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TRIENNIAL REPRODUCTION SYMPOSIUM: Beef heifer development and lifetime productivity in rangeland-based production systems[1,2]

A. J. Roberts,*[3] R. N. Funston,† E. E. Grings,‡[4] and M. K. Petersen*

*USDA-ARS, Fort Keogh Livestock and Range Research Laboratory, Miles City, MT 59301; †University of Nebraska West Central Research and Extension Center, North Platte 69101; and ‡South Dakota State University, Department of Animal Science, Brookings 57007

ABSTRACT: Nutritional and environmental factors have been shown to cause epigenetic changes that influence characteristics of the offspring throughout life. In livestock, small differences in nutrition during gestation may alter lifetime production efficiency of offspring. Therefore, the potential for fetal programing should be considered when determining supplemental feeding strategies during gestation. For example, female offspring born to cows grazing dormant winter pasture supplemented with 1.1 kg/d of alfalfa hay during the last third of gestation were 10 kg heavier and had greater BCS at 5 yr of age than those from dams supplemented with 1.8 kg/d of alfalfa hay. These differences were beneficial for maintaining reproductive performance in offspring managed with fewer harvested feed inputs. Evaluation of female offspring from cows wintered on either low-quality or high-quality pasture for 30 to 45 d during the fifth to sixth month of gestation indicated a trend for longer duration of productivity in daughters from cows wintered on improved pasture. In recent studies comparing offspring from cows with or without protein supplementation while grazing dormant winter range during late gestation, heifers from protein-supplemented dams had greater BW at weaning. This BW increase persisted throughout pregnancy and to subsequent calving, and pregnancy rates were greater in heifers from protein-supplemented dams. Heifers from protein-supplemented dams had lower G:F compared with heifers from unsupplemented dams. Therefore, in utero exposure to nutritionally limited environments (nonsupplemented dams) may promote greater feed efficiency in the heifer offspring later in life. Nutrition during postweaning development may also affect lifetime productivity. Heifers developed on low-quality native range with RUP supplementation had greater retention beyond 3 yr of age than cohorts developed in a feedlot with higher quality feed and greater ADG. Collectively, these examples show nutritional management strategies used during gestation and development may influence lifetime productivity.

Key words: fetal programing, lifetime productivity, nutritional supplementation

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[3]Corresponding author: andy.roberts@ars.usda.gov

[4]Present address: US Agency for International Development, Bureau for Food Security, Washington, DC.

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INTRODUCTION

Traits important for production efficiency are regulated by both genetic and environmental factors. Phenotype may also be influenced by interaction of genotype and environment. Furthermore, nutrition and other environmental factors encountered during intrauterine development may result in epigenetic changes altering offspring phenotype later in life (Hales and Barker, 2001; Anway et al., 2005; Wu et al., 2006). Epigenetic modifications affecting gene expression can be inherited through subsequent generations (Goldberg et al., 2007). The scenario that gene expression can be altered in an entire cohort of individuals by exposure to common stimuli during uterine development has great consequences to population changes. Rate of phenotypic change resulting from epigenetic processes may be much greater than that achieved through selection or gene mutation. As such, it is logical that epigenetic processes likely play key roles in adaptation processes.

Research demonstrating generational impacts caused by environment arose from human populations that had been subjected to extreme nutritional stress (reviewed in Hales and Barker, 2001). Subsequently, animal models have facilitated tightly controlled studies to provide insight into physiological mechanisms mediating impact of under- and overnutrition during pregnancy on offspring function later in life (Wu et al., 2006; Reynolds et al., 2010; Ford and Long, 2012). Recently, it became apparent that relatively small nutritional differences imposed under common production practices may lead to metabolic programing that alters production characteristics of the offspring (Funston et al., 2012a,b; Endecott et al., 2013). This paper reviews results from 3 locations that evaluated different nutritional paradigms conducted under common beef cattle production practices expected to be representative of conditions commonly occurring in range beef cattle production, with emphasis on impacts on lifetime reproductive performance.

REVIEW AND DISCUSSION

Lifetime Productivity Study

In 2001, a long-term research project began at the USDA, ARS, Fort Keogh Livestock and Range Research Laboratory (Miles City, MT). The objective of this research was to assess lifetime productivity of cows managed under 2 levels of harvested feed input during postweaning development and winter grazing. A major impetus for conducting this long-term study revolved around whether the industry-recommended practice of supplemental feeding to improve reproductive performance minimized selection pressure for more efficient animals. A hypothesis of the study was that long-term management with lesser inputs would result in increased selection pressure against cows with greater nutritional requirements. If true, it would be expected that cows remaining in the population would better maintain reproductive function in nutritionally limited environments. Two possible modes of action leading to the expected result would be 1) change in genetic composition or 2) a metabolic adaptation to function with less input. Genetic change would require a relatively long period of time compared with metabolic adaptation. The adaptation process could also result in altered uterine function bringing about epigenetic changes in the offspring. At the time the study was initiated, evidence for either of these possibilities was scarce. Subsequently, Vonnahme et al. (2006) provided evidence that response to nutritional restriction was markedly different for ewes originating from a common genetic population but managed for several generations under very divergent nutritional environments. Ewes from a university flock managed in a relatively sedentary lifestyle with a diet that always met or exceeded NRC recommendations exhibited greater loss in BW and BCS and greater suppression in placental efficiency and fetal growth in response to nutritional restriction than ewes from a herd maintained in an extensive semiarid range environment. These results paralleled expectations in the present study.

