INFLUENCE OF ANIMAL-, ENVIRONMENT-, AND MANAGEMENT-RELATED FACTORS ON GRAZING BEHAVIOR AND PERFORMANCE OF RANGELAND BEEF HEIFERS

BY

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ABSTRACT

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Three different studies were carried out at the USDA-ARS Fort Keogh Livestock and Range Research Laboratory in Miles City, MT to evaluate the influence of animal-, environment-, and management-related factors on grazing behavior and performance of rangeland beef heifers. In the first study, I evaluated the influence of post-weaning development method and the dam's lifelong feeding regime on rangeland grazing patterns of beef heifers during winter. I compared behavior of heifers wintered on rangeland (group-fed cake, GFC or self-fed protein, SFP supplements) whose mothers were supplemented during the last third of their gestation period with an adequate (CT) or marginal (MG) level of protein to meet their nutrient requirements. I found that post-weaning development protocols modified movement and activity of heifers during winter. Restricted feeding of dams during the last third of their gestation period appeared to not affect the behavior of the offspring when conditions during the post-weaning development met the nutrient requirements of the heifers. In the second study, I evaluated the influence of post-weaning development method on rangeland grazing patterns of beef heifers during early and late spring. I compared behavior of heifers wintered on rangeland (GFC or SFP) or in a pen where they were (pen fed silage, PFS). I found that post-weaning development protocols modified movement, activity, and habitat use of heifers during early spring. Initial animal state and/or metabolic memory may have been responsible for the differences observed. Such differences, however, were possibly attenuated through time by social facilitation. In the third study, I compared the precision of two methods of estimating activity of rangeland heifers monitored with collars equipped with GPS (Global Positioning System) and motion sensors. I found that GPS alone (vs. GPS + motion sensors) might be a reliable method to estimate activities within certain limits, but software adjustments are necessary to reduce the bias. Also, further research to estimate activities using different breeds and ages (heifers vs. mature cows) of cattle on different rangeland types, as well as additional validation is needed to determinate whether these results can be generalized.

Keywords: Northern Great Plains, winter heifer development, GPS collars, heifer grazing behavior, activity classification, sensors.

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CHAPTER I

LITERATURE REVIEW

INTRODUCTION

Management of winter feeding of recently weaned replacement heifers is one of the critical factors that affect production costs in the rangeland cow-calf systems of the Northern Great Plains, especially as this involves the cost of feed until heifers achieve puberty (Roberts et al., 2009). Supplementation is a strategy that is used to supply additional nutrients to cover the energy and protein requirements of animals. In the Northern Great Plains, this strategy is suggested as a complement to the dormant native range during winter (forage present < 6% crude protein) to cover the nutritional requirements of pregnant cows and to improve growth and reproductive performance of heifers (Roberts et al., 2009; Adam & Short, 1987). The main effect of a protein supplement is an increase in low-quality forage intake by increasing its digestibility (McCollum III & Horn, 1990). Fortunately, studies have shown the possibility of reducing the feeding cost by developing heifers with less mature weight at breeding without affecting their reproductive performance in the short term (Roberts et al., 2016; Endecott et al., 2013; Funston et al., 2012, Clanton et al., 1983). However, although research has been conducted considering reproductive aspects, little is known about the performance of the offspring in terms of grazing behaviors when mothers are fed in restricted conditions.

Additionally, how heifers are developed from weaning to breeding influences the long-term sustainability of the herd. Preliminary studies suggested that the post-weaning method of heifer development (supplementation and rangeland or dry lot) could affect subsequent grazing distribution patterns of the cow herd, consequently impacting rangeland pasture utilization patterns (Hojer et al., 2012, Perry et al., 2013, Perry et al., 2015).

Finally, not only will the rangeland distribution be affected by the post-weaning method, the dam's history, and the feeding of heifers, but environment-related factors such as vegetation-type rangeland, elevation, slope, distance to water, and the weather will also influence heifer-grazing habits when they come from different management practices. For this reason, the objective of this review is to explore what is known about how behavior and performance of rangeland-developed heifers are affected by the biophysical environment in which they graze and by a heifer’s and its dam’s feeding regime. Additionally, I will explore what is known about the use of remotely sensed vegetation phenology dynamics on rangelands and how the combination of the global positioning system (GPS), geographic information system (GIS), and remote sensing will allow us to implement a comprehensive approach to study how livestock interacts with extensive and heterogeneous rangeland pastures.

This thesis attempts to provide information to the development of management strategies based on manipulating grazing rangelands, not only for efficient livestock production, but also for suitable landscape management.

FACTORS THAT INFLUENCE GRAZING BEHAVIOR AND PERFORMANCE OF RANGELAND-DEVELOPED HEIFERS

Animal-related factors

Different factors influence the grazing behavior of cattle. The first involves the physical characteristics of the animal. Cattle have a flat muzzle with a tongue, a broad mouth, and absence of the cleft and therefore, their selective ability and the quality of their diets tend to be lower than in other ruminant species (Ellis & Travis, 1975). Body size is proposed as another factor that influences their grazing distribution pattern. Laca et al. (2010) studied the effect of grazing distribution on the selection pattern of animals in the short term and found that cattle are less selective than sheep, and the reason is associated with the body size. Smaller ruminants, may explore high-quality patches vs. larger body size counterparts. Genetics appear to be another animal-related factor that affects grazing behavior. Peinetti et al. (2011) stated that Criollo breed may explore larger areas of desert pastures compared to British breeds due in part to the smaller body size of Criollo cows compared to Angus counterparts. Criollo might also be less dependent on water than European breeds. Bailey et al. (2015a) linked animal genotype with cattle grazing patterns using genetic markers. The authors found that the GMR5 gene located on chromosome 29 might be associated with the terrain use.

Several researchers have shown that among-animal variation can play a role in how cattle use the environment. Wesley et al. (2012) found that animals who showed an excitable temperament may have differed in their forage selection pattern by exploring larger areas of a pasture and reducing their time spent in areas near water when compared to cows who exhibit a less-excitable temperament. A recent study carried out by Goodman et al. (2016) examined the connection between behavior types excitable (go-getter) vs. less-excitable temperament (laid back) and reproductive performance in a Corona Ranch herd located in NM, USA. The research revealed that cows with excitable temperaments might have a higher reproductive efficiency compared to counterparts that exhibited a less-excitable temperament. A difference in culling rates across five years (exponential trend for ‘go-getter' and the linear trend for ‘laid back') and differences in calving rates might support this hypothesis.

Physiological stage and age also appear to be linked to cattle grazing distribution. A study conducted by Black-Rubio et al. (2008) showed that cows that were pregnant or nursing tended to use reduced areas of a pasture and walked short distances as compared to open cows. Walburger et al. (2009) reported that young cattle tend to explore lower elevation areas, with higher slopes, and that are located near the water when compared to the oldest cattle. Walburger et al. (2009) stated that experience might influence the patterns they observed. Laca et al. (1998) showed that experience and long-term memory affects not only an animal’s exploration pattern but also its foraging efficiency. In that study, three different treatments were established: VR (food was randomly distributed without remaining constant); CR (food was randomly located and continued in the same place during the experiment); CC (food was located in clumps and stayed constant during the experiment). The results indicated that the constant location of the food positively affected the search pattern due to long-term memory use and, consequently, cattle were able to increase their intake rate. These results align with those of Bailey et al. (1989a), who found that short-term memory also influences the grazing distribution pattern. These authors argued that cattle might remember (around 8 hours) the areas where they previously foraged and will revisit or avoid them. In addition, Bailey et al. (1989b) claimed that steers might have the ability to remember the sites they have visited and the quantity of forage present. Launchbaugh and Howery (2005) stated that the grazing distribution pattern is influenced not only by spatial memory and experience but also the inherited and social influence of mothers and peers. It is important to note that animals can learn through operant conditioning, in which a given behavior can have either a positive or negative consequence that either increase or reduce the frequency of such behavior.

Some studies show that learning may influence foraging behaviors though time. Learning during early life through food imprinting (Immelmann, 1975), social models (Howery et al., 1998), and trial and error (Coussi-Corbel & Fragazsi, 1995) is critical for developing those skills. Different studies have shown the importance of peers in social facilitation of foraging behavior in cattle (Costa et al., 2016; Perry et al., 2015, Perry et al., 2013, Hojer et al. 2012; Jackson et al., 2010; Ksiksi & Laca, 2000).

A significant tool for studying social learning and thus animal behavior is using social network analysis (Makagon et al., 2012, Wey et al., 2008). A social network is defined as a social structure where the relationships between and among individuals are determined by the quality and content of the relationship as well as their patterns (Hinde, 1976). Social networks provide a framework to study the connection between an animal's individual behavior and its influences at the population level. Network analysis involves different statistical tools (metrics) to analyze the social structure of individuals in the environment. According to Wey et al. (2008), statistical metrics can be grouped into the following categories: individual measures (betweenness centrality, centrality, closeness centrality, degree centrality, indegree, outdegree, and node degree), intermediate measures (clustering coefficient, cliquishness, average path length, and diameter), and group measures (average path length, density, and diameter). Individual measures involve the analysis of an individual's precise location inside the network and that individual's effects on others; it implies the direct and indirect relationships with other individuals. Intermediate measures include the study of the relationships of more than a single individual, e.g., the existence of other groups in the network. Finally, group measures represent different aspects of the overall network organization.

Social networks can be mapped using adjacency matrices created, for example, by the ASSOC1 software (Weber et al., 2001). In order to create this matrix, it is necessary to define both the spatial and temporal thresholds because they are the foundation upon which the network is built, i.e., they define when individuals are considered associated. The spatial threshold is defined as the maximum distance for which two individuals are still considered associated at that moment in time, whereas the temporal threshold is the lowest quantity of time required for two individuals to be considered related or associated (Weber et al., 2001). Defining those thresholds would be a challenge because studies have shown that spatial threshold might be affected by forage quantity and season. Harris et al. (2007) found that as forage availability increased, animals foraged closer together, but when forage was limited, animals tended to be fragmented. Similar results were found by Cheleuitte-Nieves et al. (2018), although those were related to seasonal changes. These authors showed that animals exhibited dispersion patterns during the summer but aggregation during winter, thereby affecting the spatio-temporal herd dynamics. Finally, Harris et al. (2007) stated that not only should GPS data be considered to establish a correct spatial threshold, but such data should also be combined with field observations to generate a more reliable threshold.

Another interesting way to measure social interactions is by using association indices. These can also help better understand social behavior and its influence on grazing patterns. For example, Stephenson et al. (2016), using the SOCPROC software and Half-Weight Index (HWI), evaluated the strength of the relationships between cattle depending on the size of the herd. The authors found that cows in larger herds form multiple groups, whereas smaller herds tend to form a single group. Also, a weak association shown in this study implied that cows might prefer different groups instead of spending time in the same group. Stephenson et al. (2016) suggested that herd size should be considered in the design of grazing management strategies.

Environment-related factors

Topography is a well-established factor that influences the grazing distribution pattern of cattle (Bailey & Provenza, 2008; Bailey et al., 2005; Holecheck, 2011). Using a regression model, Senft et al. (1983) reported that different activities such as grazing, travel, resting, and bedding are influenced by topography. Senft et al., (1983) pointed out that cattle tend to spend more time in lowland areas than high terrain. A study by Gillen et al. (1984) examined preference and found that cattle prefer a site where the slope gradient is ≤ 10 % and avoid sites with a higher gradient of 20 %. Similar results were reported by Ganskopp and Vavra (1987), who found that cattle utilized 78 % of an area with a slope of 0-9 %, with the values presenting a downward trend as the slope gradient increased. A more recent study by Bailey et al. (2015b) examined how terrain heterogeneity influences cattle distribution and feeding site selection. Six ranches were used to study the grazing distribution patterns of cows using GPS collars, and feeding sites were created by dividing each ranch into parts according to topography, vegetation, and the number of animals per area. This study found that cows present in uniform and moderate terrain tend to change feeding sites more often than cows in an area with rugged topography or large spatial heterogeneity. The author explained that the reason is associated with the satiety hypothesis (Bailey & Provenza, 2008), which involves the connection between the time that animals need to spend in a specific area to become satiated with the forage present in it.

Several studies have shown that distance to water is another critical component of the grazing pattern (Bailey et al., 2005; Vallentine, 2001). A study conducted in Wyoming by Pinchak et al. (1991), showed that cattle preferred foraging sites near to a water resource (around 300 m.) and avoided those far away from the drinker. Similar results were reported by Gillen et al. (1984), though distances were less than the values (200 m.) reported by Pinchak et al. (1991). It is important to note that snow cover may affect the utilization of water sources. Bailey et al.

(2000) observed that cows tracked with a GPS collar tend to reduce the visit time to the water resources when snow cover was present.

Bailey et al. (2001) examined the relationship between the utilization of the terrain by cows differing in physiological stage and age and found no significant differences in the terrain used by pregnant and non-pregnant cows. However, there was a tendency for non-lactating cows to use rough topography and steep gradients compared to lactating cows. The authors explained that the higher water requirements for lactation and the presence of calves could be a constraint for lactating cows from traveling longer distances. In addition, it is important to note that, contrary to results obtained by Walburger et al. (2009), young cows (3-years old) explored areas with higher slope gradients compared to the oldest cows. Bailey et al. (2001) pointed out that these patterns might be associated with the social rank that exists among animals of different ages, which might lead to forcing young cows to explore rougher terrain. Another interesting aspect that Bailey et al. (2001) found was that breeds that originated from mountainous terrain (Tarentaise) appeared to use steeper gradients more often than breeds that originated from areas of flat terrain (Hereford).

Several studies have shown weather conditions also influence the grazing distribution. Cattle might select microclimates to maintain their thermal balance. A study conducted in Montana revealed that cows can use areas with a specific microclimate to reduce exposure to cold temperatures and high winds (Houseal & Olson, 1995). Similarly, Senft et al. (1985) claimed that, in response to maintaining thermoneutrality, cattle tend to select different topographic characteristics of the terrain. For instance, the authors found that, during the daytime, cattle tended to use warm areas during winter and cool areas during the summer, while during the nighttime, cattle selected resting areas based on their thermal exchange properties. Malecheck and Smith (1976) reported that cattle could not only reduce the grazing time during cold days, but also reduce their travel activity according to wind velocity. A study conducted in Miles City, Montana during winter (Adams et al., 1986) revealed that grazing time was significantly correlated with minimum daily temperature. Thus, lower temperature reduced the grazing time in pregnant cows by approximately 50 % when temperatures ranged between 0 and - 40 ºC.

Halasz et al. (2016) evaluated how weather conditions impact behavior of Hungarian grey cattle during four grazing seasons. A positive correlation was founded between daily distance traveled and atmospheric pressure. Halasz et al. (2016) stateed that warm-weather fronts - which bring high temperature and humidity- combined with low atmospheric pressure might generate more uncomfortable conditions for grazing animals. Another study has focused on the relationship between weather and the age of cows. Beaver and Olson (1997) suggested that as a result of learned and innate knowledge, animals could balance their activity patterns in regards to feeding and thermal needs. This study was carried out in Montana during two winters, with two groups of cows that were rotated between pastures. One group was three years old and inexperienced, whereas the other group was 7-8 years old and experienced. The young cows were not pregnant during the first winter, but were pregnant during the second winter. The oldest cows were pregnant during both periods. Their results indicated that adult cows tended to use similar microsites during both periods while the younger cows used different microsites every year. The authors suggested that young cows could have used different areas in response to the different physiological stage and the experience acquired between two years.

Grazing behavior is also influenced by forage quantity and quality. A study conducted by Ganskopp and Bohnert (2009) reported that cattle prefer areas with high crude protein values and low standing crop. Bailey (1995) pointed out that when cattle were exposed to ungrazed areas, they avoided patches with low forage quality and high quantity of dead forage and in general, preferred areas with high forage quality, which were visited more frequently than those with less quality. In addition, Bailey et al. (1989b) stated that cattle may link forage quantity with specific locations, although this association may extinguish through time (Bailey & Sims, 1998).

Management-related factors

Successful grazing management requires not only an understanding of factors that affect grazing distribution patterns of cattle but also understanding how to manipulate cattle behavior to achieve the desired goal. Strategies such as the distribution of water resources, the use of fire and fertilization, fencing and the moment of use are cited as factors that modify pasture attributes impacting grazing distribution (Bailey, 2004). There are, however, strategies to modify grazing patterns that rely on animal genetics (Bailey et al. 2015a), age (Walburger et al., 2009), and feed supplementation (Bailey & Welling, 1999).

Feed supplementation is used mainly to supply additional nutrients to animals so as to cover their energy and protein requirements. In the Northern Great Plains, feed supplements are used as a complement to dormant native range during winter to improve growth and reproductive performance of heifers (Roberts et al., 2016, Roberts et al., 2007). Protein supplements are used to influence intake and digestibility of low-quality forages (Petersen, 2006, McCollum III & Horn, 1990).

There are different ways to deliver feed supplements to cattle. Hand-feeding is defined as a method where the supplement is provided in a certain quantity that is consumed by animals over a relatively short time, while self-fed is supplied to allow *ad libitum* intake which is ususally limted by modifying the amount, physical characteristics and/or palatability of the supplement (Sawyer & Mathis, 2001). A review by Bowman and Sowell (1997) showed that the type of supplement and the delivery method might affect the responses to supplementation by influencing the variation between individuals. In this review, the authors included intake data for both, sheep and cattle considering several environments and types of supplement. They reported that the number of animals who failed to consume any supplement was higher in self-fed than in hand-self (19 % vs. 5 %, respectively), which indicated overfeeding in some animals and underfeeding in others. Factors associated with trough space, allowance, formulation and forage characteristics can also affect supplement intake (Bowman & Sowell, 1997).

Animal-related factors, social interactions, and previous experience may also influence the response to supplementation, although at a different level. For instance, Dixon et al., (2003) investigated how previous experience affected the variability in the intake when various types of the supplement were offered to heifers. Lithium sulfate was used to measure the intake, and three different experiments were conducted based on the kind of supplement and the heifer's experience. In experiment 3, groups of heifers with or without experience were supplemented with two different loose mineral mix types and inclusion or not of cottonseed meal. The first supplement included 448 g . kg^{-1} of salt, 313 g . kg^{-1} of calcium phosphate, 224 g . kg^{-1} of urea, 15 g . kg^{-1} of sulfur, and the second supplement contained 33 % less of salt, calcium phosphate, urea and sulfur plus 300 gr cottonseed meal. The voluntary intake was influenced by the type of supplement, which was a 48.1 % higher when the cottonseed was included. Similarly, the supplement consumed by heifers without experience was greater for both types of supplements than heifers with experience. The authors claimed that the quantity of urea could have generated an aversion effect, which could have impacted their results. The authors concluded that although the variability in the intake of supplement might be explained in part by the previous experience, the type of supplement offered to heifers appeared to be the main influencing intake.

Another important aspect of supplementation is the effect of the supplement on grazing behavior. Schauer et al., (2005) investigated the effect of supplementing at different time intervals on the grazing distribution patterns and cow performance in the Northern Great Basin. GPS was used to estimate different variables such as grazing time, distance traveled, and distance from water, and n-alkane was used to estimate intake, and harvest efficiency. The authors found that none of the variables they measured was influenced by the supplementation treatment or supplementation frequency. However, supplemented cows spent less time grazing compared to non-supplementated counterparts, regardless of the supplementation frequency (every day or every six days). The authors concluded that protein supplementation might have little influence on the distribution patterns of cattle in this region. Similar results were reported by Krysl and Hess (1993) who reported that grazing time is reduced when supplementation was offered to animals.

THE RELATIONSHIP BETWEEN EPIGENETICS, NUTRITION, GRAZING BEHAVIOR, AND REPRODUCTIVE ASPECTS OF HEIFERS.

"Epigenetics" is a term that was first introduced by Conrad Waddington in 1942 (Murrell et al., 2005) and that has been subject of different definitions throughout the last decades (Ibeagha-Awemu et al., 2015, Berger et al., 2009, Peaston and Whitelaw, 2006, Jablonka & Lamb, 2002). In its widespread sense, it refers to the heritable changes that occur in the chromosome but do not modify the DNA sequence. DNA methylation, histone modification, and noncoding microRNAs are the three specific mechanisms that are responsible for producing the epigenetic changes (Ibeagha-Awemu et al., 2015, Canani, et al., 2011).

Significant efforts have been made to associate maternal nutrition with the epigenetics mechanisms in relation to its impacts on the growth, development, reproduction, and feed efficiency of the progeny (Roberts, et al., 2016, Funston et al., 2013, Ford & Long, 2012, Roberts et al., 2007). Barker et al. (1992) defined "fetal programming as the event in which environmental factors alter the intrauterine environment triggering epigenetic mechanisms that change the expression of genes affecting the performance of the offspring”.

The nutrition in early gestation is necessary for the placental growth, differentiation, and vascularization as well as fetal organogenesis. Specifically, this is the period when limb, liver, lungs, thyroid, spleen, adrenal glands, brain thymus, and kidneys are developed (Hubbert et al., 1972). Van Straten et al. (2010) demonstrated that the maternal protein restriction in mice throughout gestation period affected the lipid metabolism in the fetal liver by DNA methylation.

Maternal nutrition is also associated with the skeletal muscle and fiber development. Consequently, owing to the number of fibers defined by secondary myogenesis and fixed in the early to middle gestation, undernutrition in this period will negatively impact muscle mass and therefore offspring performance (Yan et al., 2013, Du et al., 2010, Zhu et al., 2006, Zhu et al., 2004) while no effect might be observed during the embryonic stage and late gestation stage (Du, et al., 2005 and Du et al., 2010). However, it is important to note that if an undernutrition in the late gestation period occurs, the muscle fibers' size might be negatively affected (Costello et al., 2008, Greenwood et al., 1999).

On the other hand, overnutrition in gestation appears to enhance intramuscular adipogenesis and fibrogenesis in the middle pregnancy, which can improve quality by improving the marbling and subsequently palatability factors such as the juiciness and flavor (Dobson et al., 2010). A study conducted by Muhlhausler et al. (2007) showed that an overexpression of genes appears to contribute to the regulation of the adipogenesis and lipogenesis mechanism when maternal diet increases during the late gestation period, all of which influence the performance of offspring. Maresca et al. (2019) point out that modifying protein intake during the late gestation in cows does not affect steers' growth (progeny) in terms of body weight and growth rate throughout the finishing phase. However, the authors found differences in carcass composition and meat quality.

Peñagaricano et al. (2014) evaluated the effect of different types of diets on the expression of the fetal genome in muscle and adipose tissues during the middle-late pregnancy in sheep. Ewes were assigned one of three diets composed of fiber (alfalfa haylage), starch (corn) or fiber, protein, and fat (dried corn). After 130 ± 1 day of pregnancy, dams were necropsied to obtain the fetus and collect samples from the longissimus dorsi muscle, perirenal adipose depot, and subcutaneous adipose depot. RNA extraction was conducted in each tissue, and mapping was performed to detect different expression genes. The experiment showed that gene expression was modified by the type of diet. When the dams' diet was based on starch, an alteration in the fetal muscle was observed. Conversely, if the dams' diet was made up of fiber, protein, and fat alterations in subcutaneous and perirenal adipose tissues in the fetal stage were observed. Peñagaricano et al. (2014) argued that maternal nutrition during pregnancy could alter chromatin marks of a particular region of DNA triggering the transcriptomic modification in the fetus. The authors finally concluded that maternal nutrition during the middle of late pregnancy might produce a change in the fetal muscle and fat tissues, which might affect the performance of offspring. Additionally, a study conducted by Maresca et al. (2018) revealed that reducing the protein intake of cows during late gestation can affect postnatal growth by lowering the body mass index and modifying the head circumference of the offspring. The authors found that glucose regulation and IGF-1 concentrations were affected by altering the dam's diet during this period.

There is also evidence that the diet of the mother during gestation influences the feeding behavior of the offspring. A study conducted in sheep showed that prenatal exposure to a specific type of feed—through the mother's diet—influenced the offspring's feeding preferences later in life (Simitzis et al., 2008). This is also supported by Nolte et al. (1992), who found that the odor of herbs (garlic) would be detected in both amniotic fluid and fetal blood.

Wiedmeier et al. (2002) evaluated how animals eating low-quality forage early in life would influence their performance later in life. A group of cows was fed with low-quality forage from gestation until early lactation. After weaning, low-forage quality was replaced by high-quality diets until approximately 5 years old. Surprisingly, when cows were exposed to low-quality forage again during subsequent winters, those animals who were familiarized with low-forage quality by early experience in utero and after birth had a higher performance in terms of milk production compared to naïve cows that did not have early experience with consuming this type of forage. Additionally, Wiedmeier et al. (2012) showed how providing high-fiber diets to pregnant cows positively impacted the intake and digestibility of this type of forage in their offspring.

Vonnahme et al., (2006) studied how the nutritional restriction during early to mid-gestation in ewes can affect the weight fetal, blood glucose concentration, and placental growth and differentiation compared to ewes with adequate nutrients. One group of ewes received restricted feeding without supplementation (Baggs) while another group received adequate nutrition (UW). After that, some ewes from both groups were exposed to 50% restricted feeding during early until mid-gestation, and other ewes from both groups were subject to adequate feeding (control fed). Then, ewes were slaughtered for analysis. Weight, fetal, and blood glucose concentration decreased in those fetuses that came from restricted mothers UW from early from mid-gestation compared to mothers from control fed UW. However, no differences were found between in the fetal weight of both Baggs ewes (restricted or control). The authors suggested that their results might be explained by the capacity of ewes, which were adapted to feeding in a restricted environment to provide-- by placental transport-- the necessary nutrients to develop the fetus during mid-gestational nutrient restriction.

Thus, findings described above provide evidence that animals can adapt better to specific environments during the postnatal stage when they are exposed to similar nutrition/flavors during prenatal stage, and those would play a relevant role to production systems management and their efficiency, especially in systems where the main feed resource is the low quality of forage (e.g., rangeland).

Another interesting aspect of the importance of nutrition during gestation is the relationship with the reproductive development of the progeny. It occurs during the first third of the pregnancy, when the testicles and ovarian system develop. It is important to note that approximately by the eightieth day of pregnancy, the gonadal system development takes place (Nilsson & Skinner, 2009). It is a significant aspect that is associated with the creation of follicle and ovarian reserves, all of which help to define the reproductive life of the offspring (Hirshfield, 1994). Mossa et al. (2009) evaluated the effect of nutritional restriction in heifers on the quantity of antral follicles in female progeny. The maternal restriction was performed from conception to the end of the first pregnancy period. After the calves had been born, the number of antral follicles were measured by ovarian ultrasonography in the female offspring (7-8 weeks of age). The results showed that not only the quantity of follicles in follicular waves might be altered by maternal nutrition but also the proportion of the ovarian reserve.

Although the timing of the reproductive development in the fetus is focused during the first one-third of gestation, there is some disagreement among researchers. Warner et al. (2012) did not find evidence that protein supplementation in late gestation increased the reproductive rate in offspring. However, Martin et al. (2007) reported that heifers from dams that received protein supplement during late pregnancy exhibited higher pregnancy rates compared to their counterparts born to non-supplemented dams. Also, although Funston et al. (2010) claimed that no significant difference was exhibited in the reproductive performance of heifers between supplemented and non-supplemented dams, an increasing trend was observed in heifers born to dams that had received supplementation.

