Rangeland Habitat Use and Activity of Cattle with Divergent Molecular Breeding Values for Residual Feed Intake

by

Carly Ann Moore

A thesis submitted in partial fulfillment of the requirements for the degree of

Master of Science

in
Rangeland and Wildlife Resources

Department of Agricultural, Food and Nutritional Science
University of Alberta

Abstract

Selection for the trait residual feed intake (RFI) is an emerging tool for cattle producers to manage feed costs within the beef industry. This study explored whether cattle habitat use and activity on extensive pasture-based systems in the dry mixedgrass of Alberta differed between cattle with divergent molecular breeding values (MBV's) for RFI. Neither predicted RFI group (low vs. high) nor individual animal MBV score were found to explain cattle movement rates, resting time, or habitat use. Instead, timing of grazing (early, middle and late growing season grazing), pasture type (native mixedgrass, tame, or wetland plant community types), forage metrics (quantity and quality) and distance to water were the factors regulating cattle activity, habitat use, and performance. Cows had significantly higher activity levels (greater movement rates and lying bout frequency, less time spent lying down) early in the grazing season. Lying time decreased with increasing pasture size across all pasture types and native grasslands alone, and decreased with increasing biomass and exposure to better quality (less fibrous) grasses and forbs. Cow performance metrics during the growing season (weight and back fat gain, as well as calf weaning percentage) were not affected by MBV for RFI, activity measures or most habitat metrics studied. However, those cows spending less time within 200 m of water were found to wean larger calves and gain more back fat over the grazing season. I conclude that improving pasture-based cow/calf production through selection for low RFI requires more research into genetic markers that better predict RFI under these complex, native pasture environments. Our research showed that changing environmental conditions affected animal activity and habitat selection, and this consequently affected their performance. These results support that the identification of MBV markers unique to extensive production systems may be necessary to improve cow/calf production through selection using RFI.

Til min farfar, som gav mig en livslang lidenskab for landbrug og en forståelse for "moo-haws".

Acknowledgements

I'd like to first recognize Gemstone Cattle Company, the Doerksen family, and Nolan Bear. Your contribution to my project was vital and I so enjoyed working with you throughout the project. Thanks to my committee member Scott Nielsen and co-supervisor Graham Plastow for all your expertise, help with preparing for conference presentations and for the great discussions during our meetings. Finally to my co-supervisory Edward Bork, for being there through this whole process in spite of life's challenges. Your knowledge and passion are inspiring and I am so grateful for your time setting up the project, field work, and the support to keep me moving forward with writing and analysis. You and Kim are certainly a big part of the range family.

To the rest my range family- I feel so lucky to have you all in my life! Barry and Judy Irving, thank you for steering me down this life path and inspiring my passion for range throughout my academic life, not to mention the personal hours you put into my project. Don and Sandra Armitage, thank you for opening your home and sharing your time with me at the ranch. I so enjoyed the cattle moves, county tours and sight-seeing, and the dinners, stories and laughs. It's time to "get rich and go farming". A big thank you goes to Nicky, the most reliable partner I could have asked for on this project. I'm proud of the work that we did as a team and had a great time catching calves, bottle feeding orphans and working with the project cattle and heifers with you. Finally, the time I got to spend with fellow grad students and field assistants- as temporary roommates at Mattheis or during conferences, sharing lab and office space, going for ice cream, beers or meals, and nerding out about rangelands- made grad studies worthwhile. Thanks to Lisa Raatz, Lysandra, Kassia, Faezeh, Caroline, Sean, Angela, Ashton, Monica, Kara, Megan, and Grace for being such a big part of my journey.

To my biological family, Mom and Dad and Kyle, thanks for always being supportive of my aspirations, even when they took longer than expected. You were always excited to hear the latest news about my work, even if it involved me complaining. I love you guys. Last but never least, I have an unquantifiable amount of gratitude for my life-long partner in crime, Brett Moore. I certainly would not be writing this acknowledgement if it weren't for his assistance in the field, the innumerable hours of R-coding help, the 3.5 years of cheerleading, and for keeping me fed and partially sane while I juggled full time work and writing. You are the best.

Funding for this project came from Alberta Agriculture and Forestry, Emissions Reduction Alberta, Delta Genomics, and the University of Alberta Rangeland Research Institute.

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List of Symbols and Abbreviations

- number
% - percent
°C – degrees Celsius
ADF – acid detergent fiber
ANOVA – analysis of variance
cm - centimeters
CP – crude protein
FCR - Feed Conversion Ratio
g - grams
GIS - Geographic Information System
GPS – Global Positioning System
ha - hectare
hr - hour
kg- kilograms
km - kilometers
MBV- molecular breeding value
m - meters
mm- millimeters
n – sample size
N - Nitrogen
NFI – Net Feed Efficiency
P:E – precipitation to evaporation ratio
pRFI – predicted Residual Feed Intake
R^2 – regression goodness-of-fit measure
RFI – Residual Feed Intake
SE – standard error
SD - standard deviation

Chapter 1. A Literature Review Examining Cattle Grazing Behaviour and Production Efficiency

1.1 Residual Feed Intake

Feed expenses for maintenance alone can comprise up to 75% of the variable costs that beef producers incur in a typical production year (Okine et al. 2004). While feed prices are not always under the direct control of the producer, finding animals that efficiently use feed is an important management strategy. Measures of feed efficiency in the past have used metrics such as average daily gain or feed to gain conversion ratio (FCR), where the latter is defined as the ratio of feed intake to weight gain over a specific time period (Archer et al. 1999). However, selection of animals with greater FCR has led to the selection of larger framed animals with increased maintenance requirements, thereby not achieving the goal of improving beef production efficiency (Archer et al. 1999).

Additionally, efficiency of individual animal feed utilization has been difficult to measure until the recent introduction of automated intake measurement systems such as GrowSafe (Okine et al. 2004). GrowSafe systems (GrowSafe Systems Ltd., Airdrie, AB, CAN) enable the continuous assessment of individual animal feed intake through electronic identification of each visit of animals to a feed bunk with a built-in scale to record feed intake. The ability to track individual feed intake has shifted the focus of livestock researchers from examining group pen feed intakes to assessing each animal's metabolizable energy intake and requirements, and led to the concept of residual feed intake (RFI) or net feed efficiency (NFE). RFI is an improved measure of feed efficiency in cattle because it is independent of animal size and growth, and can be used as a tool for selecting animals with lower maintenance requirements; this reduction could therefore reduce the input cost of feed in beef operations (Basarab et al. 2003). Animals with lower RFI are more efficient because they gain proportionally more body mass per unit of feed consumed, and are likely to waste less feed via body maintenance. It is possible for animals to have a low RFI value because they are not growing well or taking in little feed, but accounting for growth and intake together can prevent this problem (Berry and Crowley 2012).

Residual feed intake is also a heritable trait (Basarab et al. 2007; Schenkel et al. 2004) that producers can use as a tool for selecting cattle that are complementary to their management goals. Additionally, studies have shown that bull reproductive success remains independent of RFI (Wang et al. 2012), and Paradis et al. (2015) found that heifers with phenotypic low RFI (more efficient animals) seemed to have stronger innate immunity (i.e. were less likely to become ill). According to Black et al. (2013), RFI phenotypes had no relationship to temperament, thereby allowing for selection of the latter without negative implications for feed consumption and weight gains. Selecting for lower RFI also had no effect on other heritable production metrics like growth rate and final size of cattle (Nkrumah et al. 2004). As production traits are vital to the success of a beef producer, independence of RFI selection is an important characteristic because improvements in RFI should not occur at the expense of other desirable production metrics.