Cows used in this study were from a stable composite gene combination (one-half Red Angus, one-fourth Charolais, and one-fourth Tarentaise) population developed at Fort Keogh (Newman et al., 1993). At initiation of the study in December 2001, pregnant cows averaged 5.2 ± 0.1 yr of age, 536 ± 4.6 kg BW, and 5.2 ± 0.04 BCS (1 = severely emaciated to 9 very obese; Herd and Sprott, 1986). Bred heifers averaged 1.6 ± 0.01 yr of age, 445 ± 5.7 kg BW, and 5.9 ± 0.1 BCS. Cows were stratified by age and weight and were then randomly assigned to be managed on 1 of 2 levels of supplementation while grazing dormant native forage from December to March of each winter. Supplement treatments included the feeding of alfalfa cubes or hay at the equivalent of 1.8 or 1.1 kg/d (as-fed basis), which was expected to be an adequate (**ADEQ**; n = 92 cows and 19 bred heifers) or marginal (**MARG**; n = 138 cows and 21 bred heifers) level of protein supplementation to meet NRC (2000) requirements based on average quality and availability of the winter forage. Greater numbers of cows were initially assigned to the MARG treatment group to accommodate for expected differences in retention rates between the 2 groups. The natural rangeland vegetation is a grama–needlegrass–wheatgrass (*Bouteloua–Hesperostipa–Pascopyron*) mixed-grass dominant rangeland (Kuchler, 1964). Additional information concerning the type and nutrient characteristics of forage at the research site was previously published (Grings et al., 2005; Grings and Roberts 2013). Pastures used for winter grazing were not grazed during the growing season and were sufficient in size to provide available forage for grazing throughout the winter grazing period. Heifer calves born from 2002 to 2011 that were retained as replacements were stratified by BW at weaning, age of dam, and dam winter supplementation treatment and were then randomly assigned to ADEQ (n = 656) or MARG (n = 655) supplemental feeding (see additional details subsequently described for postweaning treatment of these animals). Supplement treatment was annually repeated for cows out to 10 yr of age. Cows were culled from the study if they failed to become pregnant or lost their calf prior to weaning. At present, data continue to be collected on cows born during the previous 10 yr and their offspring.

Cows in each supplement group were managed on separate pastures each winter to allow for differential feeding. Pasture sizes varied from 140 to 1,220 ha. Supplement consisted of alfalfa cubes (yr 1 through 3; 20% average CP) or alfalfa hay (all other years; 20% average CP). Supplement was offered daily (yr 1 through 7 and yr 10) or every other day at quantities appropriate to achieve the targeted equivalents for daily levels of supplement intake. When snow or ice cover limited forage availability, cows were fed alfalfa hay at a rate equivalent to 10.0 or 8.3 kg/d (as-fed basis) for each cow in the ADEQ or MARG treatments, respectively. Approximately 2 to 3 wk prior to start of calving, cows were moved to small paddocks approximately 15 ha in size to facilitate observation through calving. In yr 1 through 4, multiparous cows from both supplement groups were combined into the same calving paddock and were provided alfalfa hay at a rate of 10.0 kg/d (as-fed basis) for each cow. Subsequent to yr 4, cows from the 2 supplement groups were kept in separate paddocks prior to calving and were fed either 10.0 or 8.3 kg alfalfa hay/d (as-fed basis) for each cow in the ADEQ or MARG treatments, respectively. Primaparous cows from each supplement group were combined 2 to 3 wk prior to calving each year and were fed at the rate of 10.0 kg alfalfa hay/d (as-fed basis) throughout calving in small lots or paddocks. Subsequent to calving, cows and their calves from both supplement groups were managed together for the remainder of the year until December, when cows were again separated into their respective supplement treatment groups. Breeding of cows was initiated on approximately June 1 of each year, with different approaches used throughout the course of the study. For 2002 through 2005 and 2009, cows 2 yr of age and older were subjected to estrous synchronization and timed AI followed by natural mating for a total breeding season of 49 to 51 d. In 2006, cows were given a single injection of PGF and were artificially inseminated after observed estrous during a 27-d period following PG followed by natural mating for a total 83-d breeding season. In 2007, 2008, and 2010, cows were subjected to 56 to 63 d of natural mating. From 2011 on, cows were naturally mated for 45 for 48 d. In 2003 to 2005, yearling heifers were subjected to estrous synchronization and timed AI followed by breeding by natural mating for a total breeding season of 44 to 53 d. In 2006, 2009, and 2010, heifers were given 1 or 2 shots of PG and were artificially inseminated after observed estrous followed by natural mating for a total breeding season of 45 to 59 d. Heifers were naturally bred for 62 d in 2007 and 2008 and for 46 d in 2011 and 2012. Calves were weaned from cows at approximately 6 mo of age, with an October 9 average date of weaning across years.

At weaning, heifer calves from cows in this experiment were assigned to 1 of 2 levels of nutrition during a 140-d period after weaning and fed a corn silage–based diet to appetite (**Control**) or fed at 80% of that consumed by controls adjusted to a common BW basis (Restricted), as previously described (Roberts et al., 2009a). Heifers from the Control and Restricted postweaning treatments that became pregnant were subjected to the ADEQ and MARG levels winter supplemental feed, respectively, for all subsequent years of production, as previously described.

Data collected in the study were separately analyzed for cows that were used to initiate the study (born prior to 2001) and those born in the study (after 2001) due to potential influences of winter supplement treatments during in utero development and postweaning treatments on the animals born after 2001. For cows born before initiation of the study, data for BW and BCS, and changes in these measurements over the winter treatment period were analyzed by the MIXED procedure of SAS (SAS Inst. Inc., Cary, NC), using a model that included main effects and the interaction of winter supplement treatment and cow age classification of 2, 3, 4, 5, or >5 yr and the main effect of year (2002 through 2010). Pregnancy data were analyzed by the MIXED procedure of SAS, using a model that included main effects and the interaction of year (2002 through 2007). The model for pregnancy data differed from the BCS and BW model due to limitation in data for age and year groupings. Data from cows born after initiation of the study were analyzed by the MIXED procedure of SAS using a model that accounted for main effects of birth year and the main effects and interaction of treatment and dam treatment.

