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Drivers of grazing livestock efficiency: how physiology, metabolism, experience and adaptability influence productivity

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ABSTRACT: Beef cow efficiency is a century's old debate on what the criteria, certain phenotypic traits, and definition of an "efficient" cow. However, we do know that energy utilization by the cow herd is proportionally large compared to the rest of the sector, which accounts up to 70 to 75% of dietary energy for maintenance with the residual used for pregnancy, lactation, activity and adaptation to the environment. Therefore, leveraging genetic variation in cow energy efficiency by selecting cows that require less energy for maintenance potentially reduces total energy utilization for beef cattle production, which will ultimately improve production efficiency and profitability. For livestock producers, optimizing both economic and biological efficiency is critical. The continued viability of production systems utilizing rangelands requires more rapid adoption of innovative management practices and selection tools that lend to increased profitability through optimization of nutrient utilization and increased reproductive performance. However, the implementation of a gold standard to identify energy efficient beef cows has not yet been fully realized for the beef industry. Rangeland beef cow herds are required to be biologically and reproductively efficient in an array of ever changing environmental conditions. The most efficient cows are those that easily adapt to environmental changes and have the ability to conserve or reset their maintenance requirements to match current environmental conditions. To achieve this metabolic adaptability or flexibility, beef cows need to be suited to their environment and have the ability to acclimate to environmental changes. The purpose of this proceedings paper is to identify and describe factors that influence range cow efficiency and ultimately contributes to the sustainability (both from a productivity and economic view point) of range cows in extensive enterprises.

Key words: beef cow, efficiency, metabolic flexibility, rangelands

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INTRODUCTION

The implementation of standard criteria to identify energy efficient beef cows has not been accomplished for the beef cowherd. The challenge of pinpointing efficiency traits in grazing livestock production is that livestock in the U.S. graze in a wide variety of environmental and management conditions. These various environmental differences provide a challenging situation to have a universal cow efficiency equation. For example, efficiency in one environment does not necessarily equate to efficiency in a different environment (Burns et al., 1979; Koger et al., 1979). However, certain drivers of efficiency can exist across environmental types such as matching cow type to production environment (Mulliniks et al., 2015a) and increased metabolic flexibility to environmental stress (Mulliniks et al., 2013b), which could be a primary focus for increasing efficiency of grazing beef cows.

Knowledge gaps concerning beef cow efficiency fundamentally inhibit advances in selecting for "efficiency" in grazing livestock. The need for a better understanding of the mechanisms driving cow efficiency is critical. Therefore, the objective of this review is to explore drivers and mechanisms of ener-

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getic efficiency that may be used to identify beef cows that are more efficient converters of grazed forage resources into animal products. Therefore, the definition of an energy efficient beef cow utilized for this review may be best represented as: *A reproductively competent, long-lived cow that consistently uses fewer forage resources (fewer calories needed) to produce a highly desirable energetically efficient calf.*

EXPERINCE AND ADAPTABILITY INFLUCECE PRODUCTIVITY

Behavior and Social Aspects

It is often discussed by the scientific community that grazing ruminants need to be acclimated to the environment they are being raised in. But what exactly does "acclimated" actually mean? Acclimate is merely, the grazing ruminants' ability to adjust to current environmental conditions and optimize use of available feed resources to maintain an expected level of production. If the grazing ruminant fails to make these adaptations under current environmental conditions and/or is unable to meet production goals, then management needs to consider alternatives. Range livestock are dependent on the quality and quantity of forage produced on a given rangeland. Forage production, however, is reliant on timing and amount of precipitation, optimal temperatures to promote plant photosynthesis for growth, soil type and nutrient availability, and soil microbial activity that aids in nutrient supply to plant roots, among other factors. Another key component relates to management of the rangeland, which includes the degree of utilization and season in which grazing is to occur (Grings et al., 1996; Grings et al., 2005). While all these factors are important and directly influence production of the grazing ruminant on arid and semiarid rangelands we will focus on the ability of the grazing ruminant to adapt to changing environmental conditions and how experience may or may not play a critical role in acclimation.