A number of physiological mechanisms exist for why animals with lower RFI may be more efficient, including having lower maintenance costs due to lower organ weight and reduced fat deposition (Basarab et al. 2003), or different rates of protein turnover or tissue metabolism due to stress (Richardson and Herd 2004). Efficient animals were found by Basarab et al. (2003) to have lower intakes and lower heat production, which they attributed to more optimal conversion of metabolizable energy into retained energy at low intake; as intake increases, the diet may become less efficiently metabolized and therefore more energy is lost to heat production. Alternatively, less feed may be digested and subsequently lost via fecal waste. Other important factors in determining efficiency include animal activity and diet.

Previous research has focused on testing of RFI and feed efficiency in a feedlot environment where activity and feed type, quality and intake can be tightly controlled. Applicability of RFI has been studied in pasture settings within monoculture vegetation [where dietary composition is relatively stable and the environment is uniform (Bailey 1995)], although difficulties still arise in determining accurate forage intake without intensive vegetative sampling methods (Meyer et al. 2008). As a result, observed animal performance on pasture may not be linked to RFI phenotype due to the absence of accurate intake data, complicating the interpretation of RFI utility within this production system. In addition to these limitations, typical pasturelands are very different from monocultures, as they consist of a complex mixture of different plant species at varying development stages and associated chemical composition.

Improvements in RFI may not only allow cattle producers to benefit financially from the opportunity to choose animals that efficiently use feed to achieve growth in both feedlot and pasture, but there may also be other positive environmental implications from these animals. The latter include lower methane emissions per unit of marketable beef (Hegarty et al. 2007; Nkrumah et al. 2006). These benefits would improve social license for the beef industry and give producers better assurance that consumers will continue to maintain demand for sustainable beef products in the future.

1.2 Cattle Foraging Behaviour

Rangelands contain varied topography and microclimates, which create highly diverse plant communities with marked variation in forage quality and productivity throughout the growing season. Spatial and temporal differences in forage supply are based on many factors, including soils, climate, localized vegetation composition, and historic and current rangeland management (i.e. grazing history). Heterogeneous landscapes facilitate highly selective foraging across multiple spatial scales, including at the level of feeding stations (highly localized patches), plant communities (spatial areas of uniform vegetation composition, density and height), and landscape locations (Bailey et al. 1996; Coughenour 1991; Senft et al. 1987).

Selection of grazing habitat has been examined in relation to cattle breed (Bailey et al. 2001; VanWagoner et al. 2006). Bailey et al. (2001) showed that breeds accustomed to steeper slopes (such as Tarantaise) utilize hilly landscapes more evenly than Herefords, a breed that historically was raised on more flat terrain. VanWagoner et al. (2006) found similar results with Piedmontese-sired animals using steeper slopes and vertical and horizontal distances further from water than Angus cattle. In a later study, Bailey et al. (2015) showed that grazing behaviour was a heritable trait. They found that two genetic markers on different bovine chromosomes explained 24% and 23% of the phenotypic variation in use of steep slopes and higher elevations, respectively, in topographically variable rangelands. The first marker was linked to a gene known to be associated with spatial memory, locomotion and motivation. Other markers examined accounted for 10% to 20% of the variation in terrain use indices among individual cattle (Bailey et al. 2015).

Another vital consideration in addition to genetic potential is that animals learn grazing behaviours from their dams, herd-mates, and through post-ingestive feedback from their senses. Exposure to and subsequent preference for flavours begin as early as *in-utero* (Simitzis et al. 2008), and continues to occur through suckling (Nolte and Provenza 1992a) and the first introduction to solid forages (Nolte and Provenza 1992b). The persistence of preference for flavours introduced early in life is also stronger when young are exposed to flavours with their mother, as it increases the young animal's attention and subsequent memory of flavour (Nolte and Provenza 1992b). At the landscape level, cattle will graze the same areas that they were raised in as calves, regardless of whether the animal was fostered by its own mother or a different dam as a calf, and have been found to be influenced by their early life herd mates (Howery et al. 1998). Feeding behaviours and movement patterns learned at a young age will be replicated throughout the animal's life (Launchbaugh and Howery 2005), and may be even more persistent than behaviours learned later in life (Provenza and Balph 1988). Learned behaviours also tend to be more important when applied to a similar habitat from which they originated, particularly when compared to animals that are naïve (Bailey et al. 2010; Wiedmeier et al. 2002). These behaviours and post-ingestive feedback (Provenza 1995) create part of the social and biophysical environments that interact with the animal's genome during development and shape the animal's food preferences to suit their local landscape and forage conditions (Galyean and Gunter 2016).

Past experiences allow an animal to reduce energy use and find the optimal environmental combination of forage and thermal conditions important for maintaining body condition and minimizing weight loss in winter (Beaver and Olson 1997). Herd dynamics are also an important contributor to foraging behaviour. The formation of subgroups with three to six animals of similar age is a common occurrence, with dominant animals in these subgroups vying for herd dominance (Harris et al. 2007). Harris et al. (2007) also found that older animals were generally dominant and found to be spatially closer to other dominant animals than to non-dominant cohorts. Social dominance plays a key part in habitat selection for individual animals (Bailey 1995; Sato 1982) and their subsequent performance (Bailey et al. 1996).

1.3 Mixedgrass Prairie Characteristics and Responses to Anthropogenic Impacts

The Dry Mixedgrass Natural Subregion of Alberta is found in the warm and dry south east portion of the province, and is generally flat to gently undulating in loamy areas, or moderately rolling in sandy areas. Soils range from Brown Chernozems on loamy uplands, to Humic Regosols in rolling sandy areas. Wetland areas contain Humic Gleysols. Mean annual precipitation for the study area examined here is 354 mm, with the majority of precipitation falling as summer rain, peaking in July. By August, vegetation senescence progresses rapidly on uplands due to a P:E ratio of about 0.4. Vegetation is comprised mostly of native grassland with an abundance of both cool-season (C3) and warm-season (C4) plants. Common native grasses include *Hesperostipa comata*, *Pascopyrum smithii*, *Bouteloua gracilis*, *Calamovilfa longifolia*, and *Koeleria macrantha* (Coupland 1961). *Rosa* and *Artemisia* species dominate the shrub component and there is a large diversity of native and introduced forbs.

This prairie region has had a storied past with human use. It is the primary area historically used for grazing (Coupland 1961) for settlers, and continues to be a significant contributor to beef production in the Canadian prairies (Willms and Jefferson 1993). Research by Smoliak et al. (1972), Willms (2002), Broadbent et al. (2016), and Bork et al. (2017) have shown over the years that grazing and/or defoliation intensity and frequency have significant impacts on mixedgrass biomass and community composition. Above grazing, more recent alterations have occurred to native vegetation composition and moisture regimes from anthropogenic impacts. Irrigation channels, pivots, and wetland creation by Ducks Unlimited have altered some areas to become more sub-irrigated, with vegetation shifts occurring in response. These projects increase the diversity and abundance of plants, including various wetland sedges (*Carex* and *Eleocharis* spp.) and rushes (*Juncus* spp.), but not all are native grasses and forbs (e.g., *Poa pratensis*, *Sonchus arvensis*, *Cirsium arvense*, *Crepis tectorum*, *Arctium minus*). The change in moisture regime also alters the dominance of some plant species, such as *Shepherdia argentea*, which is a native shrub that has been found to be aggressively encroaching into wetter pastures and thus having implications for cattle production, by reducing both the amount and accessibility of herbage (Dahl 2014).

