DORMANT SEASON GRAZING OF NORTHERN MIXED GRASS PRAIRIES: EFFECT OF SUPPLEMENTATION AND WINTER ENVIRONMENTAL CONDITIONS ON BEEF CATTLE GRAZING BEHAVIOR, RESIDUAL VEGETATION CONDITIONS AND VARIATION IN SUPPLEMENT INTAKE

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ABSTRACT

Dormant season grazing reduces reliance on harvested feeds, but typically requires protein supplementation to maintain animal performance and vegetation utilization across the landscape. However, information relating supplementation strategies and supplement intake behavior to individual grazing behavior and resource utilization on dormant forage is lacking. Thus, the intent of this research is to examine cattle resource utilization, supplement intake behavior, residual cover of vegetation and utilization on rangelands grazed during the dormant season. One hundred weaned heifer calves were randomly selected and placed into one of two supplementation treatments in each of 2 years (50 heifers/treatment/year); one receiving a free access 62% crude protein self-fed mineral/protein concentrate, and the other receiving a daily hand-fed 20% crude protein cake while grazing December through March. Additionally, a commercial herd of 300 bred cows ranging in age from 1- to 12-yr-old were provided a 30% crude protein self-fed supplement with 25% salt to limit intake in a SmartFeed Pro self-feeder system to measure individual animal supplement intake from November to January in each of 2 years. In both grazing trials, transects were randomly located within each pasture for measuring vegetation composition, production and quality, canopy cover and visual obstruction readings pre and post grazing. Grazing locations were monitored for individuals with Global Positioning System collars containing head position sensors that record daily space use and location of grazing activities. Data sets were used to quantify space use with generalized linear models to assess cattle resource utilization and supplementation behavior. Cattle provided the hand-fed cake selected grazing location near supplement delivery sites and spent less time grazing per day than self-fed supplemented cattle. Substantial amounts of herd-level variability in both studies suggests individual attributes are major drivers in cattle resource use. Supplement treatment and grazing intensity had little impact on residual vegetation conditions, however, the timing of grazing and year did affect the response of residual vegetation to grazing. Younger cattle consumed more supplement with less variability than older aged cattle. This research provides multidimensional insight to stakeholders concerning grazing behavior and the ecological impacts of late season use on Montana rangelands.

INTRODUCTION AND LITERATURE REVIEW

Beef cattle production on Montana ranches accounted for $1.78 billion of gross income and 42% of Montana's total agricultural sales in 2012 (USDA-NASS 2016). Montana cattle operations are primarily cow-calf production systems that rely heavily on forages to supply nutrients for both cows and calves (Galyean and Goetsch 1993). High feed and input costs have caused an increased concern in the efficiency and profitability of cattle production in all sectors of the beef cattle industry (Meyer and Gunn 2015). To improve profitability, many cow/calf producers have adopted management strategies involving dormant season grazing that minimize costs involved in feeding harvested forage (Adams et al. 1996). The primary goal in a forage-based livestock production system is to obtain optimal animal performance while effectively utilizing the forage resource base. Dormant range forage is deficient in nutrients and may result in decreased performance (Krysl and Hess 1993, Bowman et al. 1995, Mulliniks et al. 2013b). Providing supplements to grazing beef cattle during times of low forage quality can improve animal performance and provide increased economic returns (DelCurto et al. 2000). In addition, supplementation has been used with traditional livestock management to increase distribution of livestock grazing and uniform utilization across the landscape (Fuhlendorf and Engle 2001).

Although dormant forage tends to be more tolerant of grazing (Petersen et al. 2014), evidence suggests winter grazing can actually reduce vegetation production (Willms et al. 1986, Bullock et al. 1994, Petersen et al. 2014). Removal of vegetation and litter cover reduces soil organic matter and exposes soil to direct raindrop impact allowing for potential increases in erosion and runoff (Greene et al. 1994). Additionally, vegetation composition and structural heterogeneity are key habitat characteristics that influence wildlife species diversity and ecosystem function (Christensen 1997, Wiens 1997, Fuhlendorf et al. 2009). Heterogeneity of vegetation stature, composition, and biomass serve as precursors to biological diversity at most levels of ecological organization and have been proposed as the foundation of conservation and ecosystem management (Christensen 1997, Wiens 1997, Fuhlendorf and Engle 2001). However, little is known about the effects of supplementation on winter grazing behavior by beef cattle and the potential impact of dormant season grazing on residual vegetation and rangeland sustainability (Judkins et al. 1985, Krysl and Hess 1993, Schauer et al. 2005).

Ecological impacts due to grazing pressures from livestock continue to be topics of discussion and concern by ecologists and land managers. Domestic livestock may alter ecosystem processes by reducing the cover of herbaceous plants and litter, disturbing and compacting soils, reducing water infiltration rates, and increasing soil erosion (Belsky and Blumenthal 1997). The potential for ecosystem process alteration suggests that grazing plays an influential role in the ecological function of grassland communities. This makes it imperative for managers to understand grazing behavior and its application on the landscape.

Environmental Factors that Influence Grazing Behavior and Distribution

The distribution of use by cattle is dependent on a multitude of physical and environmental factors winthin a pasture (Coughenour 1991). Patterns of herbivory are constrained by spatial variation in topography and water (Coughenour 1991). For instance, distance from water and topographical constraints typically determine distribution of cattle on the landscape (Allred et al. 2011, Kohl et al. 2013). Cattle typically will not use areas ≥ 3.2-km from a water source (Kohl et al. 2013) or slopes ≥ 11° (Gillen et al. 1984, Van Vuren 2001). The costs to travel to water are increased on steeper slopes such that vertical distance above water affects cattle use (Roath and Krueger 1982). Therefore, topography and preferred grazing areas define cattle movement by determining the location of trails and grazing paths (Weaver and Tomanek 1951) resulting in the overall distribution of grazing activities across the landscape.

Cattle are central place foragers, meeting their energetic needs with least over all costs (Van Vuren 2001). Additionally, beef cattle partition their time between grazing, rumination and resting with a maximum grazing time limited to approximately 12 hours a day (Stobbs 1975). Thus, cattle grazing locations are highly influenced by spatial and temporal patterns in the quantity and quality of forage (Senft et al. 1985, Smith et al. 1992). However, as forage availability declines, the association between herbage mass and animal response increases. This association results from a limited ability to compensate declining forage availability with increased grazing time (Allden and McDWhittaker 1970, Freer 1981, Forbes and Coleman 1987). Additionally, traveling and search time influences the energy requirements of grazing livestock (Walker et al. 1985). The energetic costs associated with travel can increase maintenance requirements from 10 – 25% in grazing animals (Ribeiro et al. 1977, Havstad and Malechek 1982).

Thus, time spent grazing and distance traveled can have considerable impact on animal production.

Winter grazing typically exposes cattle to periods of severe cold which increases potential for heat loss exceeding that normally lost in animal metabolism (Webster 1970). Chronic cold exposure results in an increased resting metabolic rate associated with increased resting metabolic heat production (Young and Christopherson 1974, Beverlin 1988). Under such conditions a point is reached that requires animals to draw upon energy reserves, that could otherwise be used for growth to maintain homeothermy (Webster 1971). In addition, at cold temperatures wind induces a higher metabolic rate and heat production (Webster 1970, Christopherson et al. 1979). Increased energy demands during winter conditions results in animals altering their behavior by decreasing their grazing time and total energy expended on other activities (Brosh 2007). Thus, winter conditions can have considerable economic impacts on the energetic efficiency of cattle production on rangelands (Webster 1970).

Short-term behavioral responses may be critical to the energy balance of domestic animals under extreme weather conditions (Senft and Rittenhouse 1985). Temperature can influence livestock grazing behavior by causing animals to select for grazing locations and grazing times that provide the least amount of temperature stress (Holechek and Vavra 1983, Parsons et al. 2003). Topography affects the microclimate experienced by animals through the orientation to the sun and prevailing winds (Senft et al. 1985). Animals are capable of seeking out these microclimates to reduce their exposure to cold temperatures and wind (Beaver and Olson 1997). However, animals must regulate this behavior so that it does not conflict with obtaining food (Ingram and Dauncey 1985). In a landscape that consists of a range of available microclimates and forage resources animals may be able to graze more efficiently (Osuji 1974, Malechek and Smith 1976).

The Influence of Supplementation on Grazing Behavior and Distribution

Grazing livestock are often supplemented to make up for limited forage availability or nutrient deficiencies (Horn and McCollum 1987, Galyean and Goetsch 1993, Bowman and Sanson 1996). Supplementation alters the nutrient status of the animal which can have strong influences on grazing behavior (Allison 1985, Adams et al. 1986). It is likely that grazing behavior may vary with protein supplementation strategies and efficiency in dormant-season grazing systems (Murden and Risenhoover 1993, Odadi et al. 2013). The act of supplementation alone can alter grazing distribution on rangelands (Ares 1953) and daily grazing activities (Adams 1985), further altering the distribution of vegetation use based on timing and location of supplements. When cattle consume forages as their only energy souce, intake of available energy may not be adequate to meet desired rates of animal performance (Moore et al. 1998). Grazing animals have been estimated to expend 46% more energy than stall fed cattle (Havstad and Malechek 1982). Thus, during times of poor forage quality, cattle may require additional energy to meet the demands associated with searching for food and grazing activities. Additionally, overall energy cost for grazing activities increases as diet quality and energy intake decreases (Brosh 2007). Traditionally, concentrate feeds (cereal grains) high in non-structural carbohydrates were used to supplement energy on dormant forage diets, however, it has been found that supplements high in non-structural carbohydrates depress intake and digestibility of low quality forages (Chase and Hibberd 1987, Cordes et al. 1988, Sanson and Clanton 1989, Sanson et al. 1990, Olson et al. 1999, Bodine and Purvis 2003, Bowman et al. 2004). Dormant range forage is deficient in crude protein (< 7%) and limits voluntary dry matter intake by cattle (Krysl and Hess 1993, Bowman et al. 1995). Protein supplementation can increase intake of low quality forage, digesibility and animal performance when the forage TDN:CP ratio is >7 (deficit of N relative to available energy; Moore et al. 1998).

Supplement form and delivery method can have tremendous impacts on forage intake (Bowman and Sowell 1997), which may be reflected in animal performance, grazing behavior and pasture use. Self-fed protein supplements have been shown to improve cattle distribution on rangelands (Ares 1953, Aubel et al. 2011), while hand-fed supplementation can disrupt daily grazing activities (Adams 1985). Concentrated protein supplements provide little to no carbohydrates for energy, suggesting animals will have to graze to meet energy demands. High fiber by-products containing low levels of nonstructural carbohydrates, such as soybean hulls and wheat middlings, are highly digestible, relativily high in degradable protein, and have been shown to increase use of low quality forage and improve weight gains of cattle (Ovenell et al. 1989, Martin and Hibberd 1990, Chan et al. 1991, Ovenell et al. 1991, Horn et al. 1995). However, by-product supplements provide a portion of the animals energy demands, suggesting less of a reliance on dormant range forage for energy. Thus, variability in forage demands resulting from protein supplement form and supplementation delivery method may affect animal behavior and performance. However, little is known about the effects of crude protein supplementation on grazing behavior and its potential effects on vegetation and rangeland sustainability (Judkins et al. 1985, Krysl and Hess 1993, Schauer et al. 2005).

The reported effectiveness of supplementation programs on grazing cattle performance has been inconsistent (DelCurto et al. 1990), likely due to variation in supplement intake by individual cows. In order to meet the nutritional needs and maintain a desired level of productivity, supplemental protein is often provided to increase forage intake, dry matter digestibility (Lusby et al. 1967), and body weight gain (Bowman et al. 1995, Bodine et al. 2001). Supplementation strategies during winter grazing assume that all animals consume a targeted quantity of supplement (Bowman and Sowell 1997). Variation of supplement intake by individual animals and the potential problems associated with supplementation not occuring at targeted amounts is often ignored. If animals consume less than the target amount, the formulated nutrient intake is not received, increasing the potential for nutrient stress. Animals consuming over the targeted amount increase supplementation costs and the potential for negative impacts on forage intake and digestibility (Bowman and Sowell 1997). Deviation from the targeted consumption of supplement can have strong effects on animal nutrient status (Bowman and Sowell 1997), likely reflected in animal performance and grazing behavior.

The Effect of Cow Age on Grazing Behavior and Distribution

Cow age has been shown to be an influential factor effecting supplement intake, foraging behavior and distribution (Adams et al. 1986, Kincheloe et al. 2004, Walburger et al. 2009). Older cattle are presumably more familiar with terrain and trails to efficiently gain access to foraging locations, making older cattle more likely to graze steeper slopes, higher elevations, and areas farther from water than younger cattle (Roath and Krueger 1982, Bailey 2005, Walburger et al. 2009). Younger, inexperienced cattle are typically unfamiliar with the terrain and foraging areas, resulting in increased travel and less time spent grazing than older cattle (Bryant 1982, Adams et al. 1986, Bailey et al. 2001). Social dominance within a cow herd is often associated with age (Wagnon 1965, Arnold and Maller 1974, Friend and Polan 1974). Older dominant cattle typically consume more supplement (Bowman et al. 1999, Sowell et al. 2003, Kincheloe et al. 2004) and are less variable in their daily supplement intake than younger cows (Bowman et al. 1999). However, the interactions of environmental factors and individual animal age and supplement intake on grazing behavior and distribution are less understood (Walburger et al. 2009).

Low Input Heifer Development

Heifer development is essential to the productivity and longevity of a cow/calf operation and typically results in additional feed costs to augment diets for sufficient gains to achieve puberty before breeding (Roberts et al. 2009, Mulliniks et al. 2013a). It has been recommended heifers reach approximately 65% of mature body weight before breeding (Patterson et al. 1992). This is typically achieved by providing optimal postweaning nutrition, ensuring heifers reach a target prebreeding weight that supports ideal reproductive performance (Patterson et al. 1992). However, high feed costs have caused producers to adopt low input management strategies that minimize costs associated with providing harvested feeds (Adams et al. 1996). Late season forage quality corresponding to fall weaned heifers is typically low in quality and may put animals in a state of negative energy balance (Mulliniks et al. 2013b). Protein supplementation while grazing dormant range can enhance heifer growth, improve pubertal status at breeding and reproductive performance (Stalker et al. 2006, Martin et al. 2007). Thus, developing heifers on poor quality forages may require considerable supplementation of nutrients in order to achieve target bodyweight and reproductive efficiency (Horn and McCollum 1987, Galyean and Goetsch 1993, Bowman et al. 2004, Mulliniks et al. 2013a). However, information evaluating supplementation strategies on grazing behavior and distribution of weaned heifer calves is lacking.

Potential Impacts of Grazing on Vegetation Characteristics

Domestic livestock grazing can alter ecosystem processes by altering vegetation composition, reducing the cover of herbaceous plants and litter, disturbing and compacting soils, reducing water infiltration rates, and increasing soil erosion (Fleischner 1994, Belsky and Blumenthal 1997, Milchunas et al. 1998, Krueger et al. 2002). Although it is generally accepted that late season grazing of dormant forage has limited impact on plant health and vigor (Petersen et al. 2014), evidence suggests winter grazing can actually reduce plant production the following growing season resulting in potential changes in species composition (Willms et al. 1986, Bullock et al. 1994, Petersen et al. 2014). Thus, even in a dormant state, grazing may play an influential role in the ecological function of grassland communities. The effects grazing has on ecological function of grassland communities makes it imperative for managers to understand grazing behavior and its application on the landscape. Herbivores act as a chronic disturbance agent by altering the pathway of succession (Joern and Keeler 1995, Hobbs 1996, Riggs et al. 2000). Grazed plants can be put at a competitive disadvantage to non-grazed plants potentially resulting in a change in plant community composition along with a reduction in overall plant production and/or overall plant nutritive quality (Fleischner 1994, Walker 1995, Krueger et al. 2002). These changes in ecosystem processes, in turn, may be related to a loss in vegetation and wildlife diversity. Because forage type is a main driver of grazing behavior, it is critical to understand the interaction of grazers and vegetation community utilization, cover and structure within a pasture rather than the utilization of the pasture as a whole. This is not only relevant for cattle production but also for land management since selective herbivory can have direct and indirect influences on vegetation communities (Riggs et al. 2004).

Conclusion

The spatial component of herbivory is a central aspect of domestic livestock ecosystems, but has remained difficult to interpret (Coughenour 1991). Topography, thermal environments and forage resources, such as standing crop and nutritional quality, interact to determine an animal’s location (Beaver and Olson 1997). Distribution of livestock use has been shown to be restricted by physical characteristics of the landscape (Roath and Krueger 1982, Gillen et al. 1984, Coughenour 1991, Van Vuren 2001, Allred et al. 2011, Kohl et al. 2013), and potentially further restricted due to the increased energetic costs of grazing under winter conditions. This brings into question the energetic efficiency of livestock grazing on rangelands under winter conditions. Protein supplementation generally improves the nutrient status of the animal (Allison 1985). Nutritional status can have strong influences on grazing behavior that may vary with protein supplementation strategies and efficiency in dormant-season grazing systems (Murden and Risenhoover 1993, Odadi et al. 2013). Additionally, the act of supplementation alone can alter grazing distribution and behavior on rangelands (Ares 1953, Adams 1985), potentially altering the distribution of vegetation use and subsequently residual cover and structure imperitive for ecological integrity and habitat for wildlife (Fuhlendorf and Engle 2001). However, little is known about the effects of crude protein supplementation on grazing behavior, utilization of native forage and its potential long-term effects on sustainability (Judkins et al. 1985, Brandyberry et al. 1991, Krysl and Hess 1993, Schauer et al. 2005). Combination of supplementation strategy, topography, winter weather, and individual animal attributes (e.g. age and supplement intake) may influence grazing behavior and have significant implications in livestock, wildlife and land management.

The general influence of environmental factors such as slope, aspect, forage production, and distance to water on cattle distribution have been well documented in previous research (Mueggler 1965, Roath and Krueger 1982, Senft et al. 1985, Ganskopp and Vavra 1987, DelCurto et al. 2005, Walburger et al. 2009). However, interactions of these environmental factors with animal attributes and protein supplementation on dormant range is less understood. Our research evaluates protein supplementation, supplementation strategy, environmental factors and individual animal attributes on grazing behavior and distribution and how dormant season grazing impacts residual vegetation conditions on rangelands in the northern mixed grass prairie. In Chapter 2, we evaluate the effects of protein supplementation strategy on dormant season grazing behavior and resource use of weaned heifer calves and how dormant season grazing impacts residual vegetation conditions. In Chapter 3, we evaluate the effects of individual animal attributes (e.g. age and supplement intake) on grazing behavior and resource use by a mixed-aged cow herd on dormant season rangelands and the effects of grazing intensity on residual vegetation conditions. In Chapter 4, we evaluate the effects of cow age and winter weather conditions on protein supplement intake and behavior for a mixed-aged cow herd grazing dormant season rangelands. In Chapter 5, we provide an overall conclusion from our research and discuss how our results can contribute to future studies of grazing behavior or be utilized in cattle and land management on rangeland in the northern mixed-grass prairie.

CHAPTER TWO

DORMANT SEASON GRAZING OF NORTHERN MIXED GRASS PRAIRIES: THE EFFECT OF SUPPLEMENTATION STRATEGIES ON HEIFER RESOURCE UTILIZATION AND VEGETATION USE

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CHAPTER TWO

DORMANT SEASON GRAZING OF NORTHERN MIXED GRASS PRAIRIES: THE EFFECT OF SUPPLEMENTATION STRATEGIES ON HEIFER RESOURCE UTILIZATION AND VEGETATION USE

INTRODUCTION

Heifer development is essential to the productivity and longevity of a cow/calf operation and typically results in additional feed costs to ensure heifers reach a target prebreeding weight that supports ideal reproductive performance (Patterson et al. 1992, Roberts et al. 2009, Mulliniks et al. 2013a). However, high feed costs have caused producers to adopt low-input management strategies that minimize costs associated with providing harvested feeds (Adams et al. 1996). Late season forage corresponding to fall weaned heifers is typically low in quality, potentially putting animals in a state of negative energy balance (Mulliniks et al. 2013b). Protein supplementation while grazing dormant range can enhance heifer growth, improve pubertal status at breeding and reproductive performance (Stalker et al. 2006, Martin et al. 2007). Thus, developing heifers on poor quality forages may require considerable supplementation of nutrients in order to achieve target bodyweight and reproductive efficiency (Galyean and Goetsch 1993, Bowman et al. 2004, Mulliniks et al. 2013a).

One of the primary goals of a forage-based livestock production system is to obtain optimal animal performance while effectively utilizing the forage resource base. Thus, the spatial component of herbivory is a central aspect of domestic livestock ecosystems (Coughenour 1991). Topography, thermal environments and forage resources (e.g. standing crop and nutritional quality), interact to determine space use (Jamieson and Hodgson 1979, Adams et al. 1986, Beaver and Olson 1997). Providing a supplement alters the nutrient status of animals which can have strong influences on grazing behavior (Allison 1985, Adams et al. 1986). Supplementation changes grazing distribution on rangelands (Ares 1953, Bailey et al. 2001) and daily grazing activities (Adams 1985), altering the distribution of vegetation use based on timing, delivery method and location of supplements. Therefore, it is likely that grazing behavior may vary with protein supplementation strategies and efficiency in dormant-season grazing systems (Murden and Risenhoover 1993, Odadi et al. 2013).

Dormant forage is often perceived to be more tolerant of grazing pressure (Petersen et al. 2014), however, improperly managed dormant season grazing can have detrimental effects on vegetation production and residual cover (Willms et al. 1986, Bullock et al. 1994, Petersen et al. 2014). Vegetation composition and structural heterogeneity are key habitat characteristics that influence wildlife species diversity and ecosystem function (Wiens 1997, Bailey et al. 1998, Fuhlendorf et al. 2009). Habitat structural heterogeneity is recognized as a precursor to biological diversity at most levels of ecological organization and is proposed to be the foundation of conservation and ecosystem management (Christensen 1997, Wiens 1997, Fuhlendorf and Engle 2001). Western rangelands are inherently heterogeneous as vegetation composition and structure vary with topographic and edaphic features (Patten and Ellis 1995, Fuhlendorf and Smeins 1998, Fuhlendorf et al. 2006). However, traditionally supplementation has been used to alter grazing distribution and promote uniform vegetation utilization across the landscape (Bailey and Welling 1999). Management strategies that promote uniform utilization of vegetation results in the homogenization of rangeland landscapes and an overall decline of ecosystem structure, function and biodiversity (Derner et al. 2009, Fuhlendorf et al. 2009, Hovick et al. 2015). Maintaining heterogeneity of vegetation composition and structure in rangelands is beneficial to ecological biodiversity (Fuhlendorf et al. 2006). However, little is known about the effects of supplementation strategies on winter grazing behavior of heifers and the potential short-term impacts on residual vegetation composition, structure and heterogeneity.

Information relating supplementation strategies to individual grazing behavior by heifers and vegetation use on dormant forage is lacking. Thus, the specific objectives of this study were to evaluate how two different protein supplementation strategies during the dormant grazing season influence (1) grazing activity and resource utilization by heifers, and (2) residual vegetation cover, structure and heterogeneity. We expected dormant season grazing by supplemented livestock to have multi-faceted effects on agroecosystems in northern mixed grass prairies. System-level impacts are likely mediated by the provision of supplement, as well as, uncontrolled environmental conditions.

METHODS

This study was conducted at the Ft. Keogh Livestock and Range Research Laboratory near Miles City, Montana (46º 22' N 105º 5' W). Climate is characterized as continental and semi-arid with an average annual pecipitation of 338 mm, 60% of which occurs during the 150-day growing season (mid-April to mid-September). Vegetation is dominated by western wheatgrass [*Pascopyrum smithii* (Rydb.) Love]), threadleaf sedge [*Carex filifolia* Nutt.], needle and thread [*Stipa comata* Trin. and Rupr.] and blue grama [*Bouteloua gracilis* (H.B.K.)]. Our study occurred during the winter grazing seasons of 2015–2016 and 2016–2017. Preciptiation for both winters was similar (2.77, 2.92 cm), however, temperatures durring the 2016–2017 winter were substantially cooler than the winter of 2015–2016 (-4.85, 0.26 °C), resulting in higher amounts and prolonged periods of snow in the second year of the study (Table 1).

Appoximately 100 weaned composite heifer calves (50% Red Angus, 25% Charolais, 25% Tarentaise) were stratified by weaning weight and alloted into one of two supplementation treatments (50 heifers per treatment) while grazing late season dormant native range. Supplement treatment groups were separated by paddocks ranging in size of 56 to 80 ha. Six paddocks with similar stocking rates (~1.3 ha/AUM), topography, vegetation composition and range condition were oriented in a wagon wheel configuration at the study site. Grazing for both treatments occurred simultaneously beginning in December and continuing until the following spring green up. Paddocks were rotated throughout the winter grazing trial resulting in three winter grazing time periods (time period 1: December – mid-January, time period 2: mid-January – February, and time period 3: March – mid-April). Supplementation treatments were alternated in each paddock every other year, so that each treatment supplement group grazed each paddock once in the two year study period. One treatment group received a 62% crude protein (as-fed) self-fed mineral/protein concentrate with 35% mineral and salt (hereafter "protein"), and the other group received a daily hand-fed 20% crude protein (as-fed) cake (hereafter "cake"). The protein group was allowed free access to the supplement located at the center of the paddock wagon wheel configuation in close proximity to water. The cake group was supplemented daily at 1000h, hand-fed on the ground in bulk at ca. 1.8 kg/head in the approximate area where cattle had access to water and consume mineral.

Sampling

We established thirty, 30-m transects randomly within each paddock. We measured vegetation production, canopy cover and visual obstruction readings (VOR) at six 0.1-m^2 plots located every five meters along each transect. Canopy cover of plant functional groups (grass, forb, shrub), cover of bare ground and litter were estimated at each plot using the six cover class Daubenmire method (Daubenmire 1959). Ground cover of plant functional groups, bare ground and litter have all previously been found to influence the abundance and demography of grassland birds, who serve as indicator species for grassland ecosystems (Bock and Webb 1984, Bradford et al. 1998, Derner et al. 2009). Visual obstruction readings were measured in four cardinal directions using a 1-meter Robel pole (Robel et al. 1970). Visual obstruction is typically correlated with aboveground biomass and represents a measure of the vertical structure and density of vegetation (Robel et al. 1970, Damiran et al. 2007). All measurements were taken pre- and post-grazing prior to spring green up to evaluate how supplementation strategy affected residual vegetation structure across the paddocks. Pre-grazing vegetation functional group production was estimated using the dry weight rank method and clipping each plot (Mannetje 1963, Dowhower et al. 2001). Clipped samples were placed in a forced air oven at 60°C for 48 hours and then weighed. Pre-grazing samples from each paddock were composited by transect and ground to pass a 1-mm screen in a Wiley mill. Samples were then analyzed in duplicate for nitrogen (Leco CN-2000; Leco Corporation, St. Joseph, MI), and fiber (NDF and ADF; Ankom 200 Fiber Analyzer, Ankom Co., Fairport, NY) as indicators of vegetation quality (Table 2).

We monitored cattle grazing activity using Lotek GPS collars (3300LR; Lotek Engineering, Newmarket, Ontario, Canada) containing head position sensors that recorded daily timing and locations of grazing activities (Turner et al. 2000, Ungar et al. 2005, Brosh et al. 2010). Heifers within each treatment were stratified by bodyweight then randomly selected for GPS collars (7 collars/treatment) with new animals selected every 28 days to minimize autocorrelation in responses among grazing periods. GPS data were used for each supplement treatment to evaluate the effects of supplementation strategy on animal grazing activity (Ungar et al. 2005, Brosh et al. 2010, Valente et al. 2013). Each collar was configured to record GPS positions, head position and vertical/horizontal movements at 5-minute intervals. Each collar stored the percentage of time the head position sensor registers in the down position (grazing activity) for each sampling period. We then used the binary classification methods developed by Augustine and Derner (2013) to separate grazing from non-grazing activities to examine time spent grazing and cattle foraging distribution. Limiting observations to grazing locations allowed us to determine important foraging areas rather than general pasture occupancy (Walburger et al. 2009).

Temperature, wind speed and direction data were collected using a permanent weather station located at the experimental paddocks. Wind speeds at 30-m^2 spatial resolution were predicted across all paddocks using average daily wind measurements collected on site, ArcGIS spatial analyst tool, a digital elevation model at 30-m^2 resolution, and WindNinja wind prediction software (Brooks 2012). In addition, HOBO Pendant® Temperature/Light Data Logger (Onset Computer Corporation, Bourne, MA) were deployed at each randomly-selected transect location within each paddock and programmed to collect ambient temperature every 30 minutes. Fine-scale ambient air temperature was modeled using the collected temperature data set and generalized linear models to evaluate the effects of physical properties (e.g., aspect, elevation and slope) on fine-scale temperature of the paddocks. Model results were used to create spatially-explicit predictions of temperature and wind conditions across each paddock, which were used as covariates in subsequent resource utilization modeling.

All supplementation and water locations were located via handheld GPS (spatial error < 10 m). Using the spatial analysis tool in ArcGIS (Environmental Systems Research Institute, Redlands, CA) and a digital elevation model at 30-m^2 resolution (USGS 2017), we created additional spatial covariate layers representing slope, aspect, and horizontal and vertical distance from supplement locations at 30-m^2 resolution.

Statistical Analysis

To evaluate the effects of supplementation strategy on vegetation functional group cover and visual obstruction, we calculated the differences in average vegetation measurements collected before and after grazing at each transect for each treatment paddock in each year. The effects of supplementation treatment on patch level heterogeneity of functional group vegetation cover and VOR was obtained by subtracting the pre-grazing transect level standard deviation from the post-grazing standard deviation for each treatment paddock within each time period for both years. Due to only one treatment replication per grazing time period and paddocks alternating treatments the second year of the study, year was used as replication of treatment within grazing time period. Therefore, the effects of supplementation strategy on vegetation conditions and time spent grazing were analyzed using mixed-effects ANOVA with a generalized mixed model including treatment, time period, and a treatment by time period interaction as fixed effects with a random intercept of treatment and random slopes effect of year. Data were plotted and log-transformed if needed to satisfy assumptions of normality and homogeneity of variance. An alpha ≤ 0.05 was considered significant.

