Developmental programming and beef production

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Implications

- The major economic costs to beef producers are associated with the breeding herd, with weaning rate and maternal efficiency being the major drivers of profitability of beef production systems.
- There is increasing interest in developed and developing countries in how to manage breeding females and their offspring to either minimize the consequences of adverse environmental effects or to enhance productivity and efficiency of offspring.
- Cattle severely growth restricted early in life can have reduced body weight for age to market weight, but with only slight or no alteration to normal allometric growth patterns of carcass tissues or beef quality, at least within pasture-based systems.
- There is little information and a need for further research in beef cattle to quantify developmental programming-related effects, particularly on reproductive success and lactation performance, interactions with the environment, and intergenerational consequences.

Key words: beef quality, body composition, developmental programming, growth and development, reproduction

Introduction

The embryonic, fetal, and neonatal periods are the stages of life when most developmental processes occur and when cellular, tissue, organ, metabolic, and hormonal systems are established. Livestock scientists have been studying the consequences of maternal nutrition on growth and development during fetal life for the productivity of ruminants for many decades. However, in recent years, there has been increasing interest in how to manage breeding females and their offspring to either minimize the consequences of adverse environmental effects or to enhance productivity and efficiency. The idea that maternal nutrition at various stages of pregnancy can indelibly influence lifetime productivity and health of progeny has gained additional currency from more recent epidemiological studies of human populations and detailed experimental studies of rodents as originally proposed by the British epidemiologist David Barker and his colleagues (Barker, 2007).

Severe, prolonged undernutrition of pregnant ruminants, especially during late gestation, can permanently retard body and wool growth of their offspring (Greenwood et al., 2009a). The evidence for effects of prenatal nutrition on postnatal development of a wide variety of tissues directly related to the production of meat, milk, and wool, as well as reproduction, is now indisputable. However, despite the unqualified excitement of some researchers for these demonstrated phenomena, understanding of their quantitative significance for the productivity and management of livestock production systems is limited and requires further research.

In this article, we provide a brief overview of current understanding and commercial relevance of observed postnatal responses to the management of breeding herds and discuss some future directions for research on developmental programming in beef cattle and other livestock species. More detailed summaries and interpretation of the current evidence for developmental programming in livestock is provided in recent reviews by Robinson et al. (2013), Kenyon and Blair (2014), Bell and Greenwood (2016), and Sinclair et al. (2016).

The Importance of Beef Production and Drivers of Economic Viability

Globally, 300 million head of cattle are used in the production of 65 million tonnes of beef annually (FAO, 2017). Asia has 31% of the world’s cattle, South America 23%, Europe 14%, Africa 13%, North America 11%, Australia and New Zealand 5%, and Central America 4%. Beef represents 21% of the 314 million tonnes of meat produced worldwide from livestock each year; the other major sources being pork (37%), poultry (36%), and small ruminants, including sheep and goats (5%).

Beef production systems vary widely from subsistence husbandry to large, highly integrated enterprises, and from small intensive to extensive pastoral and rangeland-based systems. Within all these systems, at least 60% of economic costs are associated with the breeding operation, principally the nutrition of cows and their calves, which usually occur on pasture or rangelands (Bell and Greenwood, 2013). The objective of beef production systems is viable and economical production and/or marketing of cattle and beef products to satisfy household, market, and specific consumer demands. Consumer requirements for beef cuts and quality vary widely depending on socio-economic factors (Figure 1).

In developing countries, there is an increasing demand for protein of which beef is an important and growing contributor. In developed
countries, there is an increasingly segmented marketplace that demands meat products based on factors that include, for example: cost; energy, fat, and protein content; specific dietary components such as omega-3 and other fatty acids, iron, zinc, antioxidants, and other macro- and micronutrients; intramuscular fat content or marbling; organoleptic characteristics; retail attractiveness, including color; residue-free meat; organically produced meat; animal welfare considerations; and environmental impact.