A study conducted by Roberts et al. (2009) linked maternal nutrition and its impact on progeny performance. Roberts et al. (2009) evaluated the impact of the dam's nutrition on the lifetime productivity in the progeny. The feed protocols in the cow herd involved the use of the pasture during the spring, summer, and fall seasons and then separate pasture plus protein supplementation during winter (December to March), which coincided with late gestation. The supplement was based on alfalfa cake or hay, which were provided in different amounts depending on the treatment: 1.8 kg . cow^{-1} . day^{-1} (ADEQ) or 1.0 kg . cow^{-1} . day^{-1} (MARGINAL). The management of heifers involved feeding in pens after weaning. During the first month, heifers were fed ad libitum for adaptation to the new environment. After that, for 140 days, one group of heifers was fed with a supplement based on corn silage and alfalfa ad libitum (CONTROL) while another group (REST) was assigned the same type of supplement but 80% of the total that was consumed by the females in the CONTROL group. After 140 days, heifers from both groups were placed in the same pasture until the breeding season (approximately fourteen months of age). From November-December to March, the pregnant cows from CONTROL and REST groups were fed according to the ADEQ and MARGINAL schedules, respectively. This scheme was performed each year, and results of seven years is shown by the authors. Heifers in the REST group consumed less feed for three years than those in the CONTROL group during the 140 days of supplementation. Also, the heifers in the REST group weighed less than those in the CONTROL group not only during the pre-breeding period but also during the grazing season. The calves born to heifers in the REST group weighed less than those born from dams that had received the MARG treatment.

However, it is important to note that the retention rate of these cows was higher than that of REST cows from ADEQ dams, which might indicate that heifers that are restricted during growth and that come from dams that were restricted might be able to maintain their reproductive rate in times when the nutrition level is low. In conclusion, Roberts et al. (2009) argue that if the dams are managed with the marginal input of nutrients, the offspring might present the ability to sustain the reproductive rate during a period of restricted nutrient feeding.

In summary, there is evidence that maternal nutrition could affect the progeny performance by altering the gene expression via epigenetics mechanisms. This means that providing a differential nutrient level during gestation might modify the quality of progeny, all of which might impact the production system and its efficiency.

TOOLS USED TO EVALUATE FORAGING BEHAVIOR OF RANGELAND LIVESTOCK

To study foraging behavior, it is necessary to not only know the influence of the animal and environmental attributes, but also know the measurement tools that are currently being used. Global Positioning System (GPS) collars, Geographical Information Systems (GIS) software, and Remote Sensing are considered three significant technologies that can be used to monitor the foraging behavior of livestock in grazing studies (Bailey et al. 2018, Sawalhah, 2014, Swain et al., 2011, Agouridis et al., 2004, Tuner et al., 2000).

GPS technology refers to a network of satellites and sensors that are used to locate the position of an object across a coordinate system (Tomkiewics et al., 2010). GPS technology is a robust tool that permits spatiotemporal data collection and the study of the animal distribution, movement patterns and resource use by animals (Bailey et al., 2018). Some advantages in the use of GPS collars include facility of data acquisition at a rapid rate and the ability to acquire more data compared with visual observations, where the observer's presence and the fatigue genereated by that presence, can alter cattle behavior when the animals must be evaluated over an extended period of time.

Most of the GPS collars include motion sensors, which allow researchers to make inferences about animal activity. Movement sensors usually consist of two- or three-axes accelerometer units capable of recording animal neck movements. The dual-axis sensor records the number of neck movements made by the animal in the perpendicular (up-down, y-axis) and parallel (right and left side, x-axis) planes, while the triple-axis sensor includes an extra axis to record the mid-sagittal plane (z-axis). Gonzalez et al. (2015) developed an algorithm to classify behaviors and activities using data from GPS collars and 3-axis accelerometers mounted on steers, which was validated with visual observations. Their results showed that between 85.5-90.5 % of all points were classified correctly during the algorithm development and evaluation phase. The authors concluded that GPS technology combined with accelerometer devices could be used to infer scale spatio-temporal differences not only in the location but also in the activity of cattle. However, the authors mentioned that increasing the precision was associated with increasing the sample size, autonomy of the battery, and performance of the computer equipment to manage a larger quantity of data. Ungar et al. (2011) tested two methods to infer animal activity with the classification tree using GPS data (with motion and head location data) or GPS data combined with pedometer data and visual observations. The authors concluded that the misclassification rate was lower (10 %) when de Lotek GPS collars were combined with pedometers due to the possibility of improving the splitting in the classification tree. Another study conducted by Augustine and Derner (2013) used GPS technology combined with accelerometer data (head movement of the animals) to develop a classification tree based on distance and head position. It split activities into four categories (resting, grazing, traveling, and mixed activities) and was validated with visual observations. The authors found that the classification tree categorized activities with a misclassification rate of 16%. The distance traveled and the head-down movement were the most significant variables that contributed to estimating grazing activity. Guo et al. (2009) studied behavioral patterns in cattle using GPS technology combined with an accelerometer, magnetometer, and field observations. In this study, it was possible to discriminate between resting, grazing, and traveling activities using movement speed and angular velocities. Those activities were included in a behavioral model, which simulated behavior patterns at both a fine and a larger scale. The study showed that GPS technology is useful to collect specific locations that help to classify activities; however, sensor data is important to improving the classification.

To apply GPS technology in grazing studies can be expensive, especially when it is necessary to have replication of the studies to increase the statistical power for research purposes (Swain et al., 2011). This is the reason why there is increasing interest in the use of low-cost

GPS units to monitor livestock movement and activity patterns on rangelands. Clark et al. (2006) developed a low-cost GPS collar, which allows tracking animals in real-time. Those collars have the characteristics to capture data for more than three weeks wherein the user can configure the device to monitor animals at 15-minute intervals. Similarly, Knight et al. (2018) compared the performance of low-cost collars (igotU Gt-120 GPS unit) with available GPS devices (LOTEK 3300 collars). Different variables were included in the analysis, such as elevation, slope, distance traveled, and distance from water. Authors found that igotU Gt-120 GPS units recorded less GPS locations points (66.2 %) when compared to Lotek collars (99.9%). Consequently, differences were found in the distance traveled (6171 m . day^{-1} vs. 7104 m . day^{-1} to igotU Gt-120 GPS unit and Lotek collars, respectively). The authors concluded that despite the differential collection of location points compared to Lotek collars, the igotU Gt-120 GPS units still provided an adequate number of GPS positions to study behavior on Chihuahuan Desert rangeland.

However, it is significant to note that, the main limitation with low-cost collars is that they only provide GPS coordinate values, not accelerometer data. This renders head movement unobtainable. On the other hand, a significant aspect of GPS collars, that requires consideration, is the accuracy of the location regarding the actual place of the animal being tracked. This is of particular importance in certain types of experiments needing highly accurate data positioning to avoid erroneous research conclusions. Applying differential correction might be one option to improve the precision of the dataset. The decision to use it, however, might be based on the distance of the location of the experiment from the reference station. A study conducted by

Monteiro et al. (2005) showed that accuracy decreases as soon as the distance between GPS unit to reference station increases. The authors stated that one meter of accuracy might be reduced per each 150 km distance.

Different factors might influence the accuracy of the data collection: the type of receivers used may produce errors, requiring evaluating them for both static and dynamic conditions. This is of particular importance because several studies indicate that both types of conditions may result in variations due to numerous causes. Chosa et al. (2011) evaluated the performance of two different kinds of receivers and found that dynamic accuracy was different compared to static accuracy. This research supports another study conducted by Stombaugh et al. (2002) who argued that the static performance not necessarily represents the dynamic accuracy. The authors explained that differences in both types of accuracy could be due to data filtering. For example, in the same case, the static performance of a receiver may be better using the filter, while the dynamic performance may be better without using it. Stombaugh et al. (2005) stated that one of the reasons why manufacturers do not inform the dynamic performance is that there are not suitable standards that permit testing and reporting it. Therefore, the authors developed a test fix to evaluate the dynamic accuracy, contributed to facilitating the evaluation by manufacturers (commercial suppliers), and included this information in the reports of the GPS receivers. The authors concluded that the fix system might contribute to quantification of dynamic accuracy. It is important to note that, although the design of text fixt was made by agricultural operations, it is a good example to encourage the development of test fix in rangeland and behavior studies.

Another aspect that affects the accuracy of the GPS unit is the vegetation. De Cesare et al. (2005) evaluated the effect of canopy closure on GPS accuracy. The experiment was carried out northeast of Missoula, Montana. Three different grades of canopy closure were evaluated: open, low, and high (0-10, 11-39 and >40% closure, respectively). Measurement of a point in a straight line was made using GPS units (Trimble GeoExplorer® 3) and an external antenna located to 1.8 m above the terrain. GPS error was calculated as one minus the difference of the relation between the actual length and the GPS length (1 - (real length/GPS length)). The results indicated that, while no difference was observed between the open and low percentage of canopy closure ($P=0.178$), a significant difference was found between low and high ($P=0.008$) and open and high canopy closure ($P<0.001$). Furthermore, track tortuosity would seem to increase as canopy closure increases. The authors concluded that the type of canopy closure affects GPS errors and, although the errors were within the expected precision range (1-5m), the researchers warn, precautions should be considered, in order to not include bias in tracking length and tortuosity.

Topography, together with vegetation, is also considered to affect the accuracy of the GPS unit. D’ Eon et al. (2002), studied the influence of topography on the error and bias rate in GPS collars. The experiment was conducted in the Selkirk Mountains located in southeastern British Columbia. A variable defined as available sky was calculated for each terrain location to estimate the GPS unit’s performance. While high available sky indicated the open sky view, low available sky indicated presence of terrain obstructed view. Twelve locations were selected, and three sites were established at each site according to the canopy cover: open (0% canopy cover), partially closed (30-60%), and closed (80-100%). GPS units were put at 1 meter above ground, and they were placed at 15-minute intervals. The GPS Pathfinder Pro XR unit was used to determine the position and elevation level; these values were assumed to be the true location of the experiment. The results showed that the fixed rate of the GPS unit were influenced by the interaction between topography and vegetation cover. There were no significant differences between fix rates and available sky in the 0% canopy cover, which might indicate that open canopy could maintain relatively high fix rate, even if available sky is low. However, a curvilinear regression was found between fix rates and available sky with 30-100 % canopy cover, where high available sky (for example, mountain tops) had a higher fix rate than low available sky (for instance, steep valley bottoms). The authors concluded that if fix-rate bias occurs as a consequence of the interaction between topography and canopy cover, correction factors might be used to reduce the bias and arrive at better results.

Cain III et al. (2005) studied whether topography and fix interval would affect the location error and fix success rates using GPS telemetry. The authors found that both topography and fix interval might affect GPS position data, increasing location error and missing data. Consequently, it might increase the type II error, affecting the inference of the results of a study by arriving at conclusions that might be incorrect. Recio et al. (2011) found that while native and shrub cover were present, the highest effect on fix success rate, were other variables, such as tree cover, available sky, satellites, and position (horizontal dilution), that influenced the location error.

Not only the obstruction that is produced by the animal's body, but also variations in the location and direction of the GPS antenna, may cause errors and bias the results when animals are grazing, resting or traveling, affecting the accuracy of the GPS units. D'Eon et. al. (2003) worked with a fix rate bias model evaluating the influence of using uncorrected or corrected data to study the habitat selection in behavior research. The authors found that when data loss is lower than 10%, similar conclusions might be arrived about the habitat selection, so corrections might not be necessary in this case. However, it is important to note that the bias model was based on stationary data; therefore, it might not reproduce real biases. In this study, the bias in the connection with animal activities that might generate loss of data, and are not present in the model.

D'Eon and Delparte (2005) studied the effect of position and orientation of GPS units on the their performance. Five positions were evaluated (0º, 45º, 90º, 135º and 180º from vertical) and then rotated following the cardinal points without considering 0º (GPS collar antenna looked skyward) and 180º (GPS collar antenna looked at terrain). Collars were located 50 cm from the relative plane and unobstructed area and fixed using an interval of 15 minutes. Fixed rates and horizontal location error were calculated using uncorrected data. Also, positional dilution of precision was used to evaluate the location accuracy. According to the results, the orientation did not affect either the fix rate and location error. A significant difference, however, was found depending on the position of the GPS units. The 0 º was the position that had the highest fix rate (100% ±0.00) and lowest location error (3.4 m ±0.28). Conversely, 180 º was the position that had the lowest fix rate (76.0% ±7.80) and highest location error (17 m ±1.72). It is important to note that relatively high to fix rates and low to location error were obtained between 0º and 90º. Based on these results, the authors stated that animal activity influences collar position, affecting data by impact in the error and bias, which might lead to erroneous conclusions. For example, foraging and resting might present higher bias compared with walking because when animals are foraging and resting, the collar antenna might be oriented at lower angles than when they are walking.

Finally, another aspect of interest in the GPS technology and the association with animal behavior is the sampling interval. Johnson and Ganskopp (2008) studied the effect of increasing GPS sampling intervals on estimates of distance traveled and the percentage of pasture used by cattle. Three pastures were used and groups of 20 cows were assigned in each pasture. GPS collars were fitted on four cows per pasture, at five-minute intervals for 15 days. The QBasic software was used to assess intervals from 5 to 1440 minutes. In addition, point and line analysis methods were used, and regression models were fitted using the distance traveled and the percentage of visits as the dependent variable and GPS intervals as the independent variable. The results showed that the percentage of visits to different areas the pasture with the point method was lower than line method (33.8 and 36.3 % respectively). It is also noted that with the line analysis method, spatial error increased as sampling rate increased. In a similar way, the travel distance was reduced as fix interval increased. In summary, results regarding the use of pasture and distance traveled in cattle might be affected, depending on the sampling rate, so precautions should be taken, due to underestimation of these variables as GPS fix intervals increase.

Another important tool to study animal behavior is Geographic Information Systems (GIS) that emerged as an alternative to mapping, analyzing, and measuring the world (Longley et al., 2005). In a broad sense, GIS is defined as *"a robust set of tools for collecting, storing, retrieving at will, transforming and displaying spatial data from the real world for a particular set of purposes"* (Burrough & McDonnell, 1998).

GIS has been transformed into a tool that permits us not only organize the information and store it, but also access, recover, manage, summarize, and assess different alternatives to solve problems (Longley et al., 2005). Also, as a result of GIS use by different kinds of institutions such as government, academic, agencies, and corporations (Longley et al., 2005), it has become a multi-disciplinary tool to study several geographical, environmental and socio-economic problems (Longley et al., 2005).

In the field of grazing behavior, GIS is a useful tool to combine with GPS technology (Barbari et al., 2006). While GIS provides territorial spatial parameters, GPS offers information about the spatial and temporal grazing distribution of animals on rangeland. A study conducted by Sawalhah et al. (2014) showed as it is possible determine a grazing pattern for a group of cows grazing a rangeland using GPS and GIS technology. In that study, Sawalhah et al. (2014) used different ArcGIS layers to obtain spatial parameters such as slope, elevation, aspect, cover and substantial information per each pixel in combination with remotely sensed imagery. In addition, cows were tracked with GPS to determine movement within the study area, and weather data were used to explain the grazing pattern. They found that in years with high forage allowance cows reduced the grazed area by 18.7 % and increased the return interval to each pixel by 55 % compared with years where the forage allowance is low. It also noted that wet years might cause cows to reduce the pixel residence time (14.7 %) and increase the return rate to each pixel (11.1%). In conclusion, GIS combined with GPS and remotely sensed imagery allowed these authors to test the hypothesis that cows appear to generate their own grazing systems within an area with season long grazing (Coughenour, 1991).

The use of remote sensing of the vegetation is another useful tool to study behavior of grazing animals. Remote sensing is defined as "*the science and art of obtaining information about an object or phenomenon without making contact with it*" (Jensen, 2015). Remote sensing had its origin in the 19th century with the development of photography, and astronomy was one of the first disciplines to use it. However, it is not until 1956 that this tool was introduced in vegetation studies (Jones & Vaughan, 2010).

Chlorophyll is the pigment that is mostly dominant in the structure of the plant following carotenes and xanthophylls. The chlorophyll content in a plant is essential for remote sensing because it is important to generate the spectral reflectance curves, which allow one to distinguish it from the characteristics of other materials. The spectral reflectance curve of vegetation presents a low reflectance in both blue and red bands (0.45-0.67 um) due to chlorophyll absorbing most of the incident light in this region of the spectrum ("chlorophyll absorption bands"). Conversely, there is a high reflection in the green area. It is the reason why healthy vegetation appears green in color. The reflectance increases in the near infrared region. It is the region that is called "red edge" (0.68-0.75 to 1.3 um) where 40-50% of the reflectance is reached. It is interesting to note that the position and magnitude of the "red edge" allows one to distinguish the different species that are present in an image. Also, this region is interesting for detecting vegetation stress (Lillesand et al., 2008). The reflectance decreases at 1.4, 1.9, and 2.7 um because of water absorption in that region of the spectrum. The high reflectance values are observed at 1.6 and 2.2 um depend on the leaf moisture level (Lillesand et al., 2008).

Different types of sensors can be used to capture remotely sensed data. The high-resolution systems allow monitoring of vegetation at the community level and species level. Examples of high-resolution images include IKONOS, QuickBird, and Worldview-2 (Jones & Vaughan, 2010). Their main advantage consists in the high spatial resolution (2.4 to 4 m) and revisit time (1 to 3.5 days). However, the main disadvantage is the cost of the image.

Moderate-resolution systems offer the possibility to obtain remotely sensed data with free access to information. The first satellite to acquire this kind of information was Landsat-1 in 1972, followed by Landsat-2 and Landsat-3, which had 80-m spatial resolution and 18-day revisit time. The multispectral scanner was used in these satellites (MSS) that consists of an optical-mechanical system where the image is taken perpendicular to the flight line (Jensen, 2015). After that, improvements were made, and the Landsat-4 Thematic Mapper (TM) was launched into space in 1982. The most significant advantages were the spatial resolution of 30 m in six bands, with 120 m resolution in the thermal band, and the 16-day revisit time. Landsat-5 was launched in 1985 and also included the TM. Landsat-7 was launched in 1999and was equipped with the Enhanced Thematic Mapper Plus (ETM+), which allowed the modification of the spatial resolution of the thermal infrared band to 60 m and also included a panchromatic band (0.52 to 0.90 um) with a resolution of 15 m. Landsat-8 Operational Land Imager (OLI) and Thermal Infrared Sensor (TIRS) images were launched in 2013. Landsat-8 OLI includes similar spectral bands to Landsat ETM. However, other bands are included: one coastal aerosol band (band 1), one cirrus band (band 9), and two thermal infrared bands (band 10 and 11). Moderate Resolution Imaging Spectro-Radiometer (MODIS) was launched in 1999, and has two sensors: Terra EOS AM-1 and Aqua EOS PM-1. The spatial resolution is 250 m (Bands 1-2, Pan), 500 m (Bands 3-7, VNIR), and 1000 m (Bands 8-36, SWIR). It has a revisit time of 1-2 days. MODIS is very useful for studying vegetation dynamics although the coarse spatial resolution makes the local and regional studies difficult (Xie et al., 2008). Some studies such as Knight et al. (2006) have incorporated multi-temporal observations to improve the accuracy of the data. Satellite remote sensing is a key tool in vegetation studies, especially when the Vegetation Index is used to monitor the vegetation dynamics (Jones & Vaughan, 2010).

A vegetation index (VI) refers to a mathematical combination derived from radiometric data that is used to establish the photosynthetic activity of vegetation (Jensen, 2015). A VI is useful to estimate the leaf area, gross primary productivity, and plant physiological activity

(Jensen, 2015, Zhou et al., 2014). There are several different types of VI. The normalized difference vegetation index (NDVI) is the most common VI. It is an index that is based on the difference of reflectance in the near-infrared (NIR) and red (RED) bands of the electromagnetic spectrum, $NDVI = (\rho NIR- \rho RED/ \rho NIR+ \rho RED)$
where, ρNIR = near infrared band (0.75-0.90 um), which is strongly associated with radiation reflected by vegetation. The ρRED = red band (0.63-0.69 um) is associated with the area where chlorophyll absorption is maximum. In this case, active photosynthetic vegetation will have high absorption in the red band and high reflectance in the NIR band, while vegetation that is not healthy will have low absorption in the red band and low reflectance in the NIR band. Otherwise, non-vegetated areas might show high reflectance across the spectrum. An NDVI value ranges from negative to positive values. Positive values indicate green vegetation while negative values reflect un-vegetated sectors such as barren land, water, and snow.

The Soil Adjusted Vegetation Index (SAVI) is an index used in sparse areas to compensate for a soil background (Huete, 1988). The index includes a correction factor in its calculation as $SAVI = (\rho NIR- \rho RED/\rho NIR+ \rho red+L)\ (1+L)$, where L= is a correction factor.

The Enhanced Vegetation Index (EVI) is a modification of the NDVI index (Wagle et al., 2014). In this case, the index includes a soil correction factor (L), two coefficients (C_1 and C_2), and a gain factor, (G), $EVI = G\ (\rho NIR- \rho RED/\rho NIR+ C_1\ \rho red - C_2\ \rho blue +L)$.

The challenge is to find the most appropriate VI to extract accurate information from the area of interest. Generally, the VI that is most correlated with the attribute of interest might be the most adequate to use in future research.

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CHAPTER 2

INFLUENCE OF ANIMAL-, ENVIRONMENT-, AND MANAGEMENT-RELATED FACTORS ON GRAZING BEHAVIOR OF RANGELAND BEEF HEIFERS DURING WINTER

ABSTRACT

We determined the influence of winter feed supplementation method and the dam's lifelong feeding regime on rangeland grazing patterns of beef heifers during winter. We compared behavior of heifers wintered on rangeland (group-fed cake, GFC or self-fed protein, SFP supplements) whose mothers were supplemented during the last third gestation period with an adequate (CT) or marginal (MG) level of protein to meet their nutrient requirements. During 2015 and 2016, heifers (n=42) were fitted with Lotek 3300LR GPS collars and monitored 18 or 16 days (January and February, respectively). On most days, GFC heifers traveled farther, followed more sinuous trajectories and covered larger areas than SFP counterparts in both months ($P \leq 0.05$). In general, GFC heifers spent more time in resting and traveling but fewer hours grazing time compared to SFP heifers ($P<0.05$). All heifers spent more time grazing ($P<0.01$) on cloudy days with higher humidity during January ($P<0.05$). During February, however, heifers increased the grazing time as temperature and dew point increased but the response was higher in SFP heifers compared to GFC heifers ($P<0.01$). Sinuosity, was the variable that best discriminated heifers into treatment groups between supplement method and the dam's feeding regime ($P<0.01$), although the best classification was found in heifers whose mothers came from CT group. Supplement treatment modified movement and activity of heifers during winter. Restricted the dams feeding during the third gestation period appeared to not affect the behavior of the offspring when the conditions during the supplementation treatment adequately covered the nutrient requirements of the heifers.

Keywords Northern Great Plains, winter heifer development, GPS collars, heifer grazing behavior

INTRODUCTION

Feed supplementation is commonly used on western North American ranches during winter when native rangeland vegetation is dormant (forage <6% crude protein) and cannot meet the nutritional requirements of pregnant cows or growing heifers (Roberts et al., 2009; Adam & Short, 1987). Protein supplements can boost intake of low-quality forages by increasing organic matter digestibility (McCollum III & Horn, 1990).

The cost of winter feed supplementation strongly impacts the profitability of most cow calf operations across western USA. Decreasing feed inputs in heifer development programs can result in lower weight gains and delayed puberty, while increasing such inputs typically elevates production costs. Therefore, maintaining or increasing reproductive performance of heifers while maintaining harvested feed inputs low is critical to the financial sustainability of rangeland-based cattle production systems. Advancements in the fields of genetics and epigenetics have shown progress in achieving this goal (Roberts et al., 2016, Mulliniks et al., 2012, Roberts et al., 2009, Martin, et al., 2008).

Animals can adapt better to specific environments during the postnatal stage when they are exposed to similar nutritional conditions or food flavors (Weidmeier et al. 2012; 2002) or restricted feed (Vonnahme et al., 2006) during the prenatal stage. This is particularly important to managing production systems where the primary resource consists of low-quality forage (e.g., dormant forage during winter). Thus, heifers adapted to this type of environment might help reduce the feeding cost and consequently contribute to improving the system efficiency.

A number of studies have examined the effect of supplementation on spatial distribution of cows, steers, or heifers (Hojer et al., 2012, Cibils et al., 2008, Schauer et al., 2005, Bailey et al., 2004, Krysl et al., 1993). Delivery schedules and type of supplements vary greatly and can influence rangeland grazing patterns (Mathis & Sawyer, 2007). Two common methods of range cattle feeding include hand- vs. self-fed delivery of supplements (Bowman & Sowell, 1997). Hand-feeding is defined as a type of delivery method where the supplement is provided in a specific quantity that is consumed by animals in a relatively short time. Self-fed is supplied to produce ‘ad libitum’ intake, which is typically limited by modifying the amount, palatability, and physical characteristics of the supplement (Sawyer & Mathis, 2001). Supplement delivery method as well as supplement composition (energy dense or protein dense) could conceivably influence pasture use patterns of young heifers on rangeland over the short- and longer-term, but research is lacking in this area.

The objective of this study was to determine how behavior and performance of rangeland-developed heifers in the northern Great Plains are affected by weather, feed supplementation method, and the dam's feeding regime.

We hypothesized that during winter, heifers supplemented with self-fed protein dense feed would be more effective grazers causing them to travel farther and faster, explore larger areas of a pasture, follow a more sinuous path, spend more time traveling and grazing and less time resting regardless of weather, compared to heifers supplemented with hand-delivered energy dense feed. We also hypothesized that the grazing behavior of heifers whose dams had received restricted feeding during pregnancy would differ from heifers born to non-restricted dams particularly when fed protein dense vs. energy dense winter supplement.

MATERIALS AND METHODS

Study site

The experiment was conducted at the USDA-ARS Fort Keogh Livestock and Range Research Laboratory (LARRL) in Miles City, MT (Lat 46° 23' 08'' N, Long 105° 52' 26'' W). Fort Keogh covers an area of 22,258 hectares. The climate is semi-arid (Rubel & Kottek, 2010; Kottek et al., 2006) with cold winters and warm summers. Average minimum and maximum temperatures are –14.6°C (January), and 31.8°C (July), respectively, with an average of 150 frost-free days. Mean annual precipitation is 333 mm. Soils include Mollisols and Entisols and approximately 350 plant species have been identified on the research station (Petersen &

Reinhart, 2012). Most of the plant communities in the study area are composed of C_3 graminoids. *Bouteloua-Hesperostipa-Pascopyron* associations are predominant across the study area. Pastures that were used for the study (depending on the study year) ranged in size from 49.79 to 79.91 ha (Figure 2. 1.). Vegetation classes to each pasture are showed in Figure 2. 2. and Table 2. 1.

Animals and treatments

All animal procedures were approved by the Fort Keogh Livestock and Range Research Laboratory Animal Care and Use Committee. Composite bred heifers (one-half Red Angus, one-fourth Charolais, and one-fourth Tarentaise) that were sired by similar bulls, in a resident cow herd of 24 years that grazed native range until weaning. Heifers received one of two winter supplementation treatments. The group-fed cake (GFC) treatment included heifers that were developed on rangeland and fed 1.82 kg of cake supplement . d^{-1} . $heifer^{-1}$ (20 % crude protein, 1.75 % fat, and 19 % fiber) delivered daily at approximately 10:00 a.m. during winter. Cake was formulated based on 60 % alfalfa and 40 % energy grains (variable proportions of corn, wheat, barley, peas, dry distillers' grains and malt sprouts depending on cost each year) without molasses or bentonite. The self-fed protein (SFP) treatment consisted of a group of heifers that were also developed on rangeland with a self-fed supplement delivered in Grow-Safe bunks with high protein content composed primarily of ruminal escape protein sources (50 % crude protein) plus a mineral supplement designed to be consumed individually at 0.11 to 0.45 kg . $heifer^{-1}$. d^{-1} during winter (Table 2. 2.; Mulliniks et al., 2012). Treatments began in mid- December and continued until the second week of April when all groups were combined in an ungrazed pasture for approximately 113 days.