To model the influence of supplementation treatment on space use, individual GPS-collared heifers in each treatment were defined as the biological unit of interest in modeling grazing resource utilization within paddocks. We quantified space use related to habitat covariates using multiple regression in a resource utilization function analysis (RUF; Marzluff et al. 2004, Winder et al. 2014). Resource utilization functions quantify inter-animal variation in resource use and examines use as a probabilistic and continuous metric, allowing for an increase in sensitivity for detecting resource selection for individuals within each supplementation treatment (Winder et al. 2014). Additionally, RUFs treat individual animals as the experimental unit, incorporating an individual's entire distribution of use, independently, while accounting for spatial autocorrelation of multiple locations per individual and reducing errors associated location estimation and focus on specific locations (Marzluff et al. 2004, Kertson and Marzluff 2010).

Due to cattle home range being confined to paddock management units, GPS collar data were used to build resource utilization models on a third-order scale, defining animal movements and selection of environmental and vegetation conditions within each paddock (Johnson 1980). Using Geospatial Modeling Environment (Beyer 2010) we created a raster representing the period-specific utilization density distribution for the grazing locations of individuals in each paddock. Relative use values were bounded between 1 and 99, for each 30 m^2 cell based on the relative volume of utilization distribution (Marzluff et al. 2004). Environmental covariates expected to influence heifer resource utilization included temperature, wind, distance to supplement (vertical and horizontal), supplementation treatment, slope and aspect, annual forage production and quality expressed as CP, NDF and ADF. Environmental covariates and individual relative use rasters were stacked and converted to spatially explicit data files using the 'raster' function in R, as an input for the ruf.fit package (Kertson and Marzluff 2010). Individual relative use values were log-transformed prior to modeling to meet the assumptions of multiple regression models. Using the ruf.fit package in R, resource utilization functions with standardized β coefficients were generated and evaluated for each individual in both treatment groups for each time period to represent the influence of the environmental covariates on heifer resource utilization (Marzluff et al. 2004, Kertson et al. 2011).

To develop treatment level inferences, we calculated mean standardized $\hat{\bar{\beta}}$ coefficients and a population-level variance that incorporated individual animal variation for each environmental covariate by supplementation treatment and time period (Marzluff et al. 2004). Standardized coefficients with 95% confidence intervals that do not overlap zero are considered significant predictors of space use (Marzluff et al. 2004, Winder et al. 2014). If a resource utilization coefficient is significantly different from zero, we inferred that resource use was greater or less than expected based on availability of the resource within the treatment paddock (Marzluff et al. 2004, Winder et al. 2014).

A primary step in RUF analyses is to overlay spatially-explicit utilization distributions of individuals (e.g., heifers) onto geo-referenced rasters representing spatially-explicit estimates of covariate values across the entire study area (Marzluff et al. 2004, Kertson and Marzluff 2010, Winder et al. 2014). Unfortunately, spatially-continuous estimates of vegetation composition, production and quality were not available at appropriate spatial resolution for our entire study area. Therefore, the relative resource use value predicted for each individual was extracted at each transect location and paired with the corresponding vegetation measurements. To avoid overfitting our resource utilization models, we conducted a preliminary multicollinearity analysis to select uncorrelated ($|r| > 0.6$) variables that are ecologically relevant and feasible to measure (Dormann et al. 2013). If two covariates were correlated, we fitted preliminary resource utilization models and evaluated relative support of each variable using Akaike's Information Criterion adjusted for small sample sizes (AIC_c, Burnham and Anderson 2002); we retained the variable with more relative support for further modeling and discarded the correlated variable (Fieberg and Johnson 2015).

We evaluated the effects of vegetation (e.g., production, composition and quality) and supplement treatment on relative use using generalized linear mixed models with a Gaussian (normal) error structure and individual animal as a random effect. We used AIC_c to evaluate support for competing models reflecting hypotheses about the effects of various vegetation attributes and supplement treatment on relative use by heifers (Burnham and Anderson 2002). Models with $\Delta AIC_c \leq 2$ that differed from the top model by a single parameter were excluded if confidence intervals of parameter estimates overlapped 0 (ie., were non-informative; Arnold 2010). Model fit was then evaluated by calculating marginal and conditional r^2 values for generalized linear mixed models (Nakagawa and Schielzeth 2013). All statistical analyses were performed in R (R Core Team 2017).

RESULTS

Grazing behavior and space use

Average daily time spent grazing varied across treatments and time periods ($P <$ 0.01). Cattle supplemented with concentrated protein spent more time grazing than cattle supplemented with cake (6.92 ± 0.18, 6.24 ± 0.17 hr; Figure 1). Additionally, both treatments spent more time grazing durring time period 3 (7.64 ± 0.21hr) than time periods 1 and 2 (6.31 ± 0.20, 6.12 ± 0.18 hr; Figure 1).

We estimated herd-level grazing RUFs from 42 heifers under 2 supplementation treatments during 3 winter time periods (7 heifers/treatment/time period), with an average of 1852 ± 42 grazing locations per individual. Relative resource utilization by grazing heifers in the cake treatment were negatively related to horizontal distance from the supplement feeding location in time period 1 and 2 ($\hat{\beta}$ = -0.41 ± 0.16SE, -0.53 ± 0.17; Figure 2). Relative resource selection by heifers in the protein treatment tended to decrease with distance from supplement during time periods 1 and 2 ($\hat{\beta}$ = -0.22 ± 0.25, -0.39 ± 0.26); however, individual variability in habitat selection resulted in confidence intervals overlapping 0 for the herd-level responses (Figure 3). Low values of relative use coefficients indicate average temperature, wind speed, aspect, slope and vertical distance from supplement had little influence on grazing space use for all time periods for both supplementation groups. However, vertical and horizontal distance from supplement, and temperature were highly variable among individuals as drivers of space use for both supplementation treatments (Figure 3).

The relationship between vegetation composition, production, and quality, supplementation strategy, time period of grazing, and relative resource utilization by heifers were evaluated for the 42 heifers (7 heifers/treatment/time period) using pre-grazing vegetation conditions measured at 180 transect locations (30 transects/paddock) in the study area. A single model containing crude protein (%), standing biomass of perennial grass (kg/ha) and a supplementation strategy by time period interaction had 92% of the relative support of the data (Table 3). Predicted relative resource utilization of grazing heifers for both treatments increased by 5 ± 0.4% with every 100 kg/ha standing biomass of perennial grasses ($\hat{\beta}$ = 0.0005 ± 0.00004; Figure 4). Additionally, for every 1% increase in CP, relative use increased by an average of 12% ($\hat{\beta}$ = 0.12 ±

0.007; Figure 4). The protein concentrate self-fed treatment, tended to have a 43 ± 28% higher overall relative use than the cake supplementation group in time period 1, however, confidence intervals overlap 0, indicating no significant supplement treatment level effects ($\hat{\beta}$ = 0.43 ± 0.28; Figure 4). The effect sizes of relative grazing use for the self-fed protein supplement treatment decreased in time period 2 and 3 ($\hat{\beta}$ = -0.09 ± 0.44, -0.56 ± 0.07). Conversely, relative use for the hand-fed cake treatment increased in time periods 2 and 3 ($\hat{\beta}$ = 0.07 ± 0.28, 0.39 ± 0.05), resulting in similar relative use among treatments in time periods 2 and 3 (Figure 4). The top model had a conditional r^2 of 0.71; however, the marginal r^2 was only 0.07 suggesting the majority of the variation in space use by grazing heifers was explained by individual-level variation.

Vegetation structure and heterogeneity

We found no treatment effects on pre-post grazing differences in mean residual cover of litter, grass, forbs or shrubs ($P > 0.24$; Table 4). However, pre-post differences in mean litter, residual grass, and shrub cover differed among time periods ($P < 0.01$). Litter cover increased after grazing in time period 1 (11.45 ± 2.05%SE), was unchanged after time period 2 (-2.78 ± 1.5%) and was decreased after grazing in time period 3 (-15.28 ± 1.80%; Figure 5). Grass residual cover increased with grazing in time period 1 (7.57 ± 1.98%), decreased in time period 2 (-13.85 ± 1.67%) and further decreased in time period 3 (-35.95 ± 3.06%, Figure 5). Shrubs showed no grazing effect in time period 1 (1.31 ± 0.83%) but slightly decreased in time period 2 and 3 (-1.84 ± 0.83, -1.53 ± 0.68%; Figure 5). Bare ground cover displayed a treatment level effect ($P < 0.01$), where bare ground was decreased 7.29 ± 1.12% with livestock grazing in paddocks treated with protein supplementation but not in paddocks treated with cake (0.17 ± 1.31%; Figure 6). Bare ground cover was also associated with the time period of grazing ($P = 0.02$), decreasing in time period 1 and 2 (-6.88 ± 1.70, -3.42 ± 1.49%) with no effect in time period 3 (-0.89 ± 1.32%; Figure 6). A treatment by time period interaction occurred when evaluating the effects of grazing on visual obstruction ($P < 0.04$). Visual obstruction was significantly reduced by heifers grazing during time period 1 under both supplementation treatments, but only significantly reduced in the cake group during periods 2 and 3 (Figure. 7).

Supplementation treatment did not significantly alter the differences in transect-level standard deviation of vegetation conditions before and after grazing ($P > 0.09$; Table 5). However, the time period during which grazing occurred had significant effects on the pre-post transect level standard deviation of litter, residual grass and shrub cover ($P < 0.01$). Litter transect level standard deviation was increased 3.99 ± 1.19% in time period 1 and was unchanged in time period 2 and 3 (-0.17 ± 0.97%, 0.15 ± 0.96%; Figure 8). Residual grass pre-post transect level standard deviation increased 6.67 ± 1.21% in time period 1, was unchanged in time period 2 (-2.19 ± 1.30%) and decreased 9.23 ± 1.14% in time period 3 (Figure 8). Transect level standard deviation of shrub cover increased 3.22 ± 1.11% in time period 1, decreased 2.87 ± 1.12% in time period 2 and was unchanged in time period 3 (-1.91 ± 1.05%). Visual obstruction transect level standard deviation displayed a supplementation treatment by time period interaction ($P < 0.01$), where in time period 1 both treatments resulted in a net decrease of visual obstruction standard deviation, however, in time period 2 only the cake supplementation treatment resulted in a decrease, with no treatment effects found in time period 3 (Figure 9).

DISCUSSION:

We found that supplementation strategy interacted with time period to influence relative use and grazing behavior of heifers during the winter grazing season. The hand-fed cake supplementation strategy in our study resulted in animals selecting for grazing locations near supplement delivery sites for the first two time periods and an overall decrease in the average time spent grazing per day compared to the self-fed protein concentrate treatment. Our results are consistent with previous research demonstrating that hand-fed supplementation can disrupt daily grazing activities, which influence grazing behavior and result in a decrease in time spent grazing (Adams 1985). Additionally, our top model evaluating the response of relative grazing use to vegetation characteristics indicate that heifers in both supplementation treatments for all time periods increase relative use with increasing crude protein and standing biomass of perennial grasses. These results are similar to previous research where summer grazing cattle on the short grass steppe selected grazing locations based on the relative quantity or quality of available forage (Senft et al. 1985). Most of the differences in behavioral effects among supplementation treatments tended to diminish in time period 3, which may be due to paddock green up prior to the end of the grazing period. Paddock green up results in an increase of both forage availability and quality, which has been shown to reduce reliance on supplementation, possibly due to less competition for a limited nutrient supply (Wagnon 1965, Ducker et al. 1981, Bowman and Sowell 1997).

Although grazing distribution by cattle has been shown to be constrained by spatial patterns in topography (Gillen et al. 1984, Coughenour 1991, Van Vuren 2001, Allred et al. 2011, Kohl et al. 2013) and influenced by extreme weather and temperature conditions (Holechek and Vavra 1983, Senft and Rittenhouse 1985, Beaver and Olson 1997, Parsons et al. 2003), neither were significant drivers in heifer resource use in our study. This may be due to our research paddocks being relatively small ($\bar{x}$=65 ha) with little constraint or variation in weather or topographic conditions (elevation ranging from 750 to 837m; slopes < 25%; temperature variation within and across paddocks < 1.5 °C). Grazing paddocks that consist of a larger range of available microclimates and forage resources may have different results, as previous research suggests thermal environments, topography and forage resources interact to determine an animals location (Beaver and Olson 1997).

Individual animal behavior was a major source of variation in this study, displayed as wide confidence intervals for certain variables in the RUF analysis, and the random effect of individual animal explaining the majority of variation in our top model. Previous research on supplementation and grazing behavior suggests that the nutritional status of the animal can have strong influences on grazing behavior of livestock (Krysl and Hess 1993, Bodine and Purvis 2003, Schauer et al. 2005), and that grazing behavior may vary with individual supplement intake, weight and body condition in dormant-season grazing systems (Allison 1985). Thus, future research should consider evaluating individual level factors, such as, supplement intake, body weight and condition as additional drivers in determining grazing behavior and space use.

We found supplementation strategy had very little overall effect on vegetation cover and heterogeneity within paddocks grazed at similar moderate stocking rates, with the exception of bare ground cover being reduced in paddocks managed with the protein concentrate supplementation. Rather, the time period at which grazing occurred influenced the effect of winter grazing on residual vegetation and habitat conditions. As expected, early winter grazing (December – mid-January) resulted in a decrease in visual obstruction and bare ground cover and increased litter and residual grass cover and heterogeneity of litter and residual grass cover. At the initiation of the grazing trial each year, there was little snow or environmental factors limiting forage availability. Forage availability can have major effects on grazing behavior as it forms the bounds from which the animal selects its diet, thus, high forage availability allows cattle to graze selectively (Marten 1989, Reuter and Moffet 2016). Selective grazing by livestock at moderate stocking rates, as in our study, often promotes within-paddock heterogeneity resulting in paddocks that have areas of light and heavily grazed vegetation (Coughenour 1991, Bailey et al. 1998, Fuhlendorf and Engle 2001, Bailey 2005). Due to cattle having a strong preference for grass, selective grazing may then result in an increase in heterogeneity of residual grass and litter with an overall decrease in visual obstruction and bare ground cover (Vermeire et al. 2004, Augustine and Derner 2015, Bailey et al. 2015).

Grazing during the mid-winter (mid-January – February) reduced visual obstruction, grass and shrub cover and shrub heterogeneity. Heavy snow accumulations may have limited forage availability for prolonged periods of time during both years of the grazing trial (Table 1). Limited forage availability likely caused animals to consume a greater proportion of the less-preferred forage (Marten 1989), and focus grazing efforts in areas where less snow had accumulated or when the snow melted from the site. Grazing durring the mid-winter may reduce grazing selectivity resulting in a reduction in visual obstruction and vegetation cover while reducing shrub herterogeneity but having little effect on other vegetation cover conditions within the paddock. Although bare ground cover was marginally reduced by 3.42 ± 1.49% durring the mid-winter grazing period, it is likely due to sampling error, as other cover classes either decreased or remained unchanged through the grazing time period.

We observed a decrease in litter, grass and shrub cover, as well as, grass cover variability during late-winter to early-spring grazing periods. Early March received heavy snow accumulations for short durations of time, temporarily limiting forage availability, which may explain the slight decrease in shrub cover and a more substantial decrease in grass cover and heterogeneity. Grass is the dominant functional group of vegetation for the experimental paddocks, accounting for approximately 85% of the total vegetative cover. Grass cover is a primary driver of grassland bird use and demography, and residual cover and litter may be the only source of available cover and nesting material available at the beginning of the breeding season (Davis 2005, Fisher and Davis 2010). Compared to early winter grazing, we observed that cattle grazing during the late-winter to early-spring time period under both protein supplementation strategies in this study reduced average litter cover as well as spatial variability of residual grass cover. Management strategies that reduce litter and promote homogenous residual grass cover have previously been associated with declines in nesting success of grassland ground nesting birds (Bowman and Harris 1980), suggesting that the timing, but not the supplementation strategy, of dormant season grazing may have significant impacts on breeding bird habitat conditions.

IMPLICATIONS

We observed high variability in grazing site selection among individual heifers, suggesting, individual-level factors could be the dominant drivers in grazing resource use and behavior. Individual variation in supplement intake has the potential to influence individual animal nutrient status and performance, thus altering grazing behavior and paddock use. Combination of supplement type, variability of intake, weight and body condition, and winter weather may influence grazing behavior and have significant implications in animal and land management. Monitoring daily grazing behavior without accounting for individual level factors may not provide meaningful insight about the complex interrelationships that exist between grazing livestock and their environment. Future research examining the effects of supplementation strategies on grazing behavior and resource use should incorperate individual animal measurements in an attempt to account for individual animal variablity. Understanding the effects of supplementation strategies and variation in supplement intake on animal performance, behavior and paddock use are essential in the development of a cost effective and sustainable heifer development program.

Our research provides evidence that even in winter dormant forage conditions, heifers appear to still select grazing locations based on the relative quantity and quality of available forage. Additionally, supplementation strategy can have an effect on the total time spent grazing per day and grazing resource use durring early and mid-winter (December – February). However, dispite these behavioral differences between supplementation strategies, the time period of when grazing occurred had the largest effects on structural vegetation conditions. The influence of winter grazing on average vegetative conditions, as well as, spatial variability (ie. heterogeneity) appeared to improve in the early-winter, with marginal effects in mid-winter, and negative effects in late-winter early-spring. Thus, grazing in early to mid-winter may promote or have marginal effects on vegetation and habitat heterogenity, whereas grazing in late-winter early-spring could reduce residual vegetation cover and habitat heterogeneity. Previous studies suggest that a heterogeneous approach to grassland conservation is capable of maintaining biodiversity and agricultural productivity simultaneously (Fuhlendorf et al. 2006). However, the management implications of this study should be interpreted cautiously, as universal implementation of rangeland management practices often fail to meet management objectives due to lack of local management considerations.

Table 1. Average winter temperature (low, high, mean; °C), total precipitation (cm) and predicted snow fall (based on temperature and precipitation; cm) for the 2 years of grazing (2015 – 2016, 2016 – 2017) at the Fort Keogh Range and Livestock Research Laboratory, Miles City, MT

	Temperature, °C				
	Low	High	Mean	Precipitation (cm)	Snow[a] (cm)
Year 1	-6.86	6.06	0.26	2.77	27.69
Year 2	-9.90	0.19	-4.85	2.92	43.82

[a]Snow records for Miles City, MT are not recorded, values presented are predictions based on mean temperature and total precipitation (Kyle and Wesley 1997)

Table 2. Average annual production (± SE, kg/ha), Crude Protein (CP ± SE; %), Neutral Detergent Fiber (NDF ± SE; %) and Acid Detergent Fiber (ADF ± SE; %) of the experimental paddocks for the 2 years of grazing (2015 – 2016, 2016 – 2017) at the Fort Keogh Range and Livestock Research Laboratory, Miles City, MT

	Production (kg/ha)	CP (%)	NDF (%)	ADF (%)
Year 1	711.7 (22.2)	7.3 (0.13)	74.4 (0.38)	53.7 (0.37)
Year 2	1130.6 (34.7)	9.1 (0.12)	70.1 (0.36)	45.3 (0.24)

Table 3. Model selection for models evaluating the effects of vegetation quality and production and supplementation strategy on grazing resource utilization of heifers' winter grazing rangeland in 2015 – 2016 & 2016 – 2017 at the Fort Keogh Range and Livestock Research Laboratory, Miles City, MT

Model[b]	K[c]	AICc[d]	ΔAICc[e]	W_i[f]	r^2m[g]	r^2c[h]
Crude Protein + Perennial Grass + Treatment × Time Period	10	7277.96	0.00	0.92	0.07	0.71
Perennial Grass + Crude Protein x Time Period Treatment x Time Period	11	7282.84	4.88	0.08		
Constant (null)	3	7663.16	385.20	0.00		

[a]Only models with Akaike weights (w_i) ≥ 0.01 are presented except for the null model.
[b]Cow is used as a random variable in all models.
[c]K = number of parameters.
[d]Akaike's information criterion adjusted for small sample size.
[e]Difference in Akaike's information criterion adjusted for small sample size compared to the best model.
[f]Akaike weight.
[g]Marginal R^2
[h]Conditional R^2

Table 4. Pre- post differences in mean (SE) visual obstruction and residual cover classifications by supplementation strategy and grazing time period for heifers' winter grazing rangeland in 2015 – 2016 & 2016 – 2017 at the Fort Keogh Range and Livestock Research Laboratory, Miles City, MT

	Cake			Protein			P-Value		
	T1	**T2**	**T3**	**T1**	**T2**	**T3**	**Trt[b]**	**TP[c]**	**Trt × Tp[d]**
VOR[a], cm	-2.70 (0.67)	-3.33 (0.67)	-1.52 (0.67)	-3.61 (0.67)	-1.17 (0.67)	-0.55 (0.67)	0.44	< 0.01	0.04
Bare Ground, %	-3.62 (3.28)	0.10 (3.28)	3.02 (3.28)	-10.13 (3.25)	-6.95 (3.25)	-4.79 (3.25)	< 0.01	0.02	0.95
Litter, %	10.98 (2.57)	-1.09 (2.57)	-11.16 (2.57)	11.92 (3.51)	-4.47 (3.51)	-19.40 (3.51)	0.39	< 0.01	0.20
Grass, %	5.01 (3.23)	-11.51 (3.23)	-31.14 (3.23)	10.15 (3.23)	-16.20 (3.23)	-40.77 (3.23)	0.25	< 0.01	0.07
Forb, %	-5.49 (4.07)	-4.78 (4.07)	-5.72 (4.07)	-8.28 (2.33)	-5.33 (2.33)	-4.30 (2.33)	0.80	0.10	0.10
Shrub, %	0.60 (1.63)	-3.15 (1.63)	-1.11 (1.63)	2.01 (1.22)	-0.54 (1.22)	-1.94 (1.22)	0.68	0.01	0.28

[a]Visual Obstruction Reading
[b]Treatment
[c]Time Period
[d]Treatment × Time Period

Table 5. Pre-post difference in heterogeneity (as indexed by differences in standard deviation (SE) of visual obstruction and residual cover classifications by supplementation strategy and grazing time period for heifers' winter grazing rangeland in 2015 – 2016 & 2016 – 2017 at the Fort Keogh Range and Livestock Research Laboratory, Miles City, MT

	Cake			Protein			P-Value		
	T1	**T2**	**T3**	**T1**	**T2**	**T3**	**Trt[b]**	**TP[c]**	**Trt × Tp[d]**
VOR[a]	-1.34 (0.66)	-3.06 (0.66)	-0.43 (0.66)	-3.19 (0.66)	0.06 (0.66)	0.59 (0.66)	0.16	< 0.01	< 0.01
Bare Ground	2.00 (1.59)	-1.09 (1.59)	1.22 (1.59)	-1.21 (1.59)	-2.00 (1.59)	-1.26 (1.59)	0.09	0.44	0.76
Litter	5.54 (1.53)	-0.14 (1.53)	2.06 (1.53)	2.43 (1.48)	-0.20 (1.48)	-1.76 (1.48)	0.29	0.01	0.40
Grass	6.32 (3.02)	-4.31 (3.02)	-7.24 (3.02)	7.02 (1.87)	-0.08 (1.87)	-11.21 (1.87)	0.91	< 0.01	0.06
Forb	-4.34 (2.43)	-3.77 (2.43)	-3.86 (2.43)	-4.41 (1.08)	-3.94 (1.08)	-4.81 (1.08)	0.86	0.81	0.87
Shrub	2.23 (2.59)	-4.97 (2.59)	-1.99 (2.59)	4.22 (1.65)	-0.76 (1.65)	-1.83 (1.65)	0.60	< 0.01	0.42

[a]Visual Obstruction Reading
[b]Treatment
[c]Time Period
[d]Treatment × Time Period

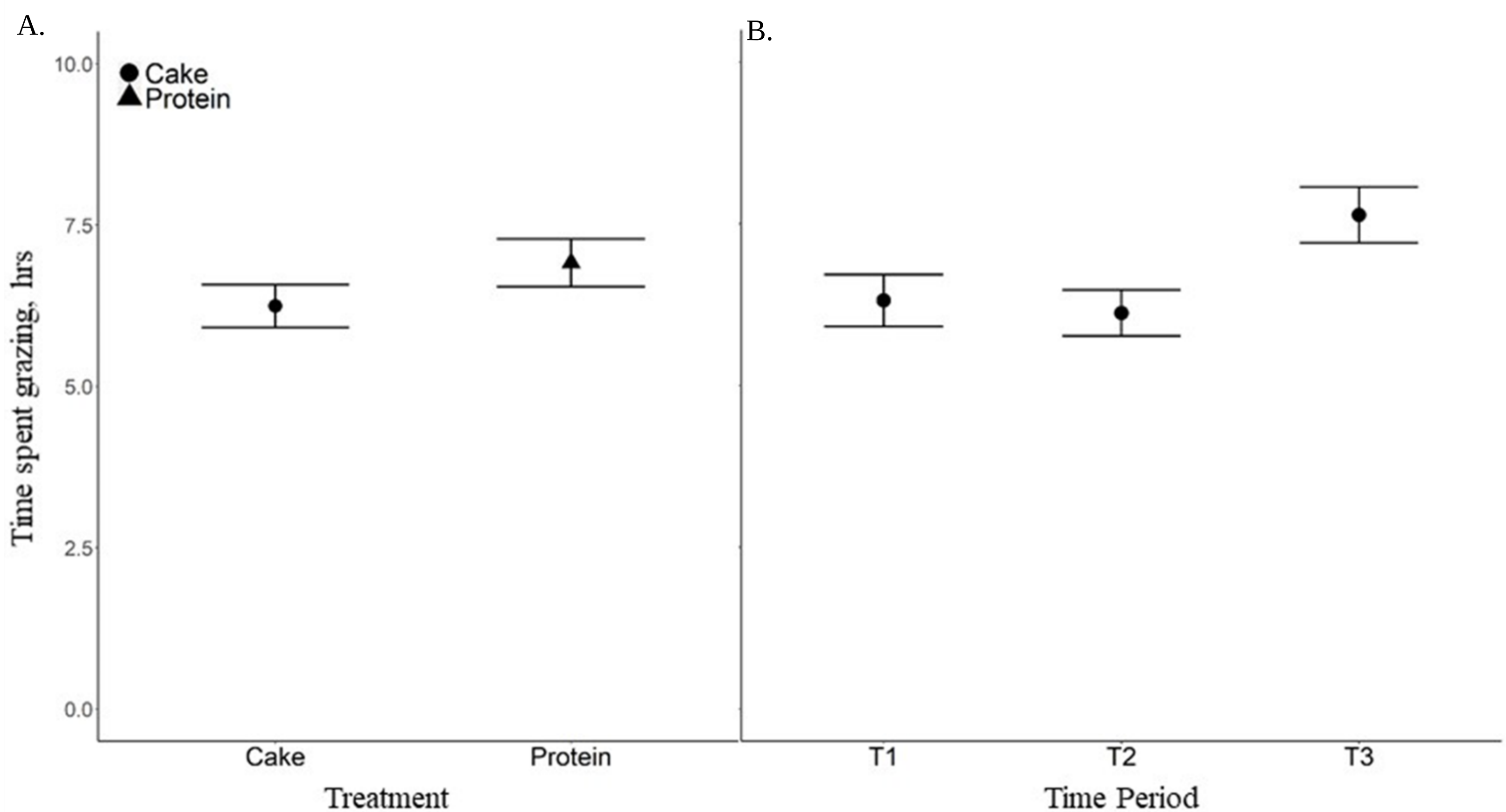

Figure 1. Average time spent grazing per day (hrs; ± 95% CI) by A) supplementation treatment and B) time period by heifers' winter grazing rangeland in 2015 – 2016 & 2016 – 2017 at the Fort Keogh Range and Livestock Research Laboratory, Miles City, MT

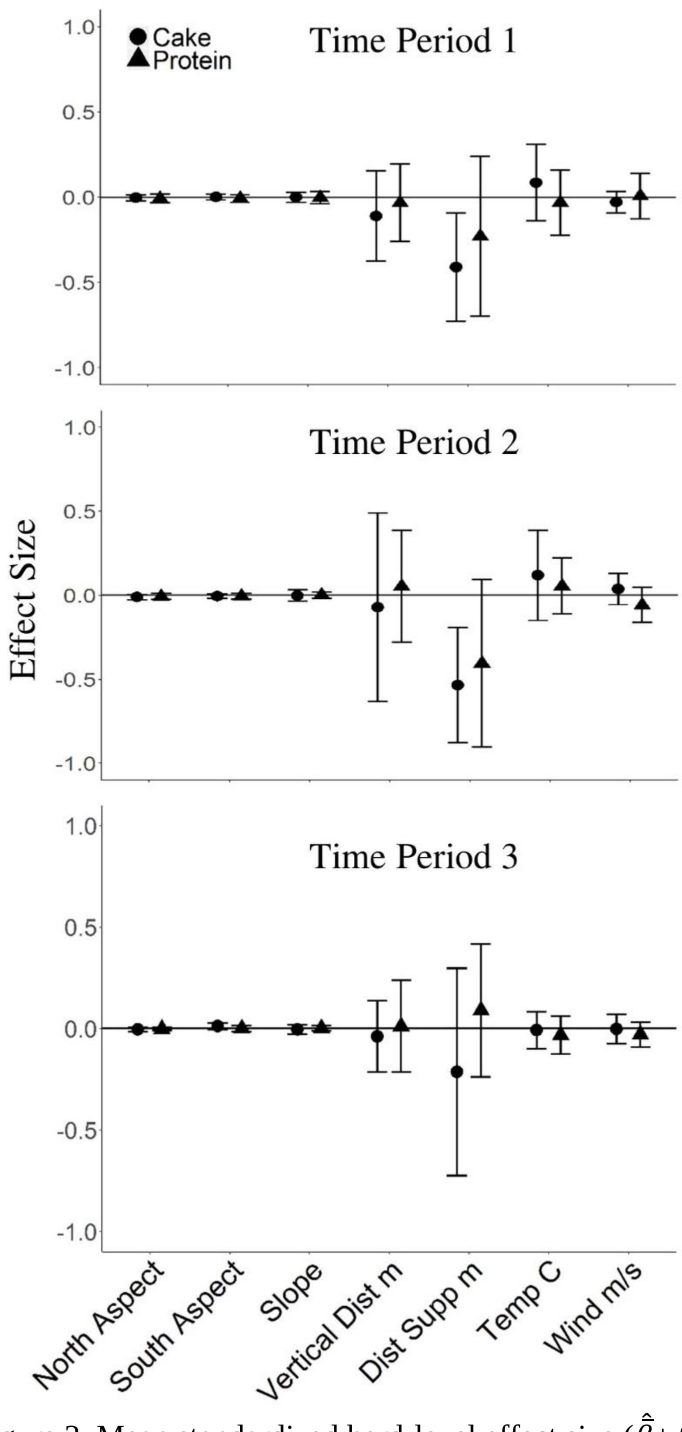

Figure 2. Mean standardized herd-level effect size ($\hat{\bar{\beta}}$± 95% CI) for heifer grazing resource utilization functions. We examined space use with two supplementation treatments for three time periods, 95% confidence intervals of $\hat{\bar{\beta}}$ that do not overlap zero denote significant responses at the population level.