For cows that were used to initiate the study in 2001, differences in the supplemental feed levels provided during the winter resulted in different BW changes throughout the winter, with ADEQ cows gaining more BW than MARG cows (least squares means for age adjusted differences over the 9 yr cows persisted in the study were

25 ± 1.3 vs. 22 ± 1.2 kg BW change for ADEQ vs. MARG, respectively; $P < 0.05$). Cows in the ADEQ group maintained BCS during the winter treatment period, whereas MARG cows experienced a 0.12 decrease in BCS ($P < 0.04$). The least squares means BCS before calving for ADEQ and MARG were 4.98 ± 0.04 and 4.86 ± 0.03, respectively (1 to 9 BCS scale; $P < 0.02$). Pregnancy rates for the 2 groups over the 2002 to 2007 breeding seasons were 92 ± 1.9% of 522 matings and 91 ± 1.6% of 327 matings for the ADEQ and MARG groups, respectively ($P = 0.8$). The absence of a marked difference in pregnancy rate indicates a greater level of performance in the MARG group than was estimated based on average forage quality available during winter grazing and NRC requirements. Forage may have been greater quality than expected throughout the 7-yr period (not supported by forage analyses), or the cattle performed better than predicted by the NRC (2000). Evidence of cows managed under extensive semiarid range environments functioning at greater levels than predicted by the NRC is accumulating (Petersen et al., 2014) and would be consistent with pregnancy rates in cows from the MARG group not differing dramatically from cows in the ADEQ group. A year × treatment interaction was not evident ($P = 0.9$), which would support adaptation of cows to MARG level of supplement and similar trends for genetic change over time for the 2 treatment groups.

Measurements collected on heifers born in 2003 through 2005 of the study indicated differences in growth, carcass, and reproductive performance due to postweaning heifer development treatment (Roberts et al., 2007, 2009a) but not nutritional treatment of their dams (data not reported). Results concerning postweaning treatment effects from these earlier analyses are further substantiated by analyses on data for all years of the study. Dam treatment and interaction of dam treatment and heifer postweaning treatment were not significant for measurements made before 18 mo of age. Figure 1 provides a summary of the growth patterns for the 2 treatments averaged over the 10 yr of the study. Measures of BW diverged ($P < 0.001$) between treatments by 28 d after initiation of restriction and remained different ($P < 0.001$) up to the time that winter supplementation treatments were initiated. Heifers developed on the Restricted level of feeding consumed an average of 26% less feed (as-fed basis) and had 0.15 kg/d less ($P < 0.001$) ADG during the 140-d postweaning trial than Control-fed heifers. Efficiency of gain during the 140-d trial was greater ($P < 0.001$) for Restricted- than for Control-fed heifers (0.114 vs. 0.107 kg G:F for Restricted vs. Control, respectively). After the 140-d trial, all heifers were provided equal access to feed or grazing. Body weight gain following the 140-d trial until pregnancy diagnosis in the fall was greater ($P < 0.001$) for Restricted than Control

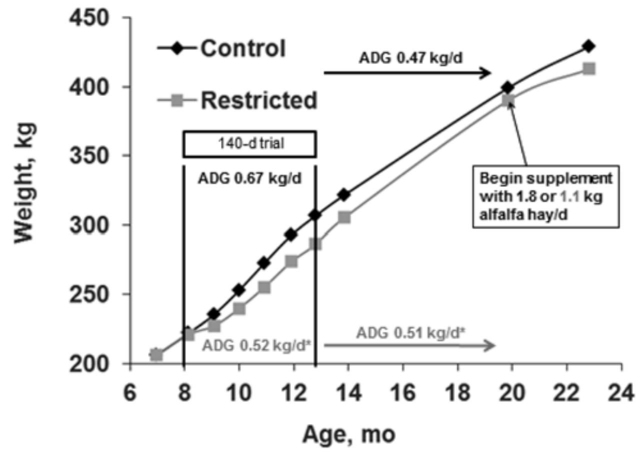

Figure 1. Patterns of growth for heifer calves fed a corn silage–based diet to appetite (Control; $n = 656$) or fed at 80% of that consumed by controls adjusted to a common BW basis (Restricted; $n = 655$) during a 140-d period after weaning (ADG = 0.67 and 0.52 kg/d for Control and Restricted, respectively; $P < 0.05$). Restricted heifers consumed 26% less feed during the 140-d period. Heifers from both treatments were managed together from 13 to 20 mo of age (ADG = 0.47 and 0.51 kg/d for Control and Restricted, respectively; $P < 0.05$). From 20 to 23 mo of age, heifers grazed dormant winter forage and were provided an equivalent of either 1.8 or 1.1 kg alfalfa hay (protein supplement)/d for Control or Restricted treatments, respectively.

heifers (Fig. 1). Although individual feed intake was not measured after the postweaning trial, data from male cohorts of the heifers also developed on 2 levels of intake exhibited greater gain after restriction occurred with feed intake levels similar to Control-reared males (Endecott et al., 2012). Therefore, it is reasonable to expect that the greater BW gain observed following restriction may have occurred without substantial differences in feed intake due to improved efficiency brought about by reduced maintenance requirements resulting from prior nutritional environment (Ferrell and Jenkins, 1985). These results, along with those previously reviewed (Funston et al., 2012a; Endecott et al., 2013), demonstrate that efficiency of developing replacement heifers may be substantially improved by nutritional environments imposed during postweaning management.