The feeding protocols in the cow herd involved the use of the pasture during the spring, summer, and fall seasons and then separate pasture plus protein supplementation during winter (December to March), coinciding with the late gestation period. The supplement was based on alfalfa cake or hay, which were provided at different rates depending on the treatment: 1.8 kg . cow^{-1} . day^{-1} (control, CT) or 1.0 kg . cow^{-1} . day^{-1} (marginal, MG). A detailed description of dams' treatments can be found in Roberts et al. (2009).

During January and February of each year, heifers in each treatment group were managed in different pastures. In January 2015 (n=134), heifers were in Lonepine R (GFC treatment) and Lonepine S (SFP treatment) while in February 2015 (n=134) heifers were moved to Lonepine T (GFC treatment) and Lonepine U (SFP treatment) pasture. In January 2016 (n=99), heifers were in Lonepine Trap (GFC treatment) and Lonepine Q (SFP treatment) while in February 2016 (n=99) heifers were moved to Lonepine S (GFC treatment) and Lonepine R (SFP treatment) pasture (Figures 1 and 2). It is important to note that most of the heifers in GFC treatment (February 2016) left the study area on some days.

GPS collars were fitted on 10 randomly selected heifers in January 2015 (n=5 GFC, and n=5 SFP) and 9 heifers in February 2015 (n=4 GFC, and n=5 SFP), 14 heifers in January 2016 (n= 7 GFC and n=7 SFP, respectively), 14 heifers in February 2016 (n=7 GFC, and n=7 SFP). Collars were configured to record position at 5-minute intervals. Different heifers were monitored for the 18-day and 16-day periods during each month (January and February, respectively) and year (2015 and 2016). Approximately half of collared heifers in each treatment group were born to dams in the CT group (see details above) while the dams of the remaining half were in the MG feeding group.

Weather variables

Weather data, including solar radiation (Langley . h^{-1}), relative humidity (%), ambient temperature (°C), rainfall (mm), wind dir (°), wind gust (m . s^{-1}), wind speed (m . s^{-1}), were retrieved from two different weather stations located at the USDA-ARS Fort Keogh LARRL in Miles City, MT (Table 2. 3.).

Movement and activity patterns

GRAZACT software (Sawalhah et al., 2016, Cao et al. unpublished) was used to calculate animal movement variables such as distance traveled (km . d^{-1}), velocity (m . s^{-1}), path sinuosity, area covered (ha . d^{-1}), and activity variables such as, resting (h . d^{-1}), grazing (h . d^{-1}), and traveling (h . d^{-1}). Sinuosity refers to straightness values, which ranges between 1 (straight path) and 0 (most sinuous path) and is the ratio of the distance between the first and last GPS location in a day, and the cumulative distance between successive 5-min GPS locations for that same day. Area covered in a day was calculated considering 288 points (GPS locations at 5-minute intervals per each animal . d^{-1}) and computing the minimum convex polygon that connects the outer points to generate a polygon around the cloud of GPS points. Activity classification of GPS points was based on movement velocity. Resting was assumed when velocity < 2 m . min^{-1}, velocities between 2 m . min^{-1} to 25 m . min^{-1} were assumed to indicate grazing, and velocities > 25 m . min^{-1} were classified as traveling. Because it was not feasible to validate velocity thresholds with visual observations, criteria to decide the velocity thresholds were based on distances used in a classification tree developed by Augustine and Derner (2013) for yearling steers grazing shortgrass prairie rangeland in Colorado, which the authors validated in a similar environment to that of the present study.

Statistical Analysis

A one-way ANCOVA in a randomized block design was conducted using a MIXED model in SAS 9.4 (SAS Institute, Cary, NC) to determine the effect of treatment (GFC, SFP) on grazing time (h . d^{-1}) controlling for weather variables. Year was considered the blocking factor and experimental unit. Treatments (GFC, and SFP) were considered a fixed effect and years (2015 and 2016) were treated as random effects. An average of grazing time of all heifers per treatment per each day (total 18 and 16 days to January and February, respectively) was used for this analysis. Each month (January or February) was analyzed separately.

Movement and activity patterns were analyzed with a blocking design with repeated measures design using a MIXED model in SAS 9.4 (SAS Institute, Cary, NC) which included the fixed effect of treatment (GFC and SFP), day (18 and 16 days to January and February, respectively) and their interaction (treatment x day). Year was the experimental unit and day was considered as a categorical variable. Each month (January and February) was analyzed separately. Years (2015 and 2016) were considered random effects. Heifers (observational unit) were considered a random effect nested within year and treatment. A type=sp (pow) option was used as the covariance structure due to the fact that in some cases measurements were unequally spaced because of outlier deletion. The ddfm=kr option was used to estimate the degrees of freedom and group option was used when the homoscedasticity assumption was not met (Little et al., 2006).

Discriminant analysis was used to classify heifers into treatment combination groups based on supplement treatment of heifers born to control or marginally fed dams (GFC-CT, GFC-MG, SFP-CT, SFP-MG) and PROC DISCRIM in SAS 9.4 (SAS Institute, Cary, NC) with the following option was used to classify the individuals: *pcov method=normal, pool=test, distance, manova, cross-validate* list. Wilks' ʎ was used to detect differences among groups ($P \leq 0.05$). A high Mahalanobis distance was interpreted to indicate higher dissimilarities, while the opposite was true of low Mahalanobis distances. Predictors used in the analysis were: distance traveled (log transformation, km . d^{-1}), area covered (ha. d^{-1}), movement velocity (log transformation, m . min^{-1}), path sinuosity (squared root transformed, 0-1), total time spent resting (h . d^{-1}), total time spent grazing (h . d^{-1}), total time spent traveling (h . d^{-1}). PROC STEPDISC in SAS 9.4 (SAS Institute, Cary, NC) was used to select the minimum set of predictors able to discriminate among groups at the $P \leq 0.05$ level. Testing for normality/multinormality of error residuals and homogeneity of variances was conducted prior to all statistical analyses to detect potential violation of assumptions. A square root transformation or log transformation was carried out on some dependent variables to normalize the residuals. Only heifers who were consistently in the study area (i.e. did not leave the study pastures) were included in this statistical analysis.

RESULTS

Weather variables

The covariates relative humidity (%), dew point (°C) and solar radiation (langley.h^{-1}) were all significantly related to grazing time ($P<0.05$) during January while the covariates temperature (°C) and dew point (°C) were l significantly related to grazing time ($P<0.01$) during February (Figure 2. 3.).

Slopes were similar for all treatments during January (P=0.28 relative humidity, P=0.60 dew point, and P=0.74 solar radiation) and February (P=0.18 temperature and P=0.17 dew point). A common model was used for all treatments (GFC and SFP) for each covariate due to the fact that distances between the regression lines (intercepts) were not significantly different for January (P=0.81 relativity humidity, P=0.85 dew point, and P=0.83 solar radiation). For each change of one unit in relative humidity, dew point or solar radiation, the average change in the mean grazing time was approximately 0.03, 0.03, and -0.13 h . d^{-1}, respectively. However, in February different models were used for GFC and SFP for each covariate (temperature and dew point) due to fact that distances between the regression lines (intecerpts) were significant ($P<0.01$ for temperature and dew point, respectively). If the temperature was 0 °C, the grazing time would be approximately 7.80 and 8.30 h . d^{-1} for GFC and SFP, respectively. In Addition, if the dew was 0 °C, the grazing time would be approximately 8.25 and 8.74 h . d^{-1} for GFC and SFP, respectively.

Movement patterns

Back-transformed movement variables LSmeans from square-root transformed data are reported in this section for path sinuosity during January. There was a significant treatment by day interaction for all movement variables (distance traveled, movement velocity, path sinuosity, and area covered) during January ($P<0.01$, Figure 2. 4.). On average, heifers in GFC walked 1.18 km . d^{-1} farther and 0.90 m . min^{-1} faster than SFP counterparts on days 1, 3, 4, 6, 8, 11, and 17 ($P<0.05$ for distance walked and movement velocities, respectively). Additionally, heifers in GFC treatment walked 0.75 km . d^{-1} farther than SFP counterparts on day 18 ($P=0.02$). Heifers in GFC treatment followed more sinuous trajectories (on average 0.24 vs. 0.30 for GFC and SFP, respectively, range 0-1) on days 2, 3, 4, 5, 8, 9, 12, and 18 ($P\leq0.05$). Similarly, heifers in GFC treatment covered a larger area than SFP heifers on days 2, 3, 4, 6, 10, 11, 16, and 18 (on average 37.74 ha . day^{-1} vs. 31.77 ha . day^{-1} for GFC and SFP, respectively, $P\leq0.01$).

There was a significant treatment by day interaction for all movement variables (distance traveled, movement velocity, path sinuosity, and area covered) during February ($P<0.01$). On average, heifers in GFC walked 0.95 km . d^{-1} farther and 0.72 m . min^{-1} faster than SFP counterparts on days 6, 10, 11, 12, 15, and 16 ($P\leq0.05$ for distance walked and movement velocities, respectively).

Heifers in GFC treatment followed more sinuous trajectories (on average 0.06 vs. 0.13 for GFC and SFP, respectively, range 0-1) on days 1, 7, 8, 10, 11, 12, and 14 ($P<0.05$). Also, heifers in GFC treatment covered a larger area of the pasture than SFP heifers on day 11 (56.82 ha . day^{-1} vs. 38.35 ha . day^{-1} for GFC and SFP, respectively, $P<0.01$) while heifers in GFC treatment covered a lower area than SFP heifers on day 4 and 14 (on average 34.11 ha . day^{-1} vs. 53.61 ha . day^{-1} for GFC and SFP, respectively, $P<0.05$).

Activity patterns

Back-transformed LSmeans from square-root transformation for time traveling are reported in this section for January. There was a significant treatment by day interaction for time spent resting ($P<0.01$), grazing ($P<0.01$), and traveling ($P< 0.01$) during January (Figure 2. 5.).

On average, heifers in GFC spent 1.35 fewer h . d^{-1} resting than SFP counterparts on day 4 ($P<0.01$), while 1.12 more h . d^{-1} resting than SFP counterparts on days 7, 10 and 12 ($P<0.01$).

In addition, heifers in GFC treatment spent more time grazing (on average 7.90 vs. 6.84 for GFC and SFP, respectively) on days 4, 8, and 14 ($P<0.05$) while heifers in GFC spent fewer time grazing (on average 7.04 vs. 7.91 for GFC and SFP, respectively) on days 7, 10, and 12.

Heifers in GFC treatment spent more time traveling (0.93 vs. 0.50 for GFC and SFP, respectively) on day 1 but fewer time traveling (on average 0.55 vs. 0.94 for GFC and SFP, respectively) on days 2, 4, 9, and 16.

There was a significant treatment effect for time spent resting and time spent grazing and a significant treatment by day interaction for time spent traveling ($P< 0.01$) during February (Figure 2. 5.). Heifers in GFC spent more time resting than SFP counterparts (15.54 vs. 15.18 for GCF and SFP, respectively, $P<0.05$). However, less time grazing was spent by GFC compared to SFP counterparts (7.66 vs. 8.18 for GCF and SFP, respectively, $P<0.01$). Finally, GFC heifers spent more time traveling than SFP counterparts on days 1, 3, 5, 10, 11, 12, 15, and 16 (on average 0.94 vs. 0.63 for GCF and SFP, respectively, $P<0.05$)

Individual classification analysis

Heifers were classified into significantly different treatment combination (GFC-CT, GFC-MG, SFP-CT, and SFP-MG) groups (ʎ Wilks = 0.52, F (3, 37) = 11.26, $P< 0.01$) when all behavior variables were considered simultaneously (Table 2. 4.). The percentage of individuals classified correctly (cross-validation) by the discriminant function was 84.62%, 0.00%, 60.00% and 0.00% for heifers in GFC-CT, GFC-MG, SFP-CT, and SFP-MG treatment combination, respectively (mean error rate = 0.59).

Classification error rates were highest for heifers who came from restricted dams whose behavior was apparently more similar to heifers who came from not restricted dams' groups (Table 2. 4.). Almost all misclassified GFC-MG heifers were placed in the GFC-CT group; only two GFC-MG heifers were misclassified as belonging to the SFP-CT group. Almost all misclassified SFP-MG heifers were placed in the SFP-CT group while three SFP-MG heifers were misclassified as belonging to the GFC-CT group. Stepwise selection using average squared canonical correlation indicated that total sinuosity (0-1, 24 hs.) was the smallest subset of behavior variables able to classify heifers into significantly different groups (P<0.01). The squared distance (Mahalanobis Distance) between heifers in GFC-CT vs. SFP-CT (3.21, P<0.01) and GFC-CT vs. SFP-MG (3.51, P<0.01) treatments and heifers in GFC-MG vs. SFP-CT (1.91, P<0.01) and GFC-MG vs. SFP-MG (2.14, P<0.01) treatments were greater than distances between heifers in GFC-CT vs. GFC-MG (0.17, P=0.39) and SFP-CT vs. SFP-MG (0.01, P=0.85) groups. Variables means are shown in Table 2. 5.

DISCUSSION

Contrary to our hypothesis, heifers supplemented with self-fed dense protein (SFP) feed traveled shorter daily distances, exhibited slower movement velocities, followed a straight path and most of the time covered smaller areas of the pasture in a day compared with peers that were supplemented with hand-fed energy-dense (GFC) feed. Heifers in SFP treatment followed a straighter path probably due to lowest overall forage quality expectations and presumed lower patch selectivity compared to heifers in GFC who received a high-energy feed supply. Heifers in GFC treatment exhibited more sinuous trajectories possibly exhibiting higher selectivity than their SFP counterparts who were possibly optimizing forage searching and foraging activities to minimize energy expenditure and maximize energy acquisition. Browning et al. 2018, who evaluated the connection between cow movement patterns with the landscape greenness, found that cows tended to follow more sinuous trajectories as vegetation greenness increased presumably due to increased opportunities to select high quality forages. Higher path sinuosity in

GFC vs. SFP heifers may have been the result of differences in level of selectivity among treatment groups. It is possible that a higher portion of nutritional requirements of GFC heifers was been met by the supplement itself, freeing up time and energy to search for patches of better forage. SFP heifers, on the other hand, who presumably met most of their energy requirements with a dormant forage diet were likely more focused on meeting daily intake requirements while conserving energy. SFP heifers spent less time on non-foraging activities (resting and traveling) and more to grazing time, which might indicate that heifers in SFP treatment expending less energy to forage due to less traveling time (Brosh et al., 2010).

The lower grazing time observed in GFC heifers compared to SFP heifers might be associated with substitution effect (Bowman & Sanson, 1996), where GFC heifers might have depressed intake and consequently, grazing time. Saker and Holmes (1974) reported that supplements with concentrates decreased the grazing time in cows. Similarly, Adams (1985) evaluated the effects of time of supplementation with corn (morning vs. afternoon) on performance and grazing behavior of steers. Authors found that supplementation not only affected the grazing time but also the interruption (morning) of regular grazing activity, which influenced both performance and grazing behavior.

All heifers spent more time grazing on cloudy days with higher humidity during January. During February, however, heifers increased the grazing time as temperature and dew point increased, but the response was higher in SFP heifers compared to GFC heifers. Adams et al., (1986) found that grazing time was significantly correlated with minimum daily temperature.

Thus, lower temperatures reduced the grazing time in pregnant cows by 50 % approximately with a temperature range within 0 to - 40 ºC. Probably, and the inverse effect might have occurred when the temperature increased, which encouraged grazing as well. However, the impact was higher in SFP heifers likely due to their overall foraging strategy described above. It is important to note that during January and February, there were days with snow in the pasture, which might have affected movement and activity patterns of both treatment groups. Bailey et al. (2000) observed that cows tracked with a GPS collars tended to reduce visit time to water when snow cover was present.

While other studies have shown that the diet of the mother during gestation influences the feeding behavior of the offspring, we found limited evidence of this phenomenon. A study with sheep showed that prenatal exposure to a specific type of feed—through the mother's diet—influenced the offspring's feeding preferences later in life (Simitzis et al., 2008). This is also supported by Nolte et al. (1992), who found that the odor of herbs (garlic) would be detected in both amniotic fluid and fetal blood. Another study by Littlejohn et al. (2015) evaluating the link between prenatal stress and postnatal calf temperament found that calves who were exposed to prenatal stress had a high cortisol level and more excitable temperament during postnatal stage (weaning) compared to calves without prenatal stress. Additionally, Maresca et al. (2018) point out that reducing the protein intake of cows during late gestation can affect postnatal growth by lowering the body mass index and modifying the head circumferences of the offspring. A review by Walterland and Garza, 1999 about metabolic imprinting showed the significant role of the nutrition during the prenatal period on the health of individuals, for example. Metabolic imprinting is the adaptive response of the fetus to variations in nutrient availability. These adaptions from early life can have permanent effects on tissues and organs. In the present study, we found limited evidence of influence of the dam's nutritional treatment during gestation. However, classification error rates using multivariate analysis were highest for heifers who came from restricted dams whose behavior was more similar to heifers who came from non-restricted dams groups. Those would suggest that the 'metabolic imprinting' could have been present, but it couldn't be expressed because the nutritional needs of heifers were possibly being met by foraging and supplementation treatments limiting opportunities for heifers to fully express behavioral adaptation to a nutritionally deficient foraging environment.

MANAGEMENT IMPLICATIONS

Post-weaning feed supplement treatments modified movement and activity patterns of heifers during winter. Restricting the dams' feeding during the last third of gestation appeared to not affect the behavior of supplemented heifers. The impact of feed supplement treatments on winter movement and activity patterns of heifers was possibly more strongly associated with the degree to which a heifer's energetic needs were met with supplements (GFC>SFP) than with the dam's lifelong feeding regime itself. However, more research is needed to determine whether advantages in foraging behavior derived from the dams' feeding regime would be observed in a situation of limited nutrient availability.

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Table 2. 1. Description of vegetation classes in Lonepine R (GFC, January 2015 and SFP, February 2016), Lonepine S (SFP, January 2015 and GFC, February 2016), Lonepine T (GFC, February 2015), Lonepine U (SFP, February 2015), Lonepine Trap (GFC, January 2016), and Lonepine Q (SFP, January 2016). Values are presented in means ± standard error.

Description	**Vegetation classes**			
	Badlands, sparsely vegetated hills	Mixed grass prairies, dominated by cool season grasses	Shrublands with mixed grass prairie understory vegetation	Cool season grasses/legumes, forbs and shrubs
Lonepine R				
Elevation (m)	2610.73 ± 1.35	2544.08 ± 1.11	2591.31 ± 0.66	2535.25 ± 1.29
Percentage covered by each class (%)	31.76	12.58	36.76	18.90
Lonepine S				
Elevation (m)	2612.30 ± 1.10	2554.60 ± 1.12	2591.71 ± 0.83	2548.60 ± 1.17
Percentage covered by each class (%)	34.02	24.09	25.98	15.91
Lonepine T				
Elevation (m)	2580.40 ± 1.22	2551.50 ± 0.94	2576.86 ± 0.54	2543.84 ± 0.90
Percentage covered by each class (%)	9.66	15.44	45.09	29.81
Lonepine U				
Elevation (m)	2574.84 ± 1.06	2536.71 ± 0.97	2564.40 ± 0.68	2526.82 ± 0.97
Percentage covered by each class (%)	18.97	13.74	43.96	23.33
Lonepine Trap				
Elevation (m)	2556.00±0.80	2523.12±0.97	2540.34±1.13	2500.18±0.78
Percentage covered by each class (%)	15.44	30.34	15.98	38.24
Lonepine Q				
Elevation (m)	2600.50 ± 0.95	2548.94 ± 1.60	2596.33 ± 0.82	2522.23 ± 2.06
Percentage covered by each class (%)	39.84	11.50	39.96	8.70

Table 2. 2. Composition of diet supplement of SelfFed (SFP) treatment.

Items	**Value**
Supplement (ingredients)	
Monensin (monensin sodium, 2000.00 g/tn)	1.00 g/lb
Pork blood meal	
Crude Protein (min, %)	85.00
Crude Fat (min, %)	1.00
Crude Fiber (max, %)	2.00
Fish meal	
Crude Protein (min, %)	60.00
Crude Fat (min, %)	6.00
Crude Fiber (max, %)	2.00
Calcium (%)	between 6.50-7.80
Phosphorus (min, %)	2.90
Ethoxyquin added preservative	
Mineral supplement (ingredients)	
Calcium (%)	between 7.00-8.00
Phosphorous (%)	8.00
Salt (%)	35.00-40.00
Potasium (%)	6.00
Magnesium (%)	6.00
Cobalt (ppm)	10.00
Copper (ppm)	2000.00
Iodine (ppm)	53.00
Manganese (ppm)	1000.00
Selenium (ppm)	20.00
Zinc (ppm)	2000.00
Vitamin A (lU/b)	120000.00

Table 2. 3. Weather variables (means ± SE) for January and February during our study at the USDA-ARS Fort Keogh LARRL in Miles City, MT.

Variables	**Period**			
	January 2015	**January 2016**	**February 2015**	**February 2016**
Solar Rad (langley. h^{-1})	7.12 ± 0.54	5.27 ± 0.56	9.81 ± 0.96	8.94 ± 0.87
Relative humidity (%)	69.11 ± 2.29	75.05 ± 1.81	64.21 ± 2.65	66.36 ± 2.70
Temperature (°C)	-0.84 ± 1.26	-6.16 ± 1.46	-5.19 ± 1.61	2.57 ± 0.68
Rainfall (mm)	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Wind Dir (°)	171.05 ± 8.92	195.82 ± 17.10	175.75 ± 11.27	175.22 ± 10.76
Wind Gust (m . s^{-1})	3.09 ± 0.43	2.26 ± 0.30	4.12 ± 0.34	4.16 ± 0.37
Wind Speed (m . s^{-1})	1.20 ± 0.25	0.81 ± 0.17	1.72 ± 0.21	1.86 ± 0.21
Dew Point (°C)	-6.22 ± 1.04	-9.99 ± 1.58	-11.44 ± 1.76	-3.98 ± 0.83

*The duration of one complete period to January and February were 18 and 16 days, respectively.

Table 2. 4. Linear Discriminant Analysis including distance traveled (log transformation, km . d^{-1}), area covered (ha. d^{-1}), movement velocity (log transformation, m . min^{-1}), path sinuosity (squared root transformed, 0-1), total time spent resting (h . d^{-1}), total time spent grazing (h . d^{-1}), total time spent traveling (h . d^{-1}) by GFC-CT (n=10), GFC-MG (n=8), SFP-CT (n=13), and SFP-MG (n=10) heifers in January and February (2015 and 2016). Heifers treatment (group-fed cake, GFC; self-fed protein, SFP) and dam's treatment (control, CT; marginal, MG).

Treatment	**Classified into treatment (%)**				**Mean Error rate**	**Pr> ChiSq**	**Wilks' Lambda**
	GFC-CT	GFC-MG	SFP-CT	SFP-MG			
GFC-CT	**90.00**	0.00	10.00	0.00	0.59	0.38	<0.01
GFC-MG	62.50	**0.00**	37.50	0.00			
SFP-CT	23.08	7.69	**61.54**	7.69			
SFP-MG	0.00	0.00	100.00	0.00			

Linear Discriminant Functions (reduced set of predictors)

GFC-CT: -42.08 + 299.56 (sinuosity)*

GFC-MG: -46.10 + 313.22 (sinuosity)*

SFP-CT: -59.61 + 359.14 (sinuosity)*

SFP-MG: -60.74 + 361.80 (sinuosity)*

*Sinuosity during 24 hs (squared root transformed, 0-1)

Table 2. 5. Means and standard error for variables included in the Linear Discriminant Analysis by GFC-CT, GFC-MG, SFP-CT, SFP-MG groups in January and February (2015 and 2016). Heifers treatment (group-fed cake, GFC; self-fed protein, SFP) and dam's treatment (control, CT; marginal, MG).

Variables	**Treatment**			
	GFC-CT	**GFC-MG**	**SFP-CT**	**SFP-MG**
Distance traveled* (km . d^{-1})	5.22 ± 0.22	5.08 ± 0.31	4.65 ± 0.17	4.93 ± 0.17
Movement velocity* (m . min^{-1})	3.99 ± 0.17	3.88 ± 0.23	3.55 ± 0.13	3.76 ± 0.13
Path sinuosity** (0-1)	0.07 ± 0.00	0.08 ± 0.00	0.11 ± 0.01	0.11 ± 0.01
Area covered (ha . d^{-1})	39.02 ± 3.11	35.73 ± 4.03	36.45 ± 2.67	38.36 ± 3.03
Total resting (h . d^{-1})	15.84 ± 0.19	16.16 ± 0.16	15.69 ± 0.20	15.34 ± 0.16
Total grazing (h . d^{-1})	7.45 ± 0.16	7.15 ± 0.10	7.67 ± 0.19	7.90 ± 0.19
Total traveling (h . d^{-1})	0.71 ± 0.05	0.68 ± 0.08	0.64 ± 0.08	0.76 ± 0.08

* Black log transform for distance traveled and movement velocity

** Black square-root transform for path sinuosity

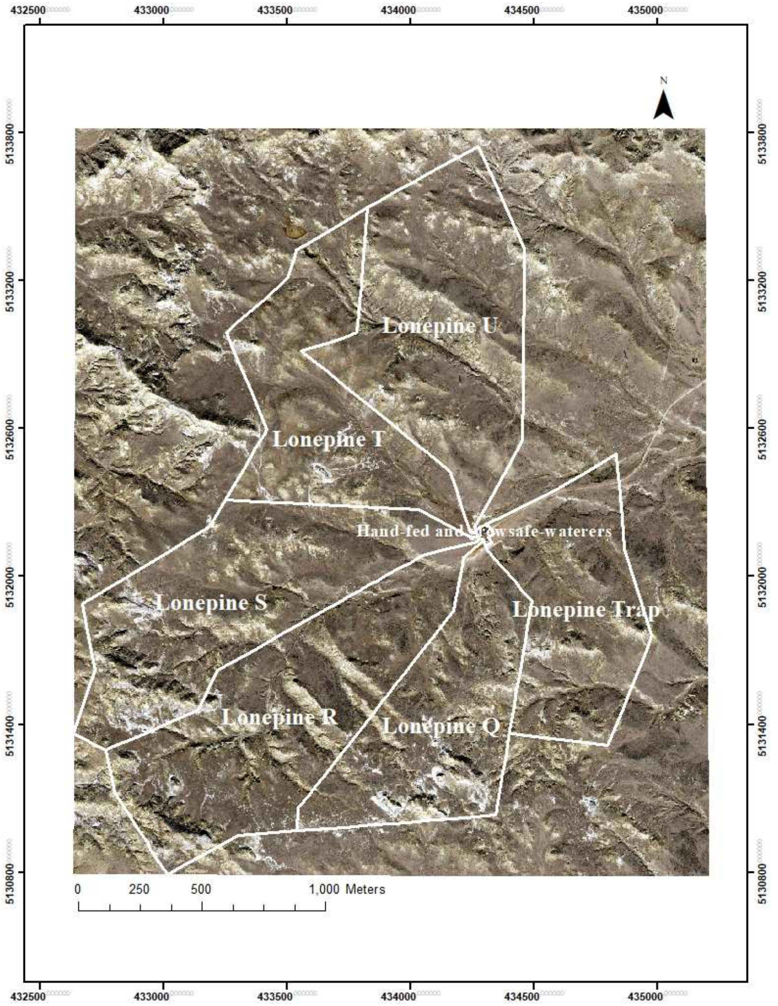


Figure 2. 1. NAIP image showing the study area outlined in white (Lonepine R, Lonepine S, Lonepine T, Lonepine U, Lonepine Q, and Lonepine Trap pasture) and location of water and GrowSafe feeders for self-fed supplement.

