slaughtered after 120 days in the feedlot, their carcasses did not differ in compositional and yield characteristics (Cafe *et al.*, 2006a).

Earlier studies within pasture-based nutritional systems also failed to demonstrate substantial differences in body or carcass composition due to nutrition and growth from birth to weaning (Berge, 1991; Hearnshaw, 1997). These authors concluded that cattle from low pre-weaning nutrition groups generally have less fat than those from high pre-weaning nutrition groups, but if compared at a constant carcass weight, differences in fatness usually disappear. As a result, calves with lower weaning weights take longer to reach carcass specifications than heavier calves.

In contrast to the above findings, severe nutritional restriction to weaning that resulted in little growth *post partum*, followed by concentrate (high energy) feeding from weaning to slaughter resulted in greater fatness at the same live and carcass weights compared with cattle well nourished prior to weaning (Tudor *et al.*, 1980). Within the same study, cattle restricted or well nourished to weaning then grown on pasture to the same slaughter weight did not differ in composition. Factors likely to have contributed to increased fatness among the small compared with large

weaners, which were subsequently fed concentrates, include the following: greater length of time on concentrate feed to reach the slaughter weight; greater weight-specific intake of nutrients following the nutritional restriction; a greater requirement for protein relative to energy at weaning and, hence, potential nutrient imbalance in the concentrate diet during the early post-weaning phase; and more limited capacity for lean tissue accretion post weaning in the small compared with large weaners.

Beef quality and myofibre characteristics. Differences in objective measurements of meat quality between cattle grown slowly or rapidly to weaning were not evident within our research (Greenwood *et al.*, 2006; Table 9). Similarly, in earlier studies, objective measures of eating quality were not adversely affected by restricted nutrition prior to weaning (Hearnshaw, 1997; Hennessy *et al.*, 2001; Hennessy and Morris, 2003). When they were affected, however, meat of cattle from low-nutrition groups was usually more tender than that of high-nutrition groups (Hearnshaw, 1997; Hennessy *et al.*, 2001). However, when compared at a constant carcass weight, in about half of the studies the meat quality differences became non-significant (Hearnshaw, 1997). Despite these findings, meat quality may be compromised if the slow growth of cattle alter weaning results in them being at least 8 to 9 months older at slaughter weight (Loxton, 1997; Purchas *et al.*, 2002). It is unclear if similar age differences resulting from growth restriction earlier in life have similar effects.

As with the above findings for meat quality, growth to weaning had little overall effect on myofibre characteristics in the *longissimus lumborum* muscle at 30 months of age, apart from a small increase in the relative area of type 1

Table 9 Consequences of growth from birth to weaning for objective measurements of *m. longissimus (striploin)* and *m. semitendinosus (eye round)* quality in beef cattle at 30 months of age (adapted from Greenwood *et al.*, 2006)

	Pre-weaning growth		Significance of difference (<i>P</i>)
	Low (<i>n</i> = 119)	High (<i>n</i> = 121)	
<i>Longissimus</i>			
Peak force (N) [†]	40.5	39.2	0.25
Compression (N) [†]	14.2	14.1	0.63
Cooking loss (%)	21.8	21.5	0.23
Ultimate pH	5.48	5.47	0.60
Colour L (lightness)	39.9	39.6	0.48
Colour a (red/green)	26.5	26.6	0.70
Colour b (yellow/blue)	13.7	13.7	0.93
<i>Semitendinosus</i>			
Peak force (N) [†]	46.3	46.3	0.89
Compression (N) [†]	22.1	22.8	0.47
Cooking loss (%)	21.5	21.3	0.45

Values are predicted means from residual maximum likelihood (REML) analyses including effects of birth weight, pre-weaning nutrition, sex, sire-genotype and their interactions. Refer to Tables 6 and 8 for growth and carcass characteristics of the cattle.

[†] Objective measures of texture, as defined by Perry *et al.* (2001).

Table 10 Consequences of growth from birth to weaning for longissimus lumborum myofibre characteristics of heifer beef cattle at 30 months of age (P. L. Greenwood and L. M. Cafe, unpublished results)

	Pre-weaning growth		Significance of difference (<i>P</i>)
	Low (<i>n</i> = 40)	High (<i>n</i> = 38)	
Weaning weight (kg)	138	203	
Live weight at 30 months (kg)	612	637	0.025
Carcass weight (kg)	345	360	0.032
Muscle weight (g)	4191	4358	0.14
Muscle CSA (cm ²)	87.3	88.4	0.58
Myofibres per mm ²	132.9	124.4	0.27
Average myofibre CSA (μm ²)	5585	5854	0.32
Total myofibre area (%)			
Type 1	23.9	21.1	0.017
Type 2C	0.59	0.67	0.75
Type 2A	22.6	22.7	0.89
Type 2AX	6.58	5.30	0.28
Type 2X	46.4	50.2	0.24

Abbreviation is: CSA = cross-sectional area.

Values are predicted means from residual maximum likelihood (REML) analyses including effects of birth weight, pre-weaning nutrition, sex, sire-genotype and their interactions. Refer to Lehnert *et al.* (2006) for myofibre classification and measurement methodology. Type 1, type 1 myosin heavy chain (MHC) ≡ slow oxidative; Type 2C, intermediate between type 1 and type 2A; Type 2A, type 2A MHC ≡ fast oxidative-glycolytic; Type 2AX, intermediate between type 2A and type 2X; Type 2X, type 2X MHC ≡ fast glycolytic.

myofibres in cattle grown slowly to weaning compared with those grown rapidly (Table 10). This is despite differences due to pre-weaning growth in the size of each myofibre type and the percentages and relative area of fast (type 2) myofibres at weaning (P. L. Greenwood, unpublished results).