Putting the grazing ruminant in perspective, one has to initially understand and recognize the behavior of domesticated range ruminants. Suites of correlated behavioral syndromes that differ among individuals across situations, context, and time (Sih et al., 2004) are useful tools to explore connections between cattle temperament and performance on rangelands. In addition, behavioral syndromes have been shown to influence an animal's fitness due to these syndromes limiting an individual's ability to adapt to varying environments (Bell, 2007). In a 2 yr study, Wesley et al. (2012) classified young beef cows into two groups ('go-getter' vs. 'laid back') based on a cluster analysis on a basis of 14 behavioral, physiological, and performance predictors. These authors reported that cows belonging to the '*go-getter*' behavioral type weaned a heavier calf, achieved BW nadir after calving 25 d sooner, and had a resumption of estrus 18 d sooner than their 'laid back' counterparts. Over a 7 yr period, Goodman et al. (2016) retrospectively analyzed culling rates of the two behavioral types and reported that the population of the herd at the Corona Range and Livestock Research Center shifted toward a population composed of 'go-getters' (Fig. 1). Which brings us to the question of how does experience and adaptability influence range livestock? The authors have chosen to mold the pursing discussion in three distinct yet related areas; 1) The academic experience of grazing or the knowledge obtained from dams or mature members of a herd; 2) The social dynamics or the hierarchical structure of herd mates: and Lastly, 3) The athleticism of individuals within a herd or the ability to use knowledge and social behaviors to optimize grazing efficiency.

The learned response of grazing begins in utero with flavors transferred from the dam to the fetus through amniotic fluid and continues after parturition as the calf suckles dams' milk (Lyons and Machen, 2000). Young grazing livestock learn what to graze and avoid from their dam and other mature herd mates (Lyons and Machen, 2000). Palatability or selection preferences for certain forages by livestock to distinguish the best forages available is a primary attribute of grazing livestock; however, ruminants will also rely on smell and sight to help select the best quality diet available. Grazing ruminants will use unfavorable experiences that cause digestive upsets to avoid forages or limit intake of those forages in future encounters (Lyons and Machen, 2000). Research from New Mexico State University indicates the relocation of animal into fresh pastures even during periods of time when forages are senescent or minimal growth is occurring can be equivalent to over 1 kg of a 40% CP supplement per cow per day (Sawyer, 2000). Furthermore, grazing livestock can still benefit from grazing senescent forages when pastures have been rested during the primary growing season. This seems to be much more beneficial for non-naïve animals or for herds that have some social structure where grazing ruminants have been in the pasture previously. Grazing ruminants retain a long-term memory (map-like representation) of foraging experiences that allow them to initially isolate areas in a landscape known to provide a high-quality diet. In addition, ruminants maintain a short-term memory (working memory), which guides them toward or away from areas recently visited (within 8 h) that are abundant or depleted of nutritional forages (Lyons and Machen, 2000). The knowledge of animals' familiar (adapted) with a given environment, when combined with those naïve animals is crucial in achieving production goals. Naïve animal introduced

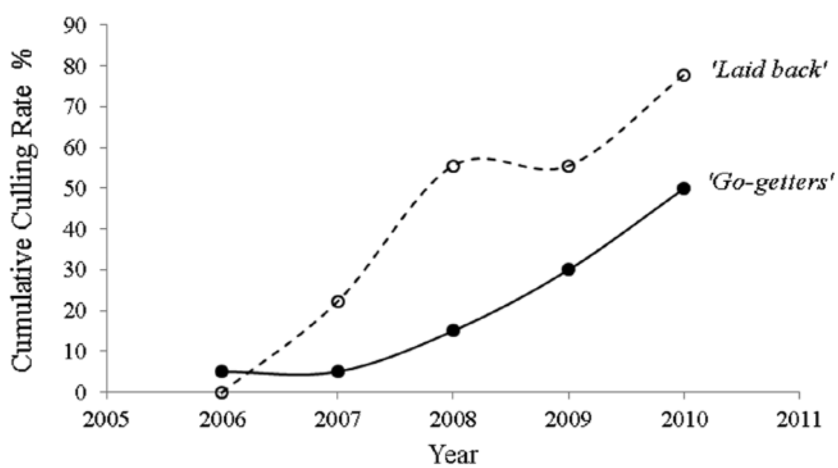

Figure 1. Cumulative culling rate for range beef cows at the Corona Range and Livestock Research Center, Corona, NM classified into two behavioral types, 'go-getters' or 'laid back'. Adapted from Goodman et al. (2016).

to a new pasture alone (no previous grazing knowledge) and not having the benefit of learning from animals with previous experience of the landscape tend to spend more time grazing which may result in eating less, traveling greater distances, and greater BW loss (Lyons and Machen, 2000).