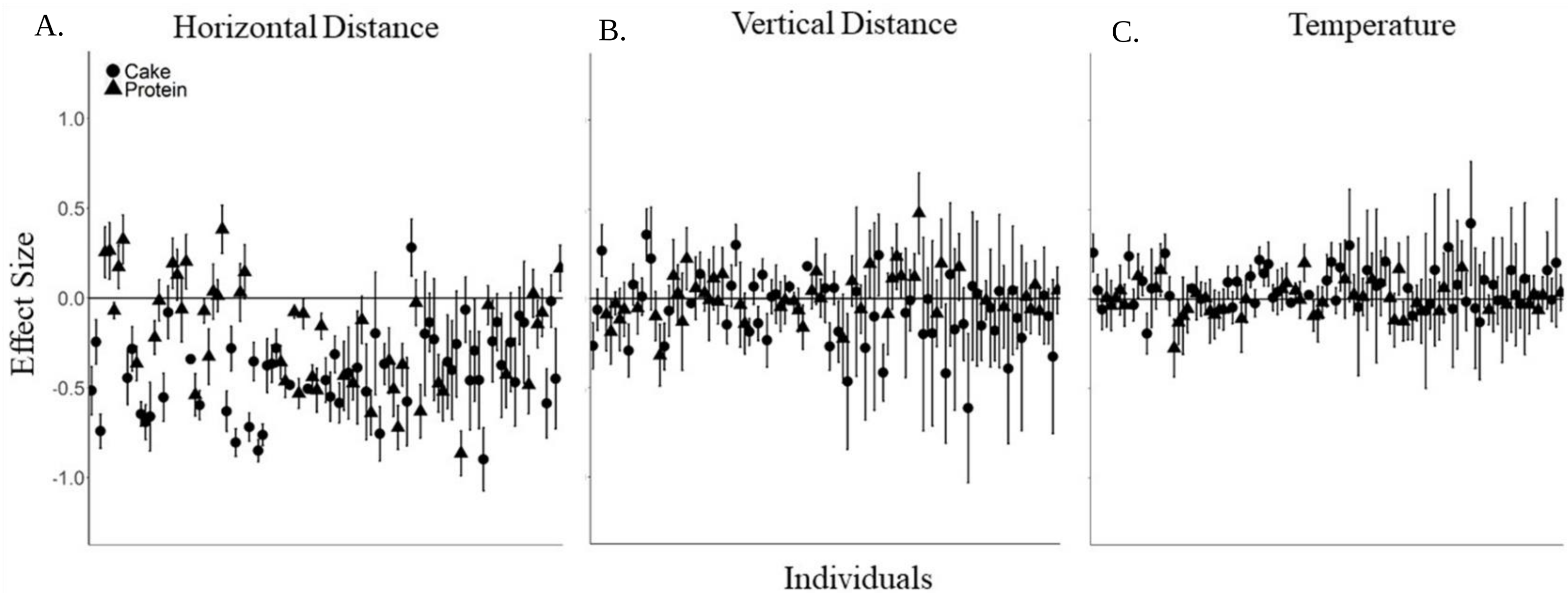

Figure 3. Mean standardized individual-level effect size ($\hat{\beta}$± 95% CI) of A) horizontal and B) vertical distance (m) and C) temperature (°C) for heifer grazing resource utilization functions. We examined space use with two supplementation treatments for three time periods, 95% confidence intervals of $\hat{\beta}$ that do not overlap zero denote significant responses at the individual level

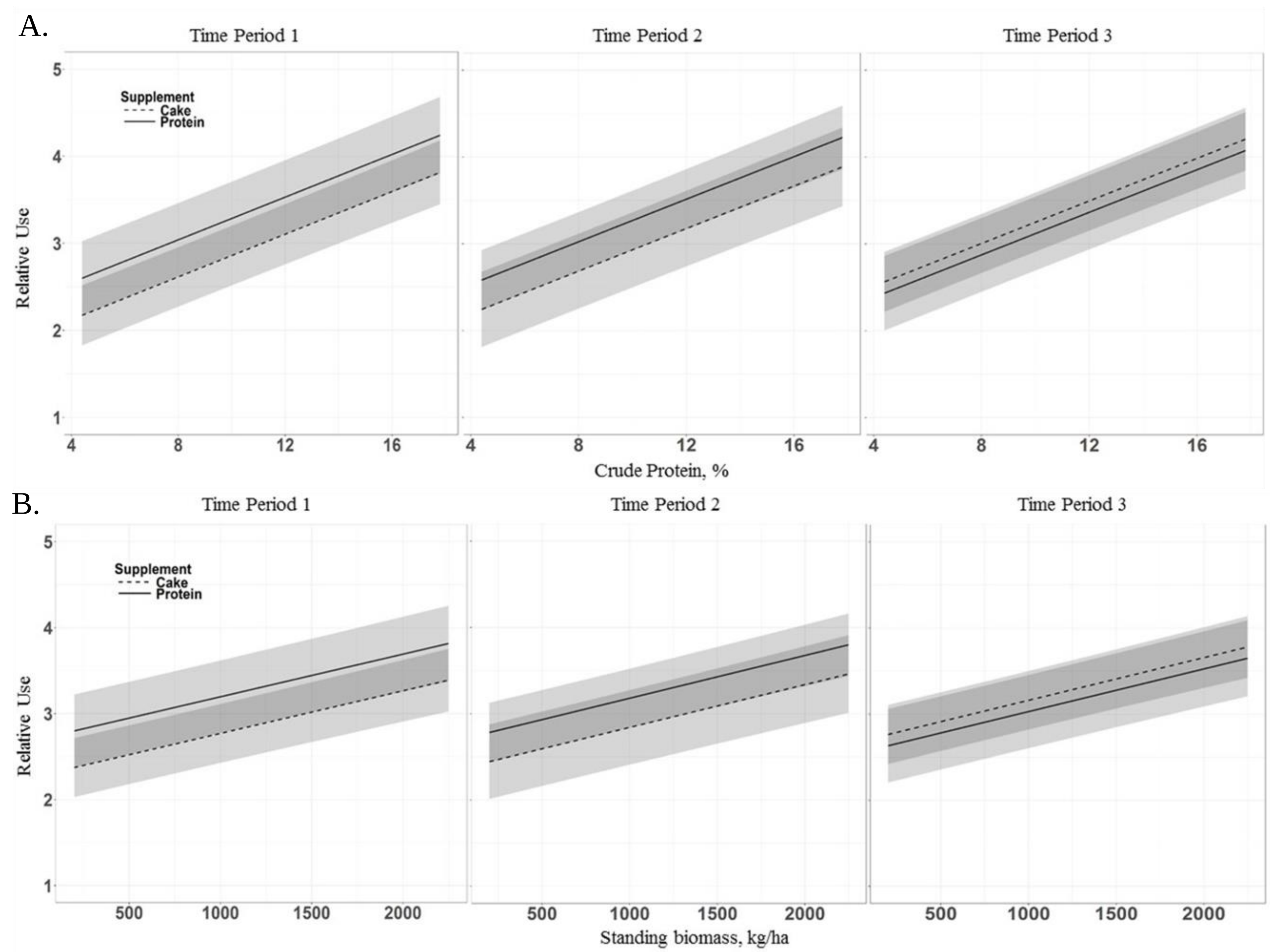

Figure 4. Predicted relationships (± 95%CI represented in the shaded area) between A) crude protein and B) standing biomass of perennial grass by time period on relative resource use by two supplementation strategies for heifers winter grazing rangeland.

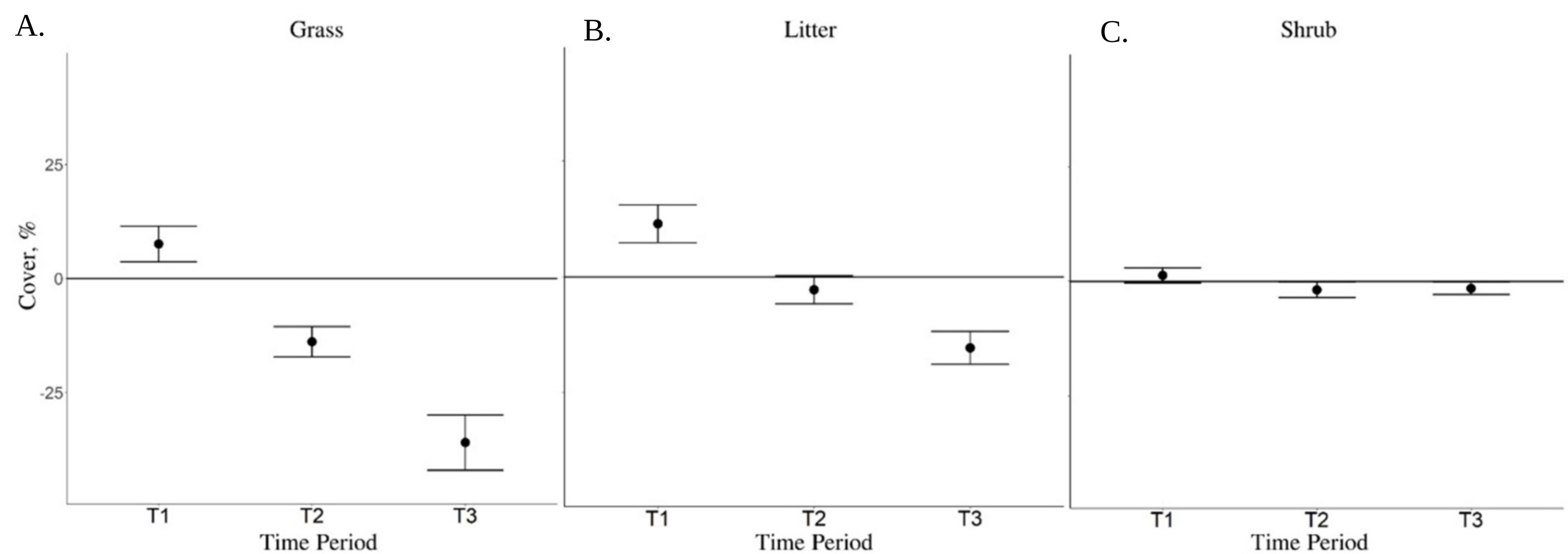

Figure 5. Pre- post differences in mean (± 95% CI) residual A) grass, B) litter, and C) shrub cover classifications by grazing time period for heifers' winter grazing rangeland in 2015 – 2016 & 2016 – 2017 at the Fort Keogh Range and Livestock Research Laboratory, Miles City, MT

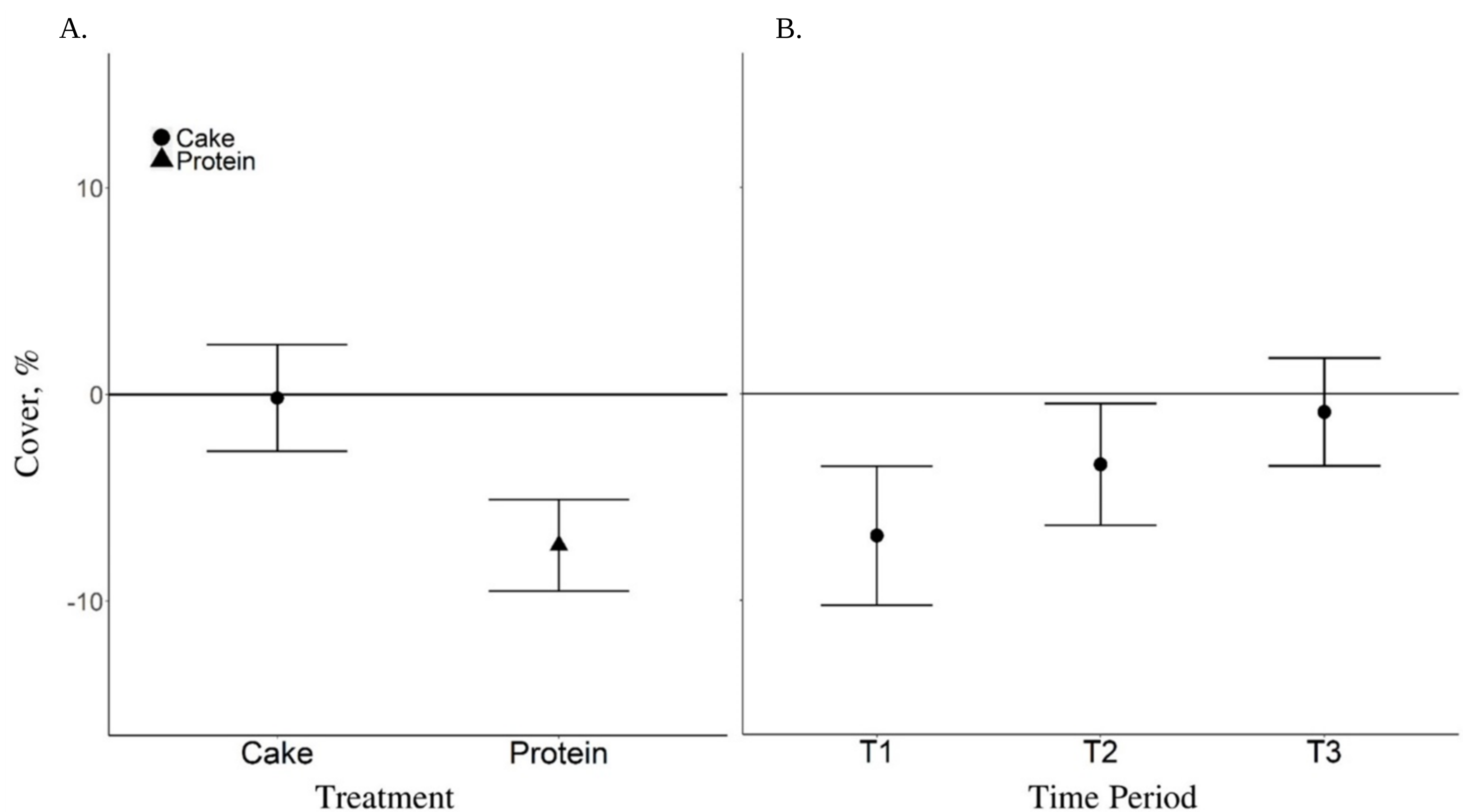

Figure 6. Pre- post differences in mean (± 95% CI) bare ground cover classification by A) supplementation treatment and B) time period for heifers' winter grazing rangeland in 2015 – 2016 & 2016 – 2017 at the Fort Keogh Range and Livestock Research Laboratory, Miles City, MT

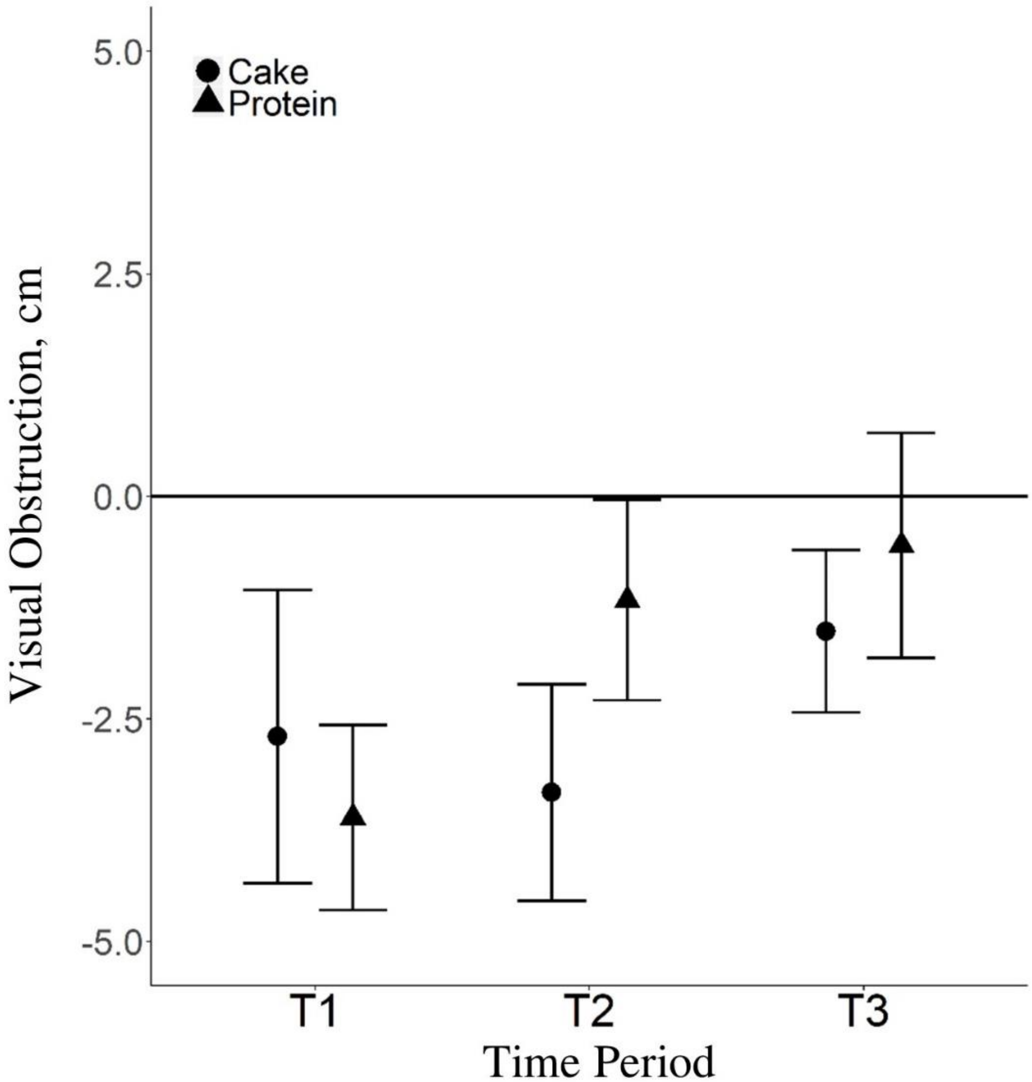

Figure 7. Pre- post differences in mean (± 95% CI) visual obstruction by supplementation treatment and time period for heifers' winter grazing rangeland in 2015 – 2016 & 2016 – 2017 at the Fort Keogh Range and Livestock Research Laboratory, Miles City, MT

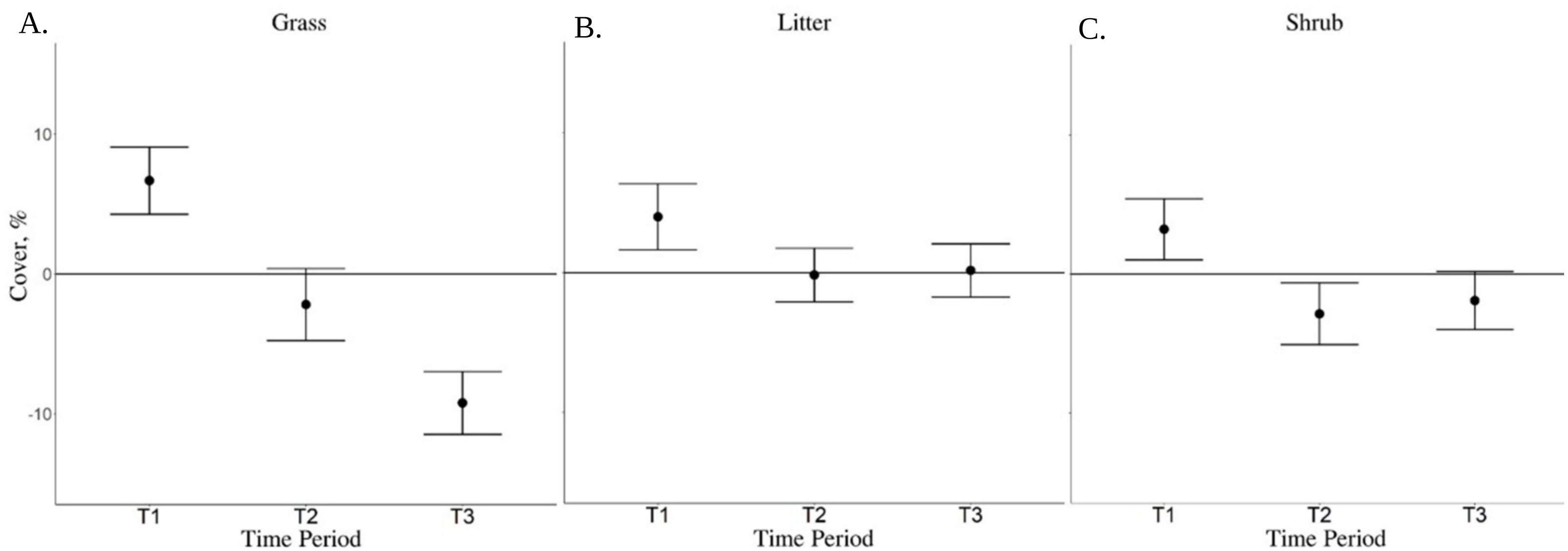

Figure 8. Pre- post difference in heterogeneity (as indexed by difference of standard deviation among transects; ± 95% CI) of A) residual grass, B) litter, and C) shrub cover classifications by grazing time period for heifers' winter grazing rangeland in 2015 – 2016 & 2016 – 2017 at the Fort Keogh Range and Livestock Research Laboratory, Miles City, MT

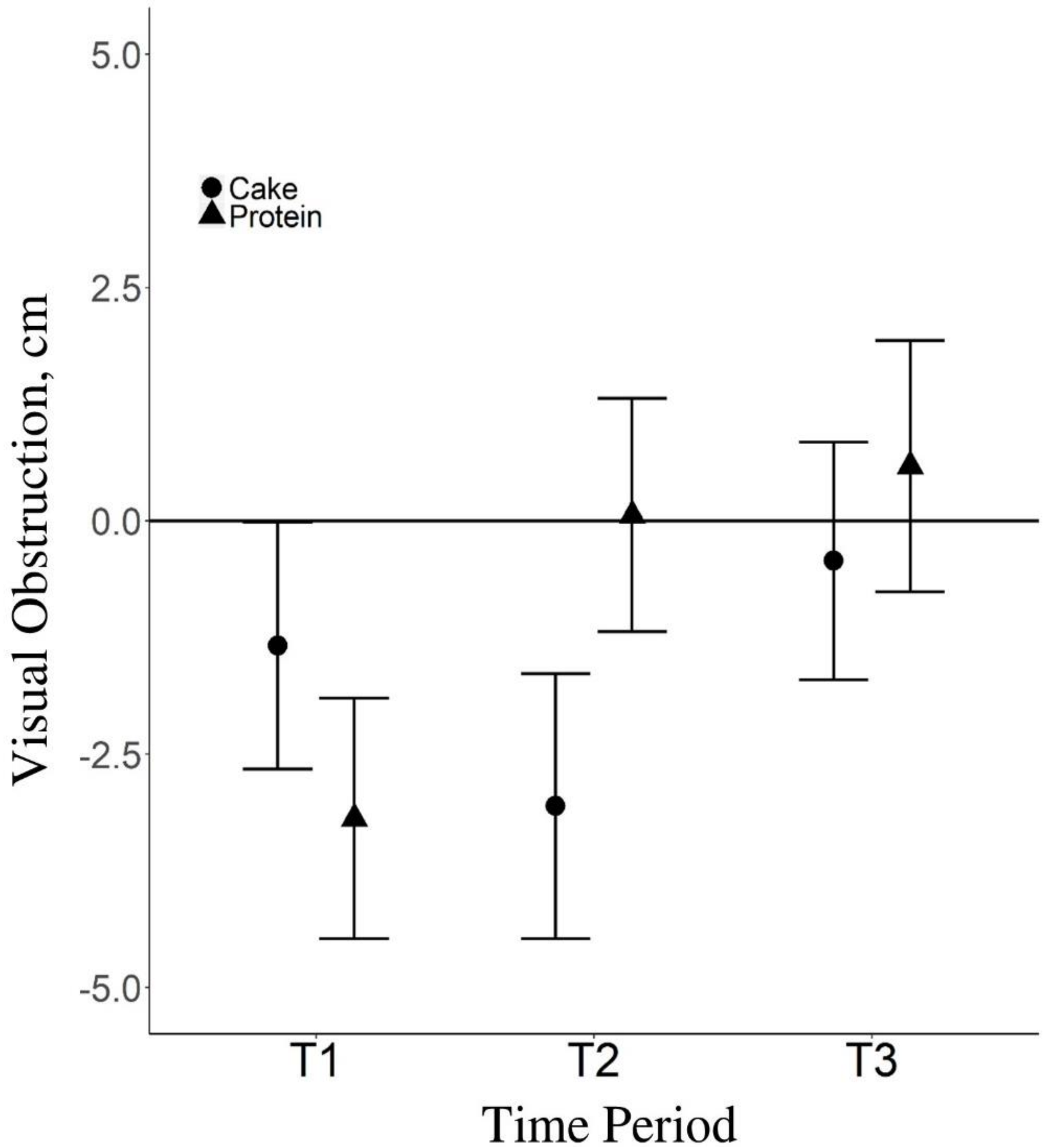

Figure 9. Pre- post difference in heterogeneity (as indexed by difference of standard deviation among transects; ± 95% CI) of visual obstruction by supplementation treatment and time period for heifers' winter grazing rangeland in 2015 – 2016 & 2016 – 2017 at the Fort Keogh Range and Livestock Research Laboratory, Miles City, MT

CHAPTER THREE

DORMANT SEASON GRAZING ON NORTHERN MIXED GRASS PRAIRIE AGROECOSYSTEMS: DOES PROTEIN SUPPLEMENTATION AND INDIVIDUAL ANIMAL VARIATION IMPACT BEEF CATTLE RESOURCE USE, VEGETATION AND RESIDUAL COVER FOR WILDLIFE

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INTRODUCTION

Economic efficiency of cattle production is threatened by high feed and input costs (Meyer and Gunn 2015). To improve profitability and transition to reduced reliance on transported harvested feeds, many cow-calf producers have adopted management strategies involving dormant season grazing (Adams et al. 1996). The primary goal in a forage-based livestock production system is to obtain optimal animal performance while effectively utilizing the forage resource base. Dormant range forage is deficient in nutrients and may result in an inability to meet production expectations (Krysl and Hess 1993, Bowman et al. 1995, Mulliniks et al. 2013b). Providing protein supplements to grazing beef cattle during times of low forage quality can improve animal performance and provide increased economic returns (Bowman et al. 1995, DelCurto et al. 2000, Bodine et al. 2001). However, supplementation strategies assume that all animals consume a targeted quantity of supplement and deviation from the target can have strong effects on animal nutirent status (Bowman and Sowell 1997).

The spatial component of herbivory is a central aspect of domestic livestock ecosystems but has remained difficult to interpret (Coughenour 1991). Mechanisms that influence grazing distribution can be classified into two factors: exogenous, the physical environment in which livestock graze, such as topography, thermal environments and forage resources (Ganskopp and Vavra 1987, Coughenour 1991, Bailey et al. 1996, Beaver and Olson 1997), and endogenous characteristics such as social learning, spatial memory, age, experience, body weight and condition (Allison 1985, Dunn et al. 1988, Bailey et al. 1996, Walburger et al. 2009). Thus, resource selection of grazing cattle can vary widely among individuals in the same pasture under the same environmental conditions (Chapter 2; Bailey 2004). Supplementation alters the nutrient status of grazing livestock, which can also have strong influences on individual grazing behavior (Allison 1985, Adams et al. 1986). The act of supplementation alone can change grazing distribution on rangelands (Ares 1953; Chapter 2) and daily grazing activities (Adams 1985; Chapter 2), altering the distribution of vegetation use based on location of supplements. Thus, it is likely that grazing behavior may vary with individual animal protein supplement intake, age, body weight and condition in dormant-season grazing systems. However, interactions of exogenous factors with endogenous attributes on grazing behavior are less understood (Walburger et al. 2009).

Grazing behavior of livestock plays a key role in grassland ecosystem function as herbivory has both direct and indirect influences on vegetative communities (Belsky and Blumenthal 1997, Riggs et al. 2004, Derner et al. 2009). Cattle alter their grazing behavior in response to nutritional factors, where providing a protein supplement often increases the intake of dormant forage and alters grazing distribution (Barton et al. 1992, Krysl and Hess 1993, Bailey and Welling 1999). Vegetation conditions of western rangelands are inherently heterogeneous (Patten and Ellis 1995, Fuhlendorf and Smeins 1998, Fuhlendorf et al. 2006), thus, protein supplementation has been used as a management tool to increase use of dormant forage and promote uniform utilization across the pasture (Bailey and Welling 1999). Although, dormant forage is typically tolerant of grazing pressure (Petersen et al. 2014), grazing management that promotes uniform utilization can result in the homogenization of vegetation conditions and an overall decline in ecosystem structure, function and biodiversity (Derner et al. 2009, Fuhlendorf et al. 2009, Hovick et al. 2015). Thus, it has been proposed that heterogeneity of vegetation structure, composition, and biomass should be the foundation of conservation and ecosystem management (Christensen 1997, Wiens 1997, Fuhlendorf and Engle 2001). Despite grazing livestock's keystone role as grassland ecosystem engineers (Derner et al. 2009), we currently have little understanding of how protein supplementation and endogenous attributes of grazing cattle interact with exogenous properties of the pasture in determining cattle use and the corresponding effects on residual vegetation cover, structure and heterogeneity.