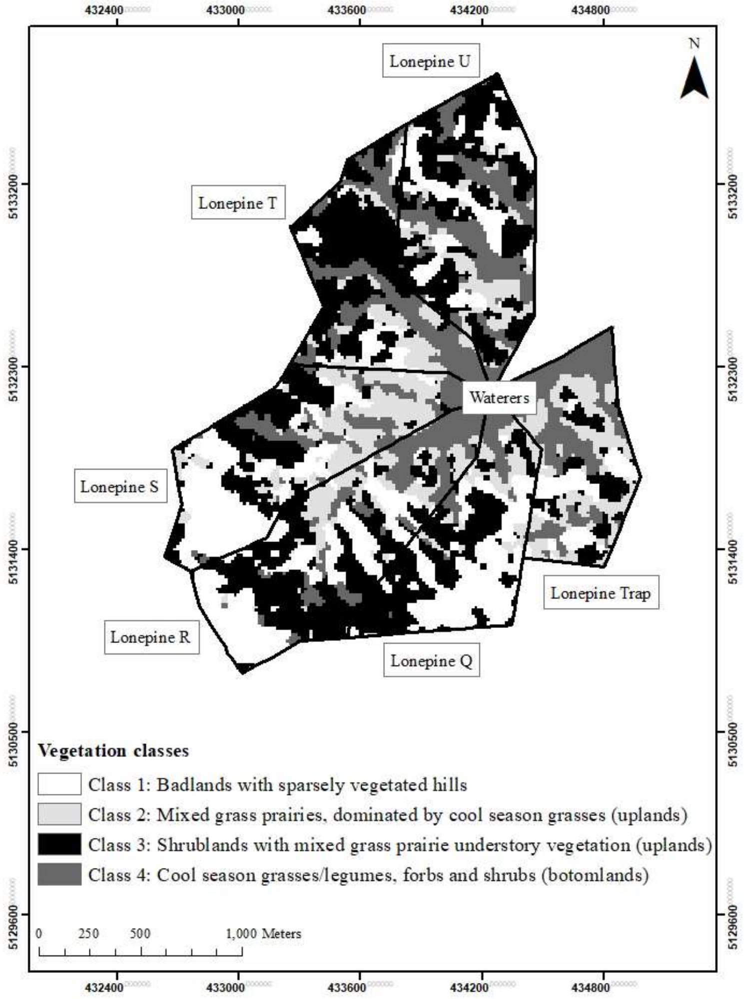


Figure 2. 2. Vegetation map for Lonepine R, Lonepine S, Lonepine T, Lonepine U, Lonepine Q, and Lonepine Trap pasture located at USDA-ARS Fort Keogh LARRL, Miles City, MT.

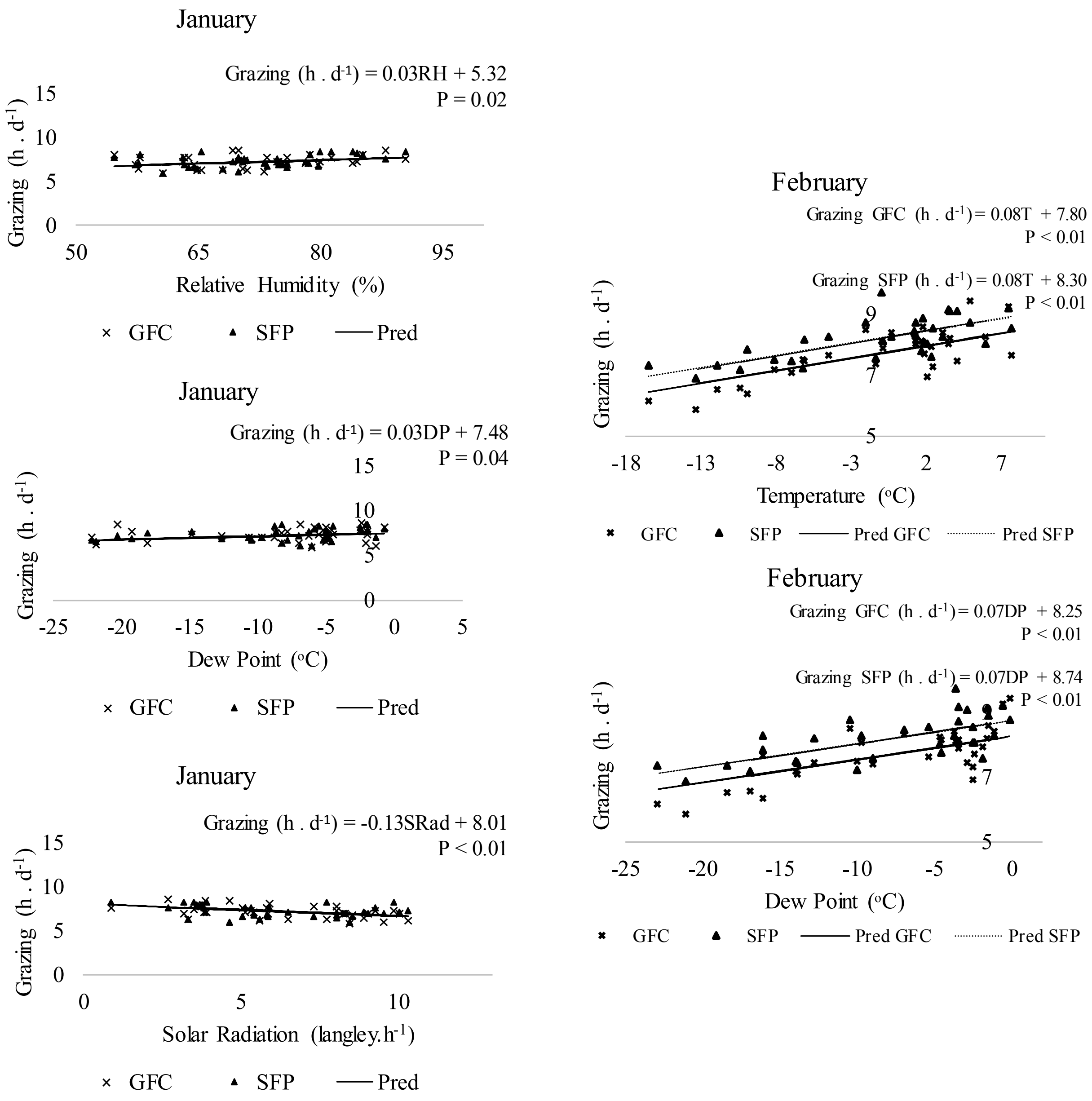
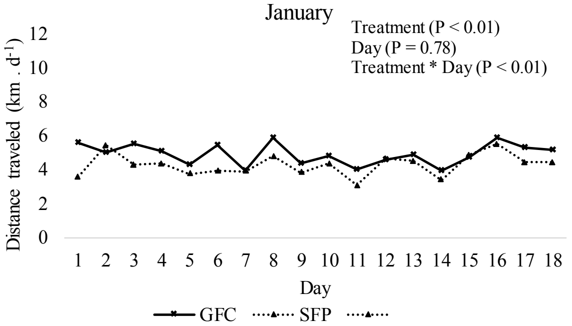
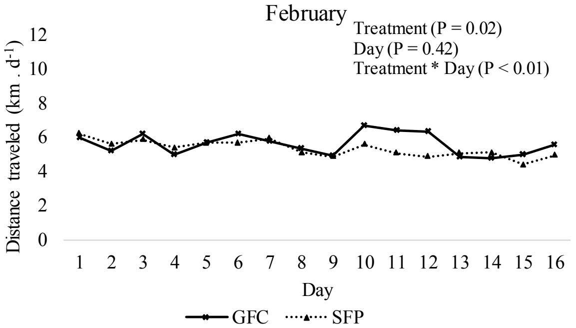
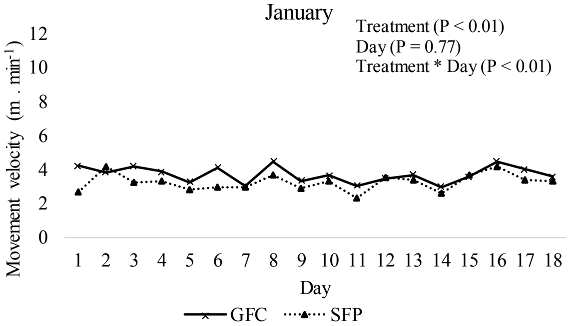


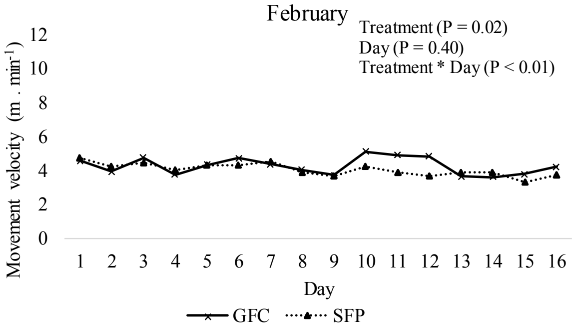
Figure 2. 3. Grazing (h . d^{-1}) vs. weather variables (relative humidity, dew point, solar radiation, and temperature) to group fed cake (GFC), and self-fed protein (SFP) treatments during January and February (2015 and 2016) in Lonepine R and Lonepine T pastures (GFC, January and

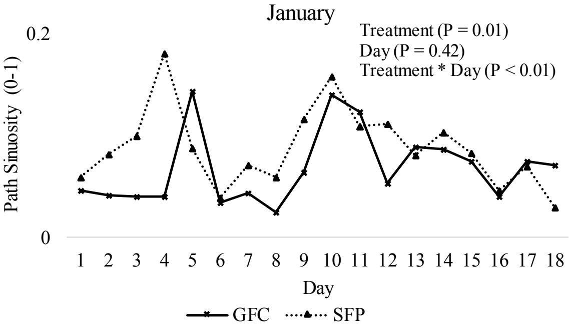
February 2015, respectively), Lonepine S and Lonepine U pastures (SFP, January and February 2015, respectively), Lonepine Trap and Lonepine S pastures (GFC, January and February 2016, respectively) and Lonepine Q and Lonepine R pastures (SFP, January and February 2016, respectively). RH = relative humidity, SRad = solar radiation, DP = dew point, T= temperature.

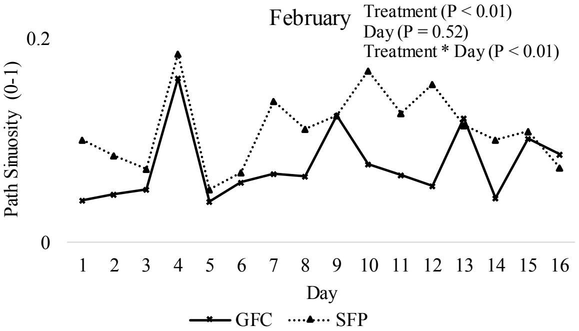

January
Treatment (P < 0.01)
Day (P = 0.78)
Treatment * Day (P < 0.01)
Distance traveled (km . d-1)
0 2 4 6 8 10 12
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18
Day
GFC
SFP

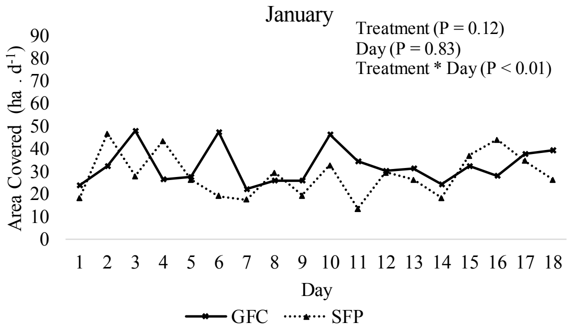

February
Treatment (P = 0.02)
Day (P = 0.42)
Treatment * Day (P < 0.01)
Distance traveled (km . d-1)
0 2 4 6 8 10 12
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16
Day
GFC
SFP


January
Treatment (P < 0.01)
Day (P = 0.77)
Treatment * Day (P < 0.01)
Movement velocity (m . min-1)
0 2 4 6 8 10 12
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18
Day
GFC
SFP


February
Treatment (P = 0.02)
Day (P = 0.40)
Treatment * Day (P < 0.01)
Movement velocity (m . min-1)
0 2 4 6 8 10 12
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16
Day
GFC
SFP


January
Treatment (P = 0.01)
Day (P = 0.42)
Treatment * Day (P < 0.01)
Path Sinuosity (0-1)
0 0.2
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18
Day
GFC
SFP


February
Treatment (P < 0.01)
Day (P = 0.52)
Treatment * Day (P < 0.01)
Path Sinuosity (0-1)
0 0.2
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16
Day
GFC
SFP


January
Treatment (P = 0.12)
Day (P = 0.83)
Treatment * Day (P < 0.01)
Area Covered (ha . d-1)
0 10 20 30 40 50 60 70 80 90
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18
Day
GFC
SFP

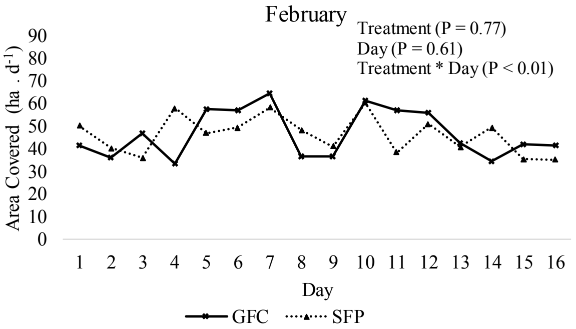

February
Treatment (P = 0.77)
Day (P = 0.61)
Treatment * Day (P < 0.01)
Area Covered (ha . d-1)
0 10 20 30 40 50 60 70 80 90
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16
Day
GFC
SFP

Figure 2. 4. Daily movement patterns (least squares means) of heifers in group fed cake (GFC), and self-fed protein (SFP) treatments during January (back transformed LSmeans from square-root transformation to path sinuosity) and February (2015 and 2016) in Lonepine R and Lonepine T pastures (GFC, January and February 2015, respectively), Lonepine S and Lonepine U pastures (SFP, January and February 2015, respectively), Lonepine Trap and Lonepine S pastures (GFC, January and February 2016, respectively) and Lonepine Q and Lonepine R pastures (SFP, January and February 2016, respectively).

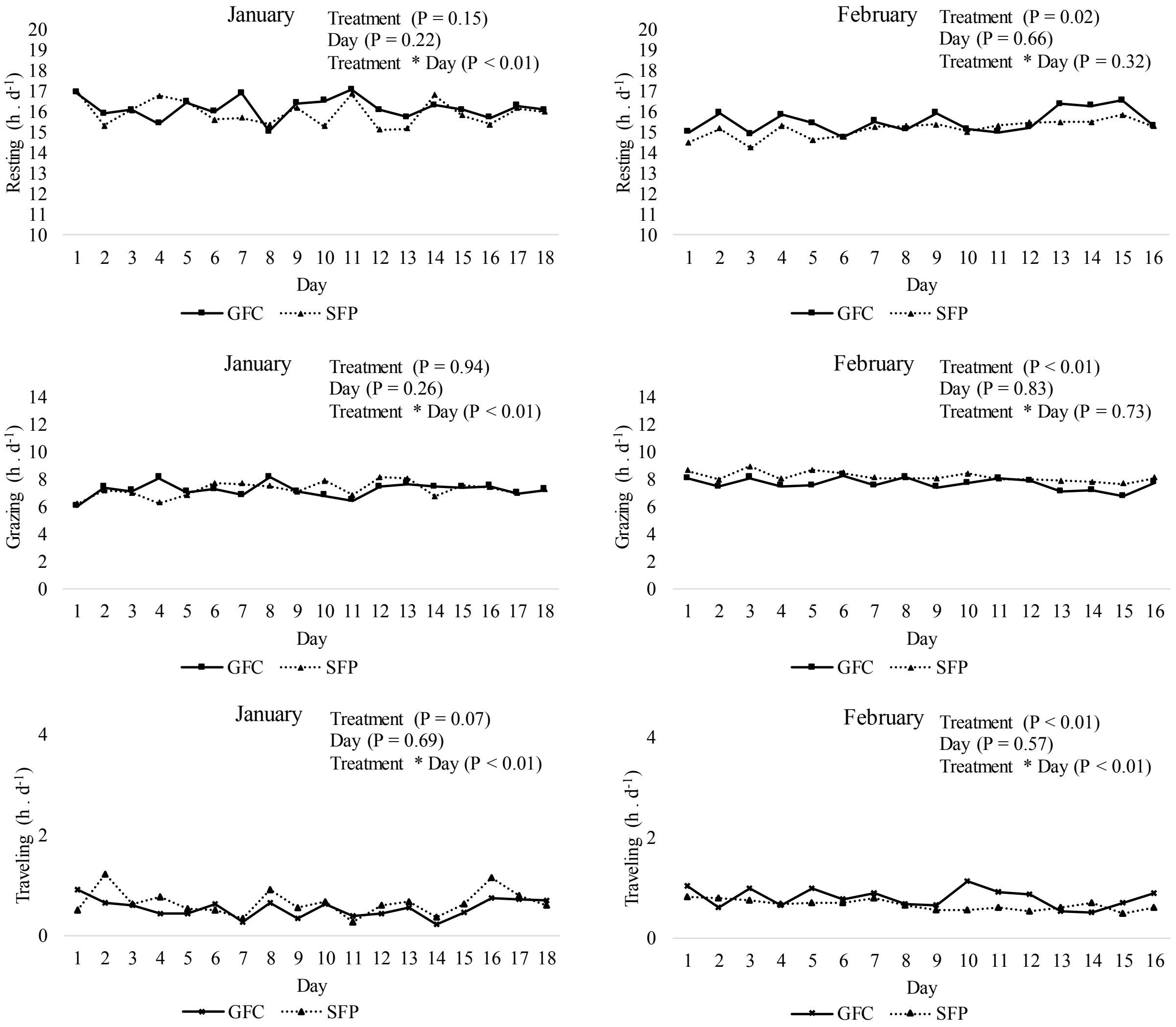


Figure 2. 5. Daily activity patterns (least squares means) of heifers in group fed cake (GFC), and self-fed protein (SFP) treatments during January (back transformed LSmeans from square-root transformation to time traveling) and February (2015 and 2016) in Lonepine R and Lonepine T pastures (GFC, January and February 2015, respectively), Lonepine S and Lonepine U pastures (SFP, January and February 2015, respectively), Lonepine Trap and Lonepine S pastures (GFC,

January and February 2016, respectively) and Lonepine Q and Lonepine R pastures (SFP, January and February 2016, respectively).

CHAPTER 3

EFFECT OF POST-WEANING DEVELOPMENT METHOD ON GRAZING PATTERNS OF RANGELAND BEEF HEIFERS DURING SPRING[1].

ABSTRACT

We determined the influence of post-weaning development method on rangeland grazing patterns of beef heifers during early and late spring. We compared behavior of heifers wintered on rangeland (group-fed cake, GFC or self-fed protein, SFP supplements during winter) or in a pen where they were pen fed silage (PFS). In April and May of each year (n=3), heifers (n=95) were fitted with Lotek 3300LR GPS collars and monitored 18 days each month. PFS heifers traveled farther than SFP and GFC counterparts on the first few days in April ($P<0.05$). PFS heifers covered larger areas of the pasture compared to GFC and SFP ($P<0.05$) counterparts during May. All heifers followed trajectories of similar sinuosity ($P>0.05$). On most days, PFS heifers allocated more time to resting (April) and traveling (April and May) than heifers in SFP treatment ($P<0.05$). SFP heifers spent significantly more time grazing than PFS and GFC counterparts during April ($P<0.01$). However, differences in foraging patterns decreased through time. All heifers spent more time grazing ($P<0.01$) on cloudy days with higher humidity during

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[1] This chapter has been submitted to Rangeland Ecology and Management in September and is currently in review. The current citation is: *Continanza, F.G. A.F. Cibils, M.K. Petersen, J.M. Muscha, A.J. Roberts, C. Steele, S. Soto Navarro, R.L. Steiner, H. Cao, Q. Gong. Effect of post-weaning development method on grazing patterns of rangeland beef heifers during spring. Submitted to Rangeland Ecology and Management*

April and less time grazing on windy and rainy days in May ($P<0.05$). Pixel Normalized Difference Vegetation Index (NDVI) appeared to influence pasture use patterns regardless of treatment. Traveling and resting time, as well as pixel residence time were the three variables that best discriminated heifers into treatment groups ($P<0.01$). Collared heifers tended to associate with heifers of their own/other treatment group (prevailing PFS-GFC or GFC-SFP heifers). The social role of a collared heifer in the herd did not appear to be associated with development treatment. Post-weaning development protocols modified movement, activity, and habitat use of heifers during early spring. Initial animal state and/or metabolic memory may have been responsible for the differences observed. Such differences, however, were possibly attenuated by social facilitation.

Keywords Northern Great Plains, Heifer development, GPS collars, cattle grazing behavior

INTRODUCTION

Developing efficient replacement heifers is critical to the success of rangeland-based beef cattle operations (Roberts et al. 2016). Ranchers typically seek to use cost-effective development programs that ensure that heifers reach breeding weights at about 15 months of age (Thomas, 2017). Some studies found that accelerating heifer growth rate during the post-weaning phase was likely to advance puberty and, consequently, improve pregnancy rates (Patterson et al. 1992). However, other studies have shown that it is possible to reduce feeding costs by managing heifer post-weaning growth to reach lighter weights at breeding without affecting reproductive performance (Roberts et al. 2016; Endecott et al., 2013; Funston et al. 2012, Clanton et al. 1983).

Post-weaning development method (rangeland or dry lot) can also influence age at puberty, conception at first breeding and subsequent grazing patterns of beef cows on rangeland. Hojer et al. (2012) found that heifers that were wintered on rangeland exhibited better use of rangeland during summer than did dry lot counterparts when they grazed separate pastures. Similarly, Perry et al. (2013) reported that heifers that were adapted to pasture conditions had higher pregnancy rates than heifers that were transferred from a dry lot to pasture directly. Another study reported that when heifers were not allowed a pasture adaptation period, they exhibited increased activity in the pasture which caused reduced weight gains and pregnancy rates (Perry et al., 2015). Collectively, these studies suggest that developing heifers in a dry lot can negatively impact their subsequent rangeland use patterns and performance as young cows although providing dry lot heifers feed supplement once they are moved to rangeland can improve their reproductive success (Perry et al., 2015).

Cattle are known to rely on previous experience to either select or avoid certain grazing areas of rangeland pastures (Bailey et al. 1996, Launchbaugh & Howery 2005, Bailey et al. 1990). An animal’s experience (both individual and social), novel stimuli, inherited traits, and spatial memory are all thought to play important roles in defining a cow’s lifelong grazing patterns on rangeland (Launchbaugh & Howery, 2005). Experience might be particularly important when comparing rangeland use patterns of animals that were raised in different environments. It is unclear if the method used to develop heifers (rangeland vs. dry lot) has a lasting influence on an individual's grazing patterns later in life or whether heifers developed in dry lots vs. rangeland interact with environment-related factors such as vegetation, topography, and weather differently.

Heifers developed on rangeland in the western United States are usually provided feed supplements during winter. Delivery schedules and type of supplements vary greatly and can influence rangeland grazing patterns (Mathis & Sawyer, 2007). Two common methods of range cattle feeding include hand- vs. self-fed delivery of supplements (Bowman & Sowell, 1997). Hand-feeding is defined as a type of delivery method where the supplement is provided in a specific quantity that is consumed by animals in a relatively short time. Self-fed is supplied to produce 'ad libitum' intake, which is achieved by modifying the amount, palatability, and physical characteristics of the supplement (Sawyer & Mathis, 2001). Supplement delivery method as well as supplement composition (energy dense or protein dense) could conceivably influence pasture use patterns of young heifers on rangeland over the short- and longer-term, but research is lacking in this area. Most studies investigating the influence of feed supplementation on rangeland beef cattle behavior have focused on mature cows (Wallace, 1992). For example, Schauer et al. (2005) investigated the effect of supplement delivery frequency on grazing distribution patterns and performance of cows in the Northern Great Basin. They used GPS data to measure grazing time, distance traveled, and distance from water, intake (inferred by n-alkanes), and harvest efficiency. The authors found that the supplementation frequency had no effect on the animal behavior variables they measured but reported that supplemented cows spent less time grazing than non-supplemented counterparts, irrespective of supplement delivery frequency (every day or every six days).

Pasture use patterns of livestock on rangeland are influenced not only by spatial memory, experience, and inheritance, but also by social influence of mothers and peers (Lauchbaugh & Howery 2005). Social facilitation can play a significant role in shaping habitat and diet selection patterns of cattle (Ralphs et al., 1999; Howery et al., 1998; Bailey et al., 2000). Therefore, it is possible that differences in foraging behavior induced by the heifer development method itself could be transient, particularly if heifers with different upbringing then graze rangeland pastures jointly as adults.

The objective of this study was to determine if post-weaning development method affects subsequent rangeland grazing patterns of beef heifers during the spring in the Northern Great Plains. We hypothesized that during spring, heifers that grazed rangeland pastures during winter would be more effective grazers causing them to travel farther, explore larger areas of a pasture, spend more time grazing regardless of weather, and use a broader range of vegetation types, compared to heifers developed in a dry lot. We also hypothesized that heifers that had been developed on winter rangeland with traditional hand fed supplements would exhibit spring grazing patterns that were intermediate compared to self-fed rangeland counterparts and dry-lot developed peers. Finally, we predicted that when grazing in a mixed treatment group, differences in grazing patterns would decrease and migrate through time to an optimal strategy due to social facilitation of foraging behaviors.

MATERIALS AND METHODS

Study site

The experiment was conducted at the USDA-ARS Fort Keogh Livestock and Range Research Laboratory (LARRL) in Miles City, MT (Lat 46° 23’ 08’’ N, Long 105° 52’ 26’’ W). Fort Keogh covers an area of 22,258 hectares. The climate is semi-arid (Rubel & Kottek, 2010; Kottek et al., 2006) with cold winters and warm summers. Average minimum and maximum temperatures are –14.6°C (January), and 31.8°C (July), respectively, with an average of 150 frost-free days. Mean annual precipitation is 333 mm. Soils include Mollisols and Entisols and approximately 350 plant species have been identified on the research station (Petersen & Reinhart, 2012). Most of the plant communities in the study area are composed of C_3 graminoids. *Bouteloua-Hesperostipa-Pascopyron* associations are predominant across the study area. Pastures that were used for the study (depending on the study year) ranged in size from 49.79 to 84.13 ha (Figure 3. 1.).

Animals and treatments

All animal procedures were approved by the Fort Keogh Livestock and Range Research Laboratory Animal Care and Use Committee. Composite bred heifers (one-half Red Angus, one-fourth Charolais, and one-fourth Tarentaise) that were sired by similar bulls, in a resident cow herd of 24 years grazed in common on native range until weaning and were used in this experiment in three different heifer development treatments that were evaluated at 12 and 13 months of age during spring. The pen-fed silage (PFS) treatment included a group of freshly weaned heifers that were developed in dry lot conditions, receiving 87 % corn silage diet, 7 % alfalfa and 6 % soy-bean meal-urea supplement described by Roberts et al. (2007) during winter (October to April). The group-fed cake (GFC) treatment included heifers that were developed on rangeland and fed 1.82 kg of cake supplement . d^{-1} . $heifer^{-1}$ (20 % crude protein, 1.75 % fat, and 19 % fiber) delivered daily at approximately 10:00 a.m. during winter. Cake was formulated based on 60 % alfalfa and 40 % energy grains (variable proportions of corn, wheat, barley, peas, dry distillers' grains and malt sprouts depending on cost each year) without molasses or bentonite. The self-fed protein (SFP) treatment consisted of a group of heifers that were also developed on rangeland with a self-fed supplement delivered in Grow-Safe bunks with high protein content composed primarily of ruminal escape protein sources (50 % crude protein) plus a mineral supplement designed to be consumed individually at 0.11 to 0.45 kg . $heifer^{-1}$. d^{-1} during winter (Table A 1., Supplementary Materials) (Mulliniks et al., 2012). Development treatments were applied in the middle of December and continued until the second week of April when all groups were combined on an ungrazed pasture during the development period (approximately 113 days). During the first week of April of each year, all heifers from each treatment were combined and managed together thereafter. In April 2015 (n=120), 2016 (n=125), 2017 (n=130) and May 2015 (n=120) heifers were in the Lonepine V pasture (Figure 1) and were provided access to the self fed protein supplement. In May 2016, heifers (n=125) were in

Lonepine U pasture but crossed the fence to the adjacent Lonepine T and S pastures on some days. In May 2017, heifers (n=130) were moved from Lonepine V to Lonepine Trap pasture due to forage allowance limitations and all heifers continued to have access to the self-fed protein.