In the majority of range livestock production systems a general gregariousness is most likely to be observed within a herd. However, during specific production events (e.g., parturition) dams initially prefer isolation, and then develop stronger social bonds with other dams during lactation (Finger et al., 2014). On the other hand, with less domesticated Zebu cattle it has been observed that the social organization is much more complex (Reinhardt and Reinhardt, 1981). As animals leave the herd for failure to meet production goals or other unforeseen reasons, new animals are developed and inserted into a herd to maintain both an environmental and economically sustainable enterprises. This results in a cyclic pattern of older animals with more grazing experience and knowledge of the rangeland having both a grazing advantage and a teaching role for younger livestock entering the herd (Howery et al., 1996). A number of studies have indicated that grazing ruminants may favor certain areas within a rangeland (e.g., riparian habitats) vs. uplands (Howery et al., 1996; Roath and Krueger, 1982) depending on forage quality and quantity (Howery et al., 1996). Within a given social structure, identification of grazing ruminants that maintain production goals and utilize a greater percentage of a landscape may prove to be of more value for selection purposes than grazing animals that travel less and camp out in an isolated area. Thus, grazing ruminants with previous knowledge of a pasture may inadvertently pass along knowledge with young naïve grazers may improve both rangeland and production efficiencies.

Acclimation

Just as athletes train for competition and adapt to training, grazing livestock are also training every day due the amount of environmental pressure a cow is expected to perform under, coupled with nutrient demands of lactation and reproduction. Animals commonly react to these variable environmental and physiological conditions by initiating adaptive responses to cope with extreme conditions such as stress (Stott, 1981). If athletes train to have an increased adaptive capacity and tolerance to stress, why don't we manage cows in a similar methodology to increase their adaptive resilience to environmental and physiological stresses? However, common livestock practices tend to manipulate livestock's nutritional environment to a degree that may completely buffer their capacity to become more adaptive and ultimately less energy efficient. In human fitness, an interesting aspect of skeletal muscle is its adaptability. If a muscle is stressed (within tolerable limits), it adapts and improves function. Conversely, if a muscle receives less stress than it's used to, it atrophies. Human research involving physical exercise and endurance has proven that physiological adaptation can be achieved through intermittent muscle contraction (Egan and Zierath, 2013). The functional adaption of skeletal muscle to continuous perturbations demonstrates the tissues malleability and adaptability to induced stress (Coffey and Hawley, 2007). Through human and animal research, an enhanced ability to maintain muscle homeostasis is an adaptive process that is the result of continuous muscular stress accompanied with increased oxygen consumption and mitochondrial respiration (Holloszy and Coyle, 1984, McGivney et al., 2009, Egan and Zierath, 2013). Therefore, adaptation requires a systematic application of environmental stress that is sufficient enough to elicit an adaptation, but not so severe that a loss in production occurs. If the stress a grazing ruminant is experiencing is insufficient to overload the body or never exceeds a certain threshold, then no adaptation occurs (Ghosh, 2004), which is where current cowherd management practices may lead by overfeeding grazing livestock. With this in mind, identification of range cows that are in better fitness may be indicative of overall production efficiencies (Roberts et al., 2009). While a thorough investigation of this concept is still incomplete for range livestock, there are strong indicators that this may be true (Roberts et al., 2009; Mulliniks et al., 2013a). In non-lactating, non-pregnant, multiparous Holstein cows exposed to exercise regimens over a 60 d period, cows exposed to exercise were considered to be in better fitness due to lower heart rate and plasma lactate concentrations at the end of that 60 d period compared to cows not exposed to exercise (Davidson and Beede, 2003). In addition, similar results were observed in non-lactating, late-pregnant multiparous Holstein cows with again fitness being improved in cows subjected to exercise (Davidson and Beede, 2009). Lastly, work from the Fort Keogh Livestock and Range Research Laboratory, indicates that heifers grazing rangeland exhibit a lower resting heart rate and experience a 0.45 kg advantage in BW compared to heifers fed in confinement (Petersen et al., 2016). This indicates that heifers grazing rangeland are in greater physical fitness over heifers fed in confinement.