1.4 Technology Applications in Animal Behaviour- GPS/GIS and Pedometers

1.4.1 Global Positioning System (GPS) collars

To improve rangeland conservation of soil and vegetation, a manager must quantify their herd's utilization and behaviours across the landscape. Visual observations can be effective but are time and labour intensive (Turner et al. 2000; Bailey et al. 1990; Harvey and Launchbaugh 1982). With the advent of GIS and remote sensing came the creation of GPS collars, which can be fitted to cattle for an extended period. These devices communicate with satellites to determine and record the animal's location (latitude and longitude in a 2-dimensional fix), as well as elevation (in the case of 3-dimensional fix). Collars activate at regular programmed intervals at which time they 'wake up', search for and connect with satellites, establish the location, and then shut down to preserve battery life. Fix intervals for data collection are user determined and location data, ambient temperature and motion sensor data are all stored on the collar. While some collars can be downloaded remotely, others are retrieved at removal, with data collection periods spanning up to half a year or more, depending on the fix interval. Spatial GPS data are particularly useful when used in conjunction with resource maps on geographic information systems to decipher habitat use or selection in space and time. Past studies with cattle have used GPS collars to determine the distribution of cattle with changing salt and water distribution (Ganskopp 2001), terrain (Bailey et al. 2004; Kaufmann et al. 2013a; Kaufmann et al. 2017), or forage quality and quantity (Ganskopp and Bohnert 2009; Kaufmann et al. 2013b; Kaufmann et al. 2017). GPS collars have also been used to identify the distribution of cattle in areas they are naïve to versus those they are accustomed to (Bailey et al. 2010), explore multi-species interactions when grazing with sheep (Putfarken et al. 2008) and understand livestock responses to virtual fencing (Umstatter et al. 2015).

Accuracy of a GPS fix location may be reduced due to atmospheric conditions, topography, vegetation cover, satellite or collar clock error, as well as satellite geometry, orbit error or multipath effects (Ganskopp and Johnson 2007). Using stationary test sites to create a probability model of location and fix rate in varying terrain and habitats is one way to account for errors (Hebblewhite et al. 2007). Positional dilution of precision information provided by GPS collars can be used to reduce locational errors (Lewis et al. 2007; D'Eon and Delparte 2005). Fixes collected at shorter time intervals have been found to have higher fix success rate (Cain et al. 2005) and to therefore be more accurate in quantifying the proportions of area that cattle use (Johnson and Ganskopp 2008). However, short fix intervals tend to catch animals being stationary in one spot, and if accompanied by random spatial errors, their locations are more likely to be inaccurately recorded, thereby creating the impression that the animal is travelling up to 15% greater distances (Ganskopp and Johnson 2007). Furthermore, assuming a straight distance travelled between fixes is a short-sighted method of determining activity alone, as grazing, moving, and lying activities can all occur within a finer time-scale than programmed collar fix intervals, and animals are unlikely to travel in a straight line between successive fixes (Schlecht et al. 2004; Swain et al. 2008). An option to alleviate these problems is to first perform a period of high fix rate to create models for predicting animal location, then in subsequent studies lower fix rates may be used with more confidence (Swain et al. 2008). Ganskopp and

Johnson (2007) reviewed methods to assist in reducing GPS error, including physically observing animals and using regression techniques, setting minimum distance thresholds, or using additional activity sensor data from collars or other technology; regression techniques were highlighted as the best methods. Our research will be using Lotek collars, which Hebblewhite et al. (2007) found to perform well, even in forested and mountainous areas. Ungar et al. (2005) found that Lotek collars also provided accurate enough records of animal activity through the sensor data.

1.4.2 Pedometers

In the case of livestock production, animal activity and its effects on energy requirements and associated production, these metrics have been studied since the 1960's (Anderson and Kothmann 1977). The fact that animals expend more energy outside (i.e., in unconfined areas) than they do inside buildings or within confined areas has been reported previously (Di Marco and Aello 2001; Osuji 1974). Horizontal travel during grazing can increase energy requirements above basal metabolism by 6-15% (Anderson and Kothmann 1980) and vertical travel (i.e. in mountainous terrain) is ten times more costly than horizontal movement (Clapperton 1964). Finally, changes in weather (e.g., heat, cold, rain and wind) and an animal's experience in an area can further influence the time that animals spend out of their thermo-neutral zone, causing wasted energy expenditure towards reducing temperature stress; Beaver and Olson (1997) found that younger cattle naïve to winter pasture were found in unprotected areas more often, and also lost more back fat and weight than experienced animals.

Pedometers are a tool that can aid in determining an animal's activity levels and are extensively used in the dairy industry to predict estrus (Roelofs et al. 2005; Rorie et al. 2002). Pedometers can also aid in the identification of disease, metabolic or digestive disorders

(Szyszka et al. 2012; Edwards and Tozer 2004), as well as lameness (Mazrier et al. 2006; O'Callaghan et al. 2003). One of the first pedometer studies done with cattle in wooded rangeland was by Anderson and Kothmann (1977). Pedometers in that study were deemed to be accurate but required manual step count resetting and pace length setting, and necessitated that animals be brought in on a weekly basis for data download and checking. Walker et al. (1985) found pedometers accurately recorded the distance an animal travels in pasture and that most variation in distance travelled was due to differences in pedometer operation and attachment.

With advances in technology, pedometers can now wirelessly send activity logs with both quantitative and qualitative attributes to reader computer stations, and software that accounts and notifies producers regarding differences among animals. By monitoring animals at all times, these systems perform further quality checks to enhance a producer's understanding of how their herd is performing and any improvements they need to make.

1.5 Knowledge Gap, Thesis Goals and Objectives

While previous studies have been conducted examining cattle RFI under feedlot conditions, no studies to date have examined the relationship between molecular breeding values for RFI, cattle habitat selection, and behaviour under open-range grazing. The goal of this research is to examine the pasture-based performance of cattle with variation in predicted RFI (based on molecular markers) while grazing on a heterogeneous rangeland during the grazing season, and interpret these responses using cattle behaviour metrics. More specifically, I will study how cattle behaviour (habitat use, activity budgets) affects cattle performance metrics (e.g. cow and calf weight gain, fall body condition score), and determine whether this relationship correlates with predicted RFI based on molecular breeding markers (MBVs). Assessment of behaviour includes investigations into animal activity collected from pedometers (e.g. resting and rates of movement) in Chapter 2. Chapter 3 explores habitat use via GPS collars and it is compared with changing forage metrics through the grazing season, including the role of pasture type and timing of grazing. The final chapter (Chapter 4) reviews the results of this research, provides implications for science and industry, and identifies further research needs and opportunities.

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Chapter 2. Activity Budgets of Rangeland Cattle with Divergent Molecular Breeding Values for Residual Feed Intake

2.1 Introduction

Livestock producers operate with the goal of maximizing animal gains and reducing feed costs. Animals take energy from feed and partition it towards either maintenance of their biological processes or production (i.e. lactation, gain in muscle mass, etc.). Feed is expensive and the amount cattle can consume is constrained by their digestive morpho-physiology, so livestock producers have looked to ways of reducing their animal's maintenance energy costs to achieve their production goals. Genomic selection using molecular breeding values (MBVs) for feed efficiency, specifically the moderately heritable (Berry and Crowley 2013) residual feed intake (RFI) trait, is an important measure in selecting for animals with lower maintenance requirements. RFI is the difference between the metabolizable energy of intake and the metabolizable energy required for maintenance and gain, and is independent of growth and maturity patterns (Okine et al. 2004).

Cattle utilize energy in the process of moving to and from feeding areas, searching for suitable feed, and in feeding itself. These energetic costs can be greater if movement is not directly associated with acquiring water or good quality food sources. In contrast, if the animal spends more time ingesting, ruminating and digesting forage, it has the potential for more of that energy to be partitioned to growth and reproduction. Feeding behaviours and activity are therefore key components that contribute to the variation of RFI in cattle, even in feedlots (Richardson and Herd 2004) where feed and water are of homogenous quality and of high availability.