GPS collars were fitted on 10 different randomly selected heifers in April (n=4 PFS, n=3 GFC, and n=3 SFP) and May 2015 (n=4 PFS, n=3 GFC, and n=3 SFP), 18 heifers in April 2016 (n=6 PFS, GFC and SFP, respectively), 14 heifers in May 2016 (n=5 PFS, n=5 GFC, and n=4 SFP), 21 heifers in April 2017 (n=7 PFS, GFC, and SFP, respectively), and 20 heifers in May 2017 (n=6 PFS, n=7 GFC, and n=7 SFP). Collars were configured to record position at 5-minute intervals. Different heifers were monitored for the 18-day periods during each month and year. In all cases, heifers were monitored upon entering a fresh pasture, except for May 2015 when heifers had been in the pasture for the previous month.

Data processing

Weather variables

Weather data, including solar radiation (Langley . h^{-1}), relative humidity (%), ambient temperature (°C), rainfall (mm), wind dir (°), wind gust (m . s^{-1}), wind speed (m . s^{-1}), were retrieved from two different weather stations located at the USDA-ARS Fort Keogh LARRL in Miles City, MT (Table 3. 1.).

Vegetation map and habitat use

Three Tier One Terrain-corrected Landsat 8 Operational Land Imager (Landsat 8 OLI T1) multispectral images for 2015, 2016, and 2017 were acquired from US Geological Survey (https://earthexplorer.usgs.gov). We also used an aerial image (1 m spatial resolution, acquired between September-October 2015) provided by the National Agriculture Imagery Program (NAIP). The NAIP imagery includes four bands covering the visible and near infrared wavelengths and a Normalized Difference Vegetation Index band (NDVI, band 5). The NDVI is a vegetation index that indicates the greenness of the forage (Rouse et al. 1973). In general, higher values of NDVI are associated with healthy, green, and dense vegetation. A raster Digital Elevation Model was created from a topographic contour -which were acquired from U.S. Geological Survey, National Geospatial Program- using ArcGIS 10.3.1 (ESRI, Redlands, CA). All the images and a digital elevation model raster were projected into a Universal Transverse Mercator, zone 13 projection.

Unsupervised classification of the NAIP imagery guided ground data collection for training supervised classification. Two-line point transects were read at 15 sites within each class to determine plant cover and species composition (Table A 2., Supplementary Materials). Four classes were established: Class 1: Badlands, with sparsely vegetated hills; Class 2: Mixed grass prairies, dominated by cool season grasses (uplands); Class 3: Shrublands with mixed grass prairie understory (uplands); Class 4: Cool season grasses/legumes and shrubs (bottomlands).

The NNDiffuse Pan Sharpening technique (ENVI software, Exelis, 2015) was used to resample the OLI multispectral data (30 m spatial resolution) to 15 by 15 m pixels and Principal Component Analysis was performed to reduce redundancy and provide the most valuable amount of spectral information. ENVI's maximum likelihood algorithm (ENVI software, Exelis, 2015) was used to classify the Layer-Stacking image to 15 meters of spatial resolution, which results of the combination of the NDVI band (NAIP), the Principal Component 1, Principal Component 2, and Principal Component 3 from each image (9 bands), and the digital elevation datasets. Stratified random points were established on the image and used as 'testing sites' to create the confusion matrix to perform an accuracy assessment. Separability of the training and testing sites was evaluated on the Layer-Stacking image.

Vegetation map produced

Cool season grasses/legumes and shrubs (class 4) covered a large area followed by mixed grass prairies, dominated by cool season grasses (class 2), then shrublands with mixed grass prairie understory vegetation (class 3), and finally Badlands, sparsely vegetated hills (class 1, Table 3. 2., Figure 3. 2.). Jeffries-Matusita and transformed divergence methods indicated separability values of 0.96 – 1.89 for testing sites and 1.95 – 2.00 for training sites (transects on terrain). Overall accuracy was 88.86 % and with Kappa=0.85.

Habitat use, movement, and activity patterns

Percentage of grazed pixels was calculated based on the proportion of pixels that heifers grazed independently of whether they were grazed in the same or different days divided by the total number of pixels in Lonepine V pasture. For this analysis, only GPS locations classified as grazing points were used.

Selection of vegetation types by heifers within the pasture was determined using Ivlev's electivity index (Jacobs 1974): $E_i = (r_i\text{-}p_i)/\ r_i{+}p_i)$, where, ri= time spent grazing a vegetation type, pi= area occupied by this vegetation type. Ivlev's E index values range from -1 (avoidance) to +1 (selection); a value of 0 indicates indifference.

GRAZPIX software (Sawalhah et al., 2016, Cao et al., unpublished) was used to calculate return interval (RI) to a given 15 m pixel (days), and residence time (RT) per pixel (min) for each animal and vegetation class. The left corner coordinates of each pixel were created using ArcGIS 10.3.1 (ESRI, Redlands, CA). Return interval is defined as average interval (days) in between visits to the same pixel. It was calculated based on pixels that were revisited on different days within the grazing period. Residence time represented the average amount of time (min) each heifer spent in each grazed pixel. It is independent of whether animal returned (the same or different days) or not to a given pixel.

GRAZACT software (Sawalhah et al., 2016, Cao et al. unpublished) was used to calculate animal movement variables such as distance traveled (km . d^{-1}), velocity (m . s^{-1}), path sinuosity, area covered (ha . d^{-1}), and activity variables such as, resting (h . d^{-1}), grazing (h . d^{-1}), and traveling (h . d^{-1}). Sinuosity refers to straightness values, which ranges between 1 (straight path) and 0 (most sinuous path) and is the ratio of the distance between the first and last GPS location in a day, and the cumulative distance between successive 5-min GPS locations for that same day. Area covered in a day was calculated considering 288 points (GPS locations at 5-minute intervals per each animal . d^{-1}) and computing the minimum convex polygon that connects the outer points to generate a polygon around the cloud of GPS points. Activity classification of GPS points was based on movement velocity. Resting was assumed when velocity < 2 m . min^{-1}, velocities between 2 m . min^{-1} to 25 m . min^{-1} were assumed to indicate grazing, and velocities > 25 m . min^{-1} were classified as traveling. Because it was not feasible to validate velocity thresholds with visual observations, criteria to decide the velocity thresholds were based on distances used in a classification tree developed by Augustine and Derner (2013) for yearling steers grazing shortgrass prairie rangeland in Colorado, which the authors validated in a similar environment to that of the present study.

Statistical Analysis

A one-way ANCOVA in a randomized block design structure was performed using a MIXED model in SAS 9.4 (SAS Institute, Cary, NC) to determine the effect of treatment (PFS, GFC, SFP) on grazing time (h . d^{-1}) controlling for weather variables. Year was considered the blocking factor and experimental unit. Treatments (PFS, GFC, and SFP) were considered a fixed effect and year (2015, 2016, and 2017) were treated as random effects. An average of grazing time of all heifers per treatment per each day (total 18 days) was used to analysis. Each month (April or May) was analyzed separately.

Vegetation electivity index (0-1), pixels grazed (%), RT (minutes), and RI (days) were analyzed using a blocking design (year) with a MIXED procedure in SAS 9.4 (SAS Institute, Cary, NC). Year was considered the experimental unit. Treatments (PFS, GFC, and SFP) were considered fixed effects, years (May 2015, April 2016, and April 2017) were treated as random effects. Heifers (observational unit) were nested within treatment, and with year were considered a random effect as well. Each vegetation class was analyzed separately. A non-parametric test (Friedman test) was used to analyze the RT (minutes) because residuals did not meet the assumptions of normality.

Movement and activity patterns were analyzed with a blocking design with repeated measures design using a MIXED model in SAS 9.4 (SAS Institute, Cary, NC) which included the fixed effect of treatment (PFS, GFC, SFP), day (18 days) and their interaction (treatment x day). Year was the experimental unit and day was considered as a categorical variable. Each month (April and May) was analyzed separately. Years (2015, 2016, and 2017) were considered random effects. Heifers (observational unit) were considered a random effect nested within year and treatment. A type=sp (pow) option was used as the covariance structure due to the fact that in some cases measurements were unequally spaced because of outlier deletion. The ddfm=kr option was used to estimate the degrees of freedom and group option was used when the homoscedasticity assumption was not met (Little et al., 2006).

Because heifer behavior cannot be defined with a single movement, activity or habitat use variable, differences among treatments were also explored via multivariate statistics. Thus, discriminant analysis was used to classify heifers into treatment groups (PFS, GFC, and SFP) using the entire suite of behavior variables listed above. PROC DISCRIM in SAS 9.4 (SAS Institute, Cary, NC) with the following option was used to classify the individuals: *pcov method=normal, pool=test, distance, manova, cross-validate* list. Wilks' Λ was used to detect differences among groups ($P \leq 0.05$). Predictors used in the analysis were: distance traveled (km . d^{-1}), movement velocity (m . min^{-1}), path sinuosity (0-1), area explored (root squared transformed, ha . d^{-1}), time spent grazing, resting or traveling (h . d^{-1}), pixels grazed (%), RI (days), and RT (minutes). PROC STEPDISC in SAS 9.4 (SAS Institute, Cary, NC) was used to select the minimum set of predictors able to discriminate among groups at the $P \leq 0.05$ level. Testing for normality/multinormality of error residuals and homogeneity of variances was conducted prior to all statistical analyses to detect potential violation of assumptions. A square root transformation was carried out on some dependent variables to normalize the residuals.

Spatial regression analysis (GeoDa software, Anselin, 2015) was used to relate pixel attributes and pixel use patterns (Return Interval and Residence Time) of heifers in each of the three treatments (PFS, GFC, SFP). Pasture attributes such as elevation (m), aspect (degree), slope (degree) were extracted to each pixel from a Digital Elevation Model using ArcGIS 10.3.1 (ESRI, 2015). Reference shapefiles were used to extract information such as distance from fence (m), distance from cow paths (m), and distance to supplement (m) and water (m). NDVI for each pixel was extracted using the same Landsat OLI images used to create the vegetation map. Model selection (ordinary least squares, spatial lag model, and spatial error model) was made using a decision tree, based on significance of the robust LM-diagnostic, robust LM-error, and robust LM-lag test statistics (Anselin, 2005). A weight variable was created to perform the spatial lag model and spatial error model using a Euclidean distance with a bandwith between 15 to 21.21 meters.

Social interaction among GPS-collared heifers was explored via association dynamics analysis using adjacency matrices created by the ASSOC1 software (Weber et al., 2001). Four different spatial thresholds (25, 50, 75, 100 meters) maintaining the same temporal threshold (55 %) were evaluated to find associations between heifers. Spatial threshold was defined as the maximum distance between associated heifers at a moment in time, while temporal threshold was lowest amount of time two heifers were together to be considered related or associated (Weber et al. 2001). Spatial thresholds were selected based on previous research on cattle social dynamics (Cheleuitte-Nieves et al., 2018; Stephenson & Bailey, 2017; Harris et al., 2007) while the temporal threshold (55 %) was selected based on preliminary exploration of the data considering different spatial thresholds (25, 50, 75, 100 m). The temporal threshold with larger number of associations was selected to conduct final analysis.

Adjacency matrices created by ASSOC1 software (Weber et al., 2001) for April 2016 and April 2017 (spatial thresholds 100 m) were used to conduct social networks analysis (Makagon et al., 2012, Wey et al., 2008) using the Gephi software version 0.9.2 (Bastian & Jacomy, 2009).

Visualization of the social network graphs was improved using the Force Atlas, Fruchterman Reingold, Yifan Hu, Yifan Hu Proportional, contraction, and Novelap algorithms, among others (Cherven, 2015). Betweenness centrality and eigenvector centrality were used as the social network metrics. Betweenness centrality refers to those individuals that are a bridge within a social network to connect with other individuals. High values indicate individuals who have control over the flow of the information transferring between individuals. If individuals who are the bridge are not present, the connections within networks will break down. Eigenvector centrality measures the influence of individuals within the network. High values represent individuals who relate to other individuals who have high values as well (Makagon et al., 2012, Wey et al., 2008).

Only April 2016, 2017 and May 2015 were included in habitat use analysis (grazed area, electivity index, Return Interval, Residence Time), spatial regression, discriminant analysis, association analysis, and social network analysis because heifers left the study area on some days during all of the other sampling dates. However, all dates were included in the analysis of movement, activity patterns, and relationship between weather variables and grazing activity.

RESULTS

Weather variables

The covariates relative humidity (%), dew point and solar radiation were all significantly related to grazing time ($P<0.01$) during April while the covariates wind gust ($m . s^{-1}$), wind speed (m . s^{-1}) and rainfall (mm) were all significantly related to grazing time ($P<0.05$) during May. Slopes were similar for all treatments during both, April ($P=0.55$ relative humidity, $P=0.85$ dew point, and $P=0.67$ solar radiation) and May ($P=0.70$ wind gust, $P=0.65$ wind speed, and $P=0.72$ rainfall). A common model was used for all treatments (PFS, GFC, SFP) for each covariate due to the fact that distances between the regression lines (intercepts) were not significantly different for April ($P=0.78$ relativity humidity, $P=0.76$ dew point, and $P=0.81$ solar radiation, Figure 3. 3.) and May ($P=0.86$ wind gust, $P=0.86$ wind speed, and $P=0.88$ radiation, Figure 3. 3.). For each change of one unit in relative humidity, dew point or solar radiation, the average change in the mean grazing time was approximately 0.02, 0.07, and -0.04 h . d^{-1}, respectively while for each change of one unit in wind gust, wind speed or rainfall, the average change in the mean grazing time was approximately -0.07, -0.11, and -2.06 h . d^{-1}, respectively.

Pasture use patterns

Heifers in all treatment groups preferred cool season grasses/legumes and shrubs (bottomlands) over all other vegetation classes (Table 3. 3.). Conversely, all heifers avoided badlands more than all other vegetation classes (Table 3. 3.). Heifers in SFP and PFS treatment groups avoided grazing in pixels classified as shrubland with mixed grass prairie understory more than GFC treatment counterparts ($P=0.02$, $P=0.04$ for GFC vs. PFS and GFC vs. SFP, respectively). Heifers in SFP treatment preferred to graze in pixels classified as mixed grass prairie dominated by cool season grasses more than PFS treatment ($P<0.01$) peers while GFC heifers showed intermediate preference levels (P=0.26, P=0.14, for GFC vs PFS and GFC vs SFP, respectively).

Heifers in SFP treatment grazed a higher percentage of pasture pixels (P<0.01) than heifers in PFS treatment while GFC heifers exhibited intermediate use values (Table 3. 3.). Heifers in SFP treatment grazed a higher percentage of mixed grass prairie pixels compared to their PFS and GFC counterparts (P<0.01 and P=0.03 for PFS and GFC, respectively). Heifers in PFS treatment grazed a smaller percentage of shrubland pixels compared to GFC counterparts (P=0.04) while SFP heifers exhibited intermediate use values (P=0.60 for PFS vs. SFP and P=0.27 for GSC vs. SFP).

Heifers in PFS treatment returned sooner to mixed grass prairie pixels and cool season grasses/legumes and shrubs pixels (exercised fewer choices) compared to GFC peers (P=0.02 and P=0.04 for mixed grass prairie pixels and cool season grasses/legumes and shrubs, respectively) while SFP heifers exhibited intermediate pixel return rates (P=0.32 for PFS and SFP to mixed grass prairie class and P=0.87 for PFS and P=0.11 for GFC for cool season grasses/legumes and shrubs class, respectively, Table 3. 3.). Heifers in GFC treatment returned to badland pixels more often than PFS and SFP counterparts (P=0.05, P=0.01 for PFS and SFP, respectively, Table 3. 3.).

Heifers in GFC treatment spent more time in badland pixels than PFS counterparts (P=0.01) while SFP heifers exhibited intermediate residence times (P=0.37, P=0.14 for PFS and GFC, respectively, Table 3. 3.). Heifers in PFS treatment spent more time in mixed grass prairie pixels than SFP counterparts (P=0.01) while GFC heifers exhibited intermediate residence times (P=0.12, P=0.56 for PFS and SFP, respectively, Table 3. 3.). NDVI was consistently a significant predictor of pixel return interval and residence time of most heifers regardless of treatment (Table 3. 4.).

Movement patterns

Back-transformed movement pattern means are reported in this section for all dependent variables except path sinuosity and area covered during May. There was a significant treatment by day interaction for both distances traveled and movement velocity during April ($P< 0.01$, Figure 3. 4.). Day 1 represents the first day all heifers from each development treatment were combined to graze the same pasture. On average, heifers in PFS walked 2.18 km . d^{-1} farther than GFC counterparts on days 1, 2, 3, 4, and 7 and 2.15 km . d^{-1} farther than SFP counterparts on days 1, 2, 3, 4 in April out of 18 days measured. Heifers in SFP treatment walked 1.48 km . d^{-1} farther than GFC counterparts only on day 3.

Similar results were found for movement velocity on days 1, 2, and 4 in April except for day 3 where PFS and SFP exhibited similar movement velocities (7.34 m . min^{-1} and 6.50 m . min^{-1} for PFS and SFP, respectively). Heifers in GFC and SFP treatments exhibited differences only on day 3 for both distances traveled and movement velocity (7.02 vs. 8.50 km . d^{-1} and 5.37 vs. 6.50 m . min^{-1}, for GFC and SFP, respectively). On the rest of the days, heifers in all treatments walked similar distances and exhibited similar movement velocity, except for day 7 where PFS again moved faster (5.31 m . min^{-1}) than GFC (4.38 m . min^{-1}).

No treatment-related differences were detected in path sinuosity (P=0.17) and area covered during April (P=0.57). Heifers followed sinuous trajectories (on average 0.06, range 0-1) and covered on average 60.61 ha day^{-1} during this month. Note that area covered included animals that were found outside the pasture on some days.

There were significant treatment differences for distance traveled during May (P=0.05). On average, heifers in PFS walked 0.4 km . d^{-1} and 0.51 km . d^{-1} more than GPC and SFP counterparts, respectively, while heifers in GFC and SFP treatment exhibited similar distance traveled during all days.

There was a significant treatment by day interaction for movement velocity during May (P=0.05) after 30 days of common grazing. On average, heifers in PFS walked 0.94 m . min^{-1} faster than GFC counterparts on day 1, and 0.92 m . min^{-1} faster than SFP counterparts on days 1 and 11 in May out of 18 days measured. Heifers in GFC and SFP treatment exhibited similar movement velocity during all days.

During May, all heifers followed sinuous trajectories (on average 0.07, range 0-1, P=0.44) while treatment-related differences were detected in area covered (P=0.01). PFS heifers covered significantly larger areas in a day (54.08 ha . d^{-1}) compared to GFC (50.05 ha . d^{-1}) and SFP (48.39 ha . d^{-1}) counterparts. Again, estimates of area covered included animals that were found outside the pasture on some days.

Activity patterns

Back-transformed traveling Lsmeans are reported in this section for April and May. There was a significant treatment by day interaction for both times spent resting ($P<0.01$) and traveling ($P< 0.01$) during April (Figure 3. 5.). Overall, heifers in PFS treatment tended to allocate more time to non-foraging activities (either resting or traveling) than heifers in SFP treatment. Heifers in the GFC treatment tended to exhibit intermediate activity levels (Figure 3. 5.).

On average, heifers in PFS spent 0.95 fewer h . d^{-1} resting than GFC counterparts on days 1 and 3 and 1.16 fewer h . d^{-1} resting than SFP counterparts on day 1, while 1.03 more h . d^{-1} resting than SFP counterparts on days 5, and 9. Heifers in GFC and SFP treatments exhibited differences only on day 7 (14.13 h . d^{-1} vs. 13.27 h . d^{-1} to GFC and SFP, respectively) during April.

There was a significant treatment by day interaction with travel time ($P<0.01$). On average, heifers in the PFS treatment group spent 65.40% more time traveling (+ 0.69 h . d^{-1}) than their GFC counterparts on days 1, 2, 3, 4, 7, and 18 in April and 56.94% more time traveling (+ 0.65 h . d^{-1}) than their SFP counterparts on days 1, 2, 4, 7, and 8 in April. Heifers in the GFC group spent, on average, 49.30% more time traveling (+ 0.28 h . d^{-1}) than their SFP counterparts on days 8 and 14 but 37.26% less time traveling than heifers in the SFP group on day 3 in April (0.58 fewer h . d^{-1}). For the remaining days, heifers in all treatments traveled similar average h . d^{-1} (between 0.76-0.81 h . d^{-1}).

There was a significant day effect for time spent grazing ($P<0.01$) during April (Figure 3. 5.). Overall, heifers in all treatments spent 1.86 fewer h . d^{-1} grazing on day 1 than on day 14, 16 and 18. In addition, in April SFP heifers spent, on average, an additional 0.58 or 0.34 h . d^{-1} grazing compared to PFS and GFC counterparts ($P<0.01$), respectively (Figure 3. 5.).

No treatment, day, or treatment by day effects were observed in time spent resting ($P=0.78$, $P=0.90$, $P=0.41$ for treatment, day, and treatment by day, respectively) or grazing ($P=0.40$, $P=0.73$, $P=0.43$ for treatment, day, and treatment by day, respectively) during May. Heifers rested on average 13.42 h . d^{-1} and grazed on average 9.84 h . d^{-1} during this month. However, differences were found between treatments ($P=0.01$) in time that heifers spent traveling. Heifers in PFS treatment spent more time traveling than GFC (0.79 h . d^{-1} vs. 0.66 h . d^{-1} for PFS and GFC, respectively) and SFP (0.63 h . d^{-1}) counterparts. GFC and SFP heifers spent similar amounts of time traveling ($P=0.87$).

Individual classification and association analysis

Heifers were classified into significantly different treatment (PFS, GFC, and SFP) groups (Λ Wilks = 0.57, F (6, 86) = 4.68, $P< 0.01$) when all behavior variables were considered simultaneously (Table 3. 5.). The percentage of individuals classified correctly (cross-validation) by the discriminant function was 75.00 %, 43.75 %, and 56.25% of heifers in PFS, GFC, and SFP treatments, respectively (mean error rate = 0.42). Classification error rates were highest for heifers in the GFC treatment whose behavior was apparently more similar to either the PFS or SFP groups (Table 3. 5.). Almost all misclassified SFP heifers were placed in the GFC group;

only one SFP heifer was misclassified as belonging to the PFS group. Stepwise selection using average squared canonical correlation indicated that time spent in non-foraging activities (daily traveling and resting time) and pixel residence time (minutes) were the smallest subset of behavior variables able to classify heifers into significantly different groups ($P<0.01$). The squared distance (Mahalanobis Distance) between heifers in SFP vs. PFS treatments and heifers in PFS vs. GFC treatments were greater than distances between heifers in GFC and SFP groups (2.71, $P<0.01$; 1.88, $P=0.01$; 1.09, $P=0.05$ for SFP and PFS, GFC and PFS, and GFC and SFP, respectively). Variable means are shown in Table 3. 6.

A larger number of different associations among collared heifers were found in the spatial threshold of 100 m during April 2016 and April 2017, maintaining a temporal threshold constant at 55%. However, only one association was found during May 2015. Associations between PFS-PFS individuals and PFS-SFP individuals tended to increase in April 2017 as compared to April 2016. Associations between GFC-GFC, SFP-SFP, and GFC-SFP tended to decrease in April 2017 compared to April 2016 while associations between PFS-GFC remained constant in both years (Table 3.7.).

A lower number of associations were found using the spatial thresholds of 75, 50, and 25 m during April 2016 and April 2017, maintaining a temporal threshold constant at 55%. Interestingly, most of these associations were found between PFS-PFS, PFS-GFC, GFC-GFC, and GFC-SFP. However, only two associations were found between PFS-SFP and SFP-SFP using the spatial threshold of 75 m.

During April 2016, heifers 15657 and 15731 (SFP treatment) were a bridge with other collared heifers facilitating the connection between them. Consequently, social facilitation was given within only one group (betweenness centrality, Figure 3. 6. a). During April 2017, heifer 16252 (PFS) was a bridge with other collared heifers. However, two groups of collared heifers were identified because three heifers were unable to connect with the larger group (betweenness centrality, Figure 3. 6. b).

Heifer 15812 (GFC), 15608 (SFP), 15657 (SFP) in April 2016 and heifer 16252 (PFS) in April 2017 tended to exhibit higher eigenvector centrality values because they were associated with heifers who presented high association with other collared heifers as well. Heifers with high eigenvector centrality values are thought to exhibit high dominance as well because of the high number of collared heifers interacting with them (incoming arrows in Figs. 3. 6. a and b).

DISCUSSION

Contrary to our hypothesis, heifers developed on rangeland traveled shorter daily distances, exhibited slower movement velocities, and covered smaller areas of the pasture in a day compared with peers that were developed in a dry lot. However, over an 18-day grazing period, rangeland-developed heifers grazed a higher percentage of pasture pixels compared to their dry lot peers, partially supporting our first hypothesis. Rangeland-developed heifers, especially those in SFP treatment, apparently used more efficient forage search tactics compared to heifers in PFS treatment. SFP heifers traveled shorter distances for every hour spent grazing or for each new pixel visited, likely expending less energy to forage. Pen fed silage-developed heifers, who were accustomed to a consistent high-quality feed supply, may have discriminated for a higher forage quality threshold for feeding sites (*as in* Bailey et al. 1996) investing more effort in search behaviors. Pen fed silage-developed heifers also appeared to apply stricter patch giving–up rules (*as in* Charnov, 1976); they tended to leave pixels sooner. This was possibly due to higher overall forage quality expectations (*as in* Charnov, 1976) derived from prior foraging experience in confinement and limited experience assessing tradeoffs (searching versus feeding behaviors to achieve optimal energy balance). Conversely, heifers raised on rangeland presumably applied less stringent feeding patch giving up rules (Bailey et al 1996, Charnov, 1976) due to their rangeland upbringing, lower initial weight gains and body condition score and experience optimizing searching (energy expenditure) and foraging (energy acquiring) activities.

Differences in pixel residence time and return interval for some vegetation classes in combination with traveling time differences suggest that, at least during the first few days, PFS heifers had higher energy expenditure compared to GFC and SFP counterparts. Brosh et al. (2010) assessed the energy cost of cattle activities using GPS data. They estimated that on average 44.45, 90.0 and 96.3 kJ . kg of body weight$^{-0.75}$. d^{-1} was the energy expended for standing, walking idle, or grazing, respectively. During April, heifers in PFS treatment spent around 61.17% more time per day traveling compared to GFC and SFP counterparts, which could have represented an extra cost of around 54.10 kJ . kg of body weight$^{-0.75}$. d^{-1} compared to rangeland raised counterparts particularly during the first couple of days when animals were moved to the pasture.

Differences in traveling time observed during May were possibly associated with exploration of a new pasture (May 2017) which likely had higher forage allowance of better quality compared to the previous pasture (Lonepine V). This would have influenced forage selection patterns which would have differed depending on the presumed forage quality expectations of the heifers in different treatments (PFS > GFC > SFP). Still, treatment differences observed in May were numerically smaller than those observed in April (especially during the first few days) likely due to the effect of social facilitation.