Average BW of heifers at start of breeding differed ($P < 0.001$) between the Control (322 ± 1.2 kg) and Restricted (305 kg ± 1.2 kg) treatments over the 10 yr of this study. These mean BW equate to 57 and 54% of the historic mature BW of the cow herd for the Control and Restricted treatments, respectively. Average pregnancy rates for the Control and Restricted treatments over 10 yr were 89 and 88%, respectively ($P = 0.63$). The interval from first day of breeding to date of first calving was not influenced by postweaning treatment ($P = 0.44$). Although not different due to treatment, pregnancy rates varied substantially across years (year effect, $P < 0.001$; Fig. 2). Although the factors contributing to annual variation in pregnancy

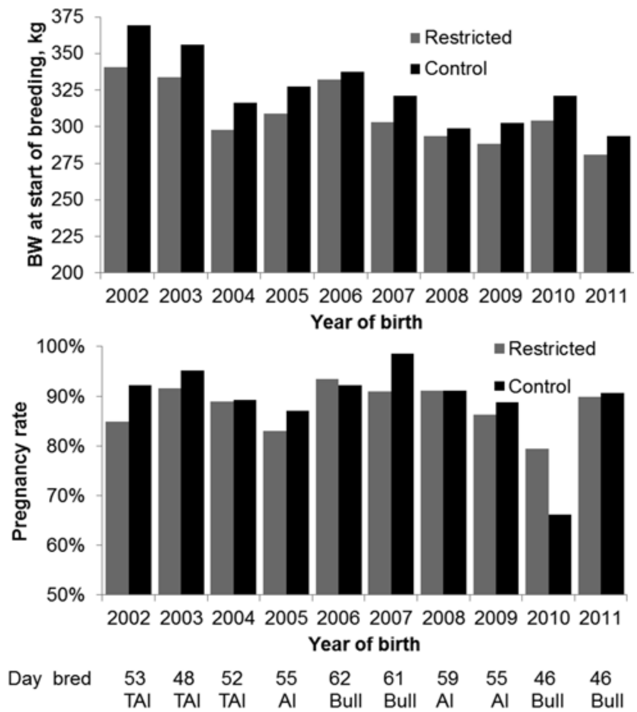

Figure 2. Prebreeding BW (top panel) and pregnancy rates (bottom panel) for heifers fed ad libitum (a corn silage–based diet to appetite [Control]; black bar) or 80% of that consumed by controls adjusted to a common BW basis (Restricted; gray bars) during a 140-d period between weaning and start of breeding. Heifer birth year is shown on the *x*-axis. Total number of d heifers were bred each year and method of breeding is shown at bottom of figure (TAI = estrous synchronization and timed AI followed by breeding by natural mating; AI entailed injection of PGF and AI after estrus followed by breeding by natural mating; Bull = natural mating). Prebreeding BW was greater ($P < 0.001$; largest SE = 4.3) for Control than Restricted heifers but pregnancy rate did not differ ($P = 0.58$; largest SE = 4.5). Prebreeding BW and pregnancy rate varied ($P < 0.001$) across years.

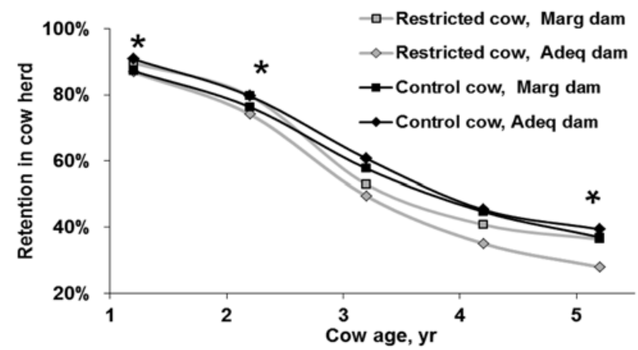

Figure 3. Impact of 2 levels of dam protein supplementation during gestation and feed level provided to daughters during postweaning development and subsequent winter supplementation on retention in the herd. Supplement treatments applied to the dams were feeding of alfalfa cubes or hay at the equivalent of 1.8 or 1.1 kg/d (as-fed basis), which was expected to be an adequate (Adeq) or marginal (Marg) level of protein supplementation to meet NRC (2000) requirements based on average quality and availability of the winter forage. Daughters of dams from each level of protein supplement were allotted by BW at weaning to be fed a corn silage–based diet to appetite (Control; $n = 656$ at first data point) or fed at 80% of that consumed by controls adjusted to a common BW basis (Restricted; $n = 655$ at first data point) during a 140-d period after weaning. Data are for animals born from 2002 through 2011, as determined in June 2015. Therefore, data are right censored due to absence of available data at 5 yr for 2011-born animals. Animals were required to get pregnant and wean a calf each year to remain in the herd. Pregnant animals grazed dormant winter forage and were provided an equivalent of either 1.8 or 1.1 kg/d protein supplement for Control or Restricted treatments, respectively. *Data points were affected by interaction ($P < 0.07$) of cow and dam treatments. Loss from 2 to 3 yr of age was greater ($P < 0.01$) for Restricted cows (gray lines) than Control cows (black lines). Loss from 3 to 4 yr of age was greater ($P < 0.03$) for cows from Adeq dam (diamonds) than cows from Marg dams (squares).

rate have not been thoroughly explored in these data, it is believed that environmental factors contributing to variations in nutritional quality of forages are involved. Nutritional variations may not be limited to what the heifers themselves experienced but may also include the nutritional environment experienced while in utero. Therefore, as subsequently discussed, the nutritional environment experienced by its dam may influence the heifer's response to limited nutrition.