While grazing on pasture, cattle exhibit complex behaviours arising from their need to balance ongoing access to resources (feed, water, thermal and protective cover), together with the maintenance of social activity. These behaviours can vary across multiple spatial and temporal scales (Bailey et al. 1996; Coughenour 1991; Senft et al. 1987). While grazing on open range, cattle theoretically partition more feed energy away from production relative to what they would expend in a feedlot. Some of the reasons for this include longer distances travelled between water sources and preferred feeding areas, the variable feed quality present in space, and the declining feed quality (and possibly quantity) evident throughout the growing season on rangelands (Bailey et al. 1996; Coughenour 1991). Complex changes in vegetation and associated feed availability and quality, in turn, change an array of feeding behaviors. For example, declines in forage abundance can lead to longer feeding times as animals spend extended periods searching for suitable feed (Osuji 1974), while decreases in feed quality can result in slower digestion and therefore longer rumination periods, in turn reducing the time spent feeding (Ruckebusch and Bueno 1978; Lofgreen et al. 1957). Di Marco and Aello (2001) found that baseline maintenance costs of cattle in pasture systems could be 8-30% greater compared to those in a feedlot, mostly from open range grazing coinciding with high bite rates. Additionally, the energetic cost of consuming fresh forage has been estimated to be twice as great as eating that same vegetation dry because of the increased time spent to achieve equivalent dry matter intake (Osuji 1973).

Pedometers are a tool that can aid in determining an animal's activity levels. Pedometers have mainly been used in confined areas or small pastures to predict estrus (Roelofs et al. 2005; Rorie et al. 2002), and aid in the detection of disease, metabolic or digestive disorders (Szyszka et al. 2012; Edwards and Tozer 2004), as well as lameness (Mazrier et al. 2006; O'Callaghan et al. 2003). One of the first pedometer studies done with cattle in rangeland was by Anderson and Kothmann (1977), where pedometers were deemed accurate but required manual step count resetting and pace length validation, and weekly removal from the animal for data download. Walker et al. (1985) found pedometers accurately assessed the distance animals travelled in pasture, with variation in precision mostly due to differences in individual pedometer operation (i.e., sensitivity to movement) and how tightly the pedometer was attached. This study built on past research by using pedometers to assess differences in activity budgets of free range cattle with divergent molecular breeding values for predicted residual feed intake. The specific objectives of this study were to determine 1) if animals with divergent MBV for RFI have different activity budgets, as demonstrated by resting time and movement rates, while grazing on pasture, and 2) if these activity budgets vary with pasture size, pasture type, or temporal changes in growing conditions, including associated forage quantity and quality. We hypothesize that animals within the low RFI MBV category will spend more time resting, and have lower movement rates, than animals within the high RFI MBV category. Additionally, we hypothesize that cattle will spend more time lying and have lower movement rates when grazing in small pastures, and when forage is relatively more abundant and of greater quality (due to quicker gut fill under favorable foraging conditions). Collectively, these behaviours are thought to be consistent with having lower maintenance costs.

2.2 Materials and Methods

2.2.1 Study Area

The Mattheis Ranch is within the Dry Mixedgrass Natural Subregion of Alberta and is comprised mostly of native grassland with an abundance of both cool-season (C_3) and warm-season (C_4) plants. Common grasses at the ranch within these areas included *Hesperostipa* *comata*, *Pascopyrum smithii*, *Bouteloua gracilis, Calamovilfa longifolia,* and *Koeleria macrantha*. *Rosa* and *Artemisia* species dominate the shrubby component of these communities, and there is a large diversity of other native and introduced plant species, with numerous chenopods found in disturbed areas. Although the cattle grazed 21 different pastures over the grazing season, only fourteen different pastures were considered in our study, because the other pastures were smaller than 13 hectares and so cows spent no more than two days in these pastures at very high stocking densities (over 50 head ha^{-1}) compared to other study pastures. Nine pastures were predominantly upland (mostly native) grassland; two pastures contained improved pastures with seeded forage (forage oats and perennial ryegrass) on irrigated pivots (called tame pastures going forward); and three pastures were comprised of open wetlands, surrounding riparian areas and abundant sub-irrigated vegetation. These latter three pastures benefited from the addition of water moved through a series of irrigation canals to wetlands created to promote waterfowl habitat. The latter areas contained a high diversity of plants, including *Poa pratensis*, various wetland sedges (*Carex* and *Eleocharis* spp.) and rushes (*Juncus* spp.), as well as abundant ruderal grasses and forbs (e.g., *Sonchus arvensis, Cirsium arvense, Crepis tectorum, Arctium minus*) adapted to mesic to hydric conditions. *Shepherdia argentea*, a native shrub, is also encroaching into these wetland pastures.

The landscape of the study area is generally flat to gently undulating in loamy areas, or moderately rolling in sandy areas, with elevations ranging from 703 to 727 m above sea level. Soils range from Brown Chernozems on loamy uplands, to Humic Regosols in rolling sandy areas. While undocumented, wetland areas likely contain Humic Gleysols. Average growing season temperatures range from 11.4°C in May to 19.2°C in July, falling to -2°C at the end of the growing season in October. Mean annual precipitation for the study area is 354 mm, with the majority of precipitation falling as summer rain, peaking in July. By August, vegetation senescence progresses rapidly on uplands due to a P:E ratio of about 0.4. The total growing season precipitation reported in 2015 was 259 mm, slightly above the 30-year average for this period (248 mm), and the average monthly temperatures from April to October in 2015 were similar to long-term norms for the period that ranged from 4 - 20 °C.

2.2.2 Cattle Herd and Collection of Production Metrics

This study used 27 animals selected from a commercial herd of 450 head of predominantly Hereford/Angus cross cattle grazing on 2750 hectares of pasture at the Mattheis Research Ranch in southeast Alberta. The whole herd was assigned MBVs for RFI using genomic best linear unbiased prediction (GBLUP) calculated from genotypes (BovineSNP50 Beadchip; Illumina Inc., San Diego, CA) generated from ear tissue samples collected using Typifix (Gene Check, Inc., Greely, CO) ear tags from cattle in 2014 (Lansink 2017). From all animals assessed, 12 of the highest and 15 of the lowest predicted RFI scoring animals were selected for behavioral monitoring. The resulting range of MBVs for the high RFI group was from 0.007 to 0.364 with a mean of 0.088 (SD ± 0.11). The low RFI group ranged from -0.149 to -0.081 with a mean of -0.102 (SD ± 0.11). The predicted accuracy of MBVs was 0.33-0.50. Cows used in this study were owned by the Gemstone Cattle Company, a local producer whose cattle are custom grazed on University of Alberta land. Calving of this herd starts in mid-April and ends in late May. Calves are then processed (vaccinated, etc.) in early June prior to being moved out to pasture with their dams for the rest of the grazing season. From early June through late October the herd was managed as a single large group and rotated through a series of 15 pastures ranging from 32-381 ha in size using a primarily once-over rotational grazing system; cows spent 5-12 days in each pasture (Appendix 1). All handling of animals during the project conformed to animal care guidelines and approvals from the University of Alberta Animal Care and Use committee (AUP #00001284).

Production metrics collected for analysis included cow gain, cow back fat gain, and calf weight gain. Early grazing season cow weight and back fat ultrasound were collected in a chute scale during calf vaccination and castration on June 11, 2015. All cows were assessed for any health concerns and these were addressed as needed. Comments were recorded on these animals. Throughout the summer, all study animals were monitored on at least a weekly basis for any health issues like foot rot or general sickness. These animals were treated as needed and their herd tag was recorded. A fall cow weight and back fat thickness measure via ultrasound were taken in a chute scale on October 28, 2015.