Conditions such as heat stress lead to reduce feed intake, endocrine dysfunction, and blood flow redistribution, which can be characterized by a decrease in animal performance (Sejian et al., 2010). However, certain animals maintain productivity and develop adaptation mechanisms under prolonged or chronic environmental pressures. For instance, tissue cells from Zebu cattle are less affected by high ambient temperatures than cells from European breeds; thus emphasizing Zebu cattle's adaptions to elevated temperatures (Hansen, 2004). At the immunological level, adaptive immune responses are characterized as antigen-specific response that evolves over a period of time (Salak-Johnson and McGlone, 2007). These adaptive immune responses help maintain homeostasis within the organism and are often necessary for survival (Salak-Johnson and McGlone, 2007). Homeorhesis is the body's ability to maintain physiological state through changes in metabolism (Bauman and Currie, 1980). During certain seasons a cow's nutrient and forage availability may become limited in particular climates. Under these conditions, a reduced energy state may occur possibly leading to negative energy balance. In humans, fasted states of exercise were more effective at eliciting cellular muscle adaptation via fat oxidation than through carbohydrate loaded exercise (Van Proeyen et al., 2011). During times of nutrient deprivation, livestock have the ability to respond through adjusting their nutrient requirements without affecting productivity (Petersen et al., 2014). In addition, Rauw et al. (2010) evaluated the BW change of ewes in resource-poor environments during a Nevada winter. The study determined that ewes that lambed the previous year where better adapted to harsh, nutrient poor conditions and lost less BW than ewes who had not lambed the year prior. Thus, homeorhetic animals are better adapted to prioritizing productivity and more efficient at mobilizing adipose tissue supplies (Rhoads et al., 2013). Often times these stressors can be viewed as supportive stimuli that enhance an animal's adaptability to situations and conditions. If the stimulus is insufficient in eliciting a response, then no adaptive process occurs. If an animal loses its ability to be adaptive then there is a potential for the animal to become less efficient. Like skeletal muscle that undergoes prolonged periods of inactivity leading to unfavorable physiological effects (Jackman and Kandarian, 2004), animals potentially will exhibit a similar effect. Also, cattle may perform well in one environment (where the potential for environmental pressures are low), but production inefficiency may develop in a different environment (Mulliniks et al., 2015a).

Adaptive Capacity and Metabolic Flexibility

The early lactation period for a cow is a time period that characterizes if a cow can cope with the metabolic load of lactation, resulting in either reproductive competence or failure to adapt. This inevitable negative energy balance (NEB) at the onset of lactation is one of the most common drivers in reproductive inefficiency. However, the adaptive response to a metabolic load such as lactation can vary greatly among animals even with the same nutrient demand (Norin et al., 2016). To test metabolic robustness of dairy cows during early lactation, Gross and Bruckmaier (2015) retrospectively ranked cows according to their greatest NEFA concentration in wk 1 to 4 postpartum. These authors reported that the greater amplitude of adaptive responses or increased plasma concentrations of NEFA, b-hydroxybutyrate, and IGF-I in high response (high NEFA cows) cows may indicate a rapid ability for the sufficient supply of mobilization-derived nutrients. Since reproduction measurements were not measured in the above study, it would be hard to speculate if the more "robust" high response cows would be more reproductive competent.

Due to the high dynamic nature of the environments and management types in beef production, an animal's ability to be adaptable during changes in environmental is essential. If adaptive, flexible management is not used, static management in the face of a dynamic problem will not yield the most favorable results (Boyd and Svejcar, 2009). In addition, the capacity for animals to cope with acute and chronic environmental changes depends on the distribution of phenotypes and the degree of phenotypic plasticity or metabolic flexibility (i.e., the phenotypic response to an environmental change) among members of the population (Hofmann and Todgham, 2010). Diversity in key physiological traits can create differential plasticity toward environmental change within a population by illustrating how individual animals can remain metabolically insensitive to one environmental stressor at the cost of being highly sensitive to another (Norin et al., 2016).