Information relating supplement intake, cow age, body weight and condition to individual grazing distribution and behavior is lacking. Previously, we found that resource selection of grazing heifers varied widely among individuals (Chapter 2). Therefore, the intent of this study was to evaluate (1) the influence of supplement intake, age, body weight and condition on grazing activity and resource utilization by cattle, and (2) the influence of dormant season use on residual vegetation cover, structure and heterogeneity. We expect that environmental factors and individual animal attributes have multi-faceted effects on distribution by supplemented cattle grazing dormant rangeland in northern mixed grass prairies. We hypothesized that cattle use is affected by endogenous attributes of the animal and distribution of use will have strong effects on vegetation structure. System-level impacts are likely mediated by the provision of supplement, as well as, uncontrolled environmental conditions.

METHODS

This study was conducted at the Thackeray Ranch (48° 21' N 109° 30' W), part of the Montana Agricultural Experiment Station located 21-km south of Havre, MT. Climate is characterized as semi-arid steppe with an average annual precipitation of 410-mm. Vegetation is dominated by Kentucky bluegrass (*Poa pratensis L*), bluebunch wheatgrass (*Pseudoregnaria spicata* [Pursh] A. Love), and rough fescue (*Festuca scabrella Torr*). Preciptiation was higher in the winter of 2017 – 2018 than 2016 – 2017 (4.06, 2.90 cm), however, temperatures durring the 2016 – 2017 winter were substantially cooler than the winter of 2017 – 2018 (-9.60, -2.90 °C), resulting in higher amounts and prolonged periods of snow in the first year of the study (Table 6).

A commercial herd of bred cows (Angus, Angus × Simmental) ranging in age from 1- to 12-year-old was grazed on a 329-ha rangeland pasture (~1.5 AUM ha^{-1}) for 2 years (272 cows with an average weight of 620 kg in the 1st year, and 302 cows with an average weight of 580 kg in the 2nd year). The winter grazing season occurred from December 1, 2016 to January 12, 2017, and November 1, 2017 to December 31, 2017. All cattle had free-choice access to a 30% CP self-fed canola meal-based (35% as-fed basis) pelleted supplement with 25% salt to limit intake. The target daily intake was 0.91-kg/cow.

Sampling

We established seventy-five 30-m transects randomly within the study pasture. Vegetation production, canopy cover and visual obstruction readings (VOR) were measured at six 0.1-m^2 plots located every five meters along each transect. We estimated canopy cover of plant functional groups (grass, forb, shrub), cover of bare ground and litter at each plot using the six-cover class Daubenmire method (Daubenmire 1959). Ground cover of plant functional groups, bare ground and litter influence the abundance and demography of grassland bird species that serve as indicators of grassland ecosystem health (Bradford et al. 1998, Derner et al. 2009). Visual obstruction readings were measured in four cardinal directions using a 1-meter Robel pole (Robel et al. 1970). Visual obstruction represents a measure of the vertical structure and density of vegetation and is typically correlated with aboveground biomass (Robel et al. 1970, Damiran et al. 2007). All measurements were taken pre- and post-grazing to evaluate the effects of relative grazing intensity on residual vegetation cover and structure across the pastures. We estimated pre-grazing vegetation functional group production using the dry weight rank method and clipping each plot (Mannetje 1963, Dowhower et al. 2001). Clipped samples were placed in a forced air oven at 60°C for 48 hours and then weighed. Pre-grazing vegetation samples were composited by transect and ground to pass through a 1-mm screen in a Wiley mill and analyzed in duplicate for nitrogen (Leco CN-2000; Leco

Corporation, St. Joseph, MI), and fiber (NDF and ADF; Ankom 200 Fiber Analyzer, Ankom Co., Fairport, NY) as indicators of vegetation quality (Table 7).

Grazing activity was monitored with Lotek GPS collars (3300LR; Lotek Engineering, Newmarket, Ontario, Canada) containing head position sensors that record daily space use, as well as, timing and location of grazing activities (Turner et al. 2000, Ungar et al. 2005, Brosh et al. 2010). All cattle were assigned to one of six age classifications (1-yr-old, 2 & 3-yr-olds, 4 & 5-yr-olds, 6 & 7-yr-olds, 8 & 9-yr-olds, and ≥ 10-yr-old) and randomly selected for GPS collars (5 collars/age class). Age classifications were based on previous research examining the influence of age on grazing behavior and distribution patterns of cattle within a large mixed-conifer allotment pasture (Walburger et al. 2009). Each individual animal was equipped with an electronic ID tag (Allflex USA, Inc., Dallas-Ft. Worth, TX) attached to the exterior of the left ear for the measurement of individual supplement intake using a SmartFeed Pro self-feeder system (C-Lock Inc., Rapid City, SD) which provided a total of 8 feeding stations. GPS data were used to evaluate the effects of age and supplement intake on animal grazing activity (Ungar et al. 2005, Brosh et al. 2010, Valente et al. 2013). Each collar was configured to record GPS positions at 15-minute intervals, and head position, vertical/horizontal movements at 5-minute intervals. We then separated grazing from non-grazing activities using the binary classification methods developed by Augustine and Derner (2013) to examine time spent grazing and cattle foraging distribution. By limiting observations to grazing locations we were able to determine important foraging areas rather than general pasture occupancy (Walburger et al. 2009).

An Onset HOBO U30-NRC Weather Station (Bourne, MA, USA) was placed near the supplement feeders and programmed to collect air temperature, relative humidity, and wind speed and direction data every 15 min for the entirety of the grazing period. We predicted fine scale wind speed (30-m^2 resolution) across all pastures using average daily wind measurements collected on site, ArcGIS spatial analyst tool, a digital elevation model at 30-m^2 resolution, and WindNinja wind prediction software (Brooks 2012). In addition, we deployed HOBO Pendant® Temperature/Light Data Logger (Onset Computer Corporation, Bourne, MA) at each randomly-selected transect location within the pasture that were programmed to collect fine-scale ambient temperature every 30-minutes. We modeled the effects of physical properties (e.g., aspect, elevation and slope) on fine-scale temperature of the pastures using generalized linear models. Model results were used to create spatially-explicit predictions of average temperature and wind conditions across the experimental pasture at a 30-m^2 resolution, which were used as covariates in subsequent resource utilization modeling.

All supplementation and water locations within the study pasture were located via handheld GPS (spatial error < 10-m). Using the spatial analysis tool in ArcGIS (Environmental Systems Research Institute, Redlands, CA) and a digital elevation model at 30-m^2 resolution (USGS 2017), we created additional spatial covariate layers representing aspect, solar radiation, terrain ruggedness (calculated by taking the sum change in elevation between a grid cell and its eight neighboring cells; Riley 1999) and horizontal distance from supplement locations and water sources at 30-m^2 resolution.

Statistical Analysis

We evaluated the effects of cow age, supplement intake, body condition and weight on time spent grazing and distance traveled with generalized linear mixed models using individual animal as a random intercept. We hypothesized that individual animal attributes could elicit one of three behavioral responses (linear, pseudothreshold, quadratic). Variables hypothesized to exhibit a pseudothreshold pattern were tested with asymptotic models by evaluating the natural log of the explanatory variable (ln[x + 0.001]; Franklin et al. 2000). We used Akaike's Information Criterion adjusted for small sample sizes (AIC_c) to evaluate support for competing models reflecting hypotheses about the effects of individual animal attributes on time spent grazing and distance traveled by cattle (Burnham and Anderson 2002). Models with $\Delta AIC_c \leq 2$ that differed from the top model by a single parameter were excluded if confidence intervals of parameter estimates overlapped 0 (ie., were non-informative; Arnold 2010). When multiple models were supported, we use model-averaged estimates of beta-coefficients ("MuMIn" package for R; Bartoń 2018). Model fit was then evaluated by calculating marginal and conditional r^2 values for generalized linear mixed models (Nakagawa and Schielzeth 2013).

To model dormant season space use by cattle, individual GPS-collared cows were defined as the biological unit of interest in evaluating grazing resource utilization within the pasture. We used multiple regression in a resource utilization function analysis to relate individual cow space use, quantified as a continuous and probabilistic variable, to pasture level covariates (RUF; Marzluff et al. 2004, Winder et al. 2014). Resource utilization functions increase sensitivity for detecting resource selection and reduce errors associated with location estimation by quantifying inter-animal variation in resource use and independently incorporating an individual's entire distribution of use while accounting for spatial autocorrelation of grazing locations (Marzluff et al. 2004, Kertson and Marzluff 2010, Winder et al. 2014).

Due to the pasture management unit defining the home range of grazing cattle, GPS data were used to build resource utilization models quantifying animal movements and selection of environmental and vegetation conditions within the pasture (third-order scale; Johnson 1980). We created a raster representing the specific utilization density distribution for the grazing locations of each individual in the pasture using Geospatial Modeling Environment (Beyer 2010). Relative use values were bound between 1 and 99, for each 30 m^2 cell based off of the relative volume of utilization distribution in that cell (Marzluff et al. 2004). Environmental covariates expected to influence resource utilization included temperature, wind, solar radiation, distance to supplement and water (horizontal), elevation, terrain ruggedness and aspect, annual forage production and quality. Using the 'raster' function in R, environmental covariate and individual relative use rasters were stacked and converted to spatially explicit data files as input for the ruf.fit package (Kertson and Marzluff 2010). Prior to modeling, individual relative use values were log-transformed to meet the assumptions of multiple regression models. Resource utilization functions with standardized β coefficients were generated using the ruf.fit package in R and evaluated for each individual to represent the influence of the environmental covariates on cattle resource utilization (Marzluff et al. 2004, Kertson et al. 2011).

Herd level inferences were developed by calculating the mean standardized β coefficients ($\hat{\bar{\beta}}$) and variance that incorporated individual animal variation for each environmental factor (Marzluff et al. 2004). Standardized coefficients with 95% confidence intervals that do not overlap zero were considered significant predictors of space use (Marzluff et al. 2004, Winder et al. 2014). If a resource utilization coefficient was significantly different from zero, we inferred that resource use was greater or less than expected based on availability of the resource within the experimental pasture (Marzluff et al. 2004, Winder et al. 2014). For environmental factors eliciting high herd-level variability in habitat selection (herd level SE of standardized coefficients > 0.25), we conducted a post hoc analysis evaluating the effects of cow age, supplement intake, body weight and condition on resource use coefficients relative to each habitat covariate using generalized linear models. We investigated three behavioral responses (linear, pseudothreshold, quadratic) that individual animal attributes may have on resource selection coefficients. We used Akaike's Information Criterion adjusted for small sample sizes (AIC_c, Burnham and Anderson 2002) to evaluate support for competing models reflecting hypotheses about the effects of animal attributes on resource use by cattle. Model fit was then evaluated by calculating a multiple r^2 value for generalized linear models.

Geo-referenced rasters representing estimates of vegetation composition, production and quality were not available at the appropriate spatial resolution to incorporate in the RUF analysis. Therefore, to evaluate the relationship of vegetation characteristics and resource use of grazing cattle, we extracted the relative resource use value for each individual at each of the transect location within the pasture and paired it with the corresponding vegetation measurements. We evaluated the effects of vegetation (e.g., production, composition and quality) and cow age, body condition, and supplement intake (linear, pseudothreshold, or quadratic response) on relative use with generalized linear mixed models using individual animal as a random effect. To avoid overfitting our resource use models, we conducted a preliminary multicollinearity analysis to select uncorrelated ($|r| > 0.6$) variables that are ecologically relevant and feasible to measure (Dormann et al. 2013). If covariates were correlated, we fitted preliminary resource utilization models and evaluated relative support of each individual variable using AIC_c (Burnham and Anderson 2002); we retained the variable with more relative support for further modeling and discarded the correlated variables (Fieberg and Johnson 2015). Support for competing models reflecting hypotheses about the effects of various vegetation and individual animal attributes on relative use by cattle were evaluated using AIC_c (Burnham and Anderson 2002). Model fit was then evaluated by calculating marginal and conditional r^2 values for generalized linear mixed models (Nakagawa and Schielzeth 2013).

To evaluate the relative effects of grazing intensity on the residual cover of vegetation functional groups and visual obstruction, we calculated the overall density of grazing locations within a 50-m radius of each transect location for both years. We then calculated the relative difference in mean transect level vegetation cover and visual obstruction from pre- to post-grazing for each year. Patch level heterogeneity of vegetation cover and visual obstruction was calculated by subtracting the pre-grazing transect level standard deviation from the post-grazing standard deviation for both years. We used an analysis of covariance (ANCOVA) with generalized linear models including year as a categorical variable, density of grazing locations (grazing intensity) as a continuous variable, and an interaction of grazing intensity by year to evaluate the effects of grazing intensity and year on residual vegetation cover, visual obstruction and patch level heterogeneity of residual vegetation cover and visual obstruction. Data were plotted and log-transformed if needed to satisfy assumptions of normality and homogeneity of variance. An alpha ≤ 0.05 was considered significant. Shrub cover as a functional group of vegetation was not analyzed as approximately 90% of the total shrub canopy cover was of deciduous species. Post-grazing samples were taken prior to leaf budding making it difficult to evaluate the effects of grazing on residual shrub canopy cover. All statistical analyses were performed in R (R Core Team 2017).

RESULTS

Grazing behavior and space use

The effects of cow age, supplement intake, and body condition and weight on time spent grazing per day and distance traveled per day were evaluated for 29 cows from December 1, 2016 to January 12, 2017 and 29 cows from November 1, 2017 to December 31, 2017. Models containing a quadratic effect of cow age received 61% of the support among candidate models for time spent grazing per day (Table 8). Models containing supplement intake, body condition, body weight and an interaction of cow body condition by cow weight were also supported, however, the parameter estimates for cow body condition ($\hat{\beta}$ = 52.74 ± 64.39), body weight ($\hat{\beta}$ = 14.55 ± 17.11) and the interaction of the cow body condition by cow weight ($\hat{\beta}$ = -8.09 ± 9.95) may be non-informative as confidence intervals of the effect size overlap 0. Time spent grazing was negatively associated with supplement intake ($\hat{\beta}$ = -0.05 ± 0.02), where time spent grazing per day decreased 3-min with for every kg of supplement intake (Figure 10). Time spent grazing was quadratically affected by cow age ($\hat{\beta}_{\text{Age}}$ = 1.54 ± 0.46, $\hat{\beta}_{\text{Age}^2}$ = -0.22 ± 0.06), indicating that cows maximized time spent grazing at ages of 4 – 7 years (Figure 10). The top model containing all supported variables among candidate models had a conditional r^2 of 0.51; however, the marginal r^2 was only 0.12 suggesting age, supplement intake, body weight and body condition only account for 12% of the variation associated with time spent grazing.

A single top model containing age and supplement intake received 40% of the relative support of the data when determining the effects of cow age, supplement intake, body condition and weight on distance traveled per day (Table 8). Body condition, body weight and the interactions of body condition by supplement intake, age by body weight, and body condition by body weight were also supported, although the parameter estimates for age ($\hat{\beta}$ = -5.56 ± 4.18), cow body condition ($\hat{\beta}$ = -16.12 ± 20.28), body weight ($\hat{\beta}$ = -5.26 ± 5.30) and the interaction of the cow body condition by body weight ($\hat{\beta}$ = 2.38 ± 3.14) and cow age by body weight ($\hat{\beta}$ = 0.83 ± 0.66) may be non-informative with confidence intervals of the effect overlapping 0. Distance traveled per day had an asymptotic association with supplement intake ($\hat{\beta}$ = 0.35 ± 0.09), indicating a rapid increase in travel with supplement intake that begins to level at 2.5-kg and is maximized at 10-kg per day (Figure 11). A supplement intake by body condition interaction was also supported ($\hat{\beta}$ = -0.15 ± 0.05), where cow body condition had a larger effect on distance traveled per day at high levels of supplement intake (Figure 11). The top model evaluating the effects on distance traveled had a conditional r^2 of 0.26 with a marginal r^2 of 0.18 suggesting age, supplement intake, body weight and body condition accounted for 18% of the variation associated with distance traveled per day.

We estimated RUFs for 58 cattle (29 per year) using an average of 910 ± 38 grazing locations per individual. Resource utilization by cattle grazing dormant season forage was negatively related to terrain ruggedness ($\hat{\hat{\beta}}$ = -0.09 ± 0.03; Figure 12). Additionally, relative selection by cattle tended to decrease with distance from supplement ($\hat{\hat{\beta}}$ = -0.84 ± 0.45); however, individual variability in selection resulted in confidence intervals overlapping 0 for the herd-level response (Figure 12). Low values of relative use coefficients indicate aspect, elevation, distance from water, solar radiation, average temperature and wind speed had little influence on grazing space use at a population level within the study pasture. However, distance from supplement, distance from water, and elevation were highly variable among individuals as drivers of space use (herd level SE of standardized coefficients > 0.25; Figure 13). Therefore, we conducted a post hoc analysis evaluating the relationship of individual cow attributes (age, body weight, body condition and average daily supplement intake) on resource utilization relative to distance to supplement, distance to water and elevation.

The probability of grazing site selection relative to distance from supplement was influenced by age, supplement intake and body weight, as a single top model containing age, supplement intake and body weight received 57% of the relative support among candidate models (Table 9). Resource utilization relative to distance from supplement was quadratically affected by cow age ($\hat{\beta}_{Age}$ = -0.63 ± 0.15, $\hat{\beta}_{Age^2}$ = 0.07 ± 0.02), indicating that cattle of all ages select for grazing locations close to supplement with cows aging 6 – 7 being the most closely associated with supplement sites (Figure 14). Likewise, resource utilization relative to distance to supplement had a quadratic relationship with supplement intake ($\hat{\beta}_{Supplement\ Intake}$ = -0.78 ± 0.21, $\hat{\beta}_{Supplement\ Intake^2}$ = 0.22 ± 0.58), where any supplement intake resulted in selection of grazing location near supplement feeders, with intakes ranging between 1.5 and 2-kg being the most closely associated with supplement sites (Figure 14). Cow body weight also exhibited a quadratic effect on resource utilization relative to distance from supplement ($\hat{\beta}_{Weight}$ = -0.01 ± 0.01, $\hat{\beta}_{Weight^2}$ = 0.001 ± 0.0001), as cattle weight increased above 650-kg they became less associated with supplement location (Figure 14).

The probability of grazing site selection relative to distance from water was also influenced by age, supplement intake and body weight, as models containing a quadratic effect of age and body weight, and an asymptotic effect of supplement intake and an interaction of supplement intake by body weight were most supported among candidate models (Table 9). However, supplement intake ($\hat{\beta}$ = 0.69 ± 1.97) and the interaction of supplement intake by body weight ($\hat{\beta}_{Supplement\ Intake \times Body\ Weight}$ = -0.002 ± 0.007, $\hat{\beta}_{Supplement\ Intake \times Body\ Weight^2}$ = 0.001 ± 0.001) may be non-informative as confidence intervals of the effect size overlap 0. Resource use relative to distance from water were quadratically affected by cow age ($\hat{\beta}_{Age}$ = 0.22 ± 0.09, $\hat{\beta}_{Age}{}^2$ = -0.03 ± 0.01), where yearling to 3-yr-old cattle selected grazing locations regardless of proximity to water, while cattle aging 6 – 7 selected grazing locations farthest from water (Figure 15). Cow body weight also elicited a quadratic effect on resource use relative to distance from water ($\hat{\beta}_{Body\ Weight}$ = 0.01 ± 0.005, $\hat{\beta}_{Body\ Weight}{}^2$ = -0.001 ± 0.0001), as the lightest and heaviest cattle neither selected for or against distance to water and cattle weighing between 600 and 700 kg selected grazing locations away from water (Figure 15).

The probability of grazing site selection relative to elevation was influenced by age and supplement intake as models containing a quadratic effect of age and supplement intake had 95% of the relative support among candidate models (Table 9). Models containing a linear effect of body weight and a quadratic effect of body condition were also supported. Resource use relative to elevation was quadratically associated with age ($\hat{\beta}_{Age}$ = 0.41 ± 0.12, $\hat{\beta}_{Age}{}^2$ = -0.04 ± 0.02), where yearlings selected grazing locations in lower elevations while older cattle selected grazing locations at higher elevations (Figure 16). Resource use relative to elevation was also quadratically affected by supplement intake per day ($\hat{\beta}_{Supplement\ Intake}$ = 0.56 ± 0.16, $\hat{\beta}_{Supplement\ Intake}{}^2$ = -0.15 ± 0.05), where cattle consuming 0 or 3 kg of supplement per day selected grazing locations regardless of elevation, as animals that consumed approximately 1.5 kg of supplement per day utilized higher elevation areas for grazing (Figure 16). Cow body condition also elicited a quadratic association on resource utilization relative to elevation ($\hat{\beta}_{Body\ Condition}$ = 3.81 ± 1.55, $\hat{\beta}_{Body\ Condition}{}^2$ = -0.34 ± 0.14), where cows with body condition of 5.5 – 6 selected areas at higher elevations to graze (Figure 16). Resource use relative to elevation was negatively associated with body weight ($\hat{\beta}$= -0.001 ± 0.0005), where lighter weight cattle selected grazing locations at higher elevations than heavier cattle (Figure 16).

The relationship of vegetation composition, production, and quality, cow age, body condition, body weight, average daily supplement intake and relative resource utilization by cattle were evaluated for the 58 cows (29 cows per year) using pre-grazing vegetation conditions measured at 75 transect locations in the study area. Models containing grass production (kg/ha), neutral detergent fiber (%), and an interaction of grass production by neutral detergent fiber received virtually all the relative support among candidate models (Table 10). Models containing crude protein (%; $\hat{\beta}$ = 0.68 ± 1.67) and an interaction of grass production by crude protein ($\hat{\beta}$ = -0.35 ± 0.18) were also supported, though effects may be non-informative as confidence intervals of the effect size overlap 0. Relative use had an asymptotic relationship with grass production ($\hat{\beta}$ = 16.58 ± 3.25), where predicted relative use increased non-linearly with grass production (Figure 17). Neutral detergent fiber also displayed an asymptotic relationship with relative use ($\hat{\beta}$ = 27.19 ± 6.03), where relative use decreased non-linearly with increasing NDF (Figure 17). However, an interaction between NDF and grass production was supported ($\hat{\beta}$ = -3.71 ± 0.77); high NDF values were selected in areas of low grass production, while low NDF values were selected in areas of high grass production (Figure 17).

Vegetation Structure and Heterogeneity

Livestock grazing did not affect pre-post differences in mean VOR ($\hat{\beta}$ = 0.001 ± 0.012), bare ground cover ($\hat{\beta}$ = 0.003 ± 0.016) and residual cover of grass ($\hat{\beta}$ = 0.05 ± 0.07; *P* > 0.22; Table 11). However, the data supported a year by density of grazing locations (grazing intensity) interaction in residual grass cover ($\hat{\beta}$ = -0.20 ± 0.09), where in year one grazing intensity had a slight positive effect on residual grass cover, while in year 2 grass cover was negatively associated with grazing intensity (Figure 18). We found a positive asymptotic relationship between residual cover of forbs and grazing intensity ($\hat{\beta}$ = 1.04 ± 0.41), where residual forb cover was reduced at all densities of grazing locations but displayed a non-linear increase in cover with density of grazing locations (Figure 18). Ground cover of litter also had a positive asymptotic relationship with density of grazing locations ($\hat{\beta}$ = 3.06 ± 0.89), where increasing density of grazing locations resulted in a non-linear increase of litter ground cover (Figure 18). Visual obstruction reading, bare ground and litter cover all displayed a significant year effect (*P* < 0.01; Table 11). Bare ground decreased by 1.41 ± 0.43 after grazing in year one with no difference in year two (1.32 ± 0.79%; Figure 19). Conversely, litter cover increased 14.19 ± 2.22% in year one with no differences in year two (0.91 ± 1.33%; Figure 19). Visual obstruction was decreased in both years, however, had a larger reduction in year two than year one (-7.96 ± 0.62 vs -5.94 ± 0.29; Figure 19).

Grazing intensity did not significantly alter the differences in transect level standard deviation of VOR ($\hat{\beta}$ = 0.009 ± 0.009), bare ground ($\hat{\beta}$ = -0.001 ± 0.021), or residual grass ($\hat{\beta}$ = -0.02 ± 0.03) and forb cover ($\hat{\beta}$ = 0.54 ± 0.39; *P* > 0.36; Table 12).

Difference in pre- post grazing standard deviation of litter had an asymptotic relationship with density of grazing locations ($\hat{\beta}$ = 2.21 ± 0.74), whereas slight increasing density of grazing locations results in a reduction in the pasture level standard deviation of litter (Figure 20). Visual obstruction reading and litter cover difference in pre- post grazing standard deviation displayed a significant year effect ($P < 0.02$; Table 12). Visual obstruction standard deviation was decreased in both years, with a larger reduction in transect standard deviation in year two than year one (-3.21 ± 0.46 vs -1.90 ± 0.27; Figure 21). Pre- post grazing difference of litter standard deviation was decreased 5.36 ± 1.50 in year one with no differences in year two (-0.57 ± 1.52; Figure 21).

DISCUSSION:

Cow age, body condition, weight and supplement intake are known to have substantial effects on intake of low-quality forage (Allison 1985, Krysl and Hess 1993, Moore et al. 1995). Our research suggests these individual level factors also have considerable effects on grazing behavior and resource use in relation to landscape variables (e.g. elevation and distance from supplement and water) that result in high amounts of herd-level variability. The cow herd in our study grazes the same pasture each winter, thus, cow age likely reflects experience. Our results are consistent with previous research that has demonstrated experienced cattle are more likely to use areas farther from water and higher in elevation (Bailey 2005, Walburger et al. 2009). Additionally, our research suggests that older cattle graze closer to supplement locations. Therefore, supplement location and previous experience likely interact in determining cattle grazing locations. Time spent grazing was greatest for mid-aged cows (4 – 7 yearsold). Previous research has established that older cows spend more time grazing than younger cows (Adams et al. 1986), however, categorical age treatments allowed inference for only 3- and 6-year-old cattle. The difference in time spent grazing per day is likely due to inexperience of younger cattle grazing dormant rangelands (Krysl and Hess 1993) and a decrease in structural soundness and production efficiency of cattle > 8 years of age (Loucks et al. 2002).

Providing supplement to cattle grazing dormant forage often results in decreased time spent grazing (Chapter 2; Krysl and Hess 1993, Schauer et al. 2005). This negative association suggests that as cattle increase supplement intake, they either decrease forage intake or increase grazing intensity and harvest efficiency. Cattle alter their grazing behavior in response to nutritional factors, where providing a protein supplement while grazing dormant forage can increase grazing intensity, harvest efficiency and forage intake with an overall decrease in total time spent grazing (Barton et al. 1992, Krysl and Hess 1993). However, cattle have been shown to decrease their intake of low quality forage if supplement is consumed greater than 0.8% of body weight (Moore et al. 1995). The average weight of cattle across both years of the study was 627 kg, suggesting that any daily supplement intake over 5 kg would depress forage intake, likely reflected in time spent grazing. In addition, NDF has been proposed as the most important factor influencing forage intake of ruminants, where a positive response of protein supplementation on forage intake would only be expected when NDF intake is less than 12.5 g/kg BW/d (Mertens 1985, Mertens 1994). During both years of our research the available forage base averaged 70% NDF, thus, if cattle were to consume a minimum

11.2 kg of forage per day the positive effects of protein supplementation on forage intake would likely be negated. Therefore, it is probable that as cattle in our study increased supplement intake, they decreased forage intake and subsequently total time spent grazing.

Traveling is believed to influence the energy requirements of grazing livestock (Walker et al. 1985). However, previous studies show mixed results on the effects of supplementation on distance traveled (Adams 1985, Barton et al. 1992, Schauer et al. 2005). The majority of these studies specifically looked at the effects of supplemented vs non-supplemented cattle and did not measure the relationship between individual animal supplement intake and distance traveled. In our study, cattle increased travel rapidly with increased supplement intake until animals consumed approximately 2.0-kg per day at which a distance traveled per day met a semi-threshold. The energetic costs associated with travel can increase maintenance requirements from 10 – 25% in grazing animals (Ribeiro et al. 1977, Havstad and Malechek 1982). Therefore, cattle in our study may have increased consumption of supplement in response to increased energy expenditure associated with traveling to the point supplement intake may limit foraging activity and consequentially distance traveled.

Additionally, we found evidence that cow body condition mediates the effects of supplement intake on distance traveled. Generally, cows consuming low levels of supplement traveled relatively little, however, cattle with relatively low body condition (< 5) traveled farther per unit increase of supplement intake than cattle with high body condition (> 6). Livestock in relatively low body condition typically increase forage intake (Bines et al. 1969, Lusby et al. 1976, Allison 1985). Although our study did not measure forage intake, our data suggests cattle may be consuming supplement as a substitute for dormant forage. Therefore, it may be reasonable to assume a similar relationship between cattle body condition and supplement intake as cattle with relatively low body condition consumed more supplement than cattle with high body condition (2.03 ± 0.06, 1.14 ± 0.17 kg). Thus, the interaction of supplement intake and body condition may reflect the nutrient status of the animal in relation to energy expenditure associated with travel.

Contrary to expectations, elevation and distance from water and supplement were not significant drivers in herd level resource use in our study. However, these parameters exhibited substantial amounts of individual-level variation, suggesting cattle resource use relative to elevation and distance from water and supplement is influenced by individual animal attributes. Individual average daily supplement intake and body weight and condition were all important factors in determining the extent of selection of grazing locations relative to elevation and distance from supplement and water. The effects of individual level factors on resource use are likely related to energetic requirement for maintenance. Energetic requirements for maintenance are directly related to the metabolic body weight of the animal ($BW^{0.75}$), with activity increasing energy requirements per unit body weight (National Research Council 2016). Thus, the energetic cost of traveling to higher elevations is increased for heavier weight cattle. This may explain why heavier cattle in our study had a lower selection for grazing locations close to supplement and higher elevations away from water. In general, supplement intake may mitigate the increased energetic cost of travel to higher elevation grazing locations for cattle. However, in our study as average daily supplement intake increased the selection of grazing locations in higher elevations only increased until animals consumed approximately 2-kg of supplement per day, after which selection for elevation decreased. High levels of supplement intake may result in cattle consuming supplement as a substitute to forage, decreasing overall forage intake and time spent grazing, resulting in the changes in resource use relative to elevation and distance from supplement.