Data collection for calf weight gain was initiated April 25, 2015 and continued through the rest of the calving season for the project cows until June 8, 2015. We went out every day with the cattle's owner or hired hand and checked the calving field for new calves. The dam of the calf was identified by herd tag number and the calf was weighed with a hanging fish scale and duffel bag, sexed, and given a herd ID ear tag. If the cow was uncooperative when trying to obtain an actual calf weight, the weight was estimated by the cattle's owner or hired hand. Both cows and calves were assessed visually for general health and treated for any ailments if needed, with comments recorded. All information was recorded in a book while in the field and transferred to a computer file at the end of the day. Fall calf weight was collected in a squeeze chute. Steers and heifers were weighed in groups on separate days, with the heifers weighed first.

2.2.3 Forage Quality and Quantity

Forage conditions were assessed within each of the study pastures throughout the summer at the time cattle were present. A soils and vegetation geodatabase of the ranch created by

Becker (2013) was used in ArcMap to select 30 random points within each pasture that were stratified by the proportional area of all soil types (n = 480 quadrats in total for the entire grazing season). Soil types were used as they effectively distinguished between upland and lowland sites within each pasture, and therefore accounted for the majority of variation in spatial distribution of primary plant communities (Becker 2013). In the field, each point was located using a handheld GPS, and a 50 cm by 50 cm quadrat of vegetation assessed for canopy composition to the nearest 5%, and then clipped to 2 cm height. Harvested vegetation was separated into grasses and grass-likes (hereafter called 'grasses'), and forbs. Where encountered, current annual growth of palatable shrubs (estimated at < 1%) was included in the forb component. Biomass was dried in an oven at 45°C for a maximum period of 48 hr, then weighed.

To assess forage quality, samples from each quadrat were first ground using a Wiley Mill to 1 mm size, then assessed for acid detergent fiber and crude protein concentration. To evaluate fiber content, the ANKOM 200 (ANKOM Technology, Macedon, NY, USA) filter bag technique was used for grasses and forbs, which is a proxy for digestibility for cattle. After the scale was tared with an empty ANKOM mesh bag on it, a 0.45-0.5 g sample of ground vegetation was weighed into the mesh bag (one sample per quadrat and growth form). All bags were sealed with a heat sealer, and then agitated in an ANKOM analysis machine with an 8% sulphuric acidic detergent for 1 hr at 100°C. Mesh bags were rinsed 3 times, for 5 minutes each, with hot water in the ANKOM fiber analyzer machine, next washed in acetone for 5 minutes to remove all water, then air dried on racks for at least 24 hr. Dried bags were reweighed and weights recorded to derive final fiber concentrations (in %). A blank mesh bag was also weighed and washed as a control and for the formulation of a correction factor. The initial and final weights of each mesh bag, along with a correction factor, were used in the following formula to determine non-digestible fiber content:

$$\%ADF\ (as\ received\ basis)\ = \frac{(W3 - (W1 \times C1))}{W2} \times\ 100$$

Where: W1 = Bag tare weight (empty bag weight)

W2 = Sample weight

W3 = Dried weight of bag with fiber after extraction process

C1 = Blank bag correction (running average of final dried weight divided by the original blank bag weight)

Crude protein concentrations were determined using a standard protocol for a LECO TruSpec CN elemental analyzer (LECO Corporation, St. Joseph, MI, USA). Drift calibrations were measured using commercial standards for every 10^{th} sample that spanned the range of expected nitrogen (N) levels within our forage samples to ensure the LECO readings were precise and accurate. Following any adjustments for the standards, all N concentrations were converted to crude protein concentrations by multiplying by a conversion factor of 6.25.

To prepare the resulting data for analysis, each quadrat's fiber, protein and biomass metrics were matched back to the soil type they occurred on. Herbage biomass was created by summing forb and grass biomass. Herbage protein was created by summing grass and forb protein values, weighted by their relative contribution based on biomass composition from the quadrat; herbage fiber was calculated similarly. Protein and acid detergent fiber yields were calculated for forb, grass and herbage. These metrics at the quadrat level were then averaged together by soil type within each pasture for further analysis. Finally, data were compiled by soil type into topographical definitions (Table 2.1).

2.2.4 Cattle Activity Monitoring

Just prior to the start of the summer grazing period on June 11, 2015, cows that had been identified as animals with the most extreme high and low MBV within each of the groups were restrained in a squeeze chute and an AfiAct II pedometer (Afimilk®, S.A.E. Afikim, Kibbutz Afikim, Israel) attached to the rear left leg using a strap. Pedometers were placed on the lower leg and were tight enough to fit a finger snugly between the leg and the pedometer. All animal handling was approved by the University of Alberta Animal Care and Use Committee (AUP #00001284).

Pedometers required Wi-Fi in order to regularly connect to a computer for downloading of data on animal activity, and necessitated a mobile network be established to achieve this (Figure 2.1). Pedometers appeared to store information for a maximum duration of 19 hours, as determined by our dataset over the summer. As cows were in pastures that were quite large, two pedometer 'reader stations' (Michigan Dairy Tech, Olivet, MI, USA) were placed in each pasture to increase the probability of data download. These reader stations were moved with the cattle through the pastures to continuously track cow activity. Stations were protected from cattle using three panels. The main reader station contained the computer and Afimilk software that all the data were downloaded onto, recorded and analyzed with, together with a router to create a mobile network between the main reader and secondary reader station, a mobile network booster, and a satellite antenna that amplified the mobile network between the stations. It also contained a receiver box that communicated with the pedometers and wirelessly sent the data to the computer, and two RV batteries with an inverter to power the station. Batteries were charged by solar panels and by manual recharging and replacement. The secondary reader station consisted of the same type of receiver box for communicating with the pedometers, a satellite antenna that sent the pedometer data to the main reader station via the mobile network created by the home station, and batteries to run the pedometer reader. At both stations, the satellite antenna was raised into the air using a tripod base to increase signal transmission. These tripod bases were secured to the ground with spikes in each of the tripod feet and ropes tied out to heavy spikes pounded into the ground (like pitching a tent).

Locations of readers were determined by looking at a map of each of the pastures and strategically placing readers near water sources, within narrow areas in the pasture that cattle were likely to pass through, or simply at positions with an attempt to cover the most pasture area. Care had to be taken to ensure that stations were close enough to communicate with each other (i.e. maintain a mobile network with a good signal for data transmission from the secondary reader to the main reader). The flat and open nature of our study area allowed data transmission to generally be successful over large distances. Even in very shrubby and hilly pastures, our reader stations were placed a maximum of 2.5 km away from each other, with a good network signal achieved.

Data collected from the pedometers on each animal included the number of steps taken since the last contact with the reader, the time (minutes) spent lying down, time (minutes) spent standing, and the number of times each cow laid down (referred to here as 'lying bouts'). Data from the secondary reader were merged seamlessly into the data collected from the main reader station with the Afimilk software, so individual cows had a relatively continuous report of their activity over the summer. Fit of the pedometers was checked visually throughout the summer. If the pedometer had slipped or appeared to be causing discomfort to the cow, the animal was captured and the pedometer adjusted. Data were recorded until October 26, 2015, at which time pedometers were removed while the cow was in a squeeze chute.