For the beef producer, primary objectives are to maximize efficiency of feed nutrient use and to minimize costs to achieve specific market requirements that maximize income. To meet this goal, it is necessary to utilize a cattle genotype capable of meeting market specifications and to provide a suitable environment that includes enough nutrients of an appropriate quality for successful reproduction and for the various stages of growth and development of that genotype. Carcass and meat composition are also important to commercial producers of beef due to their impact on growth rate and the efficiency with which nutrients are used. The profitability of processing animals for meat depends on the supply of product that is within specification, maximizing yields of saleable meat of appropriate specifications and minimizing the amount of fat that has to be trimmed from carcasses and the amount of bone relative to saleable meat.

**What Is Developmental Programming and Why Is It Important?**

The term “developmental programming” has been widely used to describe the observed effects of early life environment, particularly in utero, on the characteristics of offspring during later life, in large domestic animals as well as in humans and rodent model species (e.g., Reynolds et al., 2010).

Key elements of the concept include the existence of: (a) indelible, long-term effects on specific aspects of development and function of multiple cell types and tissues; (b) critical windows of development when programming effects are most likely to occur; and (c) transgenerational effects involving early environmental influences on offspring phenotype not only of the F1 generation, but also subsequent generations (F2 and beyond; Aikin and Ozanne, 2014).

Among various mechanisms proposed to mediate developmental programming, epigenetic modification of gene expression in embryonic and fetal tissues has been most widely touted (e.g., Sinclair et al., 2016), involving altered DNA methylation, histone acetylation, and/or expression of non-coding microRNAs. Evidence for epigenetic changes in
somatic and both maternal and paternal germline cells in rodents, elicited by maternal nutrition and other environmental factors has been reviewed, based on a recent meta-analysis of relevant studies (Aikin and Ozanne, 2014). These authors concluded that while epigenetic mechanisms almost certainly account for various examples of phenotypic variation in F1 and, possibly, subsequent generations, other mediating factors, particularly changes in “uterine environment,” also should be considered.

The concept of developmental programming is potentially important to the breeding and management of cattle and other livestock species because it could account for much of the considerable variation between individual animals not explained by genetic or postnatal environmental effects. To date, demonstration of transgenerational inheritance of environmental influences on offspring phenotypes beyond the F1 generation in these species has been challenged by their long generation intervals and genetic heterogeneity compared with inbred lines of rodents (Bell and Greenwood, 2016; Sinclair et al., 2016). These characteristics also have made it difficult to obtain evidence for the role of epigenetics and other possible mechanisms in mediation of the observed responses of F1 offspring to altered maternal nutrition and other prenatal factors, discussed below. This has led to some skepticism about the relevance of such phenomena to livestock breeding (Goddard and Whitelaw, 2014; González-Recio et al., 2015). However, these authors share the general opinion that the issue can only be settled by continued investigations of transgenerational inheritance of epimutations in livestock species.

The role of uterine environment in mediating some examples of developmental programming (Aikin and Ozanne, 2014) also deserves further

Figure 2. Consequences for the performance of offspring in nutritionally limiting and improved pastoral cow-calf production systems have been studied within the Australian Cattle and Beef Cooperative Research Centres (Cafe et al., 2006; Robinson et al., 2013).
study in large animals. This phenomenon presumably involves variation in establishment and subsequent development of placentation. Thus, in various examples of compromised pregnancy in ruminants, inadequate vascular development of the placenta has been associated with negative consequences for fetal and postnatal development (Reynolds et al., 2010). However, we also have provided preliminary evidence that in ruminants, as in rodents, negative effects of moderate maternal undernutrition on fetal development may be buffered by upregulation of genes controlling placental growth and transport functions (Bell and Greenwood, 2016).

Influences on Fetal Growth and Development and Birth Weight

Factors that regulate calf fetal growth and development and birth weight include placental size and capacity for nutrient transfer; parity, age, and size of the dam; maternal, paternal, and fetal genotypes; and litter size, thermal environment, and maternal nutrition. Fetal genetics account for approximately one-half of the variation in birth weight, with the paternal genetic influence being greater than the maternal genetic influence.