Interactions between *in utero* and pre-weaning growth

Among the numerous beef production characteristics that we investigated, the only interaction between growth

in utero and growth prior to weaning was for the eye muscle (*m. longissimus*) cross-sectional area when compared at an equivalent carcass weight at 30 months of age (Greenwood *et al.*, 2006). Cattle of low birth weight had a greater eye muscle area at slaughter than high-birth-weight cattle within the high pre-weaning growth group (91.1 v. 87.2 cm²), suggesting, perhaps, in conjunction with the results for subcutaneous fat depth, some long-term consequences of divergent foetal growth for distribution of carcass tissues. However, the eye muscle area did not differ due to birth weight within the animals that grew slowly to weaning (89.8 v. 90.5 cm², respectively). Similarly, interactions between prenatal and pre-weaning nutrition for

post-weaning growth, feed intake, feed efficiency and carcass characteristics were not evident in the study of Stalker *et al.* (2006).

Interactions between growth early in life and gender

There appear to be few studies of interactions between growth early in life and the gender of cattle on beef production characteristics. Growth of well nourished, artificially reared calves (Tudor and O'Rourke, 1980) and feed efficiency after weaning have been shown to be influenced by gender following maternal nutritional restriction (Tudor and O'Rourke, 1980). The results of Stalker *et al.* (2006) and Martin *et al.* (2007) also suggest differences between genders in the efficiency of nutrient utilisation following divergent maternal nutrition during late pregnancy. However, few interactions between gender and nutrition early in life have been demonstrated for subsequent body and carcass characteristics, with these relating mainly to bone growth (Tudor *et al.*, 1980). Within our recent studies, interactions between birth weight and gender/year cohorts were evident for carcass weight, eye muscle area, and weight of bones and retail beef at 30 months of age (Greenwood *et al.*, 2006). However, while suggestive of interactions between sex and growth early in life, our experimental design did not allow for this interaction to be specifically tested.

Interactions between growth early in life and sire-genotype

A major objective of our research has been to determine the extent to which genotype may interact with nutrition early in life to influence subsequent growth, carcass, yield and beef-quality characteristics. To achieve this objective, our research included offspring of Piedmontese (a high muscling, high-birth-weight breed homozygous for a non-functional mutation in myostatin) and Wagyu (a high marbling and lower birth weight breed) bulls. Perhaps surprisingly, no interactions between sire-genotype and growth early in life were evident for any production parameters reported here or presented by Greenwood *et al.* (2006).

Conclusions

Severe, chronic growth retardation of cattle early in life is associated with reduced growth potential, resulting in smaller animals at any given age. The capacity for long-term compensatory growth diminishes as the age of onset of severe nutritional restriction resulting in prolonged growth retardation declines, such that more-extreme intrauterine growth retardation can result in slower growth throughout postnatal life. However, within the normal limits of beef production systems, neither restricted growth *in utero* nor from birth to weaning influences the efficiency of nutrient utilisation later in life.

Retail yield from cattle severely restricted in growth during pregnancy or from birth to weaning is reduced compared with cattle well grown early in life, when compared at the same age later in life. However, retail yield and carcass composition of low- and high-birth-weight calves are similar when compared at the same carcass weight.

At equivalent carcass weights, cattle that are grown slowly from birth to weaning have carcasses of similar or leaner composition than those grown rapidly. However, there is evidence to suggest that if high energy, concentrate feed is provided following severe growth restriction from birth to weaning, then at equivalent weights post weaning the slowly growing, small weaners may be fatter than their well-grown counterparts.

Restricted prenatal and pre-weaning nutrition and growth do not adversely affect measures of beef quality including shear force, compression, cooking loss and colour. Similarly, bovine myofibre characteristics are little affected in the long term by growth *in utero* or from birth to weaning, despite specific myofibre-type-related effects at birth and weaning, respectively.

Hence, economic benefits resulting from adequate maternal nutrition, especially during pregnancy, to optimise growth of offspring to market weights are primarily due to advantages in carcass weight and retail beef yield at a given age, reduced feed costs to reach a given market weight, stocking rates and subsequent reproductive rates of breeding cows, but not due to differences in beef-quality characteristics (Alford *et al.*, 2007).

Interactions were not evident between prenatal and pre-weaning growth for subsequent growth, efficiency, carcass, yield and beef-quality characteristics, within our pasture-based production systems. Interactions between genotype and nutrition early in life studied using offspring of Piedmontese (a high muscling, higher birth weight breed, homozygous for a mutation that produces non-functional myostatin) and Wagyu (a high marbling, lower birth weight breed) sires mated to Hereford cows were not evident for any growth, efficiency, carcass, yield and beef-quality parameters.

We propose that within pasture-based production systems for beef cattle, the plasticity of the carcass tissues, particularly of muscle, allows animals that are growth-retarded early in life to attain normal carcass composition at equivalent weights in the long term, albeit at older ages. This may well relate to regulation of nutrient intake to a level appropriate for the size and lean tissue growth capacity of the animal, coupled with the capacity of the myosatellite cell population to generate myonuclei in support of muscle growth over a prolonged recovery period, as discussed previously (Greenwood *et al.*, 1998, 1999 and 2000a). However, the availability of feed and quality of nutrition during recovery from severe growth retardation early in life may be important in determining the subsequent composition of young, light-weight cattle relative to their heavier counterparts.

Finally, it needs to be emphasised that long-term consequences of more specific, acute environmental influences during specific stages of embryonic, foetal and neonatal calf development remain to be determined. This need for further research extends to consequences of nutrition and growth early in life for subsequent reproductive performance, which has been recently shown to be affected in heifers by nutrition of their dams during late pregnancy (Martin *et al.*, 2007), although neither reproductive or lactational performance were affected by birth weight (Swali and Wathes, 2006).

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