2.2.5 Data Processing

Raw data from pedometers were screened for quality and necessary cleaning prior to analysis. Pedometer activity that occurred during the first 2 days (June 10, 11) was excluded from analysis to account for the time between initialization and attachment, as well as any time animals spent standing in the processing pens before being released. The same was done for the last 3 days of the monitoring period (October 26, 27, 28) to account for the 2 days that cows had calves weaned and the time during which pedometers were removed. Times were also excluded for dates and times that pedometer adjustment occurred on any one animal and when the herd was moved to a new pasture, including an hour afterward to provide sufficient time for animals to settle back into their pre-human disturbance routine. In addition, based on visual assessment, it appeared that data were overwritten on the pedometers after 19 hr of no contact with a pedometer station. As all data (steps taken, lying times, etc.) were manually calculated by subtracting each time stamp from its previous time stamp, differences were excluded from analysis if the time between two consecutive time stamps was greater than 19 hours to ensure that activity was not under- or overestimated. Finally, pedometers had occasional miscounts of activity which resulted in some anomalies (i.e. lying durations of over 60 minutes in an hour); these were manually confirmed and excluded from the dataset. These two exclusions resulted in the loss of 3% of the maximum sampling time interval across all cows, and ranged from 2 to 4% among cows. The total amount of potential time of error-free data available was 2,760 hours. The percentage of activity that the pedometers collected over the grazing season ranged from 10% to 38%, with the pedometers collecting an average of 28% of total activity time (95% CI [25.7, 30.4]). Our study focused on activity during peak grazing times so we further pared down the data to include only times of 4:00- 10:00 AM and 4:00-10:00 PM, as used elsewhere in previous studies (Ganskopp 2001; Ganskopp and Bohnert 2006; Lofgreen et al. 1957). After adjustment, the total amount of potential time of error-free data available was 1,380 hours. The percentage of activity that the pedometers collected throughout grazing ranged from 11% to 43%, with the pedometers collecting an average of 33% of total activity time (95% CI [29.8, 35.3]).

Gaps in data collected throughout the grazing season due to inconsistent connectivity between pedometers and reader stations required standardization of data so all animals could be compared to one another. Lying and standing time were evaluated as the proportion of total sampling time available. Movement rates (step counts per hour) and the frequency of lying bouts (number of times an animal got up and down within an hour) within each grazing period were used for analysis. Movement rate was determined by dividing the total number of steps by the total hours spent standing in a grazing period [total steps/(total standing minutes/60)]. Lying bout frequency was determined by dividing the total number of lying bouts per animal for the grazing season by the total length of time logged for the animal (# lying bouts per hour of total logged activity time). The proportion of time spent lying down by grazing period was calculated for each pedometer by taking the total time lying (by season), dividing it by the total monitoring time, and then multiplying by 100 to get a percent. Percentages of standing time by period of grazing were calculated for each pedometer by subtracting 100 from the percent time lying.

2.2.6 Data Analysis

The resulting dataset included activity data for up to 27 cows for each of 15 pastures and across three seasonal grazing periods. The data included the frequency of lying bouts (# hr^{-1} of total time), the proportion of total activity time cows spent lying down (%), and the movement rate of cattle (steps hr^{-1} of standing and/or moving time). All metrics were determined relative to the amount of total time available for evaluation for each cow, and were further partitioned into the following periods and pasture conditions: the early growing period while on native pastures (June 12 - June 20), the mid- growing period on native pasture (July 23 - August 14), and the dormant period on native pastures (August 31 - October 25). Data were additionally partitioned for cultivated pastures (early season: June 26 - July 14; middle season: August 15 - August 31) and wetland pastures (early season: June 20 - 26; middle season: July 14 - July 23). All pedometer data were examined for normality using frequency histograms prior to analysis. Cow movement rates were square root transformed to improve normality, while the % lying time and lying bout frequency data were normally distributed and did not require transformation.

Activity data were then analyzed using two separate models with analysis of variance (ANOVA). As native pastures were grazed during all three grazing times (early, mid and late season), an initial ANOVA was run using mixed models with RFI grouping and time of grazing as fixed effects, and individual animal as the random factor. Pasture size was included as a covariate in the model. The second ANOVA evaluated cow activity among all pasture types (native, tame and wetland) within the early and mid-grazing times only, with RFI, pasture type, and time of grazing as fixed effects; pasture size was again included as a covariate, and individual animal was random. Least-squares non-transformed means are presented for all analyses, with transformed data used to obtain ANOVA test results where necessary. For all significant main effects and interactions ($P < 0.05$), a post-hoc test was conducted using an LSD with $P < 0.05$. Pasture size was found to be a significant covariate in most of the analyses, so regressions were performed between the cattle activity metrics and pasture size for both native only, and all pasture types across the early and mid-season grazing time datasets.

To characterize forage biomass and quality, these data were examined for normality prior to analysis. Forb biomass and all protein and fiber yields required square root transformations, while grass biomass, fiber and protein concentrations were log transformed. Forb protein and fiber concentrations required no transformation. ANOVA was then used to assess differences in forage metrics across grazing times (early, mid and late season), topographic/soil types (grouped into categories representing moisture regimes- see Table 2.1 and Appendix 3) and their interaction, within native pastures. Soil type and season were used as fixed effects and pasture as the random variable. In this process individual clip plots were assumed to be subsamples for soil type within each pasture. Post-hoc comparisons were conducted on least squares means using an LSD test at an alpha of 5%. Responses in native pasture activity to changing native forage metrics were also explored using multiple linear regression. Uncorrelated forage metrics (Table 2.2) at the soil type level (Table 2.1) went through stepwise regression to find the best prediction model for each activity type.

Finally, to relate cow activity to the performance metrics of cow weight and body fat gain, as well as calf weaning weights, activity metric data from the entire grazing season were summarized per animal. These performance metrics were individually regressed against movement rate, lying bout frequency and lying time.

2.3 Results

2.3.1 Cow Activity within Native Pastures

RFI group, both alone and in combination with season of grazing, did not contribute to the movement rate of cows ($P \geq 0.23$; Table 2.4). Cow movement rates were effected by season of grazing ($P < 0.0001$, Table 2.4): movement rates were highest in the early season and declined progressively in late summer and fall (Figure 2.2). Movement rates of cows within native pastures did not vary with pasture size ($P = 0.36$, Table 2.4).

Pasture size and season of grazing, both alone and in combination with RFI group, had no effects on the frequency of lying bouts ($P \geq 0.45$, Table 2.4). Total lying time was not altered by RFI, alone or in combination with season of grazing ($P \geq 0.87$, Table 2.4). Lying time was altered by season of grazing ($P = 0.0004$, Table 2.4). Cattle spent approximately 29% of their time in the early grazing season lying down, which increased significantly to 42% in the mid-summer grazing period, and then declined to around 32% in the fall (Figure 2.3). Cow lying times also varied with pasture size ($P < 0.0001$, Table 2.4). Further analysis with regression indicated pasture size accounted for 20% of the variation in lying time, with lying time declining overall with increasing pasture size ($P < 0.001$, Figure 2.4).

2.3.2 Cow Activity among Different Pasture Types

RFI grouping, alone and in combination with pasture type, season of grazing, or the three-way interaction among these variables, did not affect cow movement rate ($P \geq 0.21$, Table 2.5). Cattle movement rates were affected by pasture type ($P = 0.007$, Table 2.5), with animals spending less time moving about in wetland pastures than tame and native pastures (Figure 2.5). Season of grazing also altered movement rates ($P \leq 0.0001$; Table 2.5). Cattle moved less in the middle of the grazing season, compared to early season (Figure 2.6). Interactions between seasonality and pasture type were also found ($P = 0.0004$, Table 2.5). Cattle moved more in tame and native pastures than wetland pastures in the early season (Figure 2.7), and took more steps earlier in the grazing season within tame pastures (Figure 2.8).

Lying bout frequency did not vary with RFI grouping, or any interaction thereof with season of grazing or pasture type ($P \geq 0.14$, Table 2.5). Lying bout frequency was significantly affected by pasture type and season of grazing (P = 0.0004 and 0.006, respectively, Table 2.5). Tame pastures had the highest lying bout frequency, followed by wetland pastures and then native pastures (Figure 2.9). Cattle got up and down more frequently in the early season grazing period than in the mid-season period (Figure 2.10). Pasture size did not affect lying bout frequency (P = 0.15, Table 2.5).