This metabolic flexibility is the capacity for an organism to adapt fuel oxidation to fuel availability (Galgani et al., 2008). However, a more appropriate term in many cases with grazing livestock is "metabolic inflexibility". The inability of livestock or organisms to modify oxidation in response to changes in nutrient availability has been implicated in metabolic imbalance and metabolic disorders (ie., insulin resistance). Nutrient supply over the course of a production year for grazing livestock is highly dependent on environmental conditions, which play a role in the ability for livestock to efficiently sequester nutrient into their tissues. For example, Waterman et al. (2007) reported as forage quality declines, tissues become less responsive to insulin, resulting in longer glucose half-life. As tissue sensitivity to insulin declines, circulating concentration of glucose increases, resulting in a buildup of b-hydroxybutyrate that can eventually lead to metabolic dysfunctions.

The capacity for animals to cope with environmental changes may depend on the degree of their metabolic flexibility (i.e., the phenotypic response to an environmental change). Having a high metabolic flexibility may be significantly tied to the adaptability to dynamically changing nutrient supply levels. Mulliniks et al. (2013b) illustrated the ability of livestock to modify metabolically in response to changes in nutrient availability was correlated to their timing of conception. This study indicated that cows with elevated blood ketone concentrations, manifested from metabolic imbalance, before breeding season had a prolonged interval from calving to conception. Therefore, ketone concentrations may be a useful indicator of adaptive capacity during metabolically challenging physiological periods.

Adaptive capacity confers resilience to nutritional insults, given that livestock have the ability to modify their nutrient requirements with minimal losses of production. Petersen et al. (2014) illustrated that cows experiencing a dynamic environment are coping with the change by altering nutrient requirements compared with those that are in relatively static surroundings. Conversely, cows managed in the more controlled situations or static environment have a decreased aptitude for energy utilization efficiency. To illustrate this, Mulliniks et al. (2015a) utilized datasets from research stations in New Mexico and Tennessee. Although, nutritional supply during the breeding season is much greater in Tennessee, pregnancy rates were significantly less (88 vs. 96% in TN and NM; respectively) in Tennessee than in the nutrient restricted environment of New Mexico. Input cost to achieve these production measures has to be considered in calculating efficiency differences. Current annual cost of production in Tennessee is \$800/cow; whereas New Mexico is roughly half at \$440/cow. In addition, Mayfield (2012) reports that longevity in the Tennessee herd was only 3.5 yr, which is quite a bit lower than the 61% retention rate of the heifers remaining in the herd after 5 yr of age (Mulliniks et al., 2013a), illustrating short- and long-term effects of adaptive capacity on cow-herd productivity.

So what happens if we take environmentally adapted heifers out of their dynamic environment and develop them in a static nutritional environment? In New Mexico, Mulliniks et al. (2013a) showed the impact of programming animals to fit their given production environment. These researchers developed yearling beef heifers on native range receiving one of two protein supplements (low-RUP vs. high-RUP) or a control set of heifers developed in a feedlot. During the developmental treatment period, heifers developed in the feedlot had increased ADG (0.68 kg/d) from the initiation of treatments to the start of breeding compared with range-raised heifers consuming low-quality range with protein supplementation (0.26 kg/d). Even with the low ADG until breeding, retention rate through 5 yr of age for range-developed heifers fed a high-RUP supplement was 68% compared with 41% heifers fed a lower-RUP supplement and 42% for heifers developed in a feedlot (Fig. 2). This study may indicate the influence that management animals for adaptive responses early in life can have on long-term impacts on biological and economic efficiency. In addition, engrained adaptability from long-term management may be inhibited by short-term managerial decisions, such as managing and feeding animals considerable above what their respected environment resource can provide.