Regardless of development method, heifers exhibited similar preference for or avoidance of vegetation types with high- vs low-quality forage, respectively. Spatial regression analysis showed that NDVI values explained pixel selection patterns in most cases suggesting that heifers were possibly relying mostly on visual cues to select daily feeding sites (Howery et al., 2013). Highest NDVI values were found in lower elevation pixels with cool season grasses and legumes (high quality forage), whereas pixels with lowest NDVI were badlands with less forage.

During early spring (April) all heifers, irrespective of treatment, tended to spend more time grazing on cloudy days (lower solar radiation) with higher humidity (higher relative humidity and dew point temperature). On such days, heifers may have had a reduced need to travel to the drinker to meet their water requirements that were perhaps lower due to cooler ambient conditions and/or additional forage moisture derived from dew drops during early morning hours. Sun et al. (2014) found that steers were less dependent on drinking water by consuming forage moisture, which included not only plant internal water but also external moisture (dew, intercepted rainwater, and guttation) produced by weather (temperature, global radiation, sunshine hours, and relative humidity) and soil conditions. In May, heifers in all treatments tended to spend less time grazing on windy or rainy days on which they may have prioritized staying in more sheltered sites. Those results agree with Schütz et al. (2010) who found that intake was reduced when dairy cows were exposed to wind and rain.

During early spring (April), heifers that were developed on rangeland with hand fed supplements exhibited movement and activity patterns that were most of the time similar to dry lot-developed counterparts and sometimes differed significantly from self-fed rangeland-developed peers. Although GFC heifers continued to exhibit movement and activity patterns that were intermediate between PFS and SFP counterparts, treatment differences decreased through time such that by late spring (May) behavior of all heifers was statistically similar. Therefore, our second hypothesis was only partially supported by our findings. A number of prior studies investigated the effect of supplement feeding on grazing patterns of range cattle during winter (Schauer et al., 2005; Krysl & Hess, 1993) and several studies measured the carryover effects of winter supplementation or dry lot feeding on spring grazing patterns (Perry et al., 2015; Perry et al., 2013; Hojer et al., 2012; Olson et al., 1992). Several of these authors argued that heifers raised on rangeland should be more productive than dry lot-wintered heifers because they had acquired superior grazing skills during the post weaning phase and assumed that those abilities would be used during subsequent spring grazing. Our results suggest that the impact of development method on spring movement and activity patterns of heifers was possibly more strongly associated with the degree to which a heifer's energetic needs were met with bunk ration or supplements (PFS>GFC>SFP) vs. dormant winter forages (SFP>GFC) than with the foraging environment itself (rangeland pasture vs. dry lot). Metabolic memory observed in cows subjected to feed restrictions (Soca et al., 2013; Blanc et al., 2006) could explain the differences we observed between GFC and SFP heifers.

Early-life nutrition can have long-term effects on animal metabolism. Reddy et al. (2017) found that feeding early weaning calves with high-energy diets during early life, altered meat quality in later life (metabolic imprinting). In a similar way, differential nutrition during the post-weaning phase during winter could have had a long-term metabolic impact that resulted in foraging behavior differences during spring. This imprinting response could have been stronger in heifers who received a low-energy but high-protein supplement during winter. Mulliniks et al. (2019), Mulliniks et al. (2016), and Petersen et al. (2014), argued that exposure of animals to mild stress conditions, sufficient to develop adaptation but not severe enough to reduce production (fitness), could help animals to adapt to unpredictable events, such as extreme fluctuations in forage production due to year-to-year rainfall variability. Differences in foraging behavior of SFP heifers may have reflected greater flexibility to respond to environmental variability.

Our findings largely supported our third hypothesis that when grazing in a mixed treatment group, differences in grazing patterns would decrease through time due to social facilitation of foraging behaviors. Association analysis and descriptive metrics showed that collared PFS heifers were sometimes found in the proximity of GFC (more frequently) or SFP (more rarely) collared peers during spring, which might indicate that GFC heifers could be the best heifers to learn from. Those interactions probably gave the opportunity for PFS heifers to 'copy' (*as in* Laland, 2004) behaviors of GFC (especially) and SFP counterparts who presumably had superior rangeland foraging abilities acquired during winter months at pasture. Costa et al. (2016) found that naïve heifers learned grazing skills more rapidly from experienced peers compared to situations where they co-grazed with other naïve counterparts. Similarly, Hojer et al. (2012) who evaluated the influence of post-weaning method on grazing patterns during the subsequent summer found that heifers developed in a dry lot required a longer learning period to achieve foraging skills compared to heifers developed on rangeland. Other studies have shown that heifers developed in a dry lot decreased their average daily weight gain when they were moved to pasture, presumably due to a decrease in nutrient intake, as well as a lack of a period of adaptation (Perry et al., 2015, Perry et al., 2013) and an increase in energy expenditure. However, differences in body weight (dry lot-developed > rangeland- developed), and thus maintenance requirements, may also contribute to differences in daily weight gain.

Learning is known to influence foraging behaviors though time. Provenza and Balph (1988) argued that foraging behavior learned early in life was critical and could occur through food imprinting (Immelmann, 1975) or learning from social models such as the dam and peers (Howery et al., 1998). Many other studies have also shown the importance of peers in social facilitation of foraging behavior in cattle (Costa et al., 2016; Bailey et al., 2000; Jackson et al., 2010; Ksiksi & Laca, 2000). Asocial learning, through trial and error, also plays an important role in shaping foraging behavior (Coussi-Corbel & Fragazsi 1995). It is possible that PFS heifers relied on both asocial and social learning during the two-month period of our study and those might also have influenced how PFS changed vegetation site selection. Association results showed that interactions among collared PFS, SFP, and GFC heifers occurred even though the temporal threshold we used was lower than that used by Cheleuitte-Nieves et al. (2018), Stephenson et al. (2017), and Harris et al. (2007). Coussi-Korbel and Fragazsi (1995) argued that association among individuals usually entails knowledge acquisition from each other; therefore, it is possible that the associations we detected among PFS, GFC, and SFP heifers provided opportunities for heifers to imitate each other. It is interesting to note that heifers with central social roles (high centrality eigenvalues) who would be expected to have a stronger social influence on others (Laland, 2004) did not belong to a specific treatment group. In April 2016, heifer number 15812 (GFC), 15608 (SFP), and 15657 (SFP) heifer number 15608 (SFP) apparently had important social standing in the herd (they connected with many others) whereas in April 2017, heifer 16252 (PFS) fulfilled this role. Although our analysis of social interactions is limited to collared animals, it appears that social facilitation of movement and activity patterns occurred regardless of the post-weaning development method of heifers identified as being socially influential. Still, collared PFS heifers appeared to exhibit a higher number of associations with GFC counterparts and may have learned to mimic their behavior. This would explain why PFS and GFC movement and activity patterns tended to be more similar than that of PFS vs. SFP heifers. It is important to note that we were not able to compare pre- and post-weaning foraging skills of heifers. It is possible that the pre-weaning rangeland-based upbringing (learning from social models early in life) of PFS heifers was as important as the subsequent exposure to experienced peers in the convergence of behavioral patterns observed. More research is needed to identify critical periods during a heifer's first year of life responsible for shaping lifelong patterns of grazing on rangeland.

MANAGEMENT IMPLICATIONS

Heifers developed using different post-weaning protocols showed differences in movement and activity patterns during early spring. Such differences tended to decrease over time presumably due to social facilitation. Differences in pasture use patterns, however, tended to persist. Developing heifers on rangeland providing a self-fed high protein supplement during winter tended to encourage energy-conserving foraging skills that persisted for the duration of the experiment. Heifers with stronger social connections did not belong to a specific treatment group, which might indicate that personalities or temperament may have a high impact on how social facilitation occurs when heifers developed using different protocols graze together during spring. The degree to which heifers' requirements were met with non-range forage feeds, whether supplements or bunk silage (PFS>GFC>SFP) appeared to exert a stronger influence on a heifer's grazing patterns than the winter foraging environment itself (dry lot vs. rangeland).

Additional information about indicators of metabolic memory (i.e., body condition and initial weight) would significantly improve understanding about the mechanisms underlying the grazing behavior patterns observed in this study.

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Table 3. 1. Weather variables (means ± SE) for April and May during our study at the USDA-ARS Fort Keogh LARRL in Miles City, MT.

Variables	**Period***					
	April 2015	April 2016	April 2017	May 2015	May 2016	May 2017
Solar Rad (Langley . h^{-1})	20.24 ± 1.28	16.74 ± 1.14	17.46 ±1.16	18.71 ±1.21	24.51 ± 1.40	25.11 ± 1.37
Relative humidity (%)	46.42 ± 1.28	63.48 ± 1.29	64.83 ±1.15	59.94 ±1.28	59.73 ± 1.22	58.36 ± 1.13
Temperature (°C)	9.16 ± 0.36	9.89 ± 0.34	9.45 ± 0.28	11.28 ± 0.30	13.47 ± 0.39	14.21 ± 0.33
Rainfall (mm)	0.03 ± 0.01	0.10 ± 0.03	0.05 ± 0.02	0.04 ± 0.01	0.09 ± 0.02	0.01 ± 0.01
Wind Dir (°)	178.09 ± 4.60	207.49 ± 4.76	196.97 ± 5.03	213.45 ± 4.89	194.60 ± 5.64	164.06 ± 4.53
Wind Gust (m . s^{-1})	4.38 ± 0.16	4.50 ± 0.13	4.33 ± 0.14	4.35 ± 0.13	4.53 ± 0.17	4.22 ± 0.15
Wind Speed (m . s^{-1})	1.85 ± 0.10	2.01 ± 0.08	1.83 ± 0.09	1.76 ± 0.08	1.96 ± 0.11	1.68 ± 0.08
Dew Point (°C)	-4.57 ± 0.28	1.61 ± 0.24	1.93 ± 0.19	1.79 ± 0.27	4.05 ± 0.19	4.70 ± 0.17

*The duration of one complete period was 18 days.

Table 3. 2. Description of vegetation classes in Lonepine V, Lonepine Trap, and Lonepine U. Values are presented in means ± standard error.

Description	**Vegetation classes**			
	Badlands, sparsely vegetated hills	Mixed grass prairies, dominated by cool season grasses	Shrublands with mixed grass prairie understory vegetation	Cool season grasses/legumes, forbs and shrubs
Lonepine V				
Elevation (m)	2574.86 ± 1.22	2513.87 ± 0.67	2555.27 ± 1.11	2501.39 ± 0.58
Percentage covered by each class (%)	16.82	25.84	22.10	35.22
NDVI average	0.24 ± 0.001	0.31 ± 0.000	0.28 ± 0.001	0.32 ± 0.001
Cover (%)				
Bare ground	60.00 ± 5.37	10.67 ± 3.82	36.00 ± 4.08	3.50 ± 2.06
Shrubs	45.82 ± 9.72	0.00 ± 0.00	13.30 ± 4.02	15.60 ± 1.32
Warm season grasses	4.45 ± 1.74	11.92 ± 3.53	19.6 ± 4.34	0.35 ± 0.35
Cool season grasses	38.90 ± 9.39	27.40 ± 4.44	50.500 ± 5.11	52.08 ± 2.76
Annual grasses	7.17 ± 3.70	58.02 ± 2.90	9.55 ± 1.58	13.58 ± 4.51
Introduced forbs	0.98 ± 0.98	1.67 ± 0.65	0.000 ± 0.000	16.13 ± 3.64
Natural forbs	2.70 ± 1.80	0.97 ± 0.31	6.95 ± 4.11	2.30 ± 0.78
Lonepine Trap				
Elevation (m)	2556.58 ± 0.79	2523.76 ± 0.96	2540.71 ± 1.14	2499.47 ± 0.73
Percentage covered by each class (%)	15.39	29.99	15.52	39.08
NDVI average	0.24 ± 0.002	0.31 ± 0.001	0.29 ± 0.001	0.34 ± 0.001
Cover (%)				
Bare ground	38.50 ± 12.42	7.00 ± 1.92	18.00 ± 3.27	12.00 ± 6.68
Shrubs	31.63 ± 4.99	3.10 ± 1.07	16.50 ± 3.09	3.98 ± 0.56
Warm season grasses	1.68 ± 1.04	19.15 ± 5.96	16.63 ± 3.01	0.000 ± 0.000
Cool season grasses	47.23 ± 4.59	31.08 ± 4.44	45.98 ± 5.83	72.93 ± 10.31
Annual grasses	9.70 ± 4.80	37.15 ± 4.57	18.30 ± 4.25	10.10 ± 6.00
Introduced forbs	3.33 ± 2.51	3.93 ± 0.93	1.35 ± 0.92	11.05 ± 4.18
Natural forbs	6.43 ± 0.95	5.60 ± 1.95	1.28 ± 0.44	1.93 ± 0.80
Lonepine U				
Elevation (m)	2575.19 ± 1.04	2537.31 ± 0.96	2565.14 ± 0.67	2528.29 ± 1.00
Percentage covered by each class (%)				
NDVI average	0.30 ± 0.001	0.37 ± 0.002	0.35 ± 0.001	0.39 ± 0.001
Cover (%)	18.77	13.72	44.04	23.47

Bare ground	77.00 ± 13.00	23.50 ± 5.06	42.50 ± 16.60	17.50 ± 12.04
Shrubs	21.65 ± 0.55	0.83 ± 0.50	8.58 ± 3.11	7.20 ± 3.32
Warm season grasses	3.95 ± 3.95	21.90 ± 3.12	14.45 ± 3.55	1.68 ± 1.68
Cool season grasses	62.55 ± 3.25	39.28 ± 4.86	43.93 ± 13.60	64.50 ± 3.11
Annual grasses	0.00 ± 0.00	35.08 ± 6.11	28.48 ± 14.52	11.58 ± 2.61
Introduced forbs	1.85 ± 1.85	1.28 ± 0.54	2.70 ± 0.92	14.50 ± 4.84
Natural forbs	10.05 ± 4.75	1.65 ± 0.34	1.85 ± 0.87	0.58 ± 0.33

NDVI = Normalized Difference Vegetation Index.

Table 3. 3. LS-means of the pixel-use patterns of heifers developed in a pen and fed silage (PFS) or on rangeland (group-fed cake, GFC or self-fed protein, SFP) that grazed Lonepine V pasture for 18 days during May 2015, April 2016, and April 2017.

		Vegetation class*				
Response Variable	**Trt**	Bandlands, sparsely vegetated hills	Mixed grass prairie, dominated by cool season grasses	Shrubland with mixed grass prairie understory	Cool season grasses/legumes and shrubs	Total
Ivlev's electivity index (0-1)	PFS	-0.27 ± 0.09	0.01^{A} ± 0.02	-0.11^{A} ± 0.02	0.13 ± 0.02	
	GFC	-0.31 ± 0.07	0.03^{AB} ± 0.02	-0.04^{B} ± 0.02	0.11 ± 0.01	
	SFP	-0.36 ± 0.08	0.06^{B} ± 0.02	-0.10^{A} ± 0.02	0.12 ± 0.02	
	P	*0.80*	*<0.01*	*0.01*	*0.78*	
Pixels grazed (%)	PFS	3.81 ± 0.92	9.75^{A} ± 0.62	6.53^{AC} ± 0.24	16.72 ± 0.14	36.49^{B} ± 0.96
	GFC	3.35 ± 0.46	10.22^{A} ± 0.62	7.41^{B} ± 0.24	16.44 ± 0.75	37.31^{BA} ± 0.96
	SFP	3.14 ± 0.59	10.98^{B} ± 0.62	6.86^{BC} ± 0.24	16.98 ± 0.79	38.65^{A} ± 0.97
	P	*0.86*	*<0.05*	*0.05*	*0.94*	*<0.05*
Return Interval (days)	PFS	5.84^{A} ± 0.22	5.43^{AC} ± 0.16	5.99 ± 0.34	5.43^{A} ± 0.07	5.51 ± 0.09
	GFC	5.07^{B} ± 0.22	5.88^{B} ± 0.16	5.92 ± 0.30	5.68^{B} ± 0.07	5.67 ± 0.05
	SFP	6.03^{A} ± 0.23	5.65^{BC} ± 0.16	5.91 ± 0.36	5.48^{BA} ± 0.07	5.58 ± 0.07
	P	*0.01*	*0.02*	*0.96*	*0.04*	*0.36*
Residence Time (minutes)**	PFS	10.92^{B} ± 0.89	19.36^{A} ± 0.98	12.31 ± 0.46	20.36 ± 1.22	15.84 ± 0.61***
	GFC	13.61^{A} ± 0.89	17.88^{BA} ± 0.98	13.47 ± 1.01	19.99 ± 0.56	16.30 ± 0.47***
	SFP	12.03^{BA} ± 0.89	17.11^{B} ± 0.98	13.43 ± 1.53	19.90 ± 0.92	15.59 ± 0.48***
	P	*0.01*	*0.01*	*0.62*	*0.96*	*0.55*

Trt= treatment

A-C Means with different letters by column are significantly different (Tukey's HSD, $p<0.05$).

* Each vegetation class was analyzed separately.

** Calculated based on grazed pixels. It is independent whether animal return or not to pixel.

*** Residence Time total expressed in means values due to non-normality.

Table 3. 4. Spatial regression models relating 15 m pixel attributes and pixel use patterns by heifers developed in a pen and fed silage (PFS) or on rangeland (group-fed cake, GFC or self-fed protein, SFP) during May 2015, April 2016, April 2017 in Lonepine V pasture.

Response Variable	Model*	R^2	SE	AIC
Pixel Return Interval (days) ***				
PFS	7.25 (NDVI)**	0.06	1.85	9505.04
GFC	-0.0009 (water-sup) + 0.001(aspect) + 0.001 (fence)	0.07	1.85	9431.69
SFP	-0.0008 (water-sup) + 8.64 (NDVI)	0.09	1.88	10015.90
	Model*	**R^2**	**SE**	**AIC**
Pixel Residence Time (min) ****				
PFS	-203.33 + 0.06 (elevation) + 142.43 (NDVI)	0.31	24.08	35617.0
GFC	-271.66 + 0.09 (elevation) + 130.59 (NDVI)	0.32	24.06	35581.7
SFP	-389.41 + 0.13 (elevation) + 216.58 (NDVI)	0.33	22.87	35285.1

*Model type= PFS and HFC (Spatial Lag), SFP (Spatial error); $P < 0.01$

** NDVI: 15 m pixel normalized difference vegetation index; Water-sup: Distance to drinker and supplement feed (m); Aspect (degrees); Fence: distance to fenceline (m); Elevation (m).

*** It was calculated based on pixels that animals returned to graze.

****Calculated based on grazed pixels. It is independent whether animal return or not to pixel.

Table 3. 5. Linear Discriminant Analysis including distance traveled (km . d^{-1}), area covered (squared root transformed, ha . d^{-1}), movement velocity (m . min^{-1}), path sinuosity (0-1), total time spent resting (h . d^{-1}), total time spent grazing (h . d^{-1}), total time spent traveling (h . d^{-1}), 15 m pixel return interval (d), 15 m pixel residence time (min), and percent 15 m pixels grazed (%) by PFS (n=16), GFC (n=16), SFP (n=16) heifers in May 2015, April 16, April 2017 (Lonepine V pasture). PFS= pen-fed silage, GFC= group-fed cake, SFP= self-fed protein.

Treatment	**Classified into treatment (%)**			**Mean Error rate**	**Pr> ChiSq**	**Wilks' Lambda**
	PFS	GFC	SFP			
PFS	75.00	6.25	18.75	0.42	0.82	<0.01
GFC	31.25	43.75	25.00			
SFP	6.25	37.50	56.25			

Linear Discriminant Functions (reduced set of predictors)

PFS: -369.30 + 101.32 (travel)* + 42.83 (rest)** + 3.84 (pixel residence time)***

GFC: -357.59 + 96.89 (travel) + 41.98 (rest) + 4.19 (pixel residence time)***

SFP: -333.44+ 93.35 (travel) + 40.73 (rest) + 3.85 (pixel residence time)***

* Daily time spent traveling (h . d-1)
** Daily time spent resting (h . d-1)
***Pixel residence time (min).

Table 3. 6. Means and standard error for variables included in the Linear Discriminant Analysis by PFS, GFC, and SFP in May 2015, April 16, April 2017 (Lonepine V pasture). PFS= pen-fed silage, GFC= group-fed cake, SFP= self-fed protein.

Variables	**Treatment**		
	PFS	**GFC**	**SFP**
Distance traveled (km . d^{-1})	6.96 ± 0.17	6.41 ± 0.26	6.42 ± 0.24
Movement velocity (m . min^{-1})	5.32 ± 0.13	4.90 ± 0.19	4.90 ± 0.18
Path sinuosity (0-1)	0.06 ± 0.00	0.06 ± 0.00	0.07 ± 0.00
Area covered* (ha . d^{-1})	59.14 ± 2.30	56.45 ± 1.45	55.15 ± 1.63
Total resting (h . d^{-1})	13.69 ± 0.14	13.62 ± 0.21	13.25 ± 0.17
Total grazing (h . d^{-1})	9.23 ± 0.14	9.50 ± 0.18	9.90 ± 0.15
Total traveling (h . d^{-1})	1.08 ± 0.05	0.88 ± 0.06	0.85 ± 0.06
Pixel return interval (d)	5.54 ± 0.08	5.71 ± 0.06	5.59 ± 0.07
Pixel residence time (min)	10.66 ± 0.47	13.35 ± 0.74	11.77 ± 0.59
Pixels grazed (%)	36.38 ± 0.62	36.99 ± 0.53	37.94 ± 0.43

*Black square-root transform for area covered

Table 3. 7. Number of associations between pairs of heifers developed in a pen-fed silage (PFS) or on rangeland (group-fed cake, GFC and self-fed protein, SFP) at increasing spatial thresholds (distance, meters) while maintaining the temporal threshold constant at 55 %.

Description *	**Spatial threshold**							
	25 m		**50 m**		**75 m**		**100 m**	
	ASO**	Association*** (%)	ASO	Association (%)	ASO	Association (%)	ASO	Association (%)
May 2015								
PFS-PFS	0	0.00 ± 0.00	0	0.00 ± 0.00	0	0.00 ± 0.00	0	0.00 ± 0.00
PFS-GFC	0	0.00 ± 0.00	0	0.00 ± 0.00	0	0.00 ± 0.00	0	0.00 ± 0.00
PFS-SFP	0	0.00 ± 0.00	0	0.00 ± 0.00	0	0.00 ± 0.00	0	0.00 ± 0.00
GFC-GFC	0	0.00 ± 0.00	0	0.00 ± 0.00	0	0.00 ± 0.00	0	0.00 ± 0.00
SFP-SFP	0	0.00 ± 0.00	0	0.00 ± 0.00	0	0.00 ± 0.00	1	55.1 ± 0.00
GFC-SFP	0	0.00 ± 0.00	0	0.00 ± 0.00	0	0.00 ± 0.00	0	0.00 ± 0.00
April 2016								
PFS-PFS	0	0.00 ± 0.00	0	0.00 ± 0.00	2	59.9 ± 1.55	4	59.4 ± 2.10
PFS-GFC	2	100.00 ± 0.00	2	100.00 ± 0.00	4	78.7 ± 78.65	8	68.8 ± 6.89
PFS-SFP	0	0.00 ± 0.00	0	0.00 ± 0.00	0	0.0 ± 0.00	4	56.4 ± 0.27
GFC-GFC	0	0.00 ± 0.00	0	0.00 ± 0.00	2	57.3 ± 1.00	3	61.2 ± 1.41
SFP-SFP	0	0.00 ± 0.00	0	0.00 ± 0.00	3	57.8 ± 1.03	8	59.4 ± 1.12
GFC-SFP	0	0.00 ± 0.00	2	55.3 ± 0.10	3	57.1 ± 0.21	14	57.9 ± 0.75
April 2017								
PFS-PFS	0	0.00 ± 0.00	1	59.5 ± 0.00	10	57.7 ± 0.56	21	59.1 ± 0.59
PFS-GFC	0	0.00 ± 0.00	1	55.1 ± 0.00	2	55.9 ± 0.00	8	57.1 ± 0.55
PFS-SFP	0	0.00 ± 0.00	0	0.00 ± 0.00	2	58.5 ± 2.45	8	58.7 ± 0.78
GFC-GFC	2	84.10 ± 0.50	2	84.9 ± 0.35	2	85.2 ± 0.35	2	86.7 ± 0.80
SFP-SFP	0	0.00 ± 0.00	0	0.00 ± 0.00	0	0.00 ± 0.00	0	0.00 ± 0.00
GFC-SFP	0	0.00 ± 0.00	0	0.00 ± 0.00	1	56.6 ± 0.00	2	60.6 ± 2.25

* PFS: pen fed silage, GFC: group fed cake, SFP: Self fed protein.

**ASO: Number of Associations.

*** Percent spatial association.

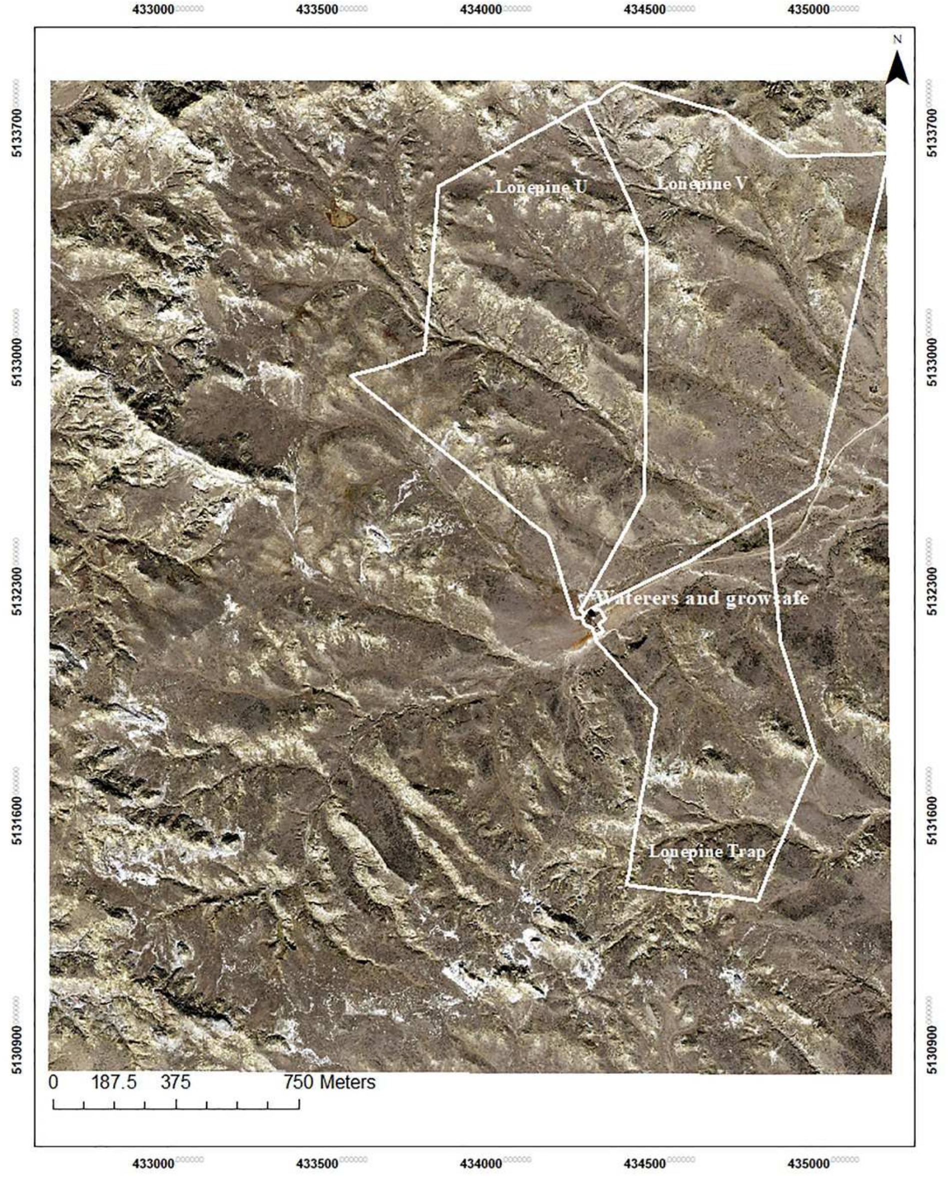


Figure 3. 1. NAIP image showing the study area outlined in white (Lonepine V, Lonepine U, and Lonpine Trap pasture) and location of water and GrowSafe feeders for self-fed supplement.