As a consequence of the various non-nutritional factors that influence calf birth weight, and because maternal metabolic adaptations protect fetal nutrient supply, it is important that these factors are assessed before attributing unexplained variation in birth weight to maternal nutrition (Bell, 2004). In our Australian Cattle and Beef Cooperative Research Centre (Beef CRC), studies on poorly fed and well-fed dams at pasture from about Day 80 of gestation to parturition (Figure 2: Cafe et al., 2006), about 20% of the variation in birth weight was explained by this very divergent nutrition during pregnancy (Figure 3 and Table 1; Robinson et al., 2013). By contrast, 50% of the variation in dam live weight at parturition was explained by nutrition during pregnancy (Table 1), with the dams on low and high nutrition during pregnancy differing on average by more than 100 kg BW at parturition (Cafe et al., 2006). These findings emphasize the capacity of the beef cow to buffer the developing fetus from the effects of nutritional limitations.

Research on Developmental Programming and Beef Production

Most research on developmental programming in cattle has focused on growth, carcass, and beef quality characteristics of offspring as affected by nutrition of the cow during pregnancy and/or lactation, with fewer, but increasing, studies on consequences for reproductive and lactation performance of offspring or on intergenerational effects.

Table 1. Effects of maternal and other factors, including growth of offspring early in life, on BW, carcass weight, and retail yield to 30 mo \((n = 228)\). Adapted from Robinson et al. (2013), which includes details of the statistical analyses and other factors that contributed less to the variation explained.

<table>
<thead>
<tr>
<th>Trait, kg</th>
<th>Mean</th>
<th>Birth weight, slope/kg</th>
<th>Weaning weight, slope/kg</th>
<th>Variation explained, %</th>
<th>Major factors contributing to variation (% of variation explained)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dam BW at parturition</td>
<td>445</td>
<td>na na</td>
<td></td>
<td>71</td>
<td>Pregnancy nutrition (50), Dam age (17)</td>
</tr>
<tr>
<td>Birth weight</td>
<td>33.7</td>
<td>na na</td>
<td></td>
<td>48</td>
<td>Dam BW at parturition (26), Sire breed (11), Sex (5)</td>
</tr>
<tr>
<td>Birth weight: model excluding dam BW at parturition</td>
<td>33.7</td>
<td>na na</td>
<td></td>
<td>43</td>
<td>Pregnancy nutrition (20), Sire breed (8), Dam age (6), Sex (4)</td>
</tr>
<tr>
<td>Weaning BW</td>
<td>189</td>
<td>1.53 na</td>
<td></td>
<td>74</td>
<td>Lactation nutrition (41), Dam BW at parturition (14), Age at weaning (6), Sex (5), Birth weight (3), Dam age (3)</td>
</tr>
<tr>
<td>End background BW</td>
<td>514</td>
<td>3.02 0.72</td>
<td></td>
<td>71</td>
<td>Weaning BW (48), Birth weight (13), Sex (9), Dam age (2)</td>
</tr>
<tr>
<td>Feedlot exit BW</td>
<td>678</td>
<td>4.39 0.78</td>
<td></td>
<td>72</td>
<td>Birth weight (34), Weaning BW (11), Dam age (2), Year (25)</td>
</tr>
<tr>
<td>Hot carcass weight</td>
<td>382</td>
<td>2.71 0.46</td>
<td></td>
<td>70</td>
<td>Birth weight (36), Weaning BW (11), Dam age (2), Year (19)</td>
</tr>
<tr>
<td>Retail yield</td>
<td>249</td>
<td>1.97 0.28</td>
<td></td>
<td>70</td>
<td>Birth weight (37), Sire Breed (9), Weaning BW (5), Dam age (2), Year (15)</td>
</tr>
<tr>
<td>Model including cold carcass weight (376 kg average cold carcass weight)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Retail yield</td>
<td>249</td>
<td>ns -0.0629</td>
<td>95</td>
<td></td>
<td>Carcass weight (87), Sire breed (7)</td>
</tr>
</tbody>
</table>

$^{a}$na = not applicable.

$^{b}$ns = not significant.