Our results are consistent with previous work that have demonstrated cattle avoid rough terrain (Ganskopp and Vavra 1987, Van Vuren 2001, Walburger et al. 2009) and select grazing locations in areas with relatively high forage production and quality (Senft et al. 1985, Smith et al. 1992, Walburger et al. 2009). Our results support an interaction between grass production and NDF, where cattle selected grazing locations with high levels of NDF in areas of low grass production while selecting areas of low NDF in high grass production cattle selected for low NDF. At our study site, low grass production areas were typically dominated by C-4 grasses (e.g. *Schizachyrium scoparium*) or bunch grasses with a low leaf:stem ratio (e.g. *Pseudoroegneria spicata*), both of which were relatively high in NDF. Therefore, we attribute the interaction of grass production and NDF on cattle resource utilization to low production areas being inherently high in NDF.

Grazing intensity assessed through density of grazing locations had a significant effect on forb and litter cover. Virtually any grazing resulted in an increase in forb cover that rapidly met a threshold. Cattle typically have a strong dietary preference for grasses

(Miller and Krueger 1976, Walburger et al. 2007, Clark et al. 2013). Thus, increases in forb cover with grazing intensity is likely an artifact of cattle removing grass biomass via grazing, increasing forb detection during the post-grazing vegetation data collection period. Grazing intensity also increased litter cover and reduced heterogeneity of litter cover, both of which rapidly met thresholds. Previous research evaluating the effects of grazing on litter suggests that dormant standing vegetation is trampled, broken into smaller pieces, and categorized as litter post-grazing (Naeth et al. 1991). Therefore, grazing intensity would be expected to increase litter cover to the point at where vegetation removal by grazing limits litter accumulations. Additionally, increases in litter cover may reduce over all heterogeneity of litter cover.

Year had a significant effect on bare ground and litter cover, VOR, and the effect of grazing intensity on grass cover. This effect is presumably due to weather differences between the two years of the grazing trial. On average, the first year of our trial was 7.6 °C colder than year two. Although year two received higher amounts of total precipitation, colder temperatures in year one resulted in an increased snowfall earlier in the grazing season and prolonged time periods of snow ground cover. The second year of the study also received snowfall early in the grazing period, however, warm temperatures limited prolonged periods of snow ground cover until late in the trial. Snow cover could limit forage availability of grazing cattle (Senft et al. 1985, Willms and Rode 1998). Forage availability can have major effects on grazing behavior as it forms the bounds from which the animal selects its diet, thus, high forage availability allows cattle to graze selectively (Marten 1989, Reuter and Moffet 2016). Limited forage availability likely caused animals to consume a greater proportion of the less-preferred forage (Marten 1989), and focus grazing efforts in areas where less snow had accumulated. Our data supports this behavioral response as grazing intensity had little to no effect on grass cover in year one, even though cattle have strong dietary preference for grass (Miller and Krueger 1976, Walburger et al. 2007, Clark et al. 2013). However, the second year of the grazing trial resulted in a strong negative association between grass cover and grazing intensity. Limited forage availabilty is further evident as the first year of the study resulted in an increase in litter with a subsequent decrease litter heterogeneity and bare ground, while in the second year neither were changed. Snow covered vegetation unavailable for grazing would likely result in an increase in litter cover and homogenity post grazing. Visual obstruction readings and heterogeneity displayed greater decreases the second year than in year one of the grazing trial, however, it is unclear if these findings are due to forage availability in relation to snow cover or the fact that the grazing season in the second year was approximately 2 weeks longer than the first year.

IMPLICATIONS

We observed high individual variability in grazing site selection of cattle, suggesting individual-level factors could be the dominant drivers in grazing resource use and behavior. Our research shows that the combination of age, supplement intake, and weight and body condition, can interact with the environmental attributes of the landscape to influence grazing behavior resulting in significant implications in animal and land management. Cattle experience, nutrient status and the energetic cost of grazing activity may be dominant drivers in cattle resource utilization. Individual variation in supplement intake has the potential to influence individual animal nutrient status and performance, thus altering grazing behavior and paddock use. Monitoring daily grazing behavior without accounting for individual level factors may not provide meaningful insight about the complex interrelationships that exist between grazing livestock and their environment. Future research examining the effects of supplementation on grazing behavior and resource use should incorporate individual animal measurements in an attempt to account for individual animal variablity. Incorporating measurements of animal performance, forage intake and energetic costs associated with travel and grazing activities could provide meaningful insight to the mechanisms driving grazing behavior and distribution. Understanding the effects of supplementation and variation in supplement intake on animal performance, behavior and paddock use are essential in the development of a cost effective and sustainable supplementation program for dormant season grazing.

Our research provides evidence that even in winter dormant forage conditions, cattle select grazing locations based on the relative quantity and quality of available forage. Additionally, supplement intake can have an effect on the distance traveled, total time spent grazing per day and grazing resource use. For landscape attributes with substantial variablity in herd-level resource use, individual-level measurements (body weight and condition, age, supplement intake) were found to be significant predictors cattle resource use. Grazing intensity had little effect on vegetation conditons and spatial variability, however, this may be related to pasture vegetation and weather conditions at the time of grazing. The effect of winter grazing on vegetative conditions, as well as, spatial variability of vegetation (ie. heterogeneity) appeared to be strongly influenced by the weather conditions. Prolonged periods of snow cover presumably limited forage availability, reducing grazing selection and the overall effects of grazing on vegetation conditions.

Table 6. Average winter temperature (low, high, mean; °C) and total precipitation (cm) for the 2 years of grazing (2016 – 2017, 2017 – 2018) at the Northern Agricultural Research Center Thackeray ranch, Havre, MT

	Temperature, °C			
	Low	High	Mean	Precipitation (cm)
Year 1	-22.70	3.80	-9.60	2.90
Year 2	-24.30	14.90	-2.00	4.06

Table 7. Average annual grass production (± SE, kg/ha), Crude Protein (CP ± SE; %), Neutral Detergent Fiber (NDF ± SE; %) and Acid Detergent Fiber (ADF ± SE; %) of the experimental paddock for the 2 years of grazing (2016 – 2017, 2017 – 2018) at the Northern Agricultural Research Center Thackeray ranch, Havre, MT

	Grass Production (kg/ha)	CP (%)	NDF (%)	ADF (%)
Year 1	3128.03 (21.78)	6.85 (0.03)	70.46 (0.08)	43.92 (0.05)
Year 2	2709.42 (23.71)	7.07 (0.03)	70.09 (0.08)	4.46 (0.05)

Table 8. Model selection for models evaluating the effects of cow age, body condition and supplement intake on time spent grazing per day (hrs) and distance traveled per day (km) by cattle grazing dormant rangeland in 2016 – 2017 & 2017 – 2018 at the Northern Agricultural Research Center Thackeray ranch, Havre, MT

Model[b]	K[c]	AICc[d]	ΔAICc[e]	W_i[f]	r^2m[g]	r^2c[h]
Time Spent Grazing per Day						
Age^2 + Supplement Intake +ln(Body Condition) × ln(Body Weight)	9	10113.50	0.00	0.28	0.12	0.51
Age^2 + ln(Body Condition) × ln(Body Weight)	8	10113.53	0.03	0.28	0.11	0.51
ln(Body Condition) × ln(Body Weight)	6	10115.92	2.42	0.08	0.02	0.51
Constant (null)	3	10123.61	10.11	0.00		
Distance Traveled per Day						
ln(Age) + ln(Supplement Intake) × ln(Body Condition) + ln(Body Condition) × ln(Body Weight)	10	8643.60	0.00	0.40	0.18	0.26
ln(Age) + ln(Supplement Intake) × ln(Body Condition)	7	8646.05	2.45	0.12	0.18	0.25
ln(Age) + ln(Supplement Intake) + ln(Body Condition) × ln(Body Weight)	8	8646.16	2.56	0.11	0.18	0.26
ln(Age) × ln(Body Weight) + ln(Supplement Intake) × ln(Body Condition)	9	8646.29	2.68	0.11	0.18	0.26
ln(Age) + ln(Supplement Intake)	5	8647.31	3.71	0.06	0.17	0.25
ln(Age) + ln(Supplement Intake) × ln(Body Condition) + ln(Body Weight)	8	8647.37	3.77	0.06	0.18	0.26
Constant (null)	3	9027.40	383.80	0.00		

[a]Only models with Akaike weights (w_i) ≥ 0.05 are presented except for the null model.
[b]Cow is used as a random variable in all models.
[c]K = number of parameters.
[d]Akaike's information criterion adjusted for small sample size.
[e]Difference in Akaike's information criterion adjusted for small sample size compared to the best model.
[f]Akaike weight.
[g]Marginal R^2
[h]Conditional R^2

Table 9. Model selection for models evaluating the effects of cow age, body condition and supplement intake on the effect size of distance from supplement, distance from water and elevation from the RUF analysis of cattle grazing dormant rangeland in 2016 – 2017 & 2017 – 2018 at the Northern Agricultural Research Center Thackeray ranch, Havre, MT

Model[b]	K[c]	AICc[d]	ΔAICc[e]	W_i[f]	r^2[g]
Distance from Supplement					
Age^2 + Supplement $Intake^2$ + Body $Weight^2$	8	60.74	0.00	0.57	0.45
Age^2 + Supplement $Intake^2$ + Body $Weight^2$ + Body $Condition^2$	10	63.01	2.27	0.18	0.48
Age^2 + Body $Condition^2$ + Age^2 × Body $Condition^2$	9	65.08	4.34	0.06	0.43
Constant (null)	2	80.21	19.47	0.00	
Distance from Water					
Age^2 + ln(Supplement Intake) + Body $Weight^2$ + Body $Weight^2$ × ln(Supplement Intake)	9	-4.25	0.00	0.21	0.41
Age^2 + ln(Supplement Intake) + Body $Weight^2$	7	-3.52	0.73	0.15	0.34
ln(Supplement Intake) + Body $Weight^2$ + Body $Weight^2$ × ln(Supplement Intake)	7	-2.97	1.29	0.11	0.34
ln(Supplement Intake) + Body $Weight^2$	5	-2.10	2.16	0.07	0.26
Age^2 + ln(Supplement Intake)	5	-2.02	2.23	0.07	0.26
Age^2 + Body $Weight^2$	6	-1.84	2.41	0.06	0.29
Constant (null)	2	8.68	12.93	0.00	
Elevation					
Age Class + ln(Supplement Intake) + ln(Body Weight)	9	28.89	0.00	0.39	0.43
Age Class + ln(Supplement Intake) × ln(Body Weight)	7	29.66	0.77	0.27	0.36
Age Class + ln(Supplement Intake) + ln(Body Condition) + ln(Body Weight)	8	30.78	1.89	0.15	0.38
Constant (null)	2	43.69	14.80	0.00	

[a]Only models with Akaike weights (w_i) ≥ 0.05 are presented except for the null model.
[b]Cow is used as a random variable in all models.
[c]K = number of parameters.
[d]Akaike's information criterion adjusted for small sample size.
[e]Difference in Akaike's information criterion adjusted for small sample size compared to the best model.
[f]Akaike weight.
[g]Multiple R^2

Table 10. Model selection for models evaluating the effects of vegetation quality and production, cow age, body condition, body weight and supplement intake on grazing resource utilization by cattle grazing dormant rangeland in 2016 – 2017 & 2017 – 2018 at the Northern Agricultural Research Center Thackeray ranch, Havre, MT

Model[b]	K[c]	AICc[d]	ΔAICc[e]	W_i[f]	r^2m[g]	r^2c[h]
ln(Grass Production) × ln(Neutral Detergent Fiber) + ln(Grass Production) × ln(Crude Protein)	8	12369.22	0.00	0.51	0.05	0.13
ln(Grass Production) × ln(Neutral Detergent Fiber) + ln(Crude Protein)	7	12369.31	0.07	0.49	0.05	0.13
Constant (null)	3	12582.92	213.68	0.00		

[a]Only models with Akaike weights (w_i) ≥ 0.05 are presented except for the null model.
[b]Cow is used as a random variable in all models.
[c]K = number of parameters.
[d]Akaike's information criterion adjusted for small sample size.
[e]Difference in Akaike's information criterion adjusted for small sample size compared to the best model.
[f]Akaike weight.
[g]Marginal R^2
[h]Conditional R^2

Table 11. Pre- post differences in mean (± SE) visual obstruction and residual cover classifications by year for cattle grazing dormant rangeland in 2016 – 2017 & 2017 – 2018 at the Northern Agricultural Research Center Thackeray ranch, Havre, MT

			P-Value		
	Year 1	**Year 2**	**Year**	**Grazing Intensity**	**Year × Grazing Intensity**
VOR[a], cm	-5.94 (0.29)	-7.96 (0.62)	< 0.01	0.25	0.23
Bare Ground, %	-1.41 (0.43)	1.32 (0.79)	< 0.01	0.64	0.49
Litter, %	14.19 (2.22)	0.91 (1.33)	< 0.01	< 0.01	0.15
Grass, %	5.95 (2.60)	1.58 (2.96)	0.26	0.22	0.03
Forb, %	-6.42 (0.86)	-6.78 (0.79)	0.76	0.05	0.08

[a]Visual Obstruction Reading

Table 12. Pre-post difference in heterogeneity (as indexed by differences in standard deviation ± SE) of visual obstruction and residual cover classifications by year for cattle grazing dormant rangeland in 2016 – 2017 & 2017 – 2018 at the Northern Agricultural Research Center Thackeray ranch, Havre, MT

			P-Value		
	Year 1	Year 2	Year	Grazing Intensity	Year × Grazing Intensity
VOR[a], cm	-1.90 (0.27)	-3.21 (0.46)	0.02	0.63	0.36
Bare Ground, %	-0.64 (0.57)	1.53 (1.08)	0.08	0.63	0.71
Litter, %	-5.36 (1.50)	-0.57 (1.52)	0.02	0.01	0.20
Grass, %	-0.77 (1.31)	0.76 (1.28)	0.41	0.41	0.74
Forb, %	-5.03 (0.71)	-5.72 (0.84)	0.54	0.36	0.20

[a]Visual Obstruction Reading

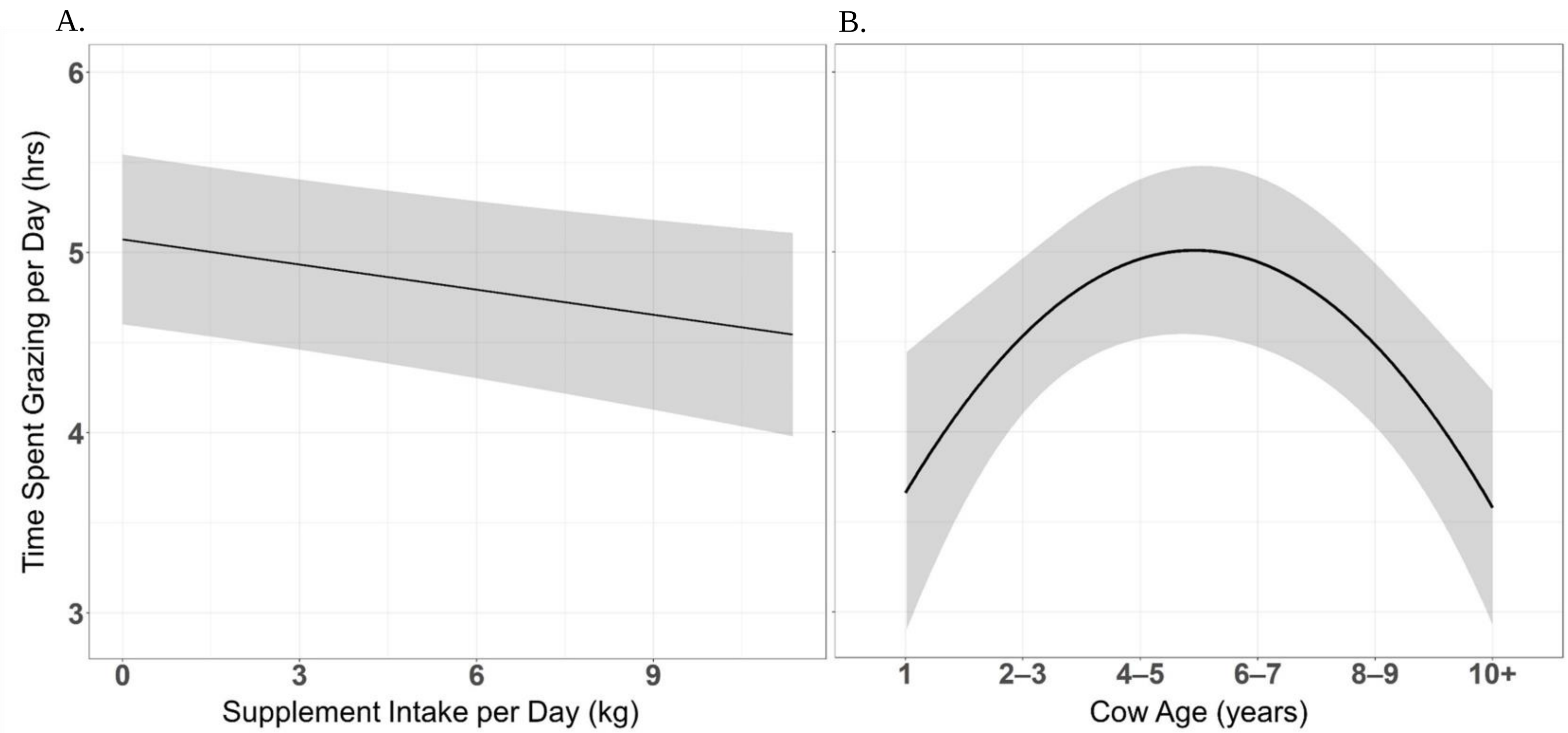

Figure 10. Predicted relationships (± 95%CI represented in the shaded area) between average A) supplement intake per day (kg) and B) cow age (years) on time spent grazing per day (hrs) by cattle grazing dormant northern mixed grass rangeland in 2016 – 2017 & 2017 – 2018 at the Northern Agricultural Research Center Thackeray ranch, Havre, MT

A.

B.

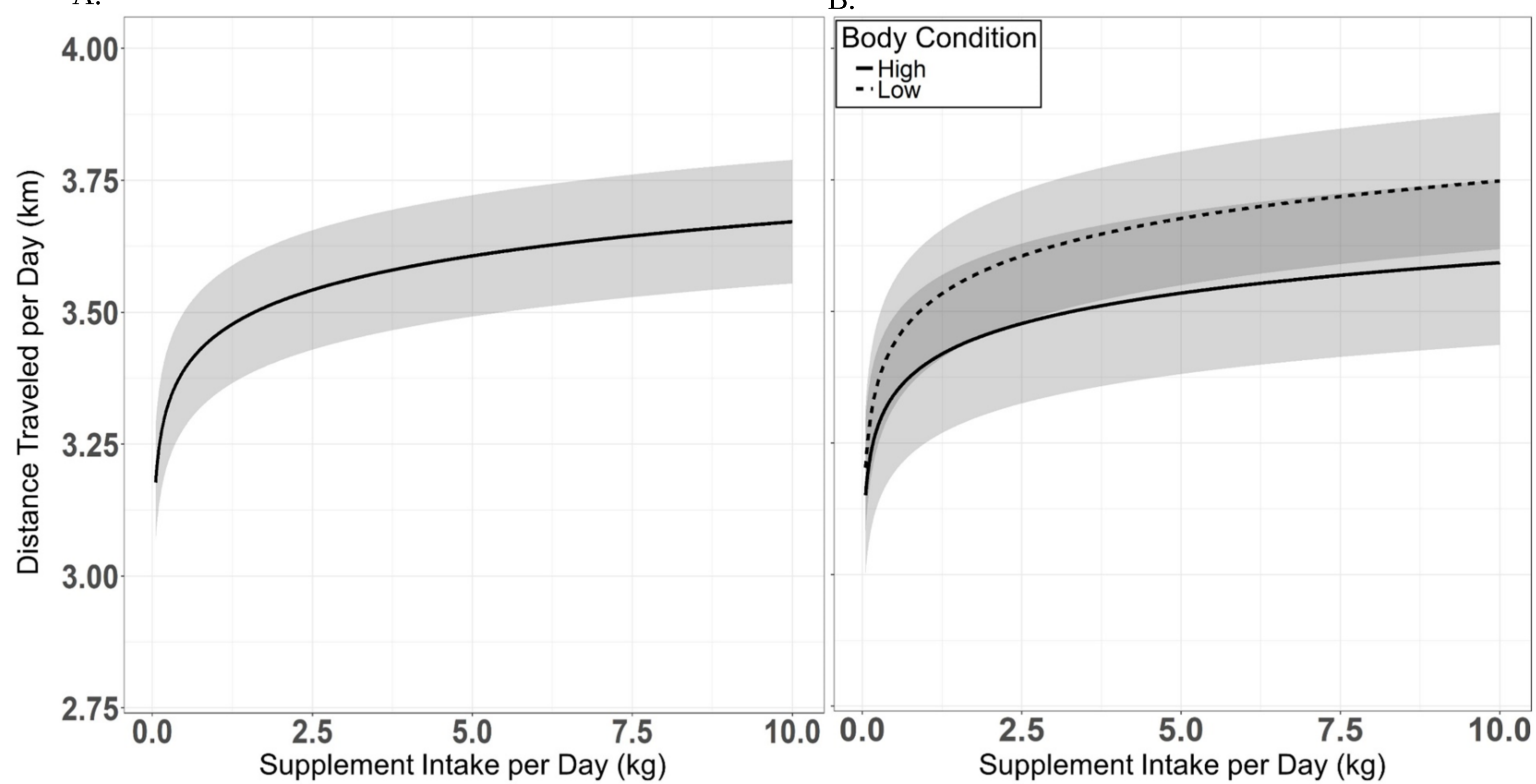

Figure 11. Predicted relationships (± 95%CI represented in the shaded area) between A) average supplement intake per day (kg) and B) the interaction of average supplement intake per day by body condition on distance traveled per day (km) by cattle grazing dormant northern mixed grass rangeland in 2016 – 2017 & 2017 – 2018 at the Northern Agricultural Research Center Thackeray ranch, Havre, MT

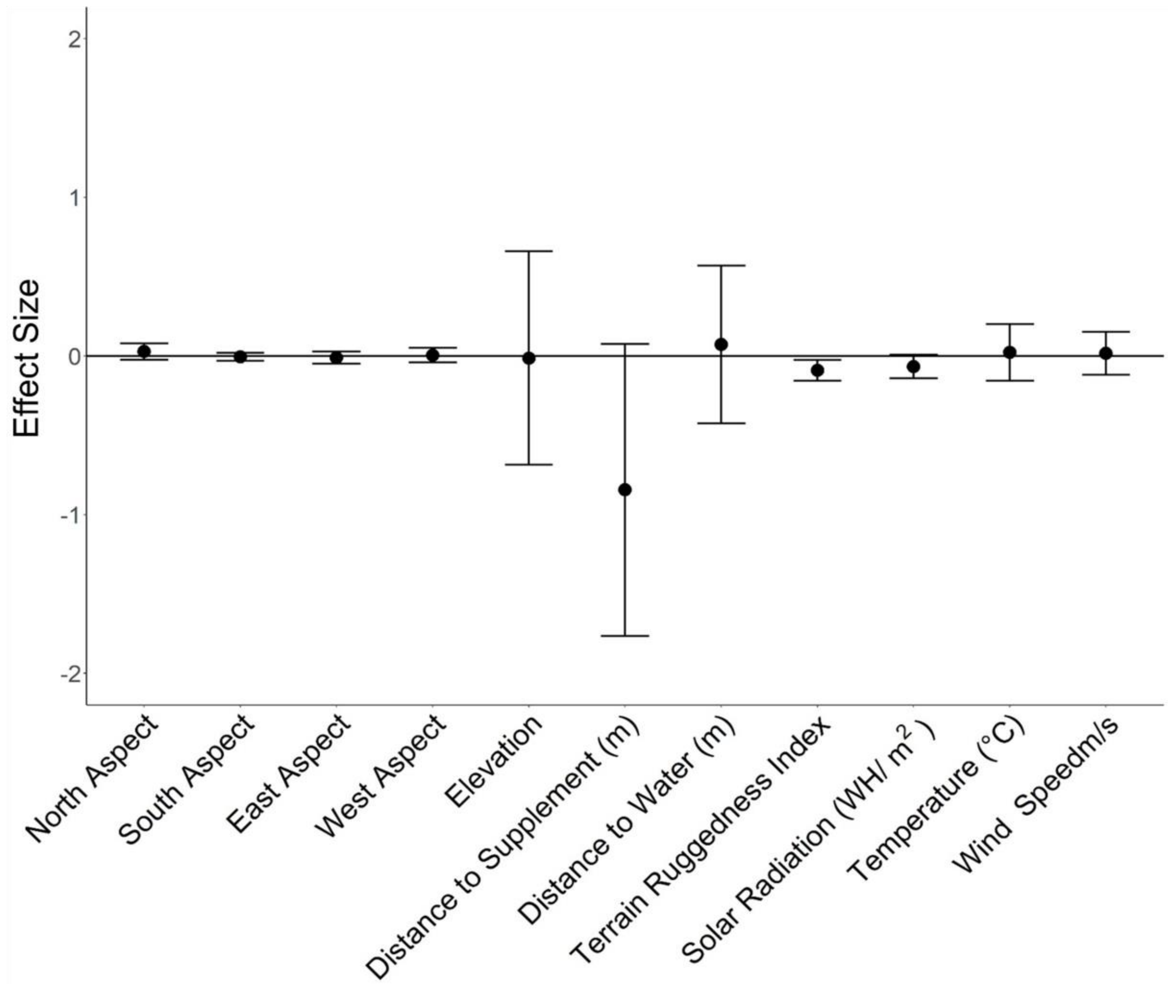

Figure 12. Mean standardized herd-level effect size ($\hat{\bar{\beta}}$ ± 95% CI) for cattle grazing resource utilization functions, 95% confidence intervals of $\hat{\bar{\beta}}$ that do not overlap zero denote significant responses at the population level

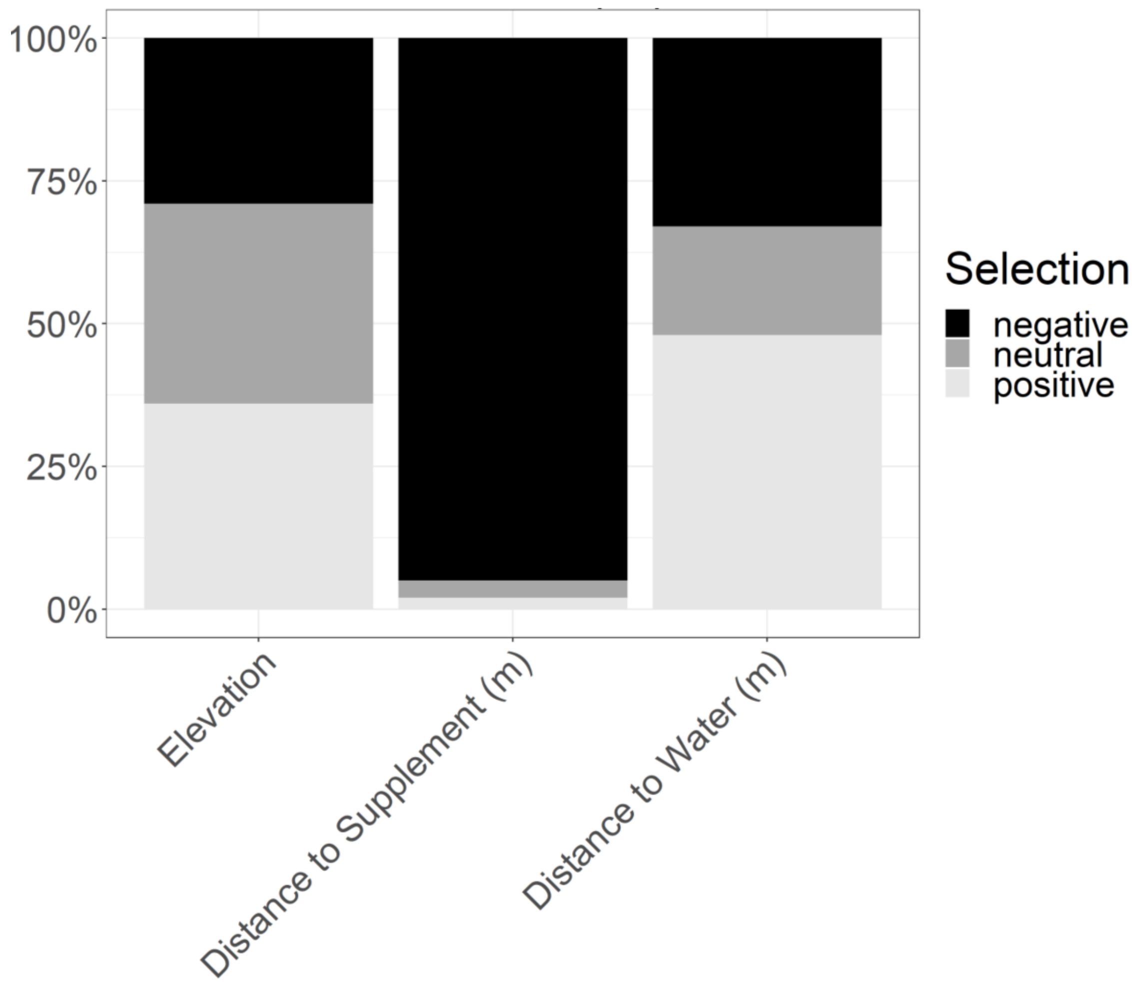

Figure 13. Percent of GPS collared cattle with positive, neutral, and negative selection coefficients relative to elevation, distance to supplement and distance to water from the resource utilization analysis for cattle grazing dormant northern mixed grass rangeland in 2016 – 2017 & 2017 – 2018 at the Northern Agricultural Research Center Thackeray ranch, Havre, MT.