Previous evaluations on the combined impacts of nutritional input during postweaning development and subsequent winter supplementation and the effects of dam treatment on retention in the herd have indicated trends for main effects and interactions of these 2 factors (Roberts et al., 2009b; Funston et al., 2012b; Endecott et al., 2013), providing evidence that fetal programming may influence individual animal response to its nutritional environment later in life. A current summary of retention in this herd is shown in Fig. 3. Analysis of these data extends the results previously reported (Roberts et al., 2009b) by including females from all years of the study represented at all time points except age 5 yr, where data from heifers born in the last year of the study are not yet available. Thus, data are not yet complete for age 5 yr. The interaction of dam treatment and heifer treatment tended ($P < 0.07$) to influence pregnancy rate and the percentages of cows retained in the herd at 2.2 and 5.2 yr of age (Fig. 3). These interactions arise from greater retention of heifers developed on restricted feed and fed MARG level of winter supplement when born from MARG dams compared with their restricted cohorts born from ADEQ dams. Pregnancy rate at 2.2 yr of age was greater ($P = 0.01$) for cows in the Control group (79%) than for cows in the Restricted group (72%), resulting in lower retention rates in Restricted cows at 3 and 4 yr of age (Fig. 3). Pregnancy rates at 3.2 yr of age were greater ($P = 0.03$) for cows born from MARG supplemented dams (79%) than ADEQ dams (72%), providing another example of fetal programing. These results provide evidence that the level of nutrition experienced during gestation can alter the developing fetus, affecting its reproductive performance later in life. The interactions observed indicate that managing cows with less feed inputs may program their offspring to better sustain reproductive performance when reared in a low-input environment. The greatest differences in retention rates depicted in Fig. 3

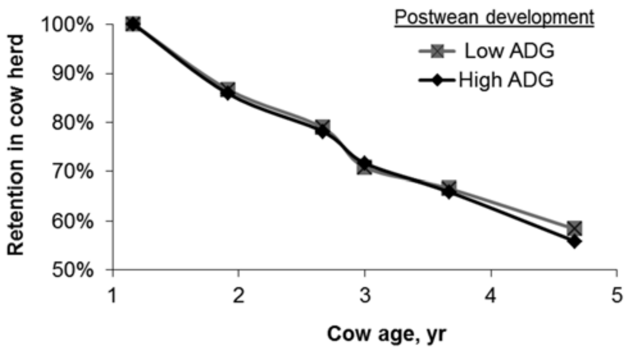

Figure 4. Growth rate between weaning and start of breeding had minimal effect on retention beyond 4 yr of age. Heifers were fed to gain either 0.50 (low ADG; *n* = 120) or 0.64 (high ADG; *n* = 120) kg/d during postweaning development, resulting in 289 and 313 kg average BW at start of breeding. Data adapted from Funston and Deutscher (2004).

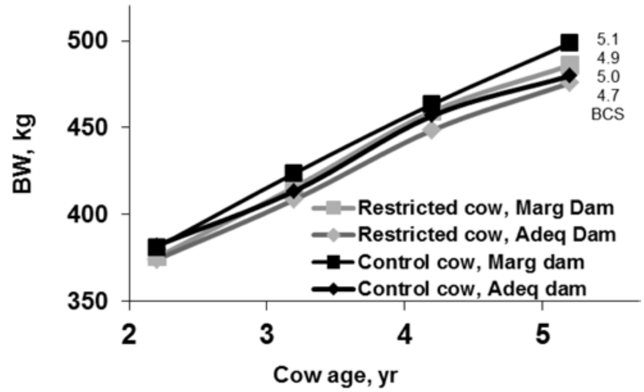

Figure 5. Impact of 2 levels of dam protein supplementation during gestation and feed level provided to daughters during postweaning development and subsequent winter supplementation on BW at start of breeding from 1 to 5 yr of age. Supplement treatments applied to the dams were feeding of alfalfa cubes or hay at the equivalent of 1.8 or 1.1 kg/d (as-fed basis), which was expected to be an adequate (Adeq) or marginal (Marg) level of protein supplementation to meet NRC (2000) requirements based on average quality and availability of the winter forage. Daughters of dams from each level of protein supplement while grazing dormant native forage were allotted by BW at weaning to be fed a corn silage–based diet to appetite (Control; *n* = 656 at first data point) or fed at 80% of that consumed by controls adjusted to a common BW basis (Restricted; *n* = 655 at first data point) during a 140-d period after weaning. Animals were required to get pregnant and wean a calf each year to remain in the herd. Pregnant animals grazed dormant winter forage and were provided equivalent of either 1.8 or 1.1 kg/d protein supplement for Control or Restricted treatments, respectively. Interaction of dam treatment and level of feed input to daughters were not observed. Postweaning development and subsequent winter supplementation treatment influenced ($P < 0.05$) cow BW at each age point, with Control cows being heavier than Restricted cows (compare black lines vs. gray lines with similar symbols). Cows born from dams receiving Marg level of winter supplement (squares) were heavier than cows born from dam receiving Adeq (diamonds) level of supplement at 3 ($P = 0.07$), 4 ($P = 0.054$) and 5 yr ($P = 0.015$) of age. Body condition scores of cows at 5 yr of age differed ($P < 0.05$) due to both cow and dam treatment, with Control cows having greater BCS than Restricted cows and cows out of Marg dams having greater BCS than cows out of Adeq dams.

are between Control and Restricted animals born from ADEQ dams. The difference between these 2 groups is consistent with data from numerous studies evaluating nutritional effects on reproduction (Richards et al., 1986; Selk et al., 1988; Spitzer et al., 1995). In contrast, the differences in retention between Control and Restricted heifers born from MARG dams would not be intuitive from previous research. These divergences in treatment response emphasize the need to consider previous herd management when interpreting results of studies evaluating nutritional impacts on reproduction. Results from studies evaluating nutritional impacts on cows that have been continuously managed to meet or exceed NRC nutritional requirements may not be indicative of results in herds managed with less inputs, as was also observed for ewes (Vonnahme et al., 2006), as previously discussed.