Extensive livestock operations in arid and semiarid rangeland environments rely heavily on the quality and quantity of forage available to achieve management production goals. While the requirements for cows experiencing weight loss (i.e., negative energy balance) are not well defined, the consequences are real and until nutrient mobilization and catabolism of body tis-

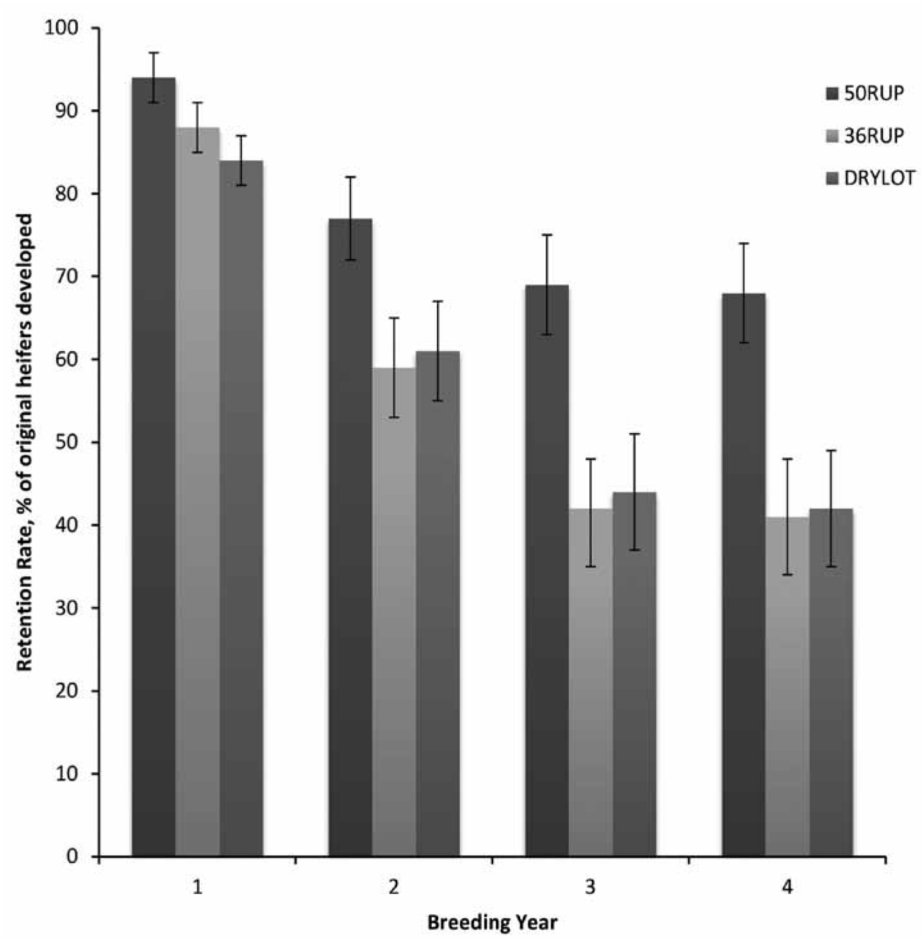

Figure 2. Retention rate of heifers grazing native dormant range with two types of protein supplementation (36RUP and 50RUP) or fed a growing diet in a drylot. Values shown in breeding yr 1 are heifer pregnancy rates. Breeding years 2 through 4 are proportion of the original heifers treated that were remaining at end of breeding in yr 2, 3, and 4. Retention tended (*$P > 0.08$) to differ among treatments in breeding yr 1 and 2, but was greater for 50RUP than 36RUP and DRYLOT cows in breeding yr 3 and 4 (**$P < 0.01$). 36RUP = 36% CP cottonseed meal base supplement fed 3 d/wk supplying 36% RUP; 50RUP = 36% CP supplement fed 3×/wk supplying 50% RUP; DRYLOT = corn silage diet fed in drylot to gain 0.68 kg/d. Adapted from Mulliniks et al. (2013a).

sue reserves are stabilized, animal performance is hindered. Metabolic dysfunctions attributed to negative energy balance are detrimental to reproductive success. Typically, research has focused on the decreased reproductive competence of animals that are in a poor plane of nutrition. However, more recent research has demonstrated that over-conditioned dairy cows mobilize more of their energy reserves than thin cows and have impaired insulin sensitivity coupled with a disposition toward metabolic dysfunction (Locher et al., 2015). Body weight loss alters oxidative metabolism (Waterman and Butler, 2010) and can directly influence reproduction, embryonic mortality, dystocia at calving, lengthened postpartum interval, and even subsequent ability to conceive (Whitman, 1975). In highly, dynamic and harsh environments, one possible method of increasing efficiency and resiliency is to select and breed for animals that have the ability to lose BW during periods when feed quantity is low and still remain reproductive competent. Borg et al. (2009) and Rauw et al. (2010) estimated moderate heritabilities for BW loss and gain in ewes grazing in rangelands. In addition, Mulliniks et al. (2012) illustrated over a 6 yr period that not all animals need to be fed to achieve a target BCS of 5 or greater at calving, which allows for utilizing body storage as a nutrient source during periods of energy deficiency to maintain reproductive competence. The cows from this study were offspring of cows that were managed in a low-input ($35 to 50 per cow per year in feed inputs) production system for multiple generations.