A. B. C.

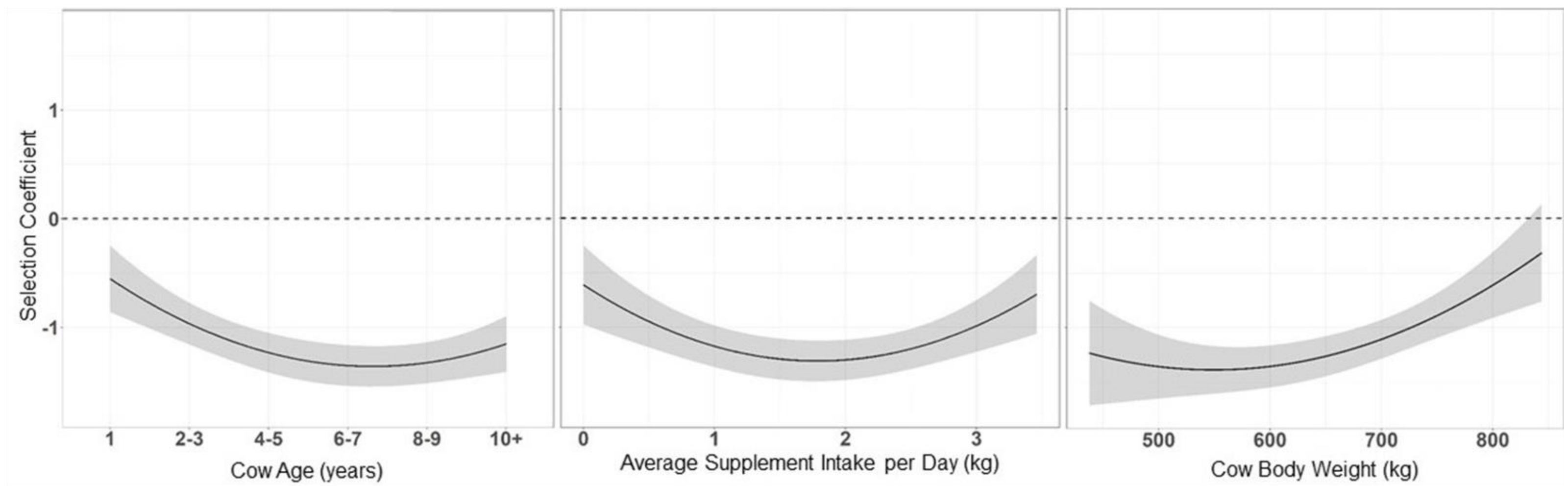

Figure 14. Predicted relationships (± 95%CI represented in the shaded area) between A) cow age (years), B) average supplement intake per day (kg) and C) cow body weight (kg) on resource utilization relative to distance from supplement by cattle grazing dormant northern mixed grass rangeland in 2016 – 2017 & 2017 – 2018 at the Northern Agricultural Research Center Thackeray ranch, Havre, MT.

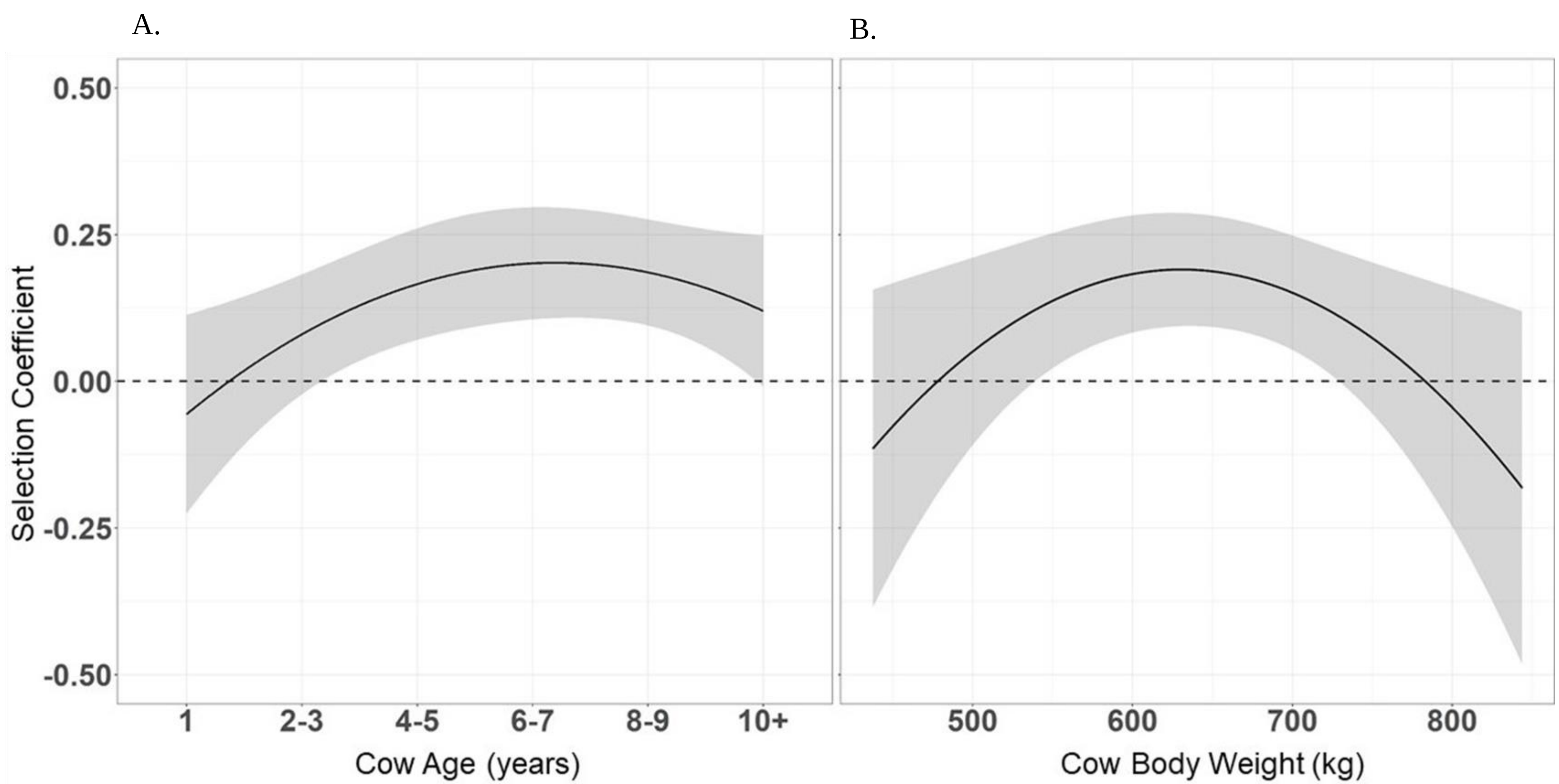

Figure 15. Predicted relationships (± 95%CI represented in the shaded area) between A) cow age (years) and B) cow body weight (kg) on resource utilization relative to distance from water by cattle grazing dormant northern mixed grass rangeland in 2016 – 2017 & 2017 – 2018 at the Northern Agricultural Research Center Thackeray ranch, Havre, MT

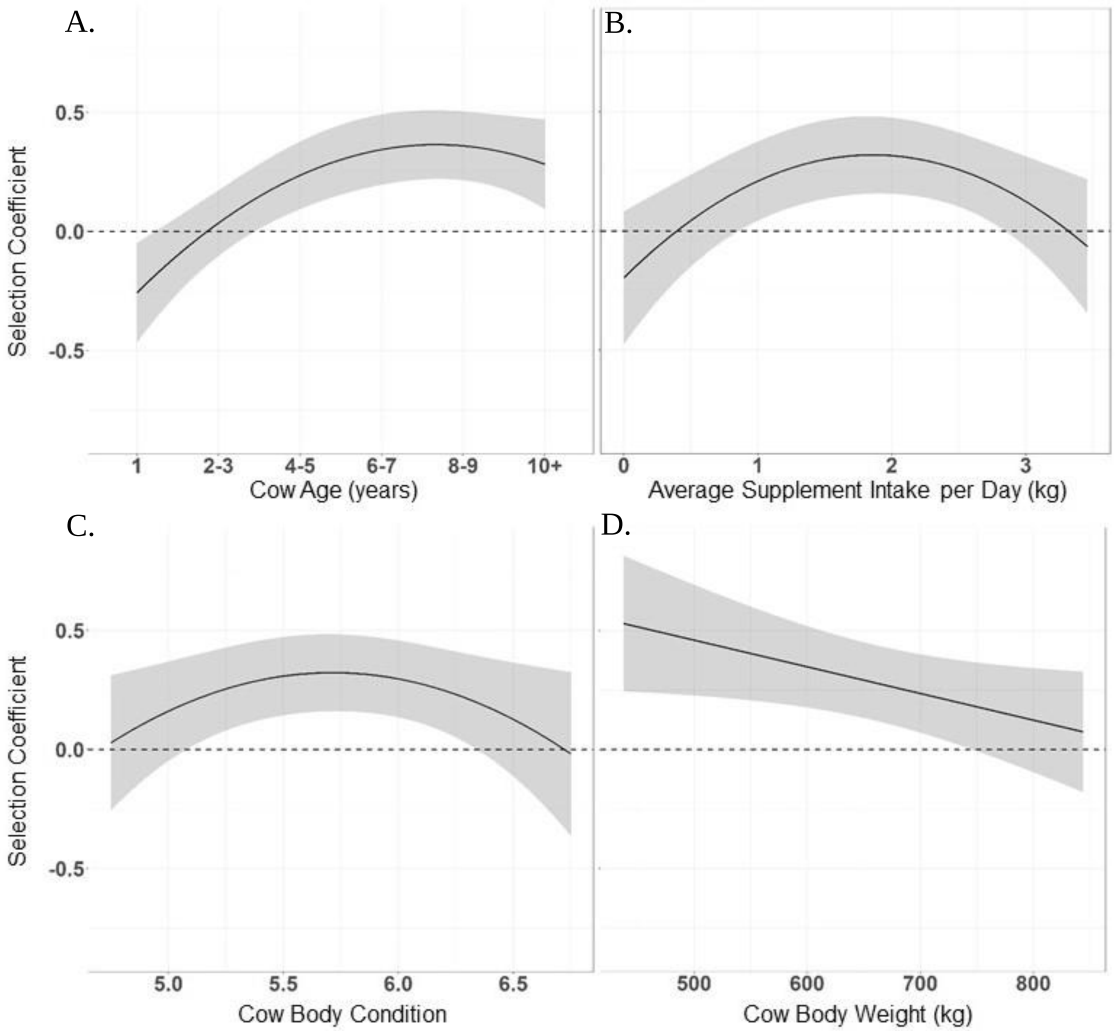

Figure 16. Predicted relationships (± 95%CI represented in the shaded area) between A) cow age (years), B) average supplement intake per day (kg), C) cow body condition and D) body weight (kg) on resource utilization relative elevation by cattle grazing dormant northern mixed grass rangeland in 2016 – 2017 & 2017 – 2018 at the Northern Agricultural Research Center Thackeray ranch, Havre, MT

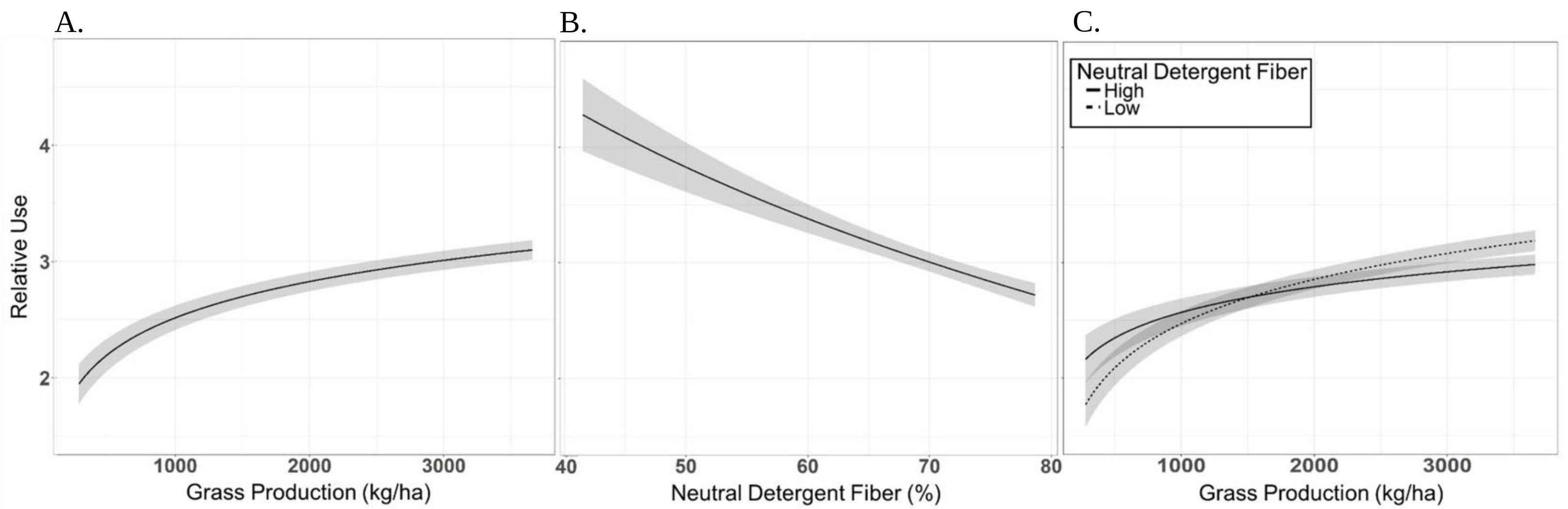

Figure 17. Predicted relationships (± 95%CI represented in the shaded area) between A) grass production, B) neutral detergent fiber, and C) the interaction of grass production by neutral detergent fiber on relative resource utilization by cattle grazing dormant northern mixed grass rangeland in 2016 – 2017 & 2017 – 2018 at the Northern Agricultural Research Center Thackeray ranch, Havre, MT.

A. B. C.

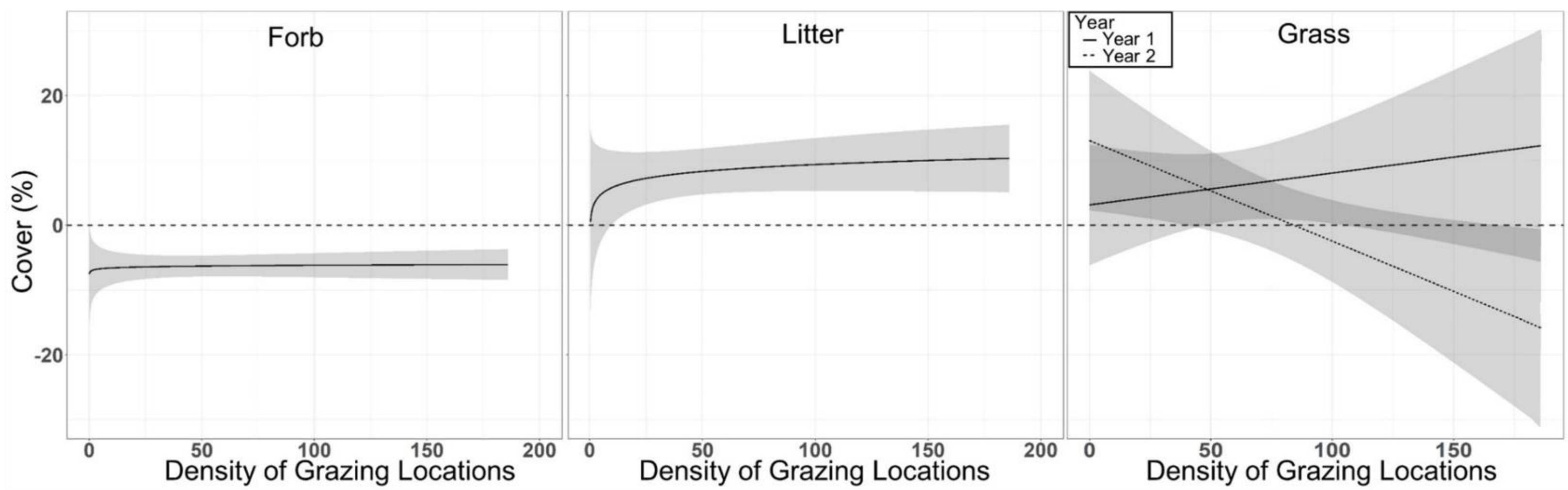

Figure 18. Predicted relationships (± 95%CI represented in the shaded area) of pre- post grazing differences of residual cover of A) forb, B) litter, C) a grass by year interaction and the density of grazing locations within a 50 m radius of transect locations by cattle grazing dormant northern mixed grass rangeland in 2016 – 2017 & 2017 – 2018 at the Northern Agricultural Research Center Thackeray ranch, Havre, MT.

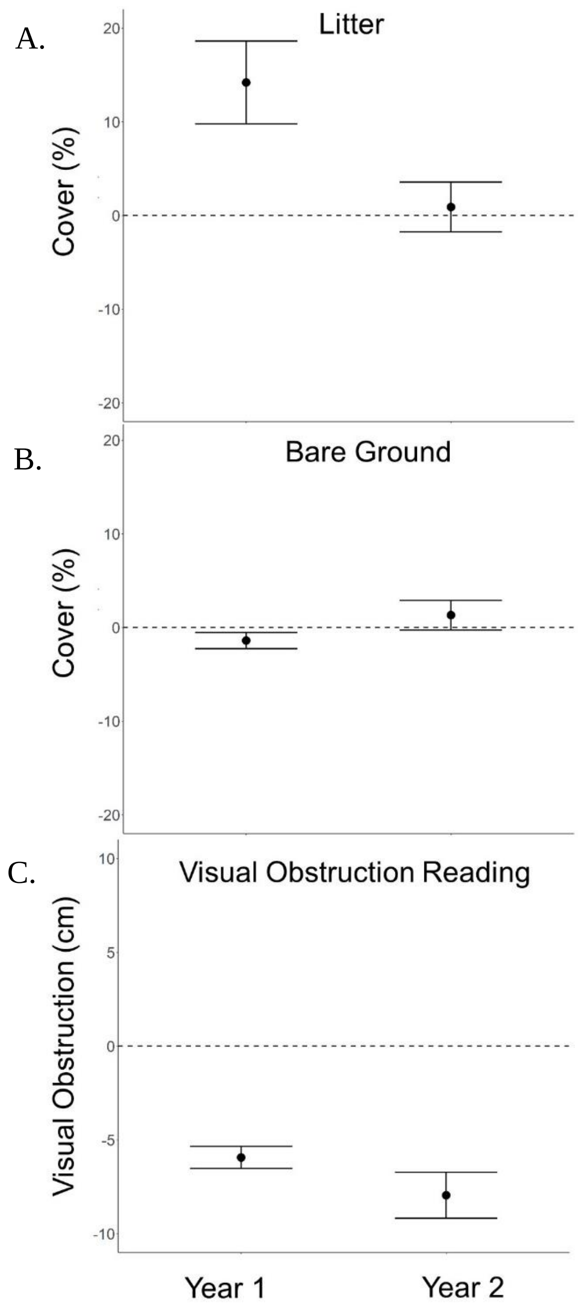

Figure 19. Pre- post differences in mean (± 95% CI) A) bare ground, B) litter and C) visual obstruction by year for dormant northern mixed grass rangeland vegetation grazed by cattle in 2016 – 2017 & 2017 – 2018 at the Northern Agricultural Research Center Thackeray ranch, Havre, MT

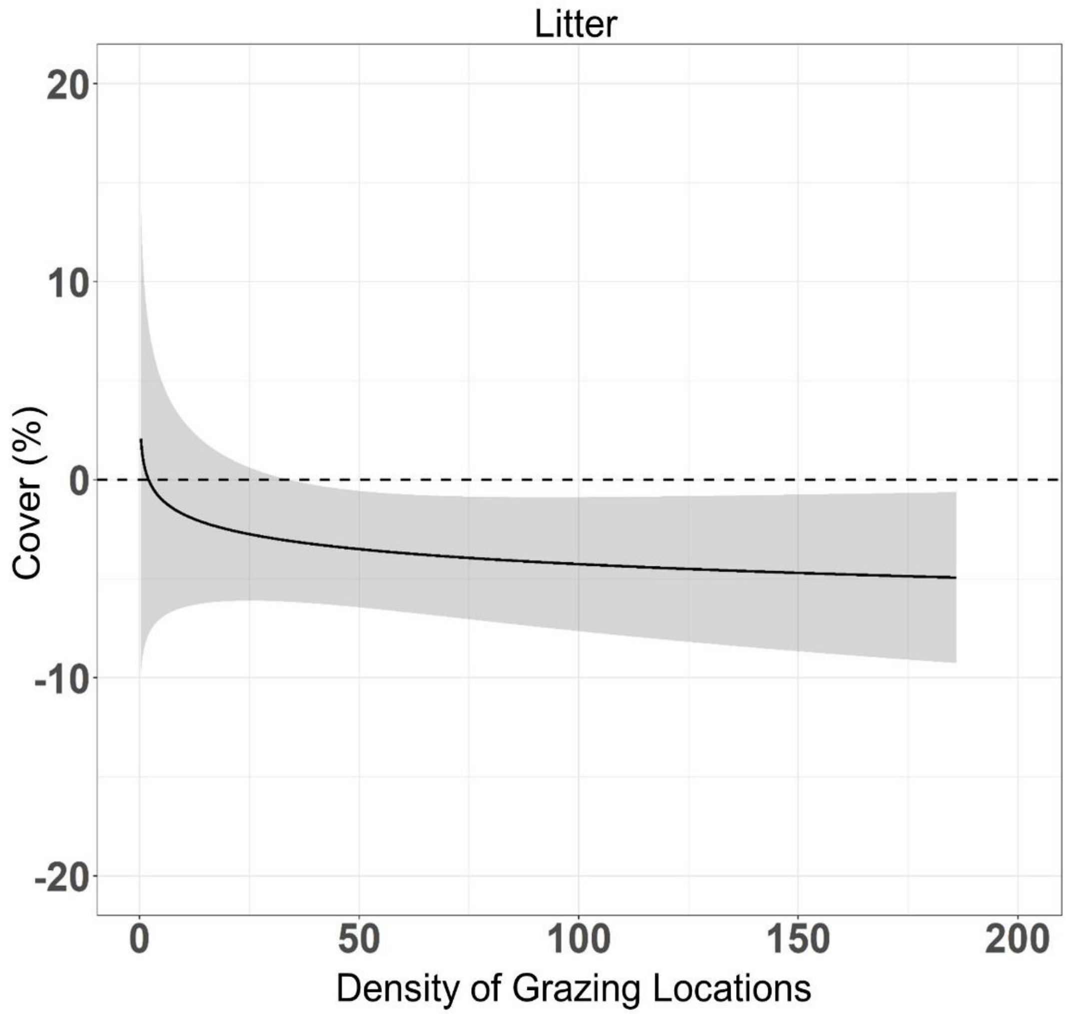

Figure 20. Predicted relationships (± 95%CI represented in the shaded area) between pre- post grazing heterogeneity (as indexed by difference of standard deviation among transects) of litter and density of grazing locations within a 50 m radius of transect by cattle grazing dormant northern mixed grass rangeland in 2016 – 2017 & 2017 – 2018 at the Northern Agricultural Research Center Thackeray ranch, Havre, MT.

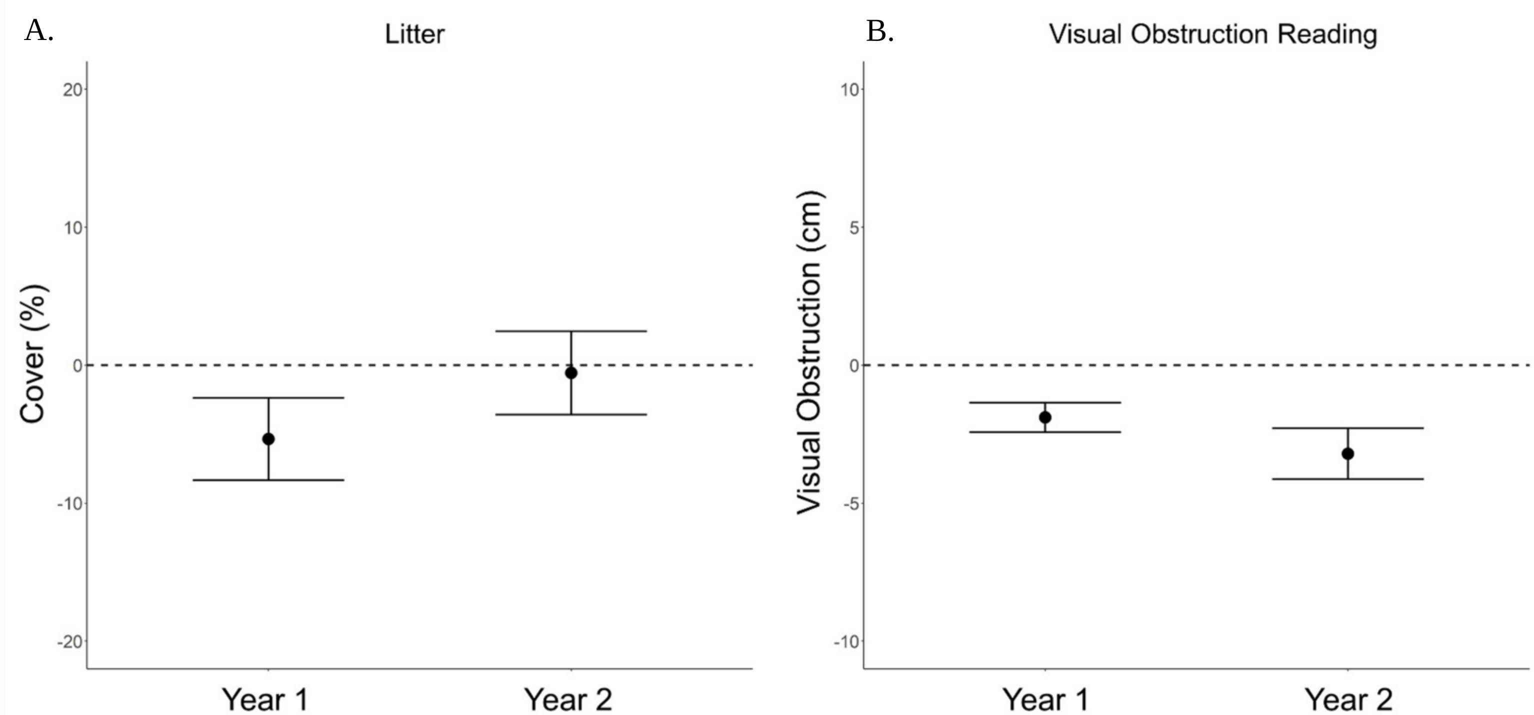

Figure 21. Pre- post difference in heterogeneity (as indexed by difference of standard deviation among transects; ± 95% CI) of A) litter cover and B) visual obstruction by year for dormant northern mixed grass rangeland vegetation grazed by cattle in 2016 – 2017 & 2017 – 2018 at the Northern Agricultural Research Center Thackeray ranch, Havre, MT

CHAPTER FOUR

THE INFLUENCE OF AGE AND ENVIRONMENTAL CONDITIONS ON SUPPLEMENT INTAKE BY BEEF CATTLE WINTER GRAZING A NORTHERN MIXED-GRASS RANGELAND IN MONTANA

Contribution of Authors and Co-Authors

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Contributions: Conceptualization, methodology, project administration, supervision, validation, writing review and editing.

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CHAPTER FOUR

THE INFLUENCE OF AGE AND ENVIRONMENTAL CONDITIONS ON SUPPLEMENT INTAKE BY BEEF CATTLE WINTER GRAZING A NORTHERN MIXED-GRASS RANGELAND IN MONTANA

INTRODUCTION

Beef cattle production on Montana farms accounted for $1.78 billion of gross income and 42% of Montana's total agricultural sales in 2012 (USDA-NASS 2016). Montana cattle operations are primarily cow-calf production systems that rely heavily on forages to supply nutrients for both cows and calves (Galyean and Goetsch 1993). High feed and input costs threatens the economic efficiency of cattle production (Meyer and Gunn 2015). Thus, many cow-calf producers have adopted management strategies involving dormant season grazing in an attempt to reduce reliance on transported harvested feeds and improve profitability (Adams et al. 1996). However, dormant range forage is deficient in nutrients typically resulting in decreased animal performance (Krysl and Hess 1993, Bowman et al. 1995, Mulliniks et al. 2013a).

Winter grazing at northern latitudes typically exposes cattle to periods of severe cold which increases energy expenditure to maintain homeothermy (Webster 1970, Webster 1971, Young and Christopherson 1974). Animals respond to the increased metabolic demand by increasing intake to meet thermoregulatory needs (Baile and Forbes 1974, Mount 1979, Weston 1982, Ames and Ray 1983, Arnold 1985, Beverlin 1988).

Thus, winter conditions can have considerable economic impact on the energetic efficiency of cattle production on rangelands (Webster 1970).

In order to meet the nutritional needs and maintain a desired level of productivity on nutrient deficient rangelands during winter months, supplemental protein is often provided to increase intake and performance (Lusby et al. 1967, Bowman et al. 1995, Bodine et al. 2001). Supplementation strategies assume that all animals consume a targeted quantity of supplement (Bowman and Sowell 1997). However, this ignores variation of supplement intake by individual animals and the potential problems associated with supplementation not occuring at targeted amounts. If animals consume less than the target amount, the formulated nutrient intake is not received, increasing the potential for nutrient stress. Animals consuming over the targeted amount increase supplementation costs and the potential for negative impacts on forage intake (Bowman and Sowell 1997). Therefore, deviation from the targeted consumption of supplement can have deleterious effects on animal performance (Bowman and Sowell 1997), reflected as decreased profit for the producer.