Figure 3. Birth weight of calves is influenced by many factors that impact on fetal growth, including: parity, age, and size of the dam; maternal, paternal, and fetal genotypes; placental size and capacity for nutrient transfer; and litter size, thermal environment, and maternal nutrition. This graph shows the distribution and wide range of birth weights from the well-nourished and poorly-nourished, mixed age and parity Hereford cows mated to high muscling or high marbling bulls in the study of Cafe et al. (2006).
Postnatal growth and body composition

The weight of evidence reviewed by Robinson et al. (2013) and Bell and Greenwood (2016) clearly indicates that intrauterine growth retardation (IUGR) induced by severe maternal undernutrition after mid-pregnancy can result in decreased postnatal growth trajectory to weaning and beyond, with negative consequences for time to reach market weight. While decreased postnatal growth due to severe fetal growth retardation may be associated with a moderate increase in body fatness in sheep, any effects of even severe prenatal growth retardation on body composition of growing and finishing beef cattle mostly can be explained by differences in BW or carcass weight (Robinson et al., 2013; Table 1).

The results of our research on cattle within pasture-based systems show that following severe, chronic nutritional restriction from Day 80 of pregnancy to calving that resulted in fetal growth retardation and reduced birth weight by an average of 3.7 kg (Cafe et al., 2006), growth-retarded offspring continued to have reduced BW until slaughter at 30 mo of age (Table 1; Robinson et al., 2013). Effects of reduced birth weight and reduced weaning BW on subsequent growth were additive, and interactions with different genotypes (Figures 4 and 5) were not evident (Table 1). Following fetal growth retardation, there was little or no evidence of compensatory growth after weaning. For every 1 kg difference in birth weight, there was a difference of 4.4 kg in feedlot exit BW, and reductions of 2.7 kg in hot carcass weight and of 2.0 kg in retail yield (Table 1 and Figure 6). In contrast, growth restriction during the period from birth to weaning resulted in partial compensation in BW for age. Every 1 kg reduction in weaning BW reduced feedlot exit BW by 0.78 kg, hot carcass weight by 0.46 kg, and retail yield by 0.28 kg (Table 1). More moderate nutritional restriction during late pregnancy has lesser or no effect on postnatal growth performance to market weight (e.g., Mulliniks et al., 2016).

In general, effects of maternal undernutrition during early to mid-pregnancy are more muted, and even when feed restriction is sufficient to affect fetal growth before late gestation, this effect can be alleviated by adequate maternal nutrition in late pregnancy, suggesting placental development was not seriously compromised, with little consequence for postnatal growth or composition (Kenyon and Blair, 2014; Bell and Greenwood, 2016). Most studies of the effects of maternal undernutrition during early to mid- or late pregnancy have used simple feed restriction as the treatment, implying a primary effect of reduced energy supply. Recent investigation of the effects of maternal protein nutrition during the first and/or second trimester in pregnant, composite (Bos indicus x B. taurus breed crosses) beef heifers found a moderate reduction in birth weight of offspring due to protein restriction during the second trimester (Micke et al., 2010b). This effect persisted transiently during the first month of postnatal life (Micke et al., 2010a), but effects thereafter on postnatal growth and fat deposition, as assessed after slaughter at almost 2 yr of age, were small and inconsistent (Micke et al., 2010a, 2011).

Feed intake and efficiency

Based on the limited available evidence on prenatal origins of postnatal variation in feed intake and efficiency, it is suggested that effects are related mainly to variation in size of the offspring (Table 2). Maternal nutrition and fetal growth retardation within pasture-based systems does not appear to contribute substantially to variation in feed intake and efficiency in the feedlot from 26 to 30 mo of age, when BW at feedlot entry is taken into account (Table 2; Cafe et al., 2009; Robinson et al., 2013). Prior lactation status of the dam (heifer, dry cow, or lactating) explained up to 8% of the variation in offspring feed conversion ratio, after accounting for differences in feedlot entry BW, which explained more than 63% of the variation (Table 2). Prior lactation status of the dam explained 8% of the variation in feedlot exit BW, and reductions of 2.7 kg in hot carcass weight and of 2.0 kg in retail yield (Table 1). More moderate nutritional restriction during late pregnancy has lesser or no effect on postnatal growth performance to market weight (e.g., Mulliniks et al., 2016).