The design of this study precludes determination of whether the effects of heifer treatment on retention in the herd are due to differences imposed during the 140-d postweaning development, winter supplementation, or the combination of the 2. Evidence that restriction during postweaning development has minimal effects on retention is provided from a study by Funston and Deutscher (2004; Fig. 4), in which heifers were developed on diets differing in quality, rather than quantity. However, growth rates achieved for the low- and high-quality diets were similar to the growth rates of Restricted and Control fed heifers depicted in Fig. 2. The 2 studies differ in that heifers in the study of Funston and Deutscher (2004) were all treated the same after postweaning development and retention was similar between the 2 postweaning treatments. Comparison of retention in these studies confirms the importance of winter nutrition in young cows.

Physiological processes responsible for the effects of dam treatment on reproductive performance reflected in retention rates (Fig. 3) remain to be identified. As observed in the classical studies leading to the concept of epigenetics previously discussed, the impact of dam undernutrition on subsequent reproductive performance exhibited by her daughter later in life may involve the altered metabolic responses contributing to the "thrifty phenotype" described by Hales and Barker (2001) and alternations in major organs as well as reproductive tissues and organs (George et al., 2012; Mossa et al., 2015). Whereas these effects have been identified in undernutrition experimental models, it remains to be determined if the effects will also be evident in marginal nutritional environments. Evidence of altered metabolism was provided by preliminary evaluation of BW and BCS of a subset of cows from the lifetime productivity study (Roberts et al., 2009b). The current paper expands on the preliminary evaluation by including females from all years of the study represented at all time points except age 5, where data from heifers born in the last year of the study are not yet available. Figure 5 depicts effects of cow and dam treatment on BW at start of breeding at 2 until 5 yr of age. Cows

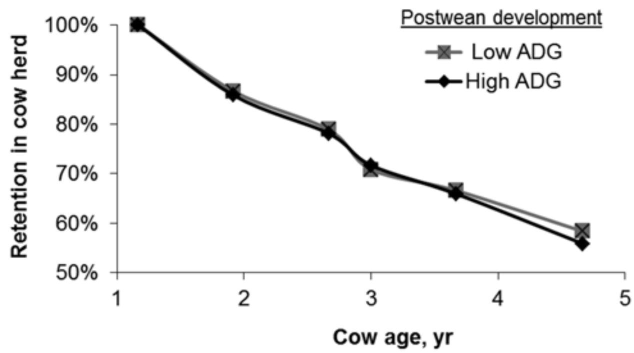

Figure 6. Retention rate of heifers grazing native dormant range provided either a 36 or 50% RUP supplementation or fed a growing diet in a feedlot during postweaning development. Retention tended ($P < 0.08$) to differ among treatments at 1 and 2 yr of age and was greater ($P < 0.01$) for range + 50% RUP than other 2 treatments at 3 and 4 yr of age. Adapted from Mulliniks et al. (2013).

born from MARG dams weighed more ($P = 0.005$) by 3 yr of age than cows from ADEQ dams. This difference persisted to 5 yr of age, the expected age at which mature BW is achieved. Body condition scores at 5 yr of age were also affected by dam treatment. Cows from ADEQ dams had lower ($P < 0.05$) BCS than cows from MARG dams (Fig. 5). Furthermore, Restricted cows from MARG dams produced calves that were lighter at birth and weaning than their contemporary herd mates born from ADEQ dams (Table 1). These differences due to dam treatment, or granddam treatment, support a role of epigenetically induced changes in metabolic pathways that improve reproductive performance leading to greater retention in the herd.

Additional evidence supporting altered metabolic function is that concentrations of IGF-1 in blood samples collected prior to and after first calving and at the start of breeding were less in Restricted cows from ADEQ dams compared with the other groups (90 vs. 98 ng IGF-1/mL; Roberts et al., 2010). The lower levels of IGF-1 coinciding with the lowest rebreeding rates in this group are consistent with IGF-1 being indicative of capacity for resumption of estrus after calving (Roberts et al., 1997; Roberts, 2008). The lack of difference in circulating IGF-1 between Restricted cows from MARG dams and Control cows from either MARG or ADEQ dams may be due to metabolic programing during uterine development, resulting in greater capacity for maintaining reproductive function under limited nutritional environments.

Table 1. Effects of feed amount provided to dam and cow on subsequent progeny performance

Dam treatment[1]	Cow treatment[2]	Calf BW at birth, kg [3]	Calf BW at wean, kg[3]
Adequate	Control	35.4	216
Marginal	Control	35.4	216
Adequate	Restricted	35.2	214
Marginal	Restricted	34.5[4]	211[4]
P-value, dam × cow treatment		0.07	0.04

[1]Cows were provided equivalent of either 1.8 (Adequate) or 1.1 kg (Marginal) protein supplement/d while grazing native range each winter.

[2]Daughters of dam treated as indicated in the first column. After weaning, these daughters were fed ad libitum during 140-d postweaning development and 1.8 kg/d supplement each winter (a corn silage–based diet to appetite [Control]) or were fed 80% of feed provided to control (common BW basis) during 140-d postweaning development and 1.1kg/d supplement each subsequent winter (80% of that consumed by controls adjusted to a common BW basis [Restricted]).

[3]Offspring from cows described in the second column; values represent 3,106 BW measurements at birth and 2,894 BW measurements at weaning collected on calves born from 2004 to 2014.

[4]Differs from other numbers in same column.