Effectiveness of supplementation programs on grazing cattle performance have been inconsistent (DelCurto et al. 1990). This inconsistency may be due to variation in supplement intake by individual cows, which is often influenced by social dominance associated with age within the herd (Wagnon 1965, Friend and Polan 1974). Cow age has been shown to be an influential factor affecting individual supplement intake, foraging behavior and distribution (Adams et al. 1986, Kincheloe et al. 2004, Walburger et al. 2009). However, interactions of environmental factors with individual animal attributes are less understood (Walburger et al. 2009). Potential changes in energetic requirements to maintain homeothermy could alter supplement intake during winter months. Short-term behavioral responses may be critical to the energy balance of domestic animals under extreme weather conditions (Senft and Rittenhouse 1985). Therefore, the goal of this research is to examine the effects of cow age and winter temperature and wind conditions on individual supplement intake by cattle grazing winter rangelands in Montana. We hypothesize that both cow age and winter environmental conditions affect the daily intake of supplement, as well as, the variation in supplement intake.

MATERIALS AND METHODS

Our study was conducted at the Thackeray Ranch (48^{o} 21' N 109^{o} 30' W), part of the Montana Agricultural Experiment Station located 21 km south of Havre, MT. Climate is characterized as semi-arid steppe with an average annual precipitation of 410 mm. Vegetation is dominated by Kentucky bluegrass (*Poa pratensis L.*), bluebunch wheatgrass (*Pseudoregnaria spicata* [Pursh] A. Love), and rough fescue (*Festuca scabrella Torr*.). Preciptiation was higher in the winter of 2017 – 2018 than 2016 – 2017 (4.06, 2.90 cm), however, temperatures durring the 2016–2017 winter were substantially cooler than the winter of 2017–2018 (-9.60, -2.90 °C), resulting in higher amounts and prolonged periods of snow in the first year of the study (Table 13).

A commercial herd of bred cows (Angus, Angus x Simmental) ranging in age from 1- to 12 grazed a 329-ha rangeland pasture (~1.5 AUM ha^{-1}) for 2 years (272 cows with an average weight of 620 kg in the 1st year, and 302 cows with an average weight of

580 kg in the 2nd year). The winter grazing season occurred from December 1, 2016 to January 12, 2017, and November 1, 2017 to December 31, 2017. All cattle had free-choice access to a 30% crude protein (CP) self-fed canola meal-based (35% as-fed basis) pelleted supplement with 25% salt to limit intake (Table 14). The target daily intake was 0.91 kg/cow. Each individual animal was equipped with an electronic ID tag (Allflex USA, Inc., Dallas-Ft. Worth, TX) attached to the exterior of the left ear for the measurement of daily individual supplement intake and the number of supplement visits using a SmartFeed Pro self-feeder system (C-Lock Inc., Rapid City, SD) that provided a total of 8 feeding stations.

The production and quality of pasture vegetation was estimated by sampling seventy-five randomly located plots prior to grazing each year. Clipped samples were placed in a forced air oven at 60°C for 48 hours and then weighed. Vegetation samples from each plot were ground to pass a 1-mm screen in a Wiley mill. Samples were then analyzed in duplicate for nitrogen (Leco CN-2000; Leco Corporation, St. Joseph, MI), and fiber (NDF and ADF; Ankom 200 Fiber Analyzer, Ankom Co., Fairport, NY) as indicators of vegetation quality (Table 15).

Cattle were assigned to one of six age classifications (1-yr-old, 2 & 3-yr-olds, 4 & 5-yr-olds, 6 & 7-yr-olds, and 8 & 9-yr-olds, and ≥ 10-yr-old) to evaluate the effects of age class on daily individual supplement intake, number of visits to the supplement feeders, and the coefficient of variation (CV) of daily supplement intake. Results of a preliminary analysis to evaluate the length of time between supplement intake readings that constitute a new visit to the supplement feeders suggested that readings more than

30-min apart delineate a new visit. This 30-min duration of time was then validated by visual observations of cattle visits to the supplement feeder. Each cow was considered an experimental unit. Supplement intake variables were analyzed using ANOVA with a mixed model including age class, year, and the interaction of age class and year as fixed effects. We included individual cow as a random intercept to account for the autocorrelation of repeated measurements of supplement intake variables for each individual cow. Least square means were separated using the pairwise method when $P < 0.05$.

An Onset HOBO U30-NRC Weather Station (Bourne, MA, USA) was placed near the supplement feeders and programmed to collect ambient air temperature, relative humidity, and wind speed and direction data every 15 min for the entirety of the grazing period. Daily average weather conditions were then paired with daily supplement intake readings for each individual animal for the duration of the grazing period. Models were developed to evaluate the influence of environmental conditions and age on daily supplement intake with generalized linear mixed models with a Gaussian (normal) error structure using individual animal as a random intercept to account for autocorrelation of repeated measurements for each individual. To avoid overfitting our models, we conducted a preliminary multicollinearity analysis to select uncorrelated ($|r| > 0.6$) environmental variables (Dormann et al. 2013). If two environmental conditions were correlated, we fit preliminary models evaluating the effect of each environmental condition on the daily supplement intake and evaluated relative support using Akaike's Information Criterion adjusted for small sample sizes (AICc Burnham and Anderson

2002); we retained the environmental condition with the most relative support for further modeling and discarded the correlated variable (Fieberg and Johnson 2015). We hypothesized that cow age and environmental conditions could elicit one of three behavioral responses (linear, pseudothreshold, quadratic). Variables hypothesized to exhibit a pseudothreshold pattern were tested with asymptotic models by evaluating the natural log of the explanatory variable (ln[x + 0.001]; Franklin et al. 2000). We used AIC_c to evaluate support for competing models reflecting hypotheses about the effects of animal age and environmental conditions on daily supplement intake (Burnham and Anderson 2002). Models with $\Delta AIC_c \leq 2$ that differed from the top model by a single parameter were excluded if confidence intervals of parameter estimates overlapped 0 (ie., were non-informative; Arnold 2010). When multiple models were supported, we use model-averaged estimates of beta-coefficients ("MuMIn" package for R; Bartoń 2018). Model fit was then evaluated by calculating marginal and conditional r^2 values for generalized linear mixed models ("MuMIn" package for R;Nakagawa and Schielzeth 2013). All statistical analyses were performed in R (R Core Team 2017).

RESULTS

The effects of age class on daily supplement intake, daily supplement intake CV and visits per day all displayed an age class × year interaction ($P < 0.01$), therefore, data are reported for each year independently (Table 16). In year 1 of the study, average daily intake decreased linearly with age class ($P < 0.01$), however, we did not observe the same relationship for year 2 ($P = 0.13$). In the second year, 2 – 3-year-old cattle consumed more supplement per day than yearlings, 4 – 5, and 6 – 7-year-old cattle ($P < 0.01$).

Visits to the supplement feeder were similar for all age classifications of cattle in year 1 (P = 0.30), however, displayed a quadratic relationship in year 2 (P < 0.01), where yearlings visited the supplement feeders less often than other age classes (P < 0.01). Daily supplement intake CV increased linearly with cow age in year 1 (P < 0.01). In year 2, daily supplement intake CV was lower for 2 – 3-year-old cattle than other age classifications (P < 0.01).

The effect of cow age, and winter environmental conditions on daily supplement intake were evaluated for 264 cows from December 1, 2016 to January 12, 2017 and 302 cows from November 1, 2017 to December 31, 2017. A single top model containing a cow age, average daily temperature and wind speed, and year received 85% of the relative support among candidate models when determining the effects of cow age and winter environmental conditions on daily supplement intake (Table 17). However, cow age ($\hat{\beta}$ = 0.0002 ± 0.009) and wind speed ($\hat{\beta}$ = 0.009 ± 0.005) may be non-informative as confidence intervals of the effect size overlap 0. Daily supplement intake increased by 0.25kg in year 2 compared to year 1 ($\hat{\beta}$ = 0.25 ± 0.02). There was a linear decrease in daily supplement intake with increasing temperature ($\hat{\beta}$ = -0.02 ± 0.002), however, there was an interaction of temperature by cow age ($\hat{\beta}$ = 0.003 ± 0.0003). Indicating that cattle decreased daily supplement intake linearly with increasing age at cold temperatures and increased daily supplement intake with cow age during warmer temperatures (Figure 22). An asymptotic effect of wind speed by year interaction was also supported ($\hat{\beta}$ = 0.03 ± 0.007), where both years had rapid increases in daily supplement intake with increasing wind speeds meeting a threshold < 5m/s, however, supplement intakes were higher per unit increase of wind speed in year 2 (Figure 22). The top model evaluating the effects of winter environmental conditions on supplement intake per day had a conditional r^2 of 0.20 with a marginal r^2 of 0.02 suggesting age, temperature and wind speed only accounted for 2% of the herd-level variation associated with supplement intake per day while the individual animal accounted for 18%.

DISCUSSION

The results of our study suggest that cow age can have a significant impact on daily supplement intake, daily supplement intake CV and daily visits to the supplement feeder. However, the effect of age on supplement intake behavior appears to vary across years, likely due to annual changing conditions. The few studies that have quantified supplement behavior of mixed age herds of cattle, have shown older cows typically consume more supplement (Bowman et al. 1999, Sowell et al. 2003, Kincheloe et al. 2004) and are less variable in their daily supplement intake than younger cows (Bowman et al. 1999). Our results contradict this conventional idea as daily supplement intake decreased and variability of daily supplement intake (indexed as % CV) increased with cow age class the first year of the study. Furthermore, 2 – 3-year-old cows had the highest daily supplement intake with the lowest variability in daily supplement intake in year 2. Maintenance energy expenditure can vary with age of cattle (National Research Council 2016). It is generally accepted that maintenance per unit of size decreases with age in ruminant livestock (Blaxter 1962, Graham et al. 1974, CSIRO 1990, 2007). Due to the poor quality of available forage in our study (approximately 70% NDF, 7% CP), younger cattle may have a higher reliance on supplement to meet their maintenance requirements in a winter environment than older cattle. Previous research has also shown that older cattle visit supplement feeders more often than younger cattle, however, these results have been inconsistent across years and studies (Bowman et al. 1999, Earley et al. 1999, Sowell et al. 2003). Our research showed no effect of age class on visits to the supplement feeder in year 1, with yearlings visiting the feeders less often than other age classes in year 2. This may be related to inexperience to winter grazing and supplementation by yearlings in year 2, as all other cattle had previous experience from the first year of the study.

All supplementation behavior measurements exhibited an age by year interaction, presumably due to substantially different weather conditions between year 1 and year 2 (Table 13). Chronic cold and wind exposure associated with northern winter grazing environments can increase the resting metabolic rate and overall energy expenditure of cattle in an effort to maintain homeothermy (Webster 1971, Christopherson et al. 1979, Keren and Olson 2006). The effect of age on daily supplement intake is mediated by ambient air temperature. Cold temperature conditions could potentially result in greater energetic needs for young cows to maintain homeothermy resulting in an increase in daily supplement intake as average daily temperatures drop. Wind appear to have varying effects on daily supplement intake across years. The inconsistency of this effect is likely due to differences in wind conditions across years and cows in the second year of the study being more experienced with grazing under winter conditions with the supplement provided.

We observed high levels of unaccounted variability in supplement intake per visit and day and the number of visits to the supplement feeders, suggesting, unmeasured individual-level and environmental factors could be dominant drivers in supplement behavior. Variation in supplement intake is positively associated with forage availability (Wagnon et al. 1966, Bowman and Sowell 1997). Snow cover could limit forage availability of grazing cattle. On average, the first year of our trial was 7.6 °C colder than year two resulting in prolonged time periods of snow ground cover. The second year of the study also received snowfall throughout the grazing period, however, warm temperatures limited prolonged periods of snow ground cover until late in the trial. Thus, varying forage availability throughout the grazing time period due to snow cover could have had an impact on behavior of supplement intake by cattle. Additionally, grazing animals have been estimated to expend 46% more energy than stall fed cattle with a 10 – 25% increase in maintenance requirements due to energetic costs associated with travel (Ribeiro et al. 1977, Havstad and Malechek 1982). Energetic requirements for maintenance are also directly related to the metabolic body weight of the animal ($BW^{0.75}$), with activity increasing energy requirements per unit body weight (National Research Council 2016). Cattle alter their grazing behavior in response to supplementation when grazing dormant forage (Barton et al. 1992, Krysl and Hess 1993, Schauer et al. 2005), which can influence the energy requirements of grazing livestock (Walker et al. 1985). Animal grazing activity and energy expenditure was not measured in our study but could be a substantial source variation in supplement intake behavior by cattle.

IMPLICATIONS

We found that cow age and winter environmental conditions can have a significant effect on supplement intake per day, supplement intake per visit, the CV of supplement intake, and visits to the supplement feeders per day. Despite some inconsistency of age and environmental effects across years, our research suggests cattle with presumed higher maintenance requirements (younger cattle) consume the most supplement, with increases in supplement intake when environmental conditions intensify metabolic demands. Thus, managers may want to ensure plenty of supplement is available when prolonged periods of cold weather are forecasted or manage younger cattle separately from older cattle. However, the management implications of this study should be interpreted cautiously, as our results are indicative of one cattle herd grazing in one location in Montana.

Our research did not quantify other indicators of animal condition that could significantly impact maintenance requirements. Thus, future research may consider tracking animal body condition, weight, forage availability and grazing activity when evaluating factors effecting supplement intake behavior. Specific factors such as cow age, environmental conditions, and supplement form need to be evaluated to determine their influence on supplement intake behavior. By providing a supplement delivery system that optimizes uniformity of consumption and minimizes economic inputs, we can effectively improve the efficiency of beef cattle production systems.

Table 13. Average winter temperature (low, high, mean; °C) and total precipitation (cm) for the 2 years of grazing (2016 – 2017, 2017 – 2018) at the Northern Agricultural Research Center Thackeray ranch, Havre, MT

	Temperature, °C			
	Low	**High**	**Mean**	**Precipitation (cm)**
Year 1	-22.70	3.80	-9.60	2.90
Year 2	-24.30	14.90	-2.00	4.06

Table 14. Supplement composition for cattle winter grazing rangeland in 2016 & 2017 at the Thackeray ranch, Havre MT (as-fed basis)

CP[1]	30.00 %
Crude fat	1.00 %
Crude fiber	8.00 %
Ca	2.00 %
P	1.00 %
Salt	25.00 %
K	0.75 %
Se	1.5 ppm
Vitamin A	9,072 IU/kg
Vitamin D	907 IU/kg
Vitamin E	9 IU/kg

[1]9.9% non-protein N

Table 15. Average annual grass production (SE, kg/ha), Crude Protein (CP; SE; %), Neutral Detergent Fiber (NDF; SE; %) and Acid Detergent Fiber (ADF; SE; %) of the experimental paddock for the 2 years of grazing (2016 – 2017, 2017 – 2018) at the Northern Agricultural Research Center Thackeray ranch, Havre, MT

	Grass Production (kg/ha)	CP (%)	NDF (%)	ADF (%)
Year 1	3128.03 (21.78)	6.85 (0.03)	70.46 (0.08)	43.92 (0.05)
Year 2	2709.42 (23.71)	7.07 (0.03)	70.09 (0.08)	4.46 (0.05)

Table 16. Mean (SE) daily supplement intake (kg), visits per day and daily supplement intake CV (%) by age for cattle grazing dormant rangeland in 2016 – 2017 & 2017 – 2018 at the Northern Agricultural Research Center Thackeray ranch, Havre, MT

	Age						***P*-Values**		
	1	**2 & 3**	**4 & 5**	**6 & 7**	**8 & 9**	**≥ 10**	**Age**	**Linear[1]**	**Quad[2]**
Year 1									
Daily intake, kg	1.32^{a} (0.12)	1.25^{ab} (0.11)	0.88^{bc} (0.08)	0.73^{c} (0.07)	0.67^{c} (0.12)	0.78^{abc} (0.18)	< 0.01	< 0.01	0.13
Visits per day	1.32^{a} (0.02)	1.30^{a} (0.02)	1.30^{a} (0.02)	1.28^{a} (0.02)	1.24^{a} (0.03)	1.26^{a} (0.04)	0.30	0.06	0.99
Daily intake CV, %	82.06^{a} (2.24)	80.76^{a} (2.20)	92.82^{b} (2.80)	105.50^{c} (3.44)	101.74^{bc} (5.80)	99.27^{abc} (7.16)	< 0.01	< 0.01	0.09
Year 2									
Daily intake, kg	1.06^{a} (0.06)	1.59^{b} (0.08)	1.21^{ac} (0.08)	1.16^{ac} (0.06)	1.26^{abc} (0.13)	1.51^{bc} (0.16)	< 0.01	0.13	0.65
Visits per day	1.37^{a} (0.02)	1.53^{b} (0.02)	1.59^{b} (0.03)	1.57^{b} (0.02)	1.52^{b} (0.04)	1.57^{b} (0.05)	< 0.01	< 0.01	< 0.01
Daily intake CV, %	86.99^{ab} (1.66)	81.17^{b} (1.35)	89.77^{a} (2.05)	90.24^{a} (1.74)	82.77^{ab} (3.05)	86.94^{ab} (3.77)	< 0.01	0.82	0.56

[1]Linear pre-planned contrast
[2]Quadratic pre-planned contrast

Table 17. Model selection for models evaluating the effects of cow age, temperature (°C), wind speed (m/s) and year on supplement intake per visit, daily supplement intake, and daily visits to supplement feeder by cattle grazing dormant rangeland in 2016 – 2017 & 2017 – 2018 at the Northern Agricultural Research Center Thackeray ranch, Havre, MT

Model[b]	K[c]	AICc[d]	ΔAICc[e]	W_i[f]	r^2m[g]	r^2c[h]
Supplement Intake per Visit						
Age^2 + $Temperature^2$ × Year + Wind $Speed^2$	12	108830.40	0.00	0.98	0.02	0.11
Age^2 × Year + $Temperature^2$ × Year + Wind $Speed^2$	14	108838.70	8.32	0.02	0.02	0.10
Constant (null)	3	109167.20	336.76	0.00		
Daily Supplement Intake						
Age × Temperature + ln(Wind Speed) × Year	9	60013.70	0.00	0.85	0.02	0.2
Age × Temperature + ln(Wind Speed) + Year	8	60017.19	3.49	0.15	0.02	0.2
Constant (null)	3	60331.86	318.16	0.00		
Daily Visits to Supplement Feeders						
ln(Age) × Year + Temperature × Year + Wind $Speed^2$ × Year	12	22118.83	0.00	1.00	0.08	0.12
Constant (null)	3	23637.44	1518.60	0.00		

[a]Only models with Akaike weights (w_i) ≥ 0.01 are presented except for the null model.
[b]Cow is used as a random variable in all models.
[c]K = number of parameters.
[d]Akaike's information criterion adjusted for small sample size.
[e]Difference in Akaike's information criterion adjusted for small sample size compared to the best model.
[f]Akaike weight.
[g]Marginal R^2
[h]Conditional R^2

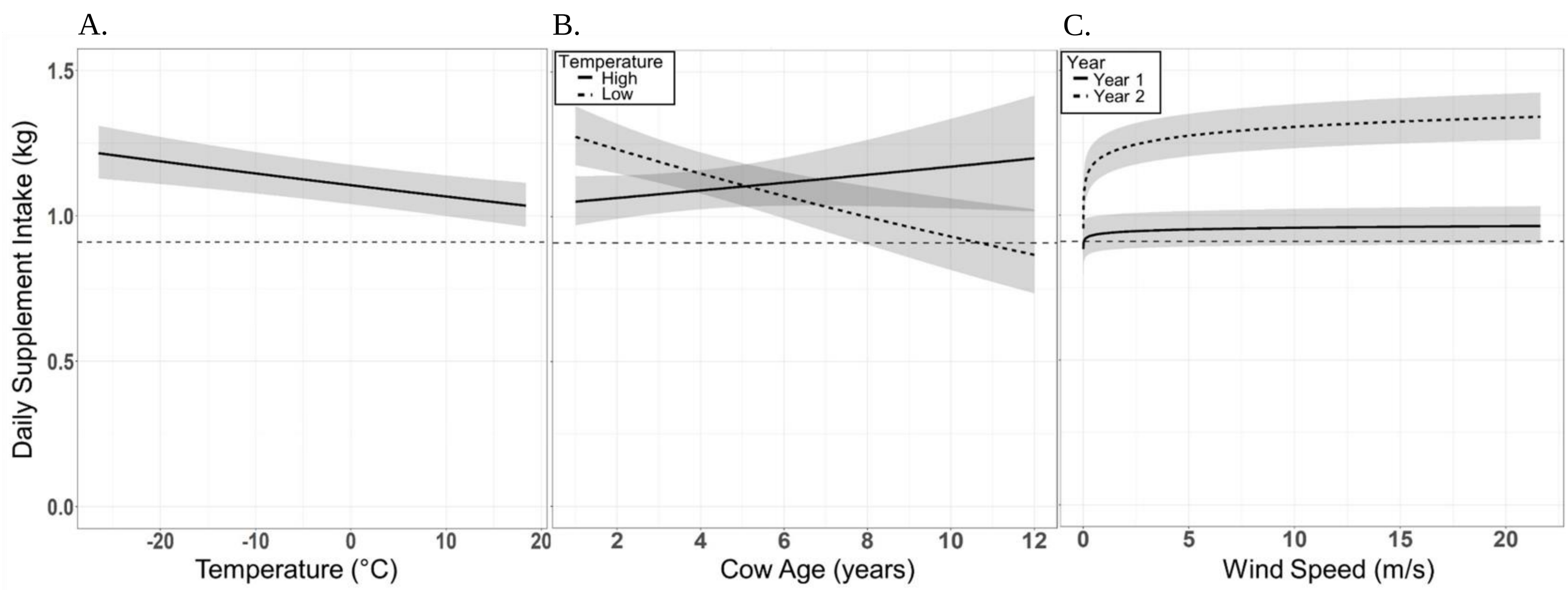

Figure 22. Predicted relationships (± 95%CI represented in the shaded area) between A) temperature (°C) B) cow age (years) and C) wind speed (m/s) on daily supplement intake (kg; dashed line represents target intake of 0.91kg/d) by cattle grazing dormant northern mixed grass rangeland in 2016 – 2017 & 2017 – 2018 at the Northern Agricultural Research Center Thackeray ranch, Havre, MT

CHAPTER FIVE

CONCLUSION AND MANAGEMENT RECOMMENDATIONS

The economic efficiency of beef cattle production is threatened by increased costs associated with harvested feeds (Meyer and Gunn 2015), resulting in the adoption of low-input management strategies including dormant season grazing (Adams et al. 1996). Dormant range forage is typically deficient in protein and often requires supplementation to meet the nutritional requirements of cattle (Krysl and Hess 1993, Bowman et al. 1995, Mulliniks et al. 2013b). Providing supplements to cattle can alter grazing distribution and behavior on rangelands (Ares 1953, Adams 1985) and has been traditionally used to promote uniform utilization of vegetation within a pasture (Bailey and Welling 1999, Fuhlendorf and Engle 2001). However, promoting uniform utilization results in the homogenization of vegetation conditions and an overall decline of ecosystem structure, function and biodiversity (Derner et al. 2009, Fuhlendorf et al. 2009, Hovick et al. 2015). Thus, the spatial component of grazing distribution is a central aspect of domestic livestock ecosystems (Coughenour 1991). Grazing distribution is influenced by both the physical environment in which livestock graze (e.g. topography; Ganskopp and Vavra 1987, Coughenour 1991, Bailey et al. 1996, Beaver and Olson 1997) and individual animal attributes (e.g. age; Allison 1985, Dunn et al. 1988, Bailey et al. 1996, Walburger et al. 2009). Prior to our study, little information was available that evaluated the interaction of protein supplementation strategies and individual animal attributes on grazing distribution, behavior and the impact on residual vegetation conditions.

Our research provides a comprehensive analysis evaluating the effects of protein supplementation, supplementation strategy, environmental factors and individual animal attributes have on grazing behavior and distribution and how dormant season grazing impacts residual vegetation conditions on rangelands in the northern mixed grass prairie. Our specific objectives were to 1) evaluate how two different protein supplementation strategies during the dormant grazing season influence grazing activity and resource utilization by heifers and how dormant season grazing impacts residual vegetation conditions and residual vegetation cover, structure and heterogeneity, 2) evaluate the influence of supplement intake, age, body weight and condition on grazing activity and resource utilization by cattle and the influence of grazing intensity on residual vegetation cover, structure and heterogeneity, and 3) examine the effects of cow age and winter temperature and wind conditions on individual supplement intake by cattle grazing winter rangelands in Montana.

Results of our studies suggest supplementation strategies have direct effects on grazing behavior and resource utilization. Hand-fed cake supplementation reduced time spent grazing per day compared to the self-fed protein concentrate. Previous work has demonstrated that hand-fed supplementation disrupts daily grazing activities, resulting in less time spent grazing and lower forage intake (Adams 1985). The effects of hand-fed supplementation on grazing behavior is likely due to the high fiber by-products contained within the supplement providing a portion of the animals energy demands, reducing reliance on dormant range forage for energy. Reduced time spent grazing and forage intake with hand-fed cake supplements may be benificial when grazing dormant season rangelands following drought conditions as forage is typically limited. Conversely, self-fed protein concentrate supplements may be a better strategy in years with high forage production and availability.

Cattle supplemented with a hand-fed cake selected for grazing locations near supplement delivery sites prior to spring greenup. Vegetation green up results in an increase of both forage availability and quality, which has been shown to reduce reliance on supplementation (Wagnon 1965, Ducker et al. 1981, Bowman and Sowell 1997). Thus, differences in relative resource use in response to supplementation strategies tended to diminish in the late winter/early spring when vegetation begin to green up and grow.

Regardless of supplementation strategy, our research indicates cattle select grazing locations on dormant rangelands relative to the quantity and quality of available forage, similar to that of summer grazing cattle on the short grass steppe (Senft et al. 1985). However, we observed high variability in grazing site selection among individuals, suggesting, individual-level factors were dominant drivers in grazing resource use and behavior. Our research evaluating the role of individual animal attributes on grazing behavior and resource use suggests age, supplement intake and body weight have considerable effects on grazing site selection. In our study, older cattle were more likely to use areas farther from water, higher in elevation and closer to supplement feeders, indicating supplement locations and experience interact in determining cattle grazing locations. Body weight and daily supplement intake also impacted grazing site selection, likely due to the relationship of these factors to the energetic requirement for maintenance of beef cattle. Heavier weight cattle in our study had a lower selection for grazing locations at higher elevations away from water. Activity increases energy requirements per unit body weight (National Research Council 2016), suggesting the energetic cost of traveling to higher elevations is increased for heavier weight cattle. In general, supplement intake may mitigate the increased energetic cost of travel to grazing locations at higher elevations. However, in our study, the selection of grazing locations in higher elevations only increased with supplement intake till animals consumed approximately 2-kg of supplement per day, after which selection for elevation decreased. Supplement intake greater than 2-kg per day may result in cattle consuming supplement as a substitute to forage, decreasing overall forage intake and time spent grazing. Thus, managers may want to consider using pastures with little elevational change for dormant season grazing and a form of supplement that is effective at limiting supplement intake to prevent animals from substituting forage for supplement.

Our results also indicate that younger cattle consume more supplement more consistently than older cattle. Maintenance energy expenditure can vary with age of cattle (National Research Council 2016), and it is generally accepted that maintenance per unit of size decreases with age in ruminant livestock (Blaxter 1962, Graham et al. 1974, CSIRO 1990, 2007). Thus, younger cattle may have a higher reliance on supplement intake to meet their maintenance requirements than older cattle when grazing dormant forage poor in quality. Additionally, we found younger animals increase supplement intake with decreasing temperature. Northern winter grazing environments often expose animals to chronic cold and windy conditions that increase the resting metabolic rate and overall energy expenditure of cattle in an effort to maintain homeothermy (Webster 1971, Christopherson et al. 1979, Keren and Olson 2006). Cold temperature conditions could potentially result in greater energetic needs for young cows to maintain homeothermy resulting in an increase in daily supplement intake as average daily temperatures drop. These findings suggest, managers may want to ensure plenty of supplement is available when prolonged periods of cold weather are forecasted or manage younger cattle separately from older cattle.

Many attributes of cattle behavior related to supplement intake were inconsistent across years, likely due to annual changing conditions. High levels of unaccounted variability suggests unmeasured environmental factors could be dominant drivers of supplement intake behavior. Forage availability is positively associated with variation in supplement intake (Wagnon et al. 1966, Bowman and Sowell 1997) and may be a substantial factor in determing cattle behavior. Varying snow cover conditions throughout the grazing season could result in fluctuating availablity of forage, which would likely be reflected in supplement intake behavior of cattle. Thus, future research may consider tracking forage availability and grazing activity when evaluating factors effecting supplement intake behavior.

When evaluating dormant season grazing on vegetation conditons, we found supplementation strategies had very little effect on residual vegetation cover and heterogeneity within pastures. However, grazing intensity and the time period at which grazing occurred did impact residual vegetation conditions. The effects of grazing intensity and the time period of when grazing occurs throughout the winter grazing season likely reflects the effect of snow cover on forage availablity. Forage availability can have major effects on grazing behavior as it directly impacts grazing selectivity (Marten 1989, Reuter and Moffet 2016). Selective grazing by livestock often promotes within-pasture heterogeneity resulting in pastures with areas of light and heavily grazed vegetation (Coughenour 1991, Bailey et al. 1998, Fuhlendorf and Engle 2001, Bailey 2005). Thus, when snow cover had minimal effect on forage availability, we found grazing decreases visual obstruction and bare ground cover and increase litter and residual grass cover and heterogeneity. However, grazing intensity had a strong negative association with grass cover. When heavy snow accumulations limited forage availability for prolonged periods of time, we found that grazing increased litter cover and reduced visual obstruction, grass and shrub cover and litter and shrub herterogeneity. Additionally, despite cattle having a strong dietary preference for grass (Miller and Krueger 1976, Walburger et al. 2007, Clark et al. 2013), grazing intensity had little to no effect on grass cover on years with heavy snow accumulations. Limited forage availability causes animals to select a greater proportion of less-preferred forage (Marten 1989), and focus grazing efforts in areas with taller statured vegetation or with little snow accumulation (Senft et al. 1985). During the late-winter, early-spring where begins to snow melt off and vegetation begins to green up, we found that grazing had the largest impact on residual vegetation conditions, with decreases in litter, grass and shrub cover, and the heterogeneity of grass cover. Reduction in snow cover and vegetation green up results in an increase in both forage availability and quality, which reduces reliance on supplementation (Wagnon 1965, Ducker et al. 1981, Bowman and Sowell 1997) and increases time spent grazing per day (Chapter 2). Previous studies suggest that a heterogeneous approach to grassland conservation is capable of maintaining biodiversity and agricultural productivity simultaneously (Fuhlendorf et al. 2006). Thus, dormant season grazing prior to snow melt/green up of vegetation may result in limited effects on vegetation conditions and spatial heterogeneity.