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Figure 5. Severely altered nutrition and growth early in life can have persistent long-term or life-long effects. This figure shows the same steers sired by high muscling (brown steers) or high marbling (black steers) bulls soon after weaning at 7 mo of age (top) and during feedlot finishing at 26–30 mo of age (bottom). The small and large steers differed in BW by over 200 kg at weaning. They show the range of weaning and subsequent BW as a consequence of divergent nutrition at pasture during pregnancy and lactation, and other factors, within the studies described by Cafe et al. (2006) and Robinson et al. (2013).
Protein supplementation of cows during late pregnancy has variable effects on post-weaning feed intake, presumably related to carryover effects on milk production of the dam and offspring growth to weaning. However, it does not affect feed efficiency within US systems where cattle are generally weaned into the feedlot (reviewed by Robinson et al., 2013).

Carcass and beef quality characteristics

Within pasture-based systems, maternal nutrition and birth weight have few long-term effects on carcass- and beef-quality characteristics beyond those explained by BW or carcass weight (Greenwood et al., 2006, 2009b; Robinson et al., 2013). At 380-kg carcass weight, there was a biologically insignificant difference (1 to 2%) in the distribution of retail beef yield between the forequarter and the hindquarter between low and high birth weight calves. Birth weight explained only 2.3% of the variation in striploin lightness (Color L*) and 1.6% of the variation in eye round (semitendinosus) compression at 30 mo of age. Our findings in cattle appear to be consistent with most other published research on consequences of nutrition across different stages of pregnancy. Protein restriction from 60 d before 24 d post conception, and for the first trimester, increased shear force in the semitendinosus muscle of bulls, and the peri-conception treatment also reduced heat soluble collagen content (Alvarenga et al., 2016a). However, protein nutrition did not affect other beef quality characteristics in the longissimus and semitendinosus muscles in that study. Supplementation during mid-pregnancy has been shown to affect fatness after accounting for carcass weight-related effects, as well as tenderness (Underwood et al., 2010). Protein supplementation in late pregnancy increased marbling score and quality grades in offspring (Larson et al., 2009), and corn, compared with hay supplementation in late pregnancy, reduced offspring marbling score and increased proportions of carcasses grading as Select (a relatively lean category in the USDA beef-grading system) but did not affect tenderness (Radunz et al., 2012).

Effects of maternal nutrition on more specific aspects of nutrient composition of meat from their offspring have not been studied in beef cattle. However, in sheep, recent evidence suggests that maternal nutrition during the peri-conceptual period may alter the metabolism of long-chain omega-3 polyunsaturated fatty acids (LCn-3PUFA) in offspring (Hopkins et al., 2014). Ewes were fed oat grain and cottonseed meal high in omega-6 PUFA, or oaten silage high in omega-3 PUFA, for 6 wk before and 3 wk following mating. When their male offspring were fed an algae high in LCn-3PUFA, the accumulation of eicosapentaenoic acid [EPA, c20:5(n-3)] and docosahexaenoic acid [DHA, c22:6(n-3)] in the longissimus muscle of their lambs was less in those lambs whose dams were fed the oats/cottonseed meal (CSM) ration compared with silage around mating (Hopkins et al., 2014). This reduced accumulation of LCn-3PUFA was also associated with a reduced relative abundance in muscle of mRNA encoding a number of genes associated with fatty acid metabolism, including fatty acid desaturase 1 and 2 (FADS-1 and FADS-2) (Alvarenga, 2016b). It is suggested based on the above evidence that further research on the consequences for beef quality of feeding specific nutrients including long-chain polyunsaturated fatty acids during the peri-conception period may be warranted.