Range vs. Feedlot Heifer Development Study

Further evidence of improved retention rates resulting from lesser feed inputs during postweaning development is provided by Mulliniks et al. (2013). In this study, postweaning growth rates differed depending on whether heifers were developed on native range or in a feedlot. Heifers developed on native range were provided the equivalent of 0.9 kg/d of a 36% CP supplement, consisting of either 109 (36% RUP) or 160 (50% RUP) g/d RUP. From January until the start of breeding in May, pasture-developed heifers gained 20 kg to achieve a prebreeding BW of 276 kg (approximately 51% of mature BW), regardless of supplement type. In contrast, heifers developed in the feedlot gained 60 kg during this same time and weighed 315 kg by the start of breeding (approximately 58% of mature BW). At the start of breeding, all heifers were combined and managed together. Rates of gain achieved during the postweaning development phase were 0.27 and 0.69 kg/d for range and feedlot, respectively. For comparison between studies, rate of gain for heifers developed on range was approximately one-half of the Restricted heifers' rate of gain shown in Fig. 1 and feedlot-developed rate of gain was similar to rate of gain of Control heifers depicted in Fig. 1. Whereas heifers developed on native range gained less than heifers in the feedlot, growth rate from the start of breeding to pregnancy diagnosis in September was greater in the range-developed heifers (0.80 and 0.85 kg/d for 36 and 50%, respectively) than feedlot-developed heifers (0.61 kg/d), resulting in similar BW of 402, 393, and 403 kg for range + 36% RUP, range + 50% RUP, and feedlot, respectively. These BW are similar to those observed at winter pregnancy diagnosis in the Control and Restricted heifers depicted in Fig. 1 for the previously described study. Whereas BW of the range and feedlot heifers were similar by fall pregnancy diagnosis, the proportion retained in the herd over 4 yr was greater for the range + 50% RUP heifers

Table 2. Impact of pasture quality grazed by dam during second trimester on subsequent productivity of daughters[1]

Trait of daughter	Pasture type: Native rangeland (6.7% CP[2])	Seeded pasture (10.2% CP[2])	P-value treatment
Days of retention in the herd	1,074 ± 213	1,480 ± 214	0.059
Total kilograms weaned calf per cow per year	108 ± 4	137 ± 4	0.027

[1]Adapted from Grings and Roberts (2013).

[2]Average CP of extrusa collected using either esophageally (yr 1 and 2) or ruminally (yr 3 and 4) cannulated mature cows.

than the other 2 groups, which did not differ (Fig. 6). As with the results of Funston and Deutscher (2004) previously discussed, these results indicate that lower growth rates during postweaning development may not be detrimental to future retention.

Studies discussed in the preceding paragraphs expand on previous reports demonstrating slow rates of postweaning development can reduce harvested feed requirements, improve feed efficiency, and, depending on type of supplements used, may increase reproductive performance (Funston et al., 2012a; Endecott et al., 2013).

Impacts of Alterations in Prepartum Dam Nutrition due to Winter Forage Type with or without Protein Supplement and Date of Weaning on Offspring Performance

Results from the lifetime productivity study discussed above demonstrate that the level of winter supplement provided to cows grazing dormant native range affects performance of female offspring. Research at the University of Nebraska (North Platte, NE) over the last decade has evaluated alternative winter feed sources and cow supplementation protocol effects on offspring performance. Many observed impacts of dam treatments on male and female offspring performance were recently reviewed (Funston et al., 2012b; Funston and Summers, 2013; Endecott et al., 2013). Information subsequently focuses on the effects of different forage types with or without supplementation during gestation on a calf's subsequent productivity as it relates to studies discussed above.

Two studies evaluated offspring performance from spring calving cows that were or were not provided a protein supplement during the last trimester while grazing dormant native forage in the Nebraska Sandhills. Martin et al. (2007) compared a 42% CP (DM) cube containing 50% sunflower meal with 47% cottonseed meal, each provided 3 times weekly at the equivalent of 0.45 kg/d. Funston et al. (2010) subsequently evaluated the provision of a 28% CP (DM) supplement consisting of mostly dried distillers' grains with solubles provided 3 times weekly at the equivalent of 0.45 kg/d. Using NRC (2000) feed values, the protein fed by Martin et al. (2007) contained approximately 33% RUP, whereas the supplement used by Funston et al. (2010) provided approximately 48% of the protein as RUP. Based on these values, supplements in the 2 studies delivered the equivalent of approximately 60 g RUP/d. Providing cows these supplements while grazing winter range increased heifer progeny BW from weaning through pregnancy diagnosis. Heifers from protein-supplemented dams attained puberty 14 d earlier than heifers from nonsupplemented dams (Funston et al., 2010) and there was a trend for (Funston et al., 2010) or significant (93 versus 80%; Martin et al., 2007) improvement in pregnancy rates of offspring from supplemented dams compared with those from nonsupplemented dams. In addition, a greater proportion of heifers from protein-supplemented dams calved in the first 21 d of the calving season than heifers from dams that were not supplemented (Funston et al., 2010).

Although the studies above reported changes in heifer performance resulting from protein supplementation of dams while grazing winter range, no effect of protein supplementation to dams grazing corn crop residue during late gestation was observed on subsequent heifer fertility (Funston et al., 2010). Similarly, Warner et al. (2011) reported no differences in heifer pregnancy rates due to protein supplementation of dams grazing corn crop residue during late gestation. Therefore, the impact of protein supplementation of dams during winter grazing on offspring performance may vary depending on type and quality of winter forage grazed.