Monitoring the effects of supplementation on grazing behavior and resource utilization without accounting for individual level factors may not provide meaningful insight about the complex interrelationships that exist between grazing livestock and their environment. The combination of supplementation strategy, age, supplement intake, and body weight can interact with the environmental attributes of the landscape to influence grazing behavior resulting in significant implications in animal and land management. Cattle experience, nutrient status and the energetic cost of grazing activity may be dominant drivers in cattle resource utilization. Individual variation in supplement intake has the potential to influence individual animal nutrient status and performance, thus altering grazing behavior and pasture use. Additionally, supplementation strategy can affect grazing behavior and resource use. However, despite the behavioral differences between supplementation strategies, the vegetation availability due to snow cover when grazing occurred may have the largest effects on structural vegetation conditions. Prolonged periods of snow cover presumably limit forage availability, reducing grazing selection and the overall effects of grazing on vegetation conditions. The influence of winter grazing on average vegetative conditions, as well as, spatial variability (i.e. heterogeneity) appeared to be marginally affected prior to snow melt, with negative effects once vegetation begins to green up. However, the management implications of this study should be interpreted cautiously, as universal implementation of rangeland management practices often fail to meet management objectives due to lack of local management considerations. Understanding the effects of supplementation and variation in supplement intake on animal performance, behavior and pasture use are essential in the development of a cost effective and sustainable supplementation program for dormant season grazing. Including measurements of animal performance, forage intake and energetic costs associated with travel and grazing activities could provide meaningful insight to the mechanisms driving grazing behavior and distribution.

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APPENDICES

APPENDIX A

PASTURE TOPOGRAPHY AND WATER, TRANSECT AND SUPPLEMENT LOCATIONS FOR STUDY AREAS

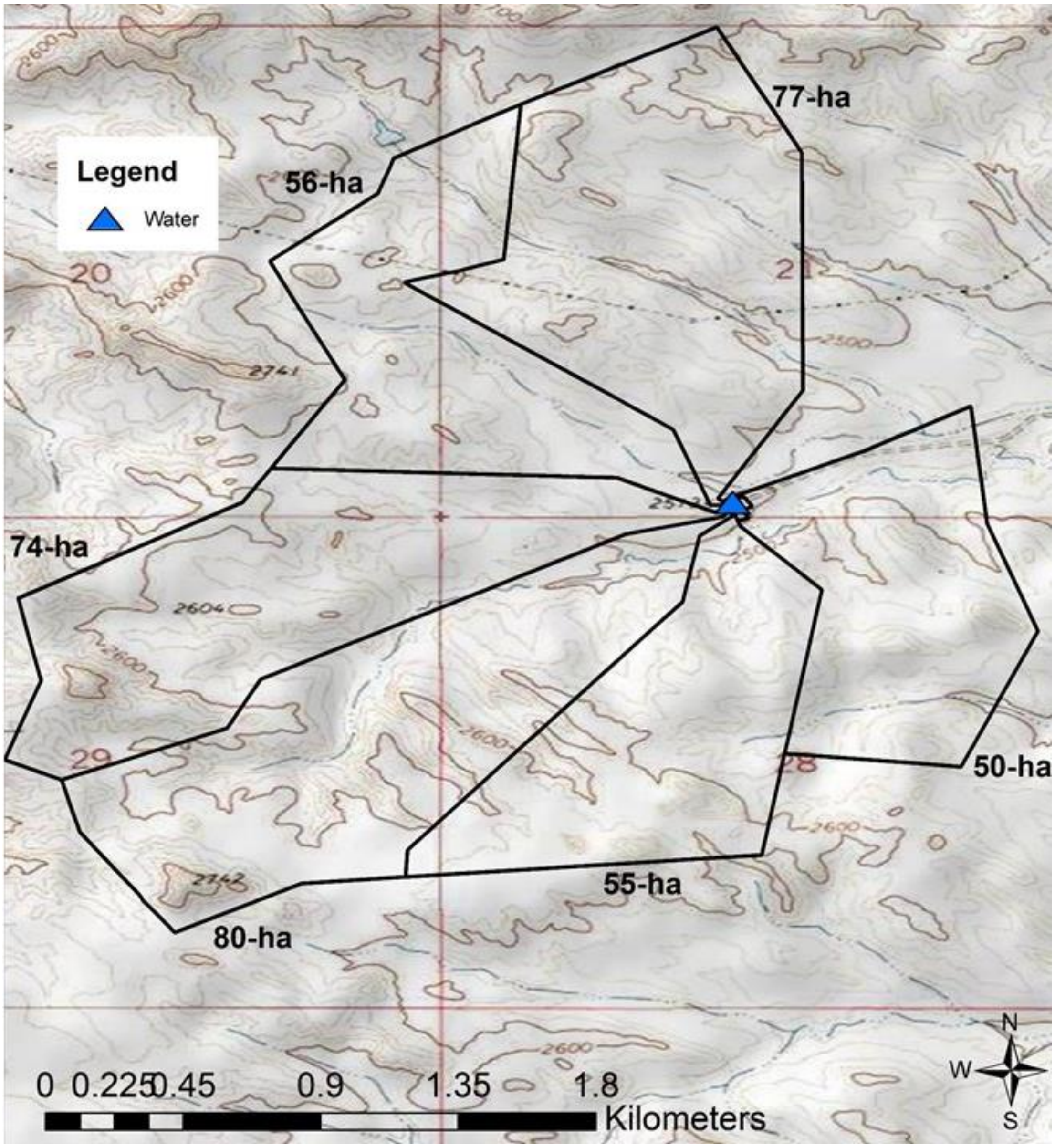

Figure A1. Topography and water location for rangeland pastures winter grazed by heifers' in 2015 – 2016 & 2016 – 2017 at the Fort Keogh Range and Livestock Research Laboratory, Miles City, MT

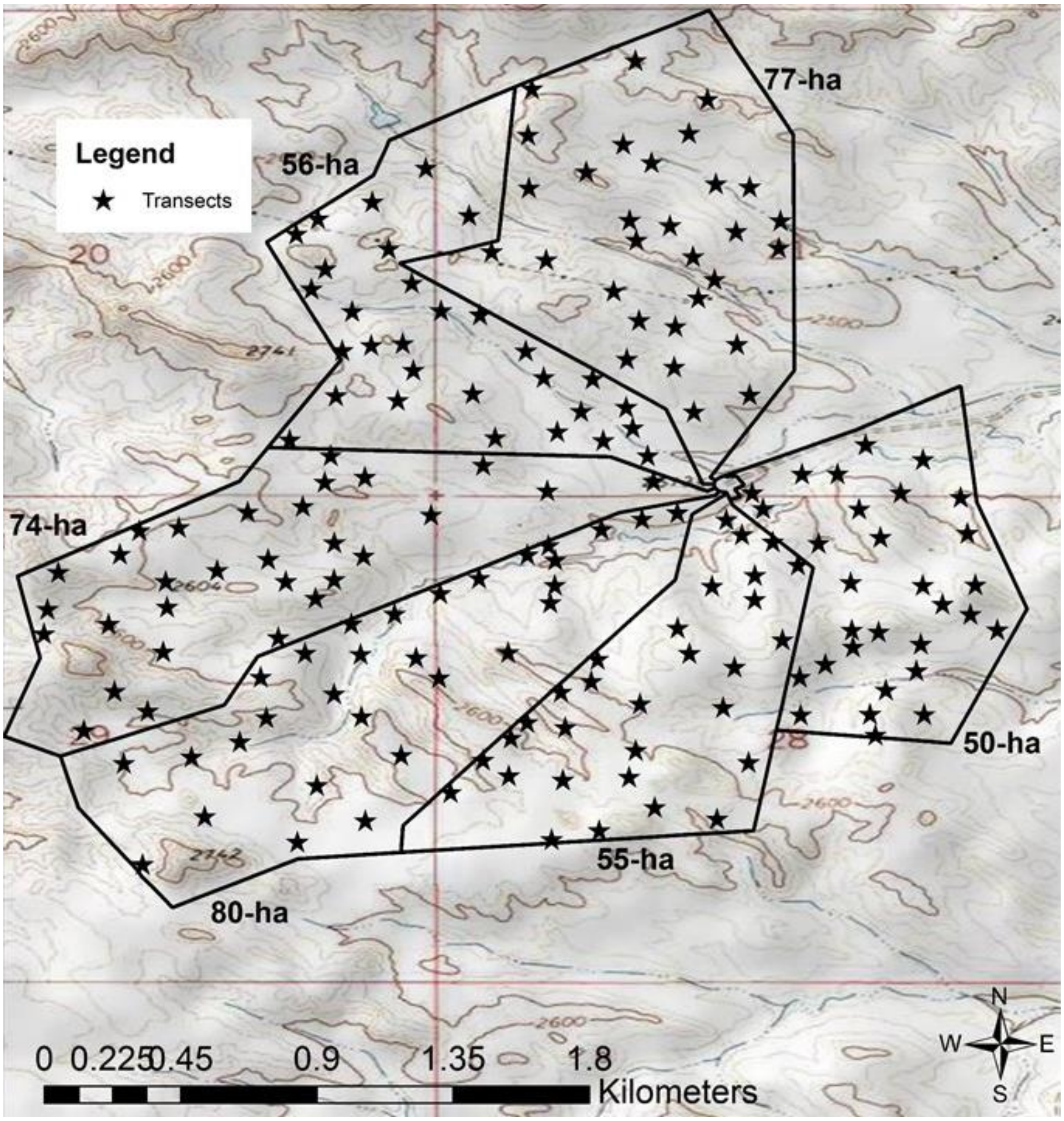

Figure A2. Transect locations for vegetation and temperature measurements for rangeland pastures winter grazed by heifers' in 2015 – 2016 & 2016 – 2017 at the Fort Keogh Range and Livestock Research Laboratory, Miles City, MT

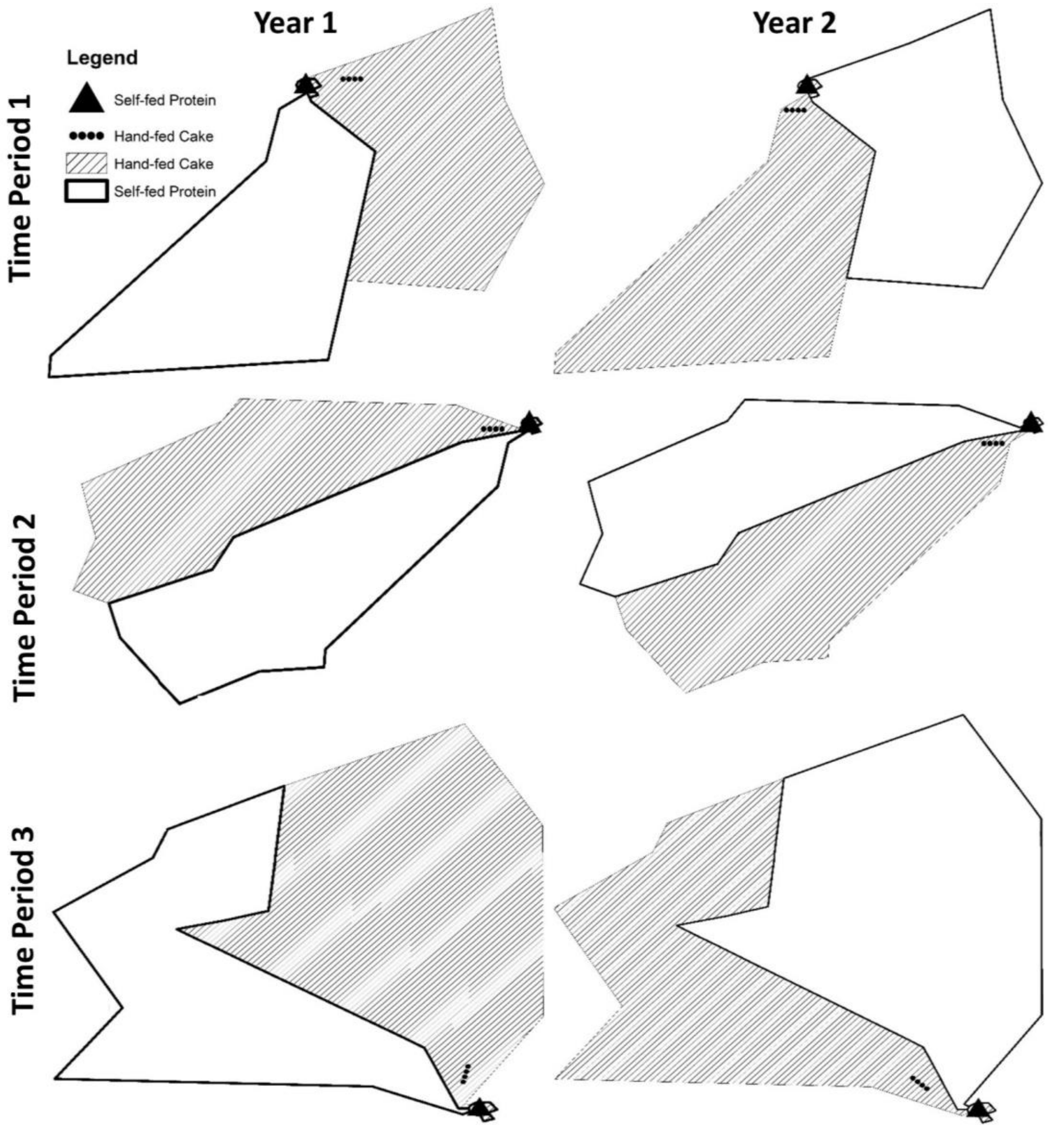

Figure A3. Pasture rotation and supplementation locations for rangeland pastures winter grazed by heifers' in 2015 – 2016 & 2016 – 2017 at the Fort Keogh Range and Livestock Research Laboratory, Miles City, MT

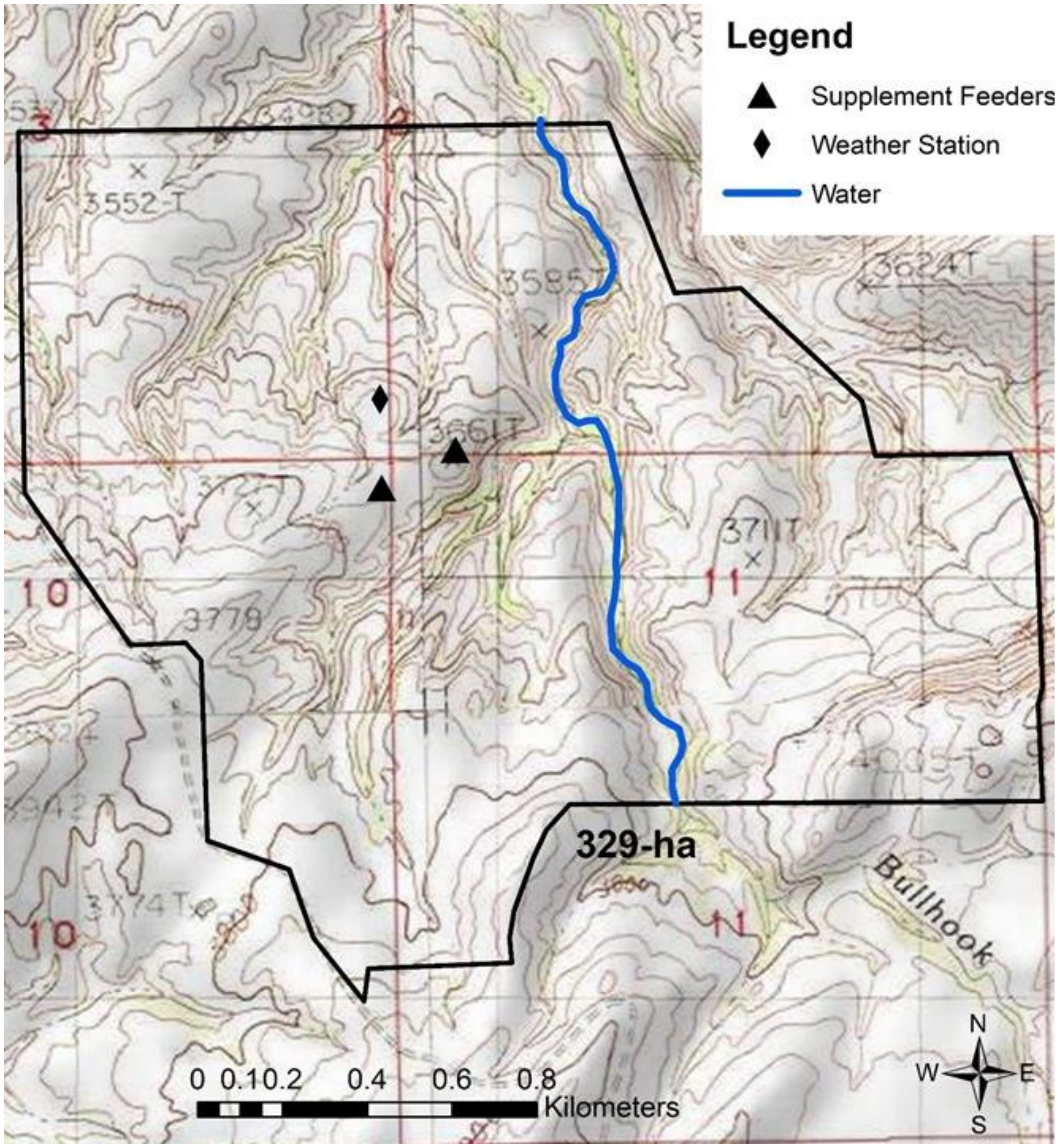

Figure A4. Topography, water, weather station and supplementation locations for the 2 years of grazing (2016 – 2017, 2017 – 2018) at the Northern Agricultural Research Center Thackeray ranch, Havre, MT

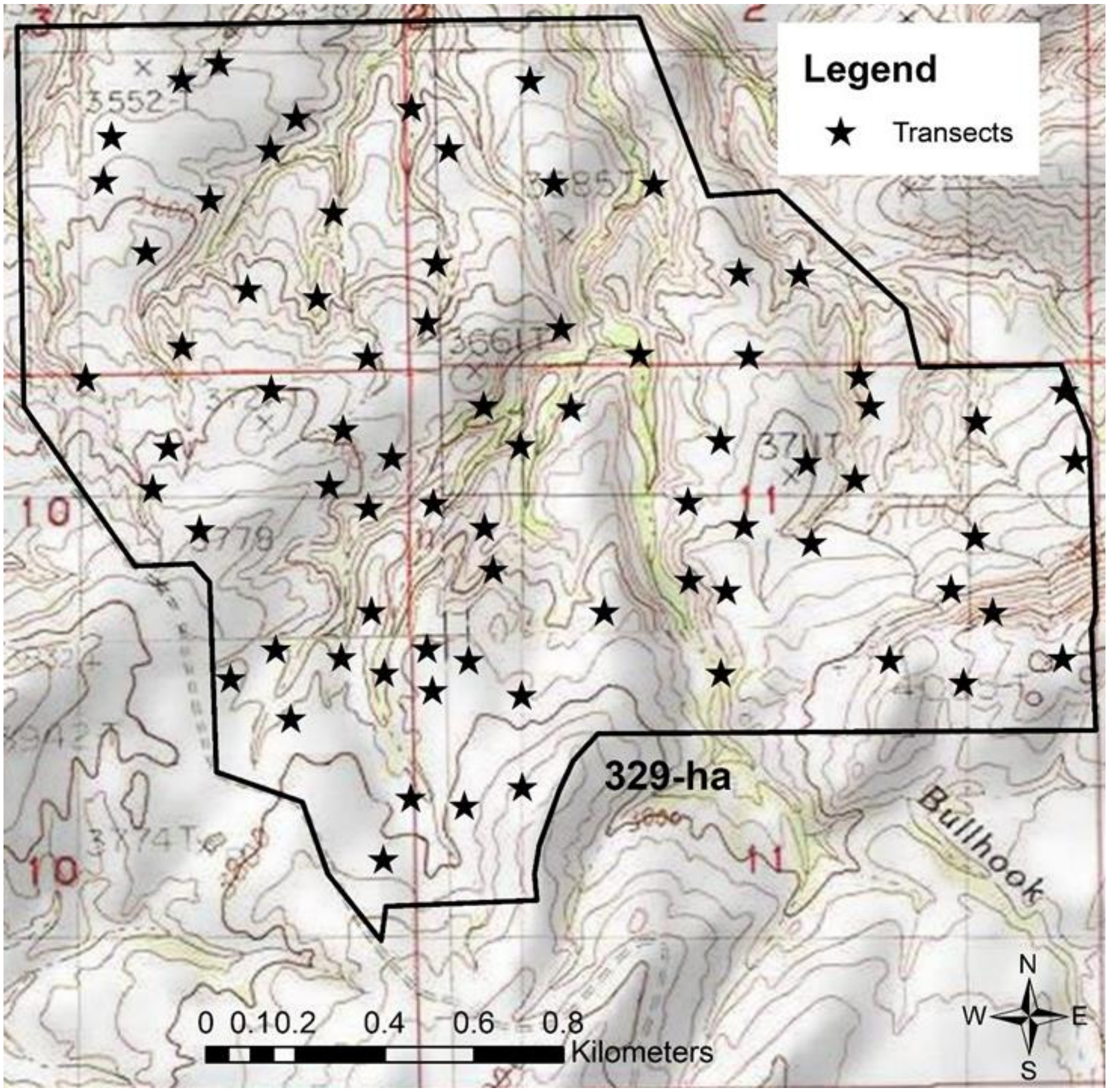

Figure A5. Transect locations for vegetation and temperature measurement for the 2 years of grazing (2016 – 2017, 2017 – 2018) at the Northern Agricultural Research Center Thackeray ranch, Havre, MT

APPENDIX B

DAILY WEATHER CONDITIONS FOR STUDY AREAS

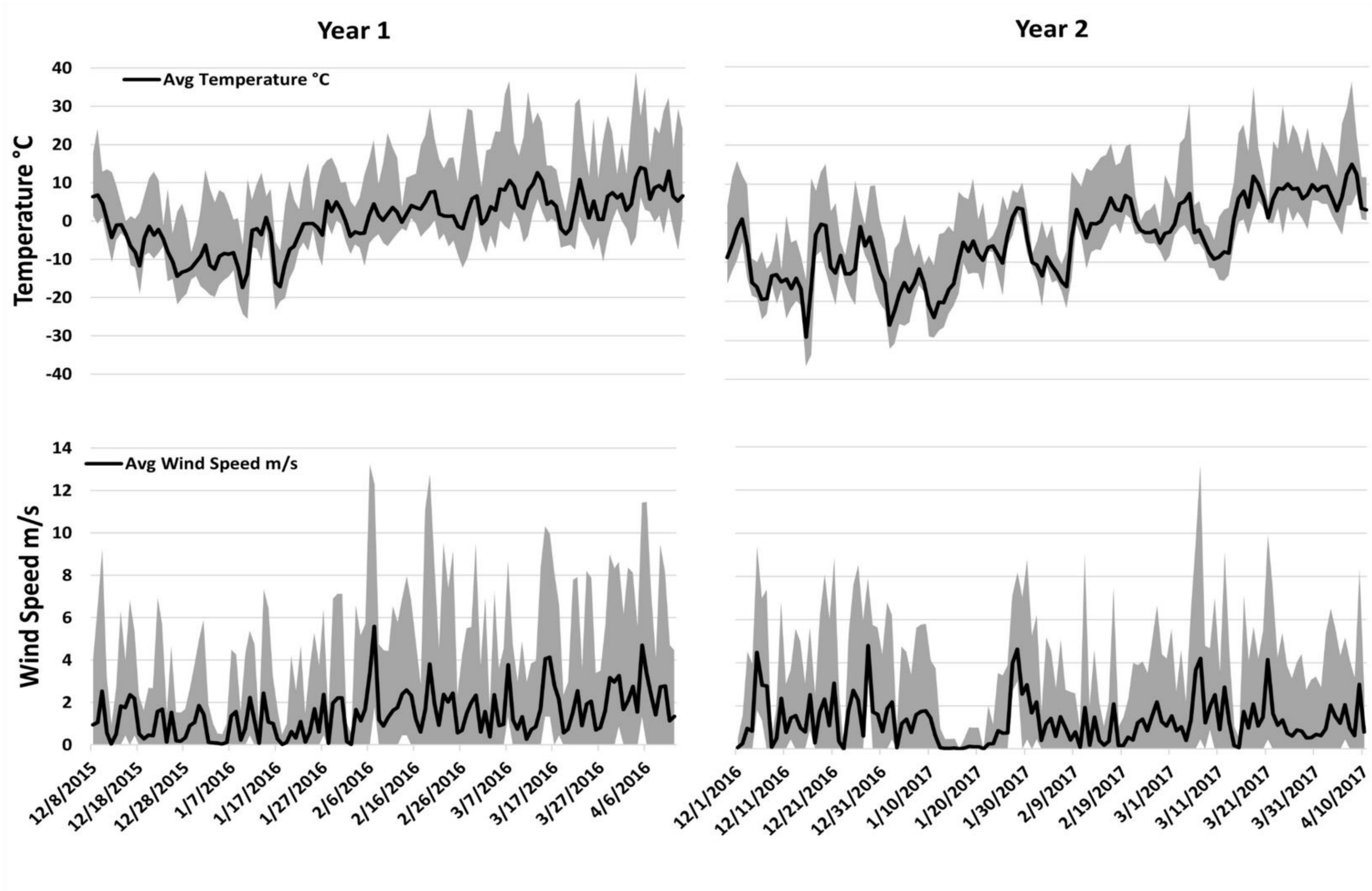

Figure 1B. Average daily temperature (°C), daily temperature range (represented in the shaded area), average daily wind speed (m/s) and daily wind speed range for the 2 years of grazing (2015 – 2016, 2016 – 2017) at the Fort Keogh Range and Livestock Research Laboratory, Miles City, MT

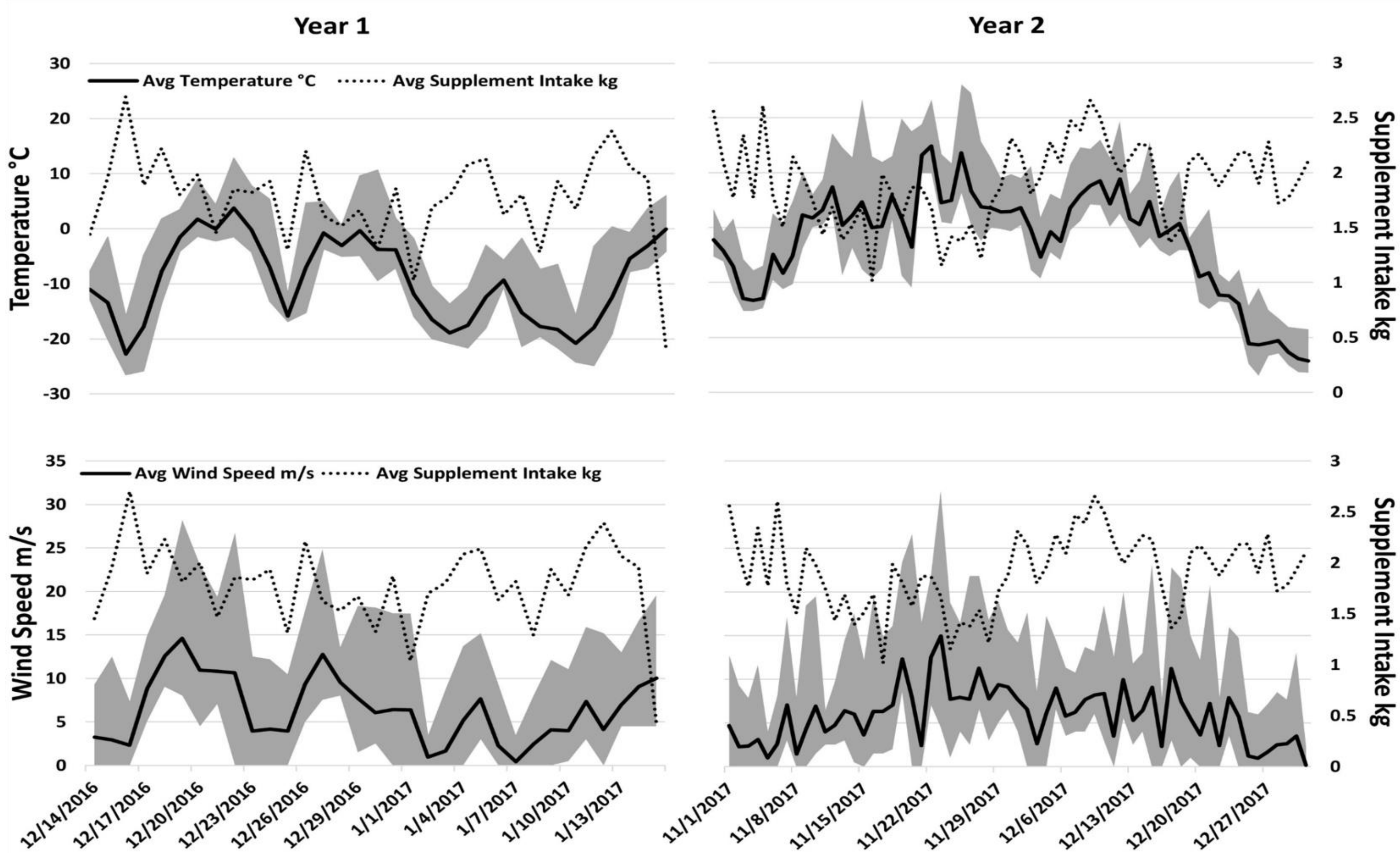

Figure 2B. Average daily temperature (°C), daily temperature range (represented in the shaded area), average daily wind speed (m/s) daily wind speed range and average supplement intake for the 2 years of grazing (2016 – 2017, 2017 – 2018) at the Northern Agricultural Research Center Thackeray ranch, Havre, MT