Reproduction

Longer-term implications of developmental programming for adult cattle reproductive performance (conception, calving, and weaning rates) largely remain to be determined, as there have been considerably fewer studies on effects of prenatal nutrition on reproduction in cattle than in sheep (reviewed by Chavatte-Palmer et al., 2014; Bell and Greenwood, 2016).
Table 2. Effects of maternal and other factors, including growth of offspring early in life, on feed intake and efficiency from 26 to 30 mo (n = 146). Adapted from Robinson et al. (2013), which includes details of the statistical analyses and other factors that contributed less to the variation explained

<table>
<thead>
<tr>
<th>Trait, kg</th>
<th>Mean</th>
<th>Birth weight, slope/kg</th>
<th>Weaning weight, slope/kg</th>
<th>Variation explained, %</th>
<th>Major factors contributing to variation (% of variation explained)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Feedlot intake, kg DM/d</td>
<td>12.1</td>
<td>0.09</td>
<td>0.009</td>
<td>75</td>
<td>Birth weight (15), Weaning BW (2), Dam age at weaning (2), Sex (56)</td>
</tr>
<tr>
<td>Feedlot intake, kg DM/d: Model including BW at feedlot entry</td>
<td>12.1</td>
<td>ns†</td>
<td>ns</td>
<td>84</td>
<td>BW at feedlot entry (63), Sex (19)</td>
</tr>
<tr>
<td>Feed conversion ratio, kg DM/kg gain</td>
<td>9.4</td>
<td>ns</td>
<td>0.022</td>
<td>38</td>
<td>Dam previous lactation status, including interaction with Sex (8), Weaning BW (6), Lactation nutrition (3), Sex, including interaction with Weaning BW (21)</td>
</tr>
<tr>
<td>Feed conversion ratio, kg DM/kg gain: Model including BW at feedlot entry</td>
<td>9.4</td>
<td>ns</td>
<td>ns</td>
<td>32</td>
<td>Dam previous lactation status (5), BW at feedlot entry, including interaction with Sex (10), Sex (18)</td>
</tr>
<tr>
<td>Residual feed intake, kg DM/d</td>
<td>0</td>
<td>ns</td>
<td>ns</td>
<td>10</td>
<td>Days pregnant at start of nutritional treatment, including interactions with Lactation nutrition and Sire breed (8), Age at weaning (2)</td>
</tr>
<tr>
<td>Feedlot exit BW</td>
<td>678</td>
<td>4.39</td>
<td>0.78</td>
<td>72</td>
<td>Birth weight (34), Weaning BW (11), Dam age (2), Year (25)</td>
</tr>
</tbody>
</table>

†ns = not significant.
‡Sex also includes effects of year.

Severe fetal growth retardation due to maternal undernutrition from early pregnancy to term decreased ovarian weight and size of large follicles in non-mated heifer progeny at 30 mo of age, more so than effects of postnatal growth retardation between birth and weaning (Wilkins et al., 2006). Other research has also shown effects of maternal restriction during pregnancy on offspring ovarian function. Feed restriction of beef heifers from just before conception through the first 4 mo or so of pregnancy diminished ovarian reserves in female progeny before and after puberty in the absence of effects of maternal nutrition on birth weight, postnatal growth, or age at puberty (Mossa et al., 2013).

Protein nutrition of pregnant beef cows can also influence the reproductive performance of heifer progeny. Protein supplementation of composite breed Bos taurus cows during late pregnancy has been shown to increase pre-breeding BW (but not birth weight), pregnancy rate, and percentage of calvings during the first 3 wk of the calving season in their heifer progeny (Martin et al., 2007). In contrast, protein supplementation of composite breed Bos taurus × B. indicus heifers during the second trimester had negative effects on ovarian follicle size and density in female offspring at about 2 yr of age, effects which were greater if the dams had not been supplemented during the first trimester (Sullivan et al., 2009). Testis development and reproductive hormone concentrations in the male offspring at 5 mo were less consistent (Sullivan et al., 2010).

It is suggested from recent evidence in sheep, that fatty acid composition of the diet fed to ewes around mating may influence the reproductive potential of their female offspring. The number of fetuses per F1 ewe at pregnancy scanning 42 d after mating was greater when their dams were fed a diet based on oats and CSM high in omega-6 fatty acids compared with ryegrass silage high in omega-3 fatty acids for 6 wk before and 3 wk following their mating (Clayton et al., 2016). Further research is warranted to assess whether such effects extend to beef cattle.