In the studies described above, Montana research evaluated the effects of 2 supplementation levels, whereas the Nebraska studies compared absence or presence of supplementation. In a recent study, Rolfe et al. (2011) evaluated offspring of March-calving cows grazing either corn crop residue or dormant winter range during the last trimester of gestation. Nutritional status for each grazing treatment was further altered by weaning in either October or December. In addition, cows grazing winter range were provided 0, 0.45, or 0.91 kg/d of a 28% CP supplement. Cows grazing corn crop residue were not supplemented. Offspring birth weight was affected by the dam's previous weaning date and grazing treatment, with average birth weights paralleling the expected nutritional environment of the dam. The greatest calf birth weights were for those born to dams that were weaned early and provided the most supplement, whereas calves from dams not provided supplement and weaned late were lightest at birth. The BW differences observed at birth were also apparent in subsequent BW throughout the first year of life.

Offspring from cows that grazed corn crop residue were similar in BW to those from cows that had received either level of protein supplement while grazing winter range. Interestingly, the previous weaning date also influenced BW of subsequent offspring, being greater for offspring from dams weaned in October rather than December. Magnitudes of the differences in offspring BW due to month of weaning in the dam were similar to differences observed in response to presence or absence of supplementation. These results provide evidence that altering the time of weaning may provide benefits to offspring performance equivalent to strategies designed to supplement forage quality. However, the proportion of heifers cycling and overall pregnancy rates did not differ due to maternal weaning treatment.

Fall Pasture Quality Study

The results from the Fort Keogh lifetime productivity study prompted an additional study to evaluate how pasture quality during autumn grazing impacted heifer offspring of cows calving in late winter (Grings and Roberts, 2013). The study was replicated 4 yr. Each year, cows were allocated to graze either pastures of seeded forage or native range. Resulting number of calves weaned following dam treatments in 2005, 2007, 2009, and 2010 were 43, 50, 39, and 43, respectively. Seeded pastures consisted of 2 replications of 26 ha each that were previously harvested for hay followed by flood irrigation in August. Forages in the seeded pasture included grasses (smooth brome, Altai wildrye, Russian wildrye, and western wheatgrass) and legumes (birdsfoot trefoil, red clover, and alfalfa). Native rangeland pastures consisted of 2 replications of 71 or 90 ha. The natural rangeland vegetation is a grama–needlegrass–wheatgrass (*Bouteloua–Hesperostipa–Pascopyron*) mixed-grass dominant rangeland (Kuchler, 1964). Extrusa samples collected using esophageally (yr 1 and 2) or ruminally cannulated (yr 3 and 4) mature cows indicated that CP differed ($P < 0.05$) between pasture forage types but digestibility did not ($P > 0.10$). Cannulated cows grazing seeded pastures had extrusa with 10.2% CP and 70% in vitro OM digestibility in yr 1 and 2 and 76% in vitro true digestibility in yr 3 and 4, DM basis, whereas extrusa from cows grazing native rangeland contained 6.7% CP and 67% in vitro OM digestibility in yr 1 and 2 and 74% in vitro true digestibility in yr 3 and 4, DM basis. Cows grazed these pastures from about September 28 to November 19 and then were moved to drylots and fed a corn silage–based diet until calving. Average calving date was February 11 ± 10 d. After calving, cows were moved to dormant native pastures and fed hay (alfalfa or grass, depending on availability each year) and/or a grain-based range cake supplement until native rangeland forage was adequate to support production based on visual estimates of forage biomass and cow's preferred consumption of native forage over harvested feed. Cows and their calves were maintained on native range until calves were weaned at approximately 190 d of age. At weaning, calves were placed in drylots. Heifers were fed a diet of 60% corn silage, 39% hay, and 1% protein and mineral supplement (as-fed basis), as previously described (Grings et al., 2005). Heifer calves born to cows in the study that were retained for replacement ($n = 42$ and $n = 32$ for seeded and native, respectively) were returned to native range in the first or second week of April and were exposed to bulls for a 35-d breeding season approximately 2 wk after return to native range. Reproductive performance of these females was evaluated.

Pasture type grazed in autumn did not result in differences in cow BW (60.8 ± 4.5 and 64.9 ± 4.5 kg change over treatment period for native and seeded pasture, respectively; $P = 0.57$) or BCS (0.33 ± 0.06 and 0.31 ± 0.06 change over treatment period for native and seeded pasture, respectively; $P = 0.8$), or offspring BW at birth ($P = 0.9$), weaning ($P = 0.9$), or 1 yr of age ($P = 0.6$). Heifer calves retained from cows grazing seeded pastures tended to remain in the herd longer than heifer calves from cows that had grazed native rangeland during the second trimester of pregnancy (Table 2). Although calf BW produced by the daughters of these cows did not differ due to pasture type (197 ± 5 and 201 ± 5 kg BW at weaning for first calf of daughters of dams that grazed native and seeded pasture, respectively; $P = 0.61$), the longer retention in the herd of daughters from cows that grazed seeded pasture resulted in more total calf production than daughters from cows that grazed native rangeland (Table 2). These results indicate that differences in forage CP levels experienced during second trimester may bring about subsequent differences in female offspring retention rate.

SUMMARY AND CONCLUSIONS

It is becoming increasingly apparent that small differences in the nutritional environment to which animals are exposed in utero and postnatally can influence traits later in life. Differences in nutrition may arise from different levels of supplementation, presence or absence of supplementation, type of supplementation, forage type and quality, or management (e.g., time of weaning). These nutritional differences are likely mediated through epigenetic or metabolic adaptation processes. Furthermore, these alterations appear to influence the capacity of future offspring to cope with nutritional stress. The implications of these generational effects on interpretations of completed and future research concerning impacts of nutrition on production need to be considered. For example, studies evaluating nutritional impacts on populations maintained in a very ample nutritional environment may not be indicative of the response expected in populations managed under limited nutritional environments.

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