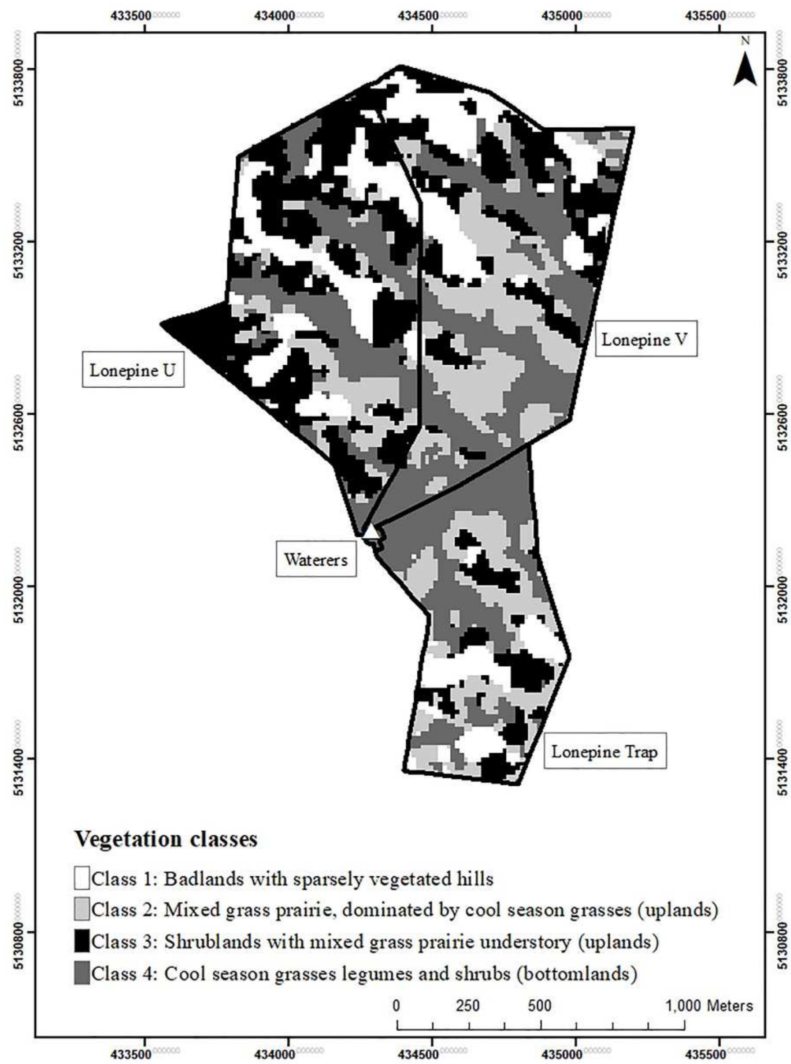


Figure 3. 2. Vegetation map for Lone pine V, Lonepine U, and Lonepine Trap located at USDA-ARS Fort Keogh LARRL, Miles City, MT.

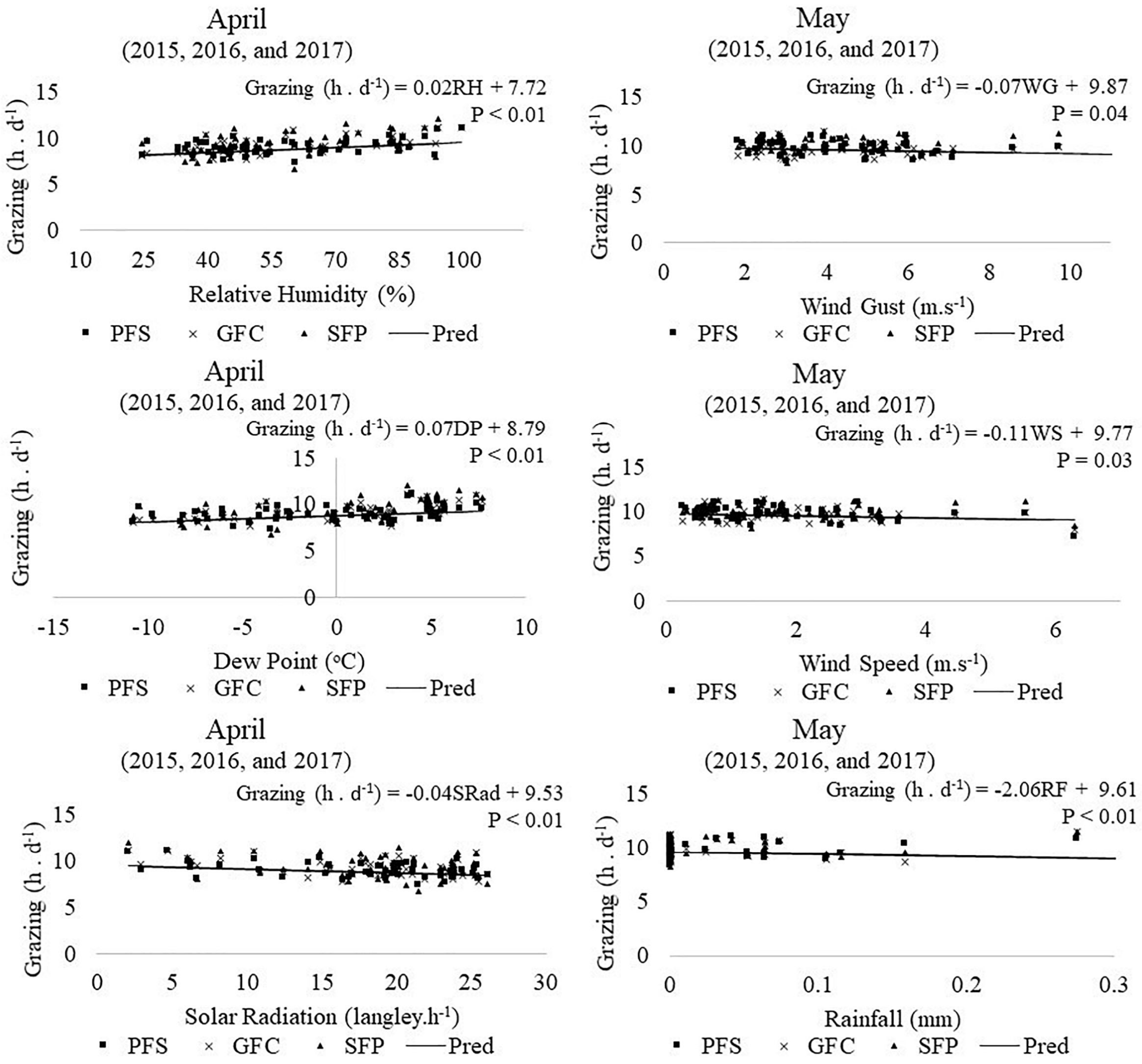
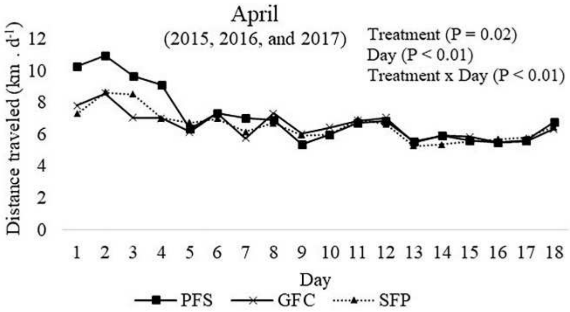
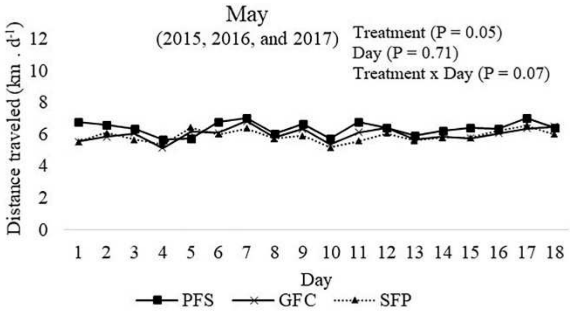
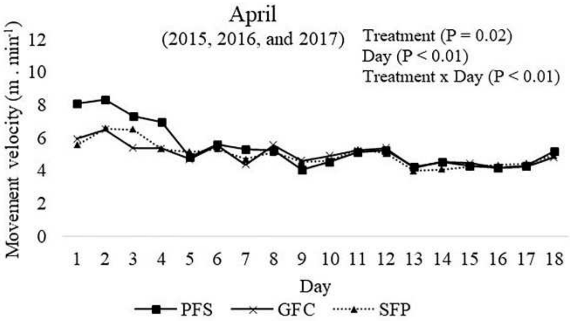


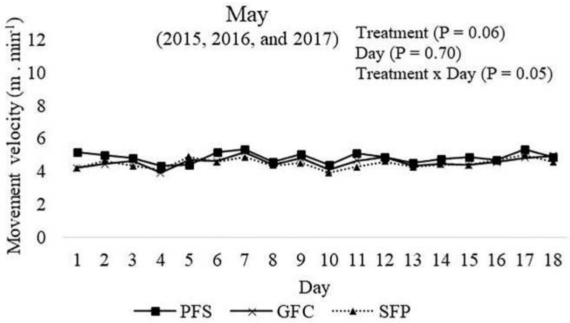
Figure 3. 3. Grazing (h . d^{-1}) vs. weather variables (relative humidity, solar radiation, dew point, wind gust, wind speed, and rainfall) to pen fed silage (PFS), group fed cake (GFC), and self-fed protein (SFP) treatments during April 2015, 2016, and 2017 in Lonepine V pasture and May 2015, 2016, and 2017 in Lonepine V, Lonepine Trap, and Lonepine U pasture. RH = relative

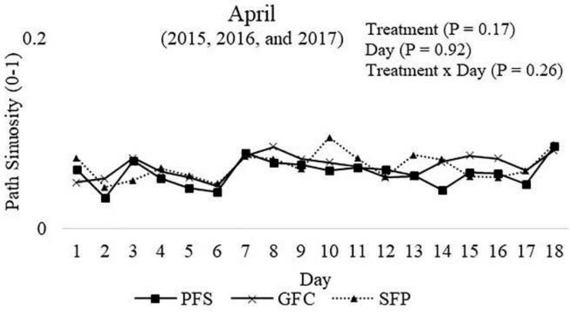
humidity, SRad = solar radiation, DP = dew point, WG = wind gust, WS = wind speed, RF = rainfall.

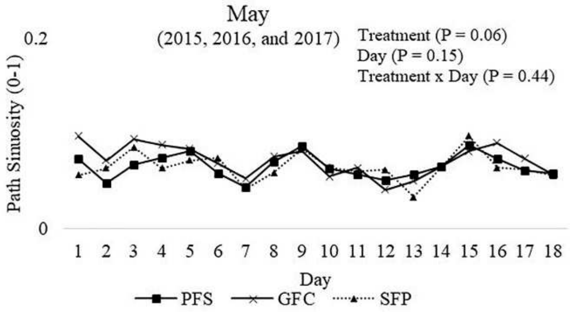

April
(2015, 2016, and 2017)
Treatment (P = 0.02)
Day (P < 0.01)
Treatment x Day (P < 0.01)
Distance traveled (km . d-1)
0
2
4
6
8
10
12
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18
Day
PFS
GFC
SFP

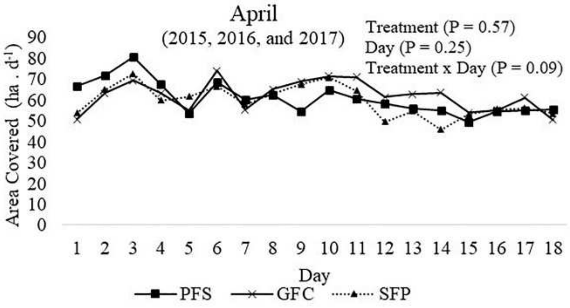

May
(2015, 2016, and 2017)
Treatment (P = 0.05)
Day (P = 0.71)
Treatment x Day (P = 0.07)
Distance traveled (km . d-1)
0
2
4
6
8
10
12
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18
Day
PFS
GFC
SFP


April
(2015, 2016, and 2017)
Treatment (P = 0.02)
Day (P < 0.01)
Treatment x Day (P < 0.01)
Movement velocity (m . min-1)
0
2
4
6
8
10
12
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18
Day
PFS
GFC
SFP


May
(2015, 2016, and 2017)
Treatment (P = 0.06)
Day (P = 0.70)
Treatment x Day (P = 0.05)
Movement velocity (m . min-1)
0
2
4
6
8
10
12
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18
Day
PFS
GFC
SFP


April
(2015, 2016, and 2017)
Treatment (P = 0.17)
Day (P = 0.92)
Treatment x Day (P = 0.26)
Path Sinuosity (0-1)
0
0.2
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18
Day
PFS
GFC
SFP


May
(2015, 2016, and 2017)
Treatment (P = 0.06)
Day (P = 0.15)
Treatment x Day (P = 0.44)
Path Sinuosity (0-1)
0
0.2
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18
Day
PFS
GFC
SFP


April
(2015, 2016, and 2017)
Treatment (P = 0.57)
Day (P = 0.25)
Treatment x Day (P = 0.09)
Area Covered (ha . d-1)
0
10
20
30
40
50
60
70
80
90
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18
Day
PFS
GFC
SFP

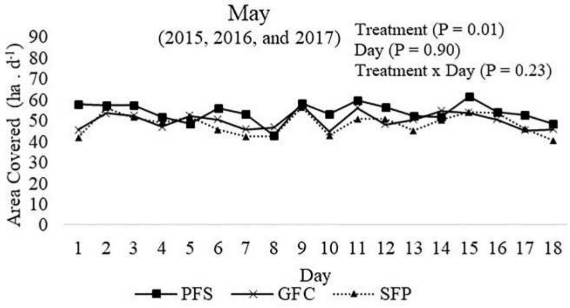

May
(2015, 2016, and 2017)
Treatment (P = 0.01)
Day (P = 0.90)
Treatment x Day (P = 0.23)
Area Covered (ha . d-1)
0
10
20
30
40
50
60
70
80
90
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18
Day
PFS
GFC
SFP

Figure 3. 4. Daily movement patterns (least squares means) of heifers in pen fed silage (PFS), group fed cake (GFC), and self-fed protein (SFP) treatments during April (back transformed LSmeans from square-root transformation) and May 2015, 2016, and 2017 (back transformed LSmeans from square-root transformation to distance traveled and movement velocity) in Lonepine V, Lonepine U, and Lonepine Trap pastures.

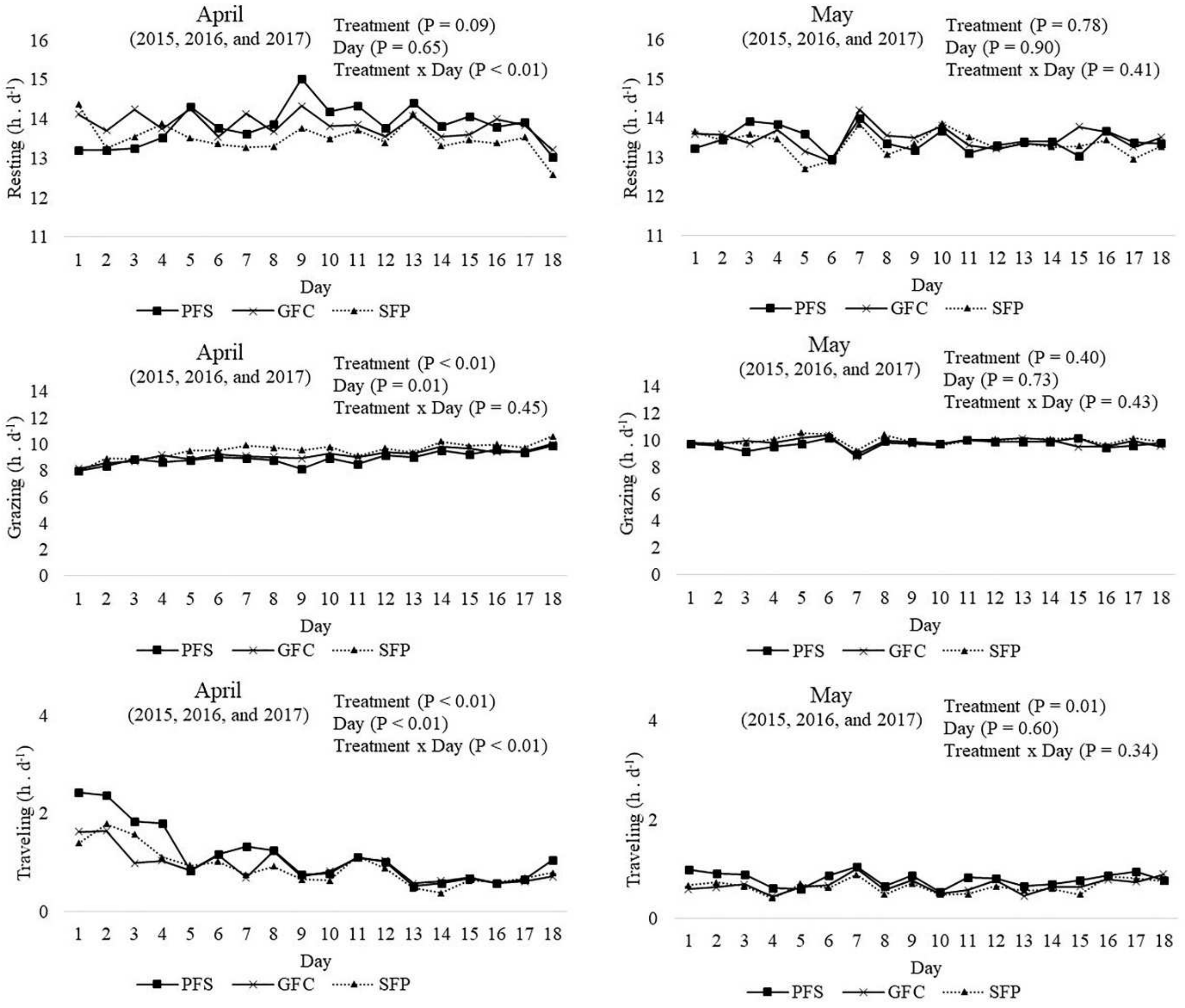
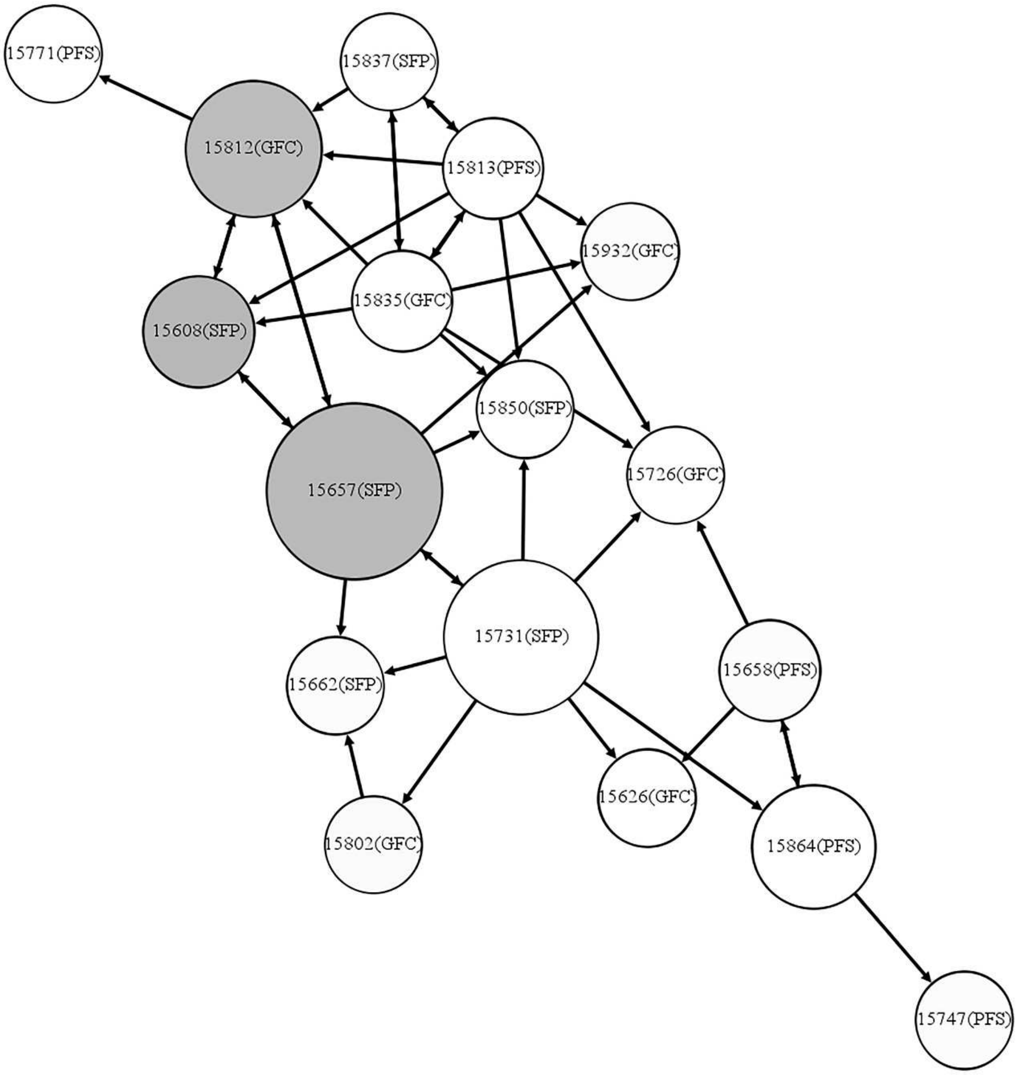


Figure 3. 5. Daily activity patterns (least squares means) of heifers in pen fed silage (PFS), group fed cake (GFC), and self-fed protein (SFP) treatments during April and May 2015, 2016, and 2017 in Lonepine V, Lonepine U, and Lonepine Trap pastures (back transformed LSmeans from square-root transformation to time traveling during April and May).

a)


15771(PFS)
15837(SFP)
15812(GFC)
15813(PFS)
15932(GFC)
15835(GFC)
15608(SFP)
15850(SFP)
15726(GFC)
15657(SFP)
15731(SFP)
15658(PFS)
15662(SFP)
15626(GFC)
15864(PFS)
15802(GFC)
15747(PFS)

b)

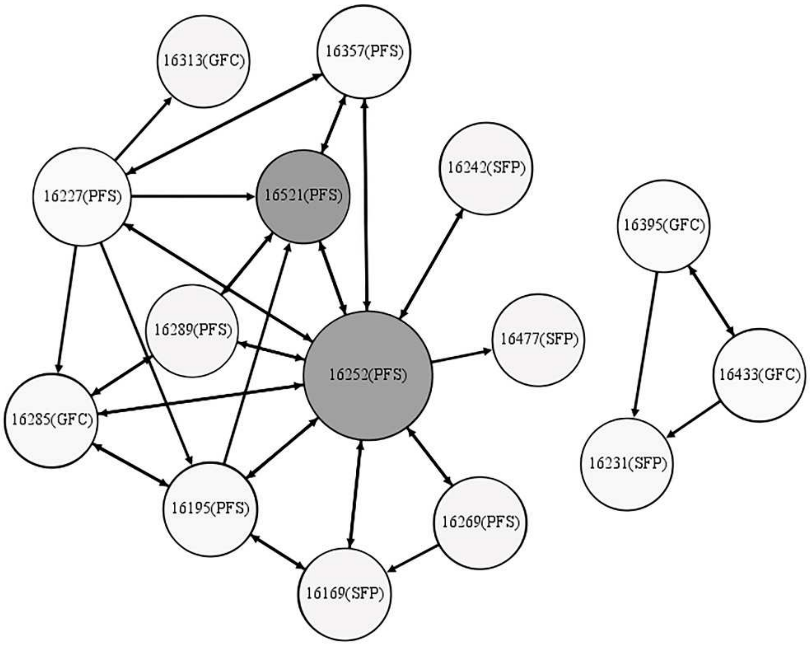


Figure 3. 6. Spatial and temporal association graph from heifers during a) April 2016 (18 days) and b) April 2017 (18 days). Temporal threshold (55 %) and spatial thresholds 100 meters. Node colored by eigenvector centrality values (highest eigenvector centrality values indicate individuals who influence other individuals); node size refers to betweenness centrality (heifers

who are important to maintain the connection between network). Number denotes the identification of heifer. Pen fed silage (PFS), group fed cake (GFC), and self-fed protein (SFP) treatments.

CHAPTER 4

A COMPARISON OF TWO METHODS TO ESTIMATE HEIFER ACTIVITY USING GLOBAL POSITIONING SYSTEM (GPS) AND ACCELEROMETER DATA

ABSTRACT

We compared the precision of two methods of estimating activity of rangeland heifers monitored with collars equipped with GPS (Global Positioning System) and motion sensors. Lotek 3300LR GPS collars with biaxial accelerometers were fitted on randomly selected crossbred heifers during winter (n=112, January, February and March, 16 days) and spring (n=79, April and May, 18 days) in three consecutive years (2015, 2016, 2017). We compared two methods of classifying heifer activity (resting, grazing, and traveling). The GPS method was based on movement velocity thresholds and the GPSA method was based on distance thresholds and 2-axis accelerometer data. Both methods yielded similar estimates for time spent resting and grazing during winter and spring (P>0.05). Differences between the two methods were found with estimated of time spent traveling in both seasons (P<0.01). Both methods presented an acceptable degree of concordance. We conclude that the GPS method might be a reliable means of estimating cattle activities within certain limits. Algorithm adjustments may necessary to reduce observed bias. Further research is needed to determine whether these results can be generalized to different breeds and ages (heifers vs. mature cows) of cattle grazing different rangeland types.

Key Words: activity classification, sensors, cattle behavior.

INTRODUCTION

Global Positioning System (GPS) tracking of livestock is now widespread and has been used to monitor habitat selection, movement patterns, and activity of cattle (Peinetti et al., 2011, Sawalhah et al., 2016, Anderson et al., 2012). Advancements in sensor technology have resulted in the development of small and lightweight accelerometers and pedometers that allow detailed tracking of animal steps or head movement. These devices are considered to have made significant advances in allowing researchers to discriminate livestock behavior patterns (Robert et al. 2009). Most commercially available GPS collars for livestock include either two- or three-axes accelerometer units capable of recording animal neck movements at very high frequencies. The dual-axis sensor records the number of neck movements made by the animal in the perpendicular (up-down, y-axis) and parallel (right and left side, x-axis) planes, while the triple-axis sensor includes an extra axis to record movement in the mid-sagittal plane (z-axis).