RFI grouping, alone or in combination with pasture size and grazing season, was not related to differences in total lying time ($P \geq 0.75$, Table 2.5). Although pasture type contributed to differences in lying time (P = 0.04, Table 2.5), no post-hoc comparisons were significant ($P \geq 0.13$). Native pastures tended to have the greatest lying time, followed by tame and cultivated pastures (31 ± 2.4, 29 ± 2.1, and 26 ± 1.4 percent lying time, respectively). Season of grazing was not a significant predictor of total lying time, and although pasture size was a significant covariate for lying time (P = 0.04, Table 2.5), it only explained 2% of the variation in lying time (Figure 2.11).

2.3.3 Native Forage Metrics and Association with Behaviour

Grass biomass, along with fiber and protein concentrations or yields, did not vary significantly over grazing season or soil type ($P \geq 0.07$, Table 2.6). Forb fiber concentration was significantly different across seasons of grazing ($P < 0.0001$, Figure 2.6). Forbs in the early grazing season were higher in fiber (i.e. less digestible) than those documented in the mid and late seasons, making them lower quality (Figure 2.12). Forb protein concentrations also varied (P= 0.008, Table 2.6) across soil types, with the midland soil types of moderate moisture having higher protein than the wettest lowland soil types (Figure 2.13). The interaction between soil type and season of grazing explained significant variation in forb crude protein levels (P = 0.03, Table 2.6). For instance, during the early season lowland (i.e. very wet) soil types showed significantly lower forb crude protein concentrations compared to midland soils with mesic moisture (Figure 2.14). Forb biomass varied over seasons of grazing ($P = 0.004$, Table 2.6), with the late season leading to significantly lower forb biomass than the mid-season periods (Figure 2.15). Similarly, forb protein and fiber yields varied across seasons of grazing ($P = 0.008$ and 0.02 respectively, Table 2.6), though further post hoc tests found no significant differences.

Multiple linear regressions of cow movement rate against the leading forage metric model explained 14% of the variation in movement rate ($P < 0.0001$, Table 2.7). Forb fiber, protein and biomass were positively related to cow movement rate ($P \leq 0.03$, Table 2.8). Both lying bout frequency and total lying time were also found to be significantly associated ($P \leq 0.02$, Table 2.7) to their respective leading forage models (Adj $R^2 = 0.02$ and 0.32, respectively, Table 2.7). Lying bout frequency was found to have a direct positive relationship with forb biomass ($P = 0.01$, Table 2.9). Lying time significantly increased with increasing forb protein and grass biomass levels, but decreased significantly as forb biomass increased ($P \leq 0.003$, Table 2.10).

2.3.4 Cow Activity and Cattle Production Metrics

Changes in cow body weight, back fat gain, and calf weaning weight, were not explained by any of the cattle activity budget measures that the pedometers tracked during the grazing season of 2015 ($P \geq 0.12$, Table 2.11). Cows that spent more time lying down tended to gain less weight and back fat over the grazing season (beta coefficients from linear models: -7.74 ± 4.7 SE and -0.005 ± 0.003 SE, respectively).

2.4 Discussion

2.4.1 RFI and Pasture Activity

Our hypothesis that efficient animals would move less and spend more time lying down and have a greater number of lying bouts than inefficient animals was rejected. These findings indicate that either the MBVs for RFI do not reflect differences in cattle activity under open-range grazing, or that activity among cattle simply does not differ in relation to this trait. The latter is perhaps more likely given that no direct relationships were found between the phenotypic expression of cows and calves (i.e. in weight, back fat, and calf weight) and the observed activity metrics, independent of MBVs for RFI.

Although it is possible that animals with divergent MBVs for RFI truly do not express any differences in activity, the patchy continuity of our data collection due to technological challenges may have had an effect on our results. In the current study, we captured an average of 33% (95% CI [29.8, 35.3]) of total grazing time activity, and this value further varied among individual animals as mentioned in Section 2.2.4. To our knowledge, the radius of reception that the Afimilk reader stations have for pedometer data collection within extensively grazed pastures was previously unstudied.

Another potential reason for the lack of differences in activity between RFI groups may be that there was not enough genetic variation among the beef cows examined. MBV’s for RFI tend to be relatively low in accuracy (0.334-0.498 for this population) and factoring in the inherent variation between the two groups of animals in this study (SD ± 0.11), actual MBV scores between these two groups could have overlapped, leading to similar expected RFI. Although data were analyzed primarily by looking for differences between groups to answer the hypotheses, when we further explored the activity responses on an individual animal level using regression, once again no significant results were found. This can be interpreted to mean that the among-animal variation that normally could be expected to be smoothed out when averaging activity responses into high or low RFI groups, did not occur, or that there simply was not enough (genetic) difference between our animals to attribute differences in activity to RFI alone.

2.4.2 Cow Activity and Season of Grazing Effects within Native Pastures

Early season grazing coincides with the highest protein and energy demands of cattle because they are supporting a calf during lactation and are simultaneously attempting to regain fat stores lost over winter (National Research Council 2000). In this study cows had their highest movement rates and shortest lying time during the early season, which supports the notion that cattle were spending increased time searching for food to meet their energetic needs (Rittenhouse and Bailey 1996). Conditions of good forage quality with limited biomass availability in early summer would require increased search time to find optimal vegetation for foraging, but also mean rapid digestion and passage rates of forage (Demment and Greenwood 1988), allowing animals to spend less time resting and ruminating.

Movement rates trended lower in the middle of the grazing season compared to earlier and coincided with cows having the highest percentage of time spent lying, and is likely indicative of highly favorable foraging conditions (i.e. high biomass) in mid-summer, allowing cows to rapidly achieve gut fill and spend more time ruminating (Cline et al. 2010; Demment and Greenwood 1988; Provenza 1995). Spending more time lying down may mean the animals are taking time to digest their food and would allow them to allocate more of their energy to production (i.e. lactation and weight gain). Moreover, declining forage quality levels in mid-summer would necessitate longer rumination periods.

The lowest observed movement rate by cows during fall could represent a shift in behaviour to decreased quality of forage (Bailey et al. 1996; Demment and Greenwood 1988). Observed forage quality metrics (protein and fiber) in the current study indicated sharp declines in quality during fall, which could discourage cattle from being selective, but also slow digestion and thereby increase forage retention times. The consequence of this action would be longer rumination times (i.e. inactivity) to process ingested forage, and lying and rumination have been found to be directly correlated (Lofgreen et al. 1957). Cows had similar lying times in early and late season, but much higher movement rates in the spring than the fall. This is likely because in the fall, there is plenty of biomass available so animals do not need to search long to find feed. However, this feed is of declining quality and takes a long time to digest.

Bailey (2005) stated that cattle are better able to select a high-quality diet in native compared to monoculture pastures because as the growing season progresses there are a greater variety of forages in different stages of vegetative development to choose from. The ability to select for a higher quality diet within larger pastures with a greater variety of vegetation patches may also explain our findings of decreased lying time as pasture size increased. Larger pastures would have a greater variety of plant communities and inherent plant species, and also lead to greater distances between preferred vegetation patches, forcing cows to spend more time travelling among preferred foraging areas. However, this pattern is only likely to occur initially during the summer when the nutritional returns from preferred patches are justified and likely to disappear during the fall season when all vegetation is under ongoing advanced senescence (i.e. forage quality declines).