Cows grazing rangelands often go through one or more periods of BW loss through a production cycle. The objective of managers and producers of these cattle is to be diligent about their management practices to observe and react to these changes sooner than later. The use of strategic supplementation and proper pasture movement can minimize effect on oxidative metabolism, which benefits the grazing ruminant and optimizes extensive operational success.

The nutrient requirements of beef cows fluctuate throughout the production cycle, with the most pivotal period of nutrient utilization occurring during late pregnancy and peak lactation. Typically, nutrient availability during these critical periods is limited and cows tend to utilize body tissue to support fetal growth and lactation (Freetly et al., 2008). Therefore, strategies to limit body tissue loss during negative energy balance generally require supplemental feed to maintain cow BW. However, research has indicated that management strategies can be developed to encourage moderate stages of feed restriction and realimentation during periods of poor nutrient availability to improve the efficiency of nutrient utilization (Freetly et al., 2008; Freetly and Nienaber, 1998). Thus, developing management systems that mimic actual production environments is instrumental to optimize production and sustainability while also minimizing production costs.

Cow BW change during late gestation is a reflection of the proportion of relative nutrient consumption compared with nutrient demands. During periods of low energy intake, mobilization of maternal nutrient lipid reserves is needed to offset energy imbalances of gestation. In a 7-yr study, Mulliniks et al. (2015b) reported overall pregnancy rates were greater in cows either losing or maintaining BW during late gestation compared with cows gaining BW. Although BW change differences were not reported up to and through breeding, this improved reproductive performance may be attributed to a decrease in nutrient requirements in cows losing BW during late gestation and an overall increase in nutrient utilization. In addition, cows that have been adapted and managed to reproduce in harsh, limited nutrient environments may have the ability to maintain normal fetal growth and development during periods of maternal nutrient restriction. Maternal undernutrition in gestating ewes adapted to nutrient limited environments did not affect fetal plasma concentrations of glucose or fetal growth (Vonnahme et al., 2006) and were able to maintain fetal concentrations of AA (Jobgen et al., 2008). This implies that there is a mutual synchrony with the dam and fetus that may provide a natural adjustment against prepartum protein undernutrition when livestock are adapted to their environment (Martin et al., 1997). Thus, pre-planned management strategies to allow for BW loss during periods of moderate feed restriction followed by nutrient realimentation during period of increase nutrient supply can be used to improve efficiency of energy utilization (Freetly et al., 2008).

Livestock are expected to survive, grow, reproduce, and cope in dynamic and unpredictable weather patterns that create diverse environmental challenges or a combination of challenges. However, if adaptive, flexible management is not utilized, static management in the face of a dynamic problem will not yield the most favorable long-term results. With that being said, adaptive management is similar to the "bend but don't break" philosophy. You allow a defined amount of stress to elicit an increased capacity to respond positively to the stress. With dynamic swings in environmental conditions, exploiting the natural ability of livestock to adapt in response to periods of nutrient imbalances may be an alternative strategy to manipulating the production environment. Implementing this approach may subsequently enhance adaptive capacity to environmental stresses, while increasing economic and biological efficiency. Flexible and opportunistic strategies are necessary for successful management in variable environments. Successful strategies have to be engrained in a clear understanding of the challenges facing the grazing animal and its natural abilities to meet and adapt to these challenges.

To recap the range cows' ability to learn, intertwine into social groups and have an elevated level of physical fitness all come together to help a grazing ruminant better adapt to the environment, and ultimately increase the efficiency of production. Some questions that need to be considered to assess the extensive range livestock production systems include: 1) Does the current grazing animal have the proper phenotypes needed to be successful in the current environment, 2) Are management decisions implemented providing the best opportunity for range livestock to meet expected production goals, lastly 3) What criteria can be used to select animals that are properly suited for a specific environment and production system.

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