Researchers that study animal behavior using GPS often combine accelerometer data with estimates of GPS-derived velocity/distance between locations to classify an animals' activity patterns. Most of such studies typically use a classification tree to discriminate GPS points into activity categories and usually validate their classification via visual observations of an animal's movement and activity patterns (Gonzalez et al., 2015, Ungar et al., 2011, Augustine & Derner, 2013 and Guo et al., 2009). However, because GPS collars are often costly, limiting the number of animals that can be tracked (Bailey et al., 2018),there is increasing interest in the use of low-cost GPS units to monitor movement and activity patterns of a larger number of animals in a herd typically in rangeland settings (Knight et al., 2018, Clark et al., 2006). The main limitation with these collars is that they lack movement sensors and only provide GPS coordinate values. But since interpretation of movement sensor data is often difficult because: 1) data are strongly influenced by how well the sensor is affixed to an animal's neck or ear (i.e. a loose-fitting collar will yield different values than a tighter-fitting one); and 2) in the case of tri-axial accelerometers, to the volume of data points produced is hard to manage and streamline, their value in improving classification of animal activities is still uncertain.

Therefore, our objective was to compare the precision of two methods to estimate the activity of rangeland heifers monitored with collars equipped with GPS and two-axis accelerometers. The first method was based on a velocity threshold using GRAZACT (Cao et al., unpublished), a Java software that helped automate classification. The second method was based on animal head movement data + distance values between recorded locations, based on parameters developed by Augustine and Derner (2013). This study hypothesized that the classification of activities using velocity thresholds would produce similar results to those of the classification of activities that consider both distance between fixes and estimates of animals head movements.

MATERIALS AND METHODS

Study area

The experiment was conducted at the USDA-ARS Fort Keogh LARRL in Miles City, MT (Lat 46° 23’ 08’’ N, Long 105° 52’ 26’’ W). The climate is semi-arid (Rubel & Kottek, 2010; Kottek et al., 2006) with cold winters and warm summers. Average minimum and maximum temperatures are –14.6°C (January), and 31.8°C (July), respectively, with an average of 150 frost-free days. Mean annual precipitation is 333 mm. Soils include Mollisols and Entisols and approximately 350 plant species have been identified on the ranch (Petersen & Reinhart, 2012). Most of the plant communities in the study area are composed of C_3 graminoids. *Bouteloua-Hesperostipa-Pascopyron* associations are predominant across the study area.

Animals and collar data

All animal procedures were approved by the Fort Keogh Livestock and Range Research Laboratory Animal Care and Use Committee. Lotek 3300LR GPS collars, with biaxial accelerometers, were fitted randomly on cross-bred heifers (½ Red Angus, ¼ Charolais, ¼ Tarentaise) during the winter and spring of 2015, 2016, and 2017 (Table 4. 1.). Different heifers were monitored each month and year during the winter and the spring.

Method 1 (GPS): This method used only GPS data to discriminate heifer activity. We classified GPS points based on movement velocity thresholds. Resting was assumed when velocity < 2 m $.\mathrm{min}^{-1}$, velocities between 2 m $.\ \mathrm{min}^{-1}$ to 25 m $.\ \mathrm{min}^{-1}$ were assumed to indicate grazing, and velocities > 25 m $.\ \mathrm{min}^{-1}$ were classified as traveling. GPS calculations were conducted by entering GPS coordinates into GRAZACT (Cao et al., unpublished), a Java software that helped automate classification. Criteria to decide the velocity thresholds was based on distances used in a classification tree developed by Augustine and Derner (2013) for yearling steers grazing shortgrass prairie rangeland in Colorado, an age class and rangeland environment similar to that of our study.

Method 2 (GPSA): This method used both distance thresholds and 2-axis accelerometer data to discriminate heifer activity. We used a classification tree model that discriminated GPS points into resting, grazing, and traveling considering the distance between GPS points and both horizontal and vertical movement values recorded by a 2-axis accelerometer. SAS 9.4 code (SAS Institute, Cary, NC) was used to create the classification tree model to calculate GPSA, which was based on parameters used by Augustine and Derner (2013).

Statistical Analysis

The results of both methods were converted to hours*day^{-1} and analyzed using PROC TTEST in SAS 9.4 (SAS Institute, Cary, NC). The differences were declared statistically significant at $P < 0.05$. The concordance correlation coefficient (CCC, Lin, 1989) was calculated to measure the agreement between two methods using SAS 9.4 (SAS Institute, Cary, NC). According to McBride et al. (2005), correlation was considered poor (CCC < 0.90), moderate (CCC between 0.90-0.95), substantial (CCC between 0.95-0.99) or almost perfect (CCC >0.99). The seasons (winter and spring) were analyzed separately, pooling data from 3 years (2015, 2016, and 2017) collected during the months of January, February, and March for winter and

April and May for spring. Testing for normality of error residuals and homogeneity of variances was conducted prior to all statistical analyses to detect potential violation of assumptions and deleting outliers. Some dependent variables were square root or log transformed to normalize the residuals. Data from May 2016 were excluded from analysis because heifers left the study area during most of the sampling period.

RESULTS AND DISCUSSION

Both methods yielded similar estimates for time spent resting (P= 0.86) and grazing (P=0.90) during winter (Table 4. 2.) and spring (P=0.07 for both resting and grazing, Table 4.2.). The confidence interval ranges showed no significant difference in the classification of resting or grazing activity between GPSA and GPS (winter and spring data); the 95% confidence interval included zero in all cases (Table 4. 2.). However, classification differences between the two methods were found with estimates of time spent traveling (P<0.01 for winter and spring, Table 4. 2.). Estimated time spent traveling was higher using GPS vs. GPSA in both seasons. The confidence interval range showed a significant difference in traveling activity between GPSA and GPS; the 95 % confidence interval did not include the zero in all cases (Table 4. 2.). The standard error tended to be smaller in the GPS compared to the GPSA method estimates for grazing activities, similar for resting and higher for the traveling activity during winter while the standard error tended to be smaller in the GPS compared to the GPSA method estimates for resting and grazing activities, and similar for the traveling activity during spring (Table 4. 2.). Although the CCC between the GPS and the GPSA methods was low for all activity patterns

(CCC<0.90), resting tended to exhibit a higher CCC (CCC=0.71) followed by grazing (CCC=0.56) and traveling (CCC=0.40) during winter. Conversely, traveling tended to present a higher CCC compared to resting and grazing during spring (CCC=0.32, 0.30, and 0.58 for resting, grazing, and traveling, respectively, Figure 4. 1.).

Both methods yielded similar estimates of time spent resting or grazing in both winter and spring, suggesting that the GPS method could be a reliable means of estimating time allocated to these activities. The lower degree of agreement (reproductivity) observed for resting, grazing, and traveling during both seasons may have been attributed to computational limitations of the GRAZACT software we used. In addition, the GPS method included only three activity classes (resting, grazing, and traveling) while the GPSA method allows for an additional category (mixed), which contains values that don't fit in any of the other three activities.

GPS estimates of time spent traveling were approximately 30 % higher than those derived with the GPSA method. Still, since time allocated to this activity is usually a very small faction of an animal's daily activity budget, in absolute terms the differences between methods are likely not biologically significant. No direct observations of animal activity were conducted in this study; therefore, we were unable to assess the accuracy of each method independently. However, Augustine and Derner (2013) who validated the GPSA method with direct observations found that inaccuracies in travel classification were higher compared to grazing and resting, which suggests that the differences in the estimates of time spent traveling are possibly associated with the inherent difficulty of correctly classifying this activity with either method.

MANAGEMENT IMPLICATIONS

Classifying livestock activities based on GPS data alone provided estimates of daily time spent in resting and grazing that were similar to those derived from more sophisticated GPS + movement sensor analyses. Our analysis used data gathered from crossbred heifers. Further research to estimate activities using different breeds and ages (heifers vs. mature cows) of cattle on different rangeland types as well as additional validation are needed to determine whether our results can be generalized.

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Table 4. 1. Description of the number of total heifers located in each pasture and numbers of collars used for the study during winter for January, February, and March (2015, 2016, and 2017) and spring for April and May (2015, 2016, and 2017).

Year	Season	Month	Pasture	Number of heifers	Numbers of collars used
2015	winter	January	Lonepine R and Lonepine S	134	10
		February	Lonepine T and Lonepine U	134	10
		March	Lonepine T and Lonepine U	134	10
2016	winter	January	Lonepine Trap and Lonepine Q	99	14
		February	Lonepine S and Lonepine R	99	14
		March	Lonepine U and Lonepine T	99	14
2017	winter	January	Lonepine Q and Lonepine Trap	105	14
		February	Lonepine Q, Lonepine R, Trap, and S	105	13
		March	Lonepine T and Lonepine V	105	13
2015	spring	April	Lonepine V	201	10
		May	Lonepine V	201	10
2016	spring	April	Lonepine V	120	18
		May	Lonepine U, T, and S	120	16
2017	spring	April	Lonepine V	125	21
		May	Lonepine Trap	125	20

Table 4. 2. Activity estimates derived from GPS vs. GPSA methods using data collected in 2015, 2016, and 2017.

Activity	GPS method		GPSA method		95% CL difference	P value[*]
	Mean (hours/day) ± SE	95% CL	Mean (hours/day) ± SE	95% CL		
Winter						
Resting[**]	1.20 (15.84) ± 0.00	1.20-1.21	1.21 (16.22) ± 0.00	1.20-1.21	-0.01-0.01	0.86
Grazing	7.27 ± 0.11	7.06-7.49	7.30 ± 0.14	7.01-7.58	-0.38-0.33	0.90
Traveling[***]	0.80 (0.63) ± 0.03	0.74-0.85	0.61 (0.37) ± 0.02	0.57-0.65	0.12-0.25	<0.01
Spring						
Resting	13.70 ± 0.08	13.53-13.85	13.94 ± 0.11	13.72-14.15	-0.51-0.02	0.07
Grazing	9.40 ± 0.08	9.25-9.55	9.12 ± 0.13	8.86-9.39	-0.03-0.58	0.07
Traveling[***]	0.94 (0.89) ± 0.02	0.91-0.97	0.81 (0.65) ± 0.02	0.77-0.84	0.09-0.18	<0.01

[*] The level of significance for all variables was set at $P<0.05$.

[**] Resting (log transformation, back log transformed data in parenthesis)

[***] Traveling (square-root transformation, back square-root transformed data in parenthesis).

GPS = classification based on GPS-derived movement velocity thresholds.

GPSA = classification based on GPS + 2-axis accelerometer data.

SE = standard error.

CI = confidence interval.

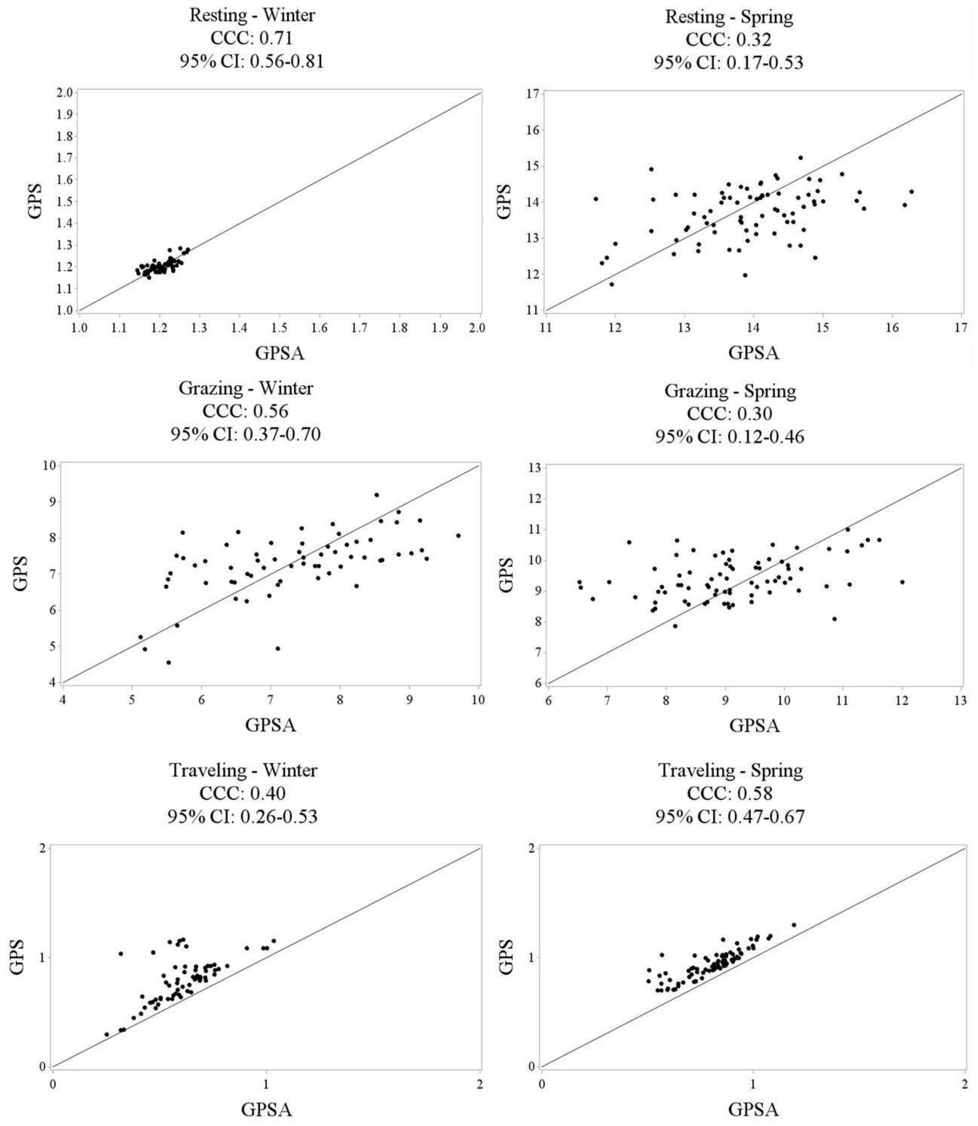

Figure 4. 1. The concordance correlation coefficient (CCC) between GPS method (y-axis) and the GPSA (x-axis) for estimates of time spent resting (log transformation for winter), grazing, and traveling (square-root transformation for winter and spring). Each black circle denotes the intersection of GPS and GPSA measurement for a specified sample (n=78). CI= confidence

interval. GPS= classification based on GPS-derived movement velocity thresholds. GPSA= classification based on GPSand 2-axis accelerometer data.

CHAPTER 5

SUMMARY OF RESEARCH AND CONCLUSIONS

The research included in this dissertation focused on how: a) winter supplement feeding and a dam's feeding history influenced grazing behavior of rangeland beef heifers during winter; and b) post-weaning development method during winter (rangeland vs. feedlot) affected subsequent spring grazing patterns of rangeland beef heifers in the Northern Great Plains. I found that restricted feeding of dams during the last third of the gestation period appeared not to affect the behavior of their female offspring when winter feeding conditions were not limiting. Winter movement and activity patterns of heifers were possibly more strongly influenced by the degree to which a heifer's energetic needs were met with supplements (group-fed cake: GFC vs. self-fed protein: SFP) than with the dam's lifelong feeding regime itself. Compared to GFC counterparts, SFP heifers grazing strategy apparently consisted of optimizing searching and foraging activities to minimize energy expenditure and maximize energy acquisition which was evident by the higher grazing time and straighter travel paths (lower path selectivity). Heifers in the GFC treatment spent more time engaged in non-foraging activities (resting and traveling) and followed more sinuous trajectories.

Post-weaning development method during winter whether supplemented on rangeland (GFC or SFP) or fed silage in a pen (PFS) affected the subsequent grazing behavior during spring when heifers in all treatment groups grazed in the same pasture. Heifers in SFP treatment continued to use more efficient forage search tactics compared to heifers in PFS treatment who appeared to apply stricter patch giving-up rules because they tended to leave pixels sooner perhaps due to higher overall forage quality expectations derived from prior foraging experience in confinement. Conversely, GFC and SFP heifers appeared to exhibit less stringent feeding patch giving up rules perhaps due to their familiarity with winter dormant forages on rangeland. Interestingly, GFC heifers tended to exhibit intermediate behaviors relative to PFS and SFP groups. Differences in grazing patterns among treatment groups decreased through time presumably due to social facilitation of foraging behaviors (all groups grazed together during spring). Interestingly, heifers that had a stronger social influence on collared peers did not belong to a specific treatment group, which might suggest that animal personality, rather than post-weaning development method, shapes the social facilitation process.

Overall, the studies I conducted suggest that restricting a dam's supplementation level during the third trimester of pregnancy does not affect subsequent grazing behavior of the offspring when nutritional requirements are met during the post-weaning phase.
Post-weaning heifer development method affected spatial distribution patterns on rangeland during winter, and those differences appeared to persist throughout spring. Heifers in the PFS treatment who were fed silage in a pen during winter might require an adaptation period when they return to graze rangelands in the spring. Supplementation may be needed for a couple of days to help offset the energy expended by these heifers while traveling and exploring the

pasture. If naive heifers grazed in a pasture with experienced heifers, differences in grazing patterns will decrease through time due to the social facilitation of foraging behaviors.

Overall, my research suggests that the method used to develop heifers during the winter influence their rangeland grazing patterns. More research is needed to determine whether differences in grazing behavior associated with heifer development protocols have life-long effects on the productivity of the herd.

APPENDIX

APPENDIX A

TABLES OF COMPOSITION OF DIET SELFFED TREATMENT AND DESCRIPTION OF DIFFERENT VEGETATION CLASSES USED IN CHAPTER THREE AT THE USDA-ARS FORT KEOGH LARRL IN MILES CITY, MT (LAT 46^{o} 23’ 08’’ N, LONG 105^{o} 52’ 26’’ W)

Table A 1. Composition of diet SelfFed treatment.

Items	**Value**
Supplement (ingredients)	
Monensin (monensin sodium, 2000.00 g/tn)	1.00 g/lb
Pork blood meal	
Crude Protein (min, %)	85.00
Crude Fat (min, %)	1.00
Crude Fiber (max, %)	2.00
Fish meal	
Crude Protein (min, %)	60.00
Crude Fat (min, %)	6.00
Crude Fiber (max, %)	2.00
Calcium (%)	between 6.50-7.80
Phosphorus (min, %)	2.90
Ethoxyquin added preservative	
Mineral supplement (ingredients)	
Calcium (%)	between 7.00-8.00
Phosphorous (%)	8.00
Salt (%)	35.00-40.00
Potasium (%)	6.00
Magnesium (%)	6.00
Cobalt (ppm)	10.00
Copper (ppm)	2000.00
Iodine (ppm)	53.00
Manganese (ppm)	1000.00
Selenium (ppm)	20.00
Zinc (ppm)	2000.00
Vitamin A (lU/b)	120000.00

Table A 2. Description of different Vegetation classes.

Vegetation class	**Pasture**		
	Lonepine V	**Lonepine Trap**	**Lonepine U**
Class 1: Badlands, which sparsely vegetated hills			
Shrubs	greasewood (*Sarcobatus vermiculatus*) wyoming big sagebrush *(Artemisia tridentate)* shadscale *(Atriplex confertifolia)* broom snakeweed *(Gutierrezia sarothrae)* rubber rabbitbrush *(Ericameria nauseosa*)	wyoming big sagebrush *(Artemisia tridentate)* greasewood *(Sarcobatus vermiculatus*)	fringed sagebrush *(Artemisia frigida*) wyoming big sagebrush *(Artemisia tridentate*) skunkbush sumac *(Rhus trilobata*) soapweed yucca *(Yucca glauca*)
Warm season grass	alkali sacaton *(Sporobolus airoides*) bluegrama *(Boutelova gracilis*) red threeawn *(Aristida purpurea*)	bluegrama *(Boutelova gracilis*) alkali sacaton *(Sporobolus airoides*)	prairie sandreed *(Calamovilfa longifolia)*
Cool season grass	western wheatgrass *(Pascopyrum smithii)* bluebunch wheatgrass *(Pseudoroegneria spicata*) slender wheatgrass *(Elymus trachycaulus*) sandberg's bluegrass *(Poa secunda*)	threadleaf sedge *(Carex filifolia*) prairie junegrass *(Koeleria macrantha*) western wheatgrass *(Pascopyrum smithii*) sandberg's bluegrass *(Poa secunda)* bluebunch wheatgrass *(Pseudoroegneria spicata*)	threadleaf sedge *(Carex filifolia*) needle-and-thread (*Hesperostipa comate*) prairie junegrass *(Koeleria macrantha)* western wheatgrass *(Pascopyrum smithii*) bluebunch wheatgrass *(Pseudoroegneria spicata*)
Annual grass	japanese brome *(Bromus arvensis)*	japanese brome *(Bromus arvensis*)	
Introduced forbs	tall tumblemustard *(Sisymbrium altissimum)*	yellow/white sweetclover *(Melilotus officinalis*)	yellow/white sweetclover *(Melilotus officinalis*)
Natural forbs	hood's phlox, spiny phlox *(Phlox hoodii*) scarlet globemallow *(Sphaeralcea coccinea)*	spiny phlox *(Phlox hoodii*) Woolly plantain *(Plantago patagonica*) american vetch *(Vicia americana*) royal penstemon *(Penstemon speciosus)*	bastard toadflax *(Comandra umbellate*) prairie thermopsis, golden pea *(Thermopsis rhombifolia*) american vetch *(Vicia americana*)
Class 2: Mixed grass prairies, dominated by cool			

season grasses			
Shrubs		winterfat *(Krascheninnikovia lanata*) fringed sagebrush *(Artemisia frigida*) wyoming big sagebrush *(Artemisia tridentate*)	fringed sagebrush *(Artemisia frigida*)
Warm season grass	bluegrama *(Bouteloua gracilis)* buffalograss *(Bouteloua dactyloides)*	bluegrama *(Bouteloua gracilis)* buffalograss *(Bouteloua dactyloides*)	bluegrama *(Bouteloua gracilis*) buffalograss *(Bouteloua dactyloides*)
Cool season grass	western wheatgrass *(Pascopyrum smithii)* green needlegrass *(Nassella viridula*) needle-and-thread *(Hesperostipa comate)*	needle-and-thread (*Hesperostipa comate*) western wheatgrass *(Pascopyrum smithii*) sandberg's bluegrass *(Poa secunda*)	threadleaf sedge *(Carex filifolia*) needle-and-thread *(Hesperostipa comate)* prairie junegrass *(Koeleria macrantha*) green needlegrass *(Nassella viridula*) western wheatgrass *(Pascopyrum smithii*) sandberg's bluegrass *(Poa secunda*) kentucky bluegrass *(Poa pratensis*)
Annual grass	japanese brome *(Bromus arvensis*) cheat grass *(Bromus tectorum*)	japanese brome *(Bromus arvensis*)	japanese brome *(Bromus arvensis*)
Introduced forbs	canadian horseweed *(Conyza Canadensis*) yellow salsify *(Tragopogon dubius*)	pale madwort *(Alyssum alyssoides*) Littlepod false flax *(Camelina microcarpa*) field cottonrose *(Logfia arvensis*) yellow/white sweetclover *(Melilotus officinalis*) yellow salsify *(Tragopogon dubius*)	littlepod false flax *(Camelina microcarpa*) field cottonros *(Logfia arvensis*) yellow salsify *(Tragopogon dubius*)
Natural forbs	scarlet globemallow *(Sphaeralcea coccinea*) woolly plantain *(Plantago patagonica*)	warty spurge *(Euphorbia spathulata*) pricklypear cactus *(Opuntia polyacantha*) Woolly plantain *(Plantago patagonica*) scarlet globemallow *(Sphaeralcea coccinea)* american vetch *(Vicia americana*)	pricklypear cactus *(Opuntia polyacantha*) woolly plantain *(Plantago patagonica)* scarlet globemallow *(Sphaeralcea coccinea*)

Class 3: Shrublands with mixed grass prairie understory			
Shrubs	wyoming big sagebrush (*Artemisia tridentate*) soapweed yucca (*Yucca glauca*) skunkbush sumac (*Rhus trilobata*)	wyoming big sagebrush (*Artemisia tridentate*)	silver sagebrush (*Artemisia cana*) white sagebrush (*Artemisia ludoviciana*) wyoming big sagebrush (*Artemisia tridentate*)
Warm season grass	bluegrama (*Bouteloua gracilis*) buffalograss (*Bouteloua dactyloides*)	bluegrama (*Bouteloua gracilis*) prairie sandreed (*Calamovilfa longifolia*) buffalograss (*Bouteloua dactyloides*) tumblegrass (*Schedonnardus paniculatus*)	red threeawn, purple threeawn (*Aristida purpurea*) bluegrama (*Bouteloua gracilis*)
Cool season grass	western wheatgrass (*Pascopyrum smithii*) green needlegrass (*Nassella viridula*) needle-and-thread (*Hesperostipa comata*)	threadleaf sedge (*Carex filifolia*) needle-and-thread (*Hesperostipa comate*) prairie junegrass (*Koeleria macrantha*) western wheatgrass (*Pascopyrum smithii*) sandberg’s bluegrass (*Poa secunda*) bluebunch wheatgrass (*Pseudoroegneria spicata*)	threadleaf sedge (*Carex filifolia*) needle-and-thread (*Hesperostipa comate*) western wheatgrass (*Pascopyrum smithii*) sandberg’s bluegrass (*Poa secunda*)
Annual grass	japanese brome (*Bromus arvensis*) cheat grass (*Bromus tectorum*) sixweeks fescue (*Vulpia octoflora*)	japanese brome (*Bromus arvensis*) sixweeks fescue (*Vulpia octoflora*)	japanese brome (*Bromus arvensis*) cheat grass (*Bromus tectorum*) sixweeks fescue (*Vulpia octoflora*)
Introduced forbs		pale madwort (*Alyssum alyssoides*) field cottonrose (*Logfia arvensis*) yellow salsify (*Tragopogon dubius*)	camelina microcarpa (*Littlepod false flax*) common pepperweed (*Lepidium densiflorum*) field cottonrose (*Logfia arvensis*) tall tumblemustard (*Sisymbrium altissimum*) yellow salsify (*Tragopogon dubius*)
Natural forbs	woolly plantain (*Plantago patagonica*) scarlet globemallow (*Sphaeralcea coccinea*) pricklypear cactus (*Opuntia*	woolly plantain (*Plantago patagonica*) scarlet globemallow (*Sphaeralcea coccinea*) showy milkvetch (*Asclepias*	woolly plantain (*Plantago patagonica*) scarlet globemallow (*Sphaeralcea coccinea*) western rockjasmine

	polyacantha) slimflower scurfpea *(Psoralidium tenuiflorum*)	*speciosa*)	*(Androsace occidentalis)*
Class 4: Cool season grasses/legumes and shrubs			
Shrubs	silver sagebrush *(Artemisia cana*)	silver sagebrush *(Artemisia cana*)	silver sagebrush *(Artemisia cana*) white sagebrush *(Artemisia ludoviciana*)
Warm season grass	bluegrama *(Bouteloua gracilis)*		bluegrama *(Bouteloua gracilis*) buffalograss *(Bouteloua dactyloides*)
Cool season grass	western wheatgrass *(Pascopyrum smithii*) kentucky bluegrass *(Poa pratensis*)	western wheatgrass *(Pascopyrum smithii*) kentucky bluegrass *(Poa pratensis*)	green needlegrass *(Nassella viridula*) western wheatgrass *(Pascopyrum smithii*) kentucky bluegrass *(Poa pratensis*)
Annual grass	japanese brome *(Bromus arvensis*)	japanese brome *(Bromus arvensis*)	japanese brome *(Bromus arvensis*)
Introduced forbs	yellow sweet clover *(Melilotus officinalis*) canada thistle *(Cirsium arvense*)	yellow sweet clover *(Melilotus officinalis*) common dandelion *(Taraxacum officinale*) field pennycress *(Thlaspi arvense*)	camelina microcarpa (*Littlepod false flax)* yellow/white sweetclover *(Melilotus officinalis)* common dandelion *(Taraxacum officinale*)
Natural forbs	american vetch *(Vicia americana*) common yarrow *(Achillea millefolium)*	scarlet globemallow *(Sphaeralcea coccinea)* american vetch *(Vicia americana*)	scarlet globemallow *(Sphaeralcea coccinea)* warty spurge *(Euphorbia spathulata*)