**Lactation**

There has been speculation that maternal nutrition and other prenatal environmental factors may influence fetal mammary development and, thence, subsequent lactation performance (e.g., Capuco and Akers, 2010). There appears to be little or no research on effects of developmental programming on mammary gland development and lactation in beef cattle. However, there is limited evidence that maternal nutrition of sheep at different stages of pregnancy can influence the milk yield of female progeny, at least during their first lactation. These relatively subtle responses need to be confirmed in large-scale studies and mechanistically linked to effects on pre- and postnatal mammary development. As we have previously discussed (Bell and Greenwood, 2016), earlier research in beef and dairy cattle has focused on later, better-defined periods of mammary development as possible windows of opportunity to influence milk production, especially those occurring before and after puberty, and during late pregnancy.

In sheep, New Zealand researchers have observed effects of maternal nutrition on fetal mammary development and subsequent milk yield of progeny (reviewed by Kenyon and Blair, 2014). Two-year-old ewes born to ewes fed at maintenance throughout pregnancy produced more milk with greater yields of lactose and crude protein in their first lactation than did ewes born to ewes ad libitum-fed throughout pregnancy, and their lambs grew faster to weaning. However, effects on milk yield were not apparent in the second to fifth lactations of the same animals (Paten et al., 2016), suggesting a lack of a permanent effect on mammary gland structure and function, and this lack of persistency was not related to plane of nutrition during pregnancy of the offspring ewes.

**Developmental programming in context: the overriding importance of maternal productivity and efficiency**

Notwithstanding our findings of influences of early life growth on subsequent growth and size of cattle and their carcasses and yields of beef, the major influence on profitability and efficiency of beef production systems is weaning rate (Alford et al., 2009). Management systems aimed at maximizing weaning rate and maternal efficiency are also likely to ensure that potentially adverse effects due to developmental programming are minimized. Hence, maternal productivity and efficiency should remain among the highest priorities for on-farm management and for research on beef production.
systems. We recently reviewed management priorities to maximize maternal efficiency, namely cow survival, environmental adaptability, reproductive performance, cow maintenance costs and weaning weight, and the biological traits that underpin them (Bell and Greenwood, 2013). The importance of maternal efficiency is highlighted by observations that the cow-calf phase of production generally accounts for at least 60% of the total economic cost of beef production, and more when heifer rearing is accounted for.

**Future directions for developmental programming research for beef production**

There remains a paucity of information and a need for research on consequences of developmental programming for performance and efficiency in beef production systems within developing and developed countries. In particular, further research is required on consequences of developmental programming for reproductive success and lactation performance in F1 and subsequent generations. This should include research on the effects of specific nutrients fed to dams including just before and/or during early stages of pregnancy for subsequent development and performance of offspring.

**Concluding comments**

A new understanding of the influences of prenatal experience on postnatal development of key tissues and functions important to animal productivity, including reproduction and lactation is emerging. With regard to the relevance of findings in beef production systems, the following observations seem appropriate.

First, while there is now convincing evidence that prenatal nutrition and other environmental factors can influence postnatal growth and reproductive performance in cattle, these effects are usually subtle and often ameliorated by postnatal nutritional experience.

Second, the relevance of developmental programming phenomena to practical management systems must be considered in the context of the major drivers of productivity, which in beef production systems, are weaning rate and maternal efficiency (Bell and Greenwood, 2013). Implementation of concepts developed in projects that adopt a whole-systems approach within contemporary production systems is required (Sinclair et al., 2016).

Finally, as noted by other reviewers (Goddard and Whitelaw, 2014; Kenyon and Blair, 2014), the magnitude and persistence of prenatal effects, including those mediated by epigenetic modifications of the genome, need to be better quantified. More particularly, the likelihood of transgenerational inheritance of epimutations should be thoroughly investigated.

**ACKNOWLEDGMENTS**

The contribution of numerous research, technical, and farm staff within the Australian Cattle and Beef Cooperative Research Centres to the outcomes of the Beef CRC research described in this article, in particular by Helen Hearnshaw, David Hennessy, Linda Cafe, Dorothy Robinson (NSW Department of Primary Industries), and John Thompson (University of New England) is gratefully acknowledged. John Wilkins and John Piltz (NSW Department of Primary Industries) are also acknowledged for their constructive comments towards the development of this paper.

**Literature Cited**


July 2017, Vol. 7, No. 3