2.4.3 Cow Activity among Different Pasture Types within Early and Mid-Season Grazing

The pattern of increased cattle movement and lying bout frequency during the early grazing season was particularly apparent within tame pastures. As discussed earlier, cows have high energy demands in spring so are likely spending much time exploring pastures in search of adequate biomass of forage, resting for a short time to digest the relatively high-quality feed ingested, and then searching again. Lying bout frequency was highest in tame pastures, which could be interpreted to mean that animals were rapidly eating and achieving gut fill, then lying down frequently to digest their forage, after which they get up and graze again. This was modelled well in our results with animals getting up and down more frequently in tame pastures. Tame pastures would be particularly prone to this pattern, as they had especially high biomass and quality, being comprised of either seeded annual forage, or high quality tame perennials (i.e. alfalfa mix).

Similar to the tame pastures, vegetation in the native and wetland pastures grazed in the middle of the grazing season would also have had time to produce plenty of biomass, which would account for lower search times required for cattle to achieve gut fill. Cow movement rates within wetlands however, were typically lower than in tame and native pastures when averaged over the whole grazing season. Although this may arise from the prevalence of large bodies of water, which could have directly limited movement by posing an obstruction (Appendix 3), it is also likely that under the sub-irrigated conditions of these pastures cattle had little need to travel far and/or search to find abundant, high quality forage, or drinking water. This would also account for the relatively high lying bout frequency observed in these areas as cows would have a frequent need to ruminate following gut fill.

Unlike tame and wetland pastures, cows within native pastures had the lowest lying bout frequency, likely because the great variation in vegetation and lower overall biomass of this forage type would have forced animals to increase their travel, search and foraging times. This was supported in this study by an increased movement rate of cattle, and a shorter time spent lying down in general.

2.4.4 Forage Metrics and Cow Activity Responses

Native pasture grass metrics did not significantly differ between soil types and seasons of grazing. In contrast, early season native pastures were characterized by plentiful forb biomass that was significantly lower in quality than subsequent seasons, with a variety in forb quality also found across different soil types. Forb protein was likely lower in the lowland soil types - both across the entire grazing season and within the early season only - because these areas were dominated by less palatable forbs such as chenopods. This brings attention to the concept that although forage quantity and quality are positively tied to water availability (Bailey and Provenza 2008), there is a limit to the benefit that water presence has. My research attempted to make connections between these responses in forb availability and quality, and cattle activity.

Although grass generally makes up the majority of cattle diets (Clark et al. 2013; Volesky et al. 2007) and grass metrics were indeed predictors of the activity models, our results showed that forb metrics were also consistently significantly associated with cattle activity. Bailey (1995) found that cattle grazing heterogeneous patches of forage selected areas with better quality regardless of the grass biomass available and developed enough preference for these areas that they were willing to travel back to them repeatedly. The significant relationship found between grass biomass (indirect) and movement rate supports Bailey’s findings; animals were not travelling to areas of greater grass biomass, but to areas of higher quality. Cattle moved more with conditions of greater forb biomass and forb protein, likely because these plants are generally palatable, of high quality, and subsequently attract animals (Galyean and Gunter 2016). Forb biomass was positively associated with lying bouts, meaning that animals were likely travelling to areas of plentiful forbs, achieving gut fill, lying down and ruminating for a short time, then getting up again and searching for more feed.

Lying time results generally supplement the results we found with other activity metrics. Grass biomass had a positive relationship to lying time, but forb biomass had a negative relationship. This is likely because forb biomass was found to increase movement rate and lying bout, which would mean that animals would subsequently be spending less time lying down. The opposite response to increasing grass biomass is likely because grasses were abundant, so animals did not need to move much to achieve gut fill and could then lay down and ruminate, two activities which have been previously found to be correlated (Zemo and Klemmedson 1970). In contrast to these explanations, increasing forb protein was found to increase lying time, and increasing grass fiber was found to decrease lying time. Rather than gut fill alone, these responses may be driven by protein-energy imbalances, which have been found to significantly alter grazing behaviours (Galyean and Gunter 2016). High protein forbs may create a protein-energy imbalance that drives selection for energy dense grasses, which have greater fiber and longer rumen retention times. Alternately, grazing low quality grass with high fiber levels may encourage a cow to search out higher quality feed and spend less time lying down.

2.4.5 Cow Activity and Cattle Production Metrics

Cattle selection is determined at the plant community, feeding station and patch level (Kaufmann et al. 2013b), with post-ingestive feedback driving preferences and intake in real-time (Provenza 1995). It would be expected that activity and performance would subsequently be influenced. However, the scale of these behaviours and responses is significantly smaller than exploring wholesale landscape effects on forage and associated animal production metrics that are the result of integrated behavior over a whole grazing season. This is likely why our cattle production metrics were not found to be significantly affected by activity, although we did find an interesting trend between increased lying time and negative impacts on fat gain and body weight gain. This trend in combination with our findings in the lying time forage model would make it appear that animals may perform better when they search for forb biomass of increased quality, balance their protein demands with higher fiber grasses, and continue to move around to expose themselves to the best combination of forage material available. This theory is in direct contrast to our hypotheses and warrants further exploration to determine when increased energy expenditure to search for improved diet quality becomes worthwhile for better performance.

2.5 Conclusion

Our research found no effects of RFI group or RFI MBV on activity patterns in cows grazing in pastures. In contrast, we found significant variation in lying time of cows, the frequency of lying bouts, and in movement rates of cattle, in relation to different seasons of grazing, pasture types, and pasture sizes. This leads us to the conclusion that environment (season of grazing and topographic/soil type), as well as management factors (i.e., pasture size) are likely more appropriate predictors of cow activity levels (movement rates and resting time) within extensively grazed pasture than MBV for RFI. Season of grazing and pasture type created marked variation in rangeland vegetation forage quality and quantity (Appendix 4 and 5), which in turn appeared to affect cattle activity. Perhaps most importantly, observed cow/calf production metrics in this investigation were not found to be related with any significance to the activity metrics observed. A more in-depth understanding of cattle activities and how they are altered with environmental changes is required to better understand the implications of activity on cattle performance. More research is also needed surrounding the use of RFI MBV's in extensively raised cattle to better account for the variation in phenotype (cattle performance) that an uncontrolled environment introduces. Ultimately, developing herd management strategies to optimize the balance of feeding and resting behaviour in cattle, while promoting more even pasture utilization, could help livestock conserve energy, optimize weight gain, and ensure sustainable use of rangeland landscapes.

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Table 2.1 Grouping of topographic/soil types by location and soil moisture effects, for analysis of forage quality changes on the landscape.

Grouping	Soil Type	Location Characteristics
Upland	Orthic Brown Chernozem (O.B.) Orthic Regosol (O.R)	Predominant grouping on upland areas that would be characterized as drier.
Midland	Orthic Eluviated Brown Chernozem (O.EB.) Gleyed Brown Chernozem (GL.B.)	Transition area between upland and lower lying areas or depressions
Lowland	Orthic Humic Gleyed Chernozem (O.HG.) Calcareous Brown Chernozem (CA.B.)	Wetland areas or those within depressional areas.

Table 2.2 Correlation table of forage metrics used to explore how forage metrics affect activity. Forage data had been averaged by topographic soil type as described in Table 2.1. Bolded values are correlated with one another and were not included in the stepwise regression to determine best models for predicting cattle activity.

Forage Variable	Forb ADF[1]	Grass ADF[2]	Forb CP[1]	Grass CP[2]	Forb Biomass[3]	Grass Biomass[4]
Forb ADF[1]	1					
Grass ADF[2]	-0.23	1				
Forb CP[1]	-0.05	-0.20	1			
Grass CP-2	-0.07	-0.54	**0.71**	1		
Forb Biomass[3]	0.17	-0.44	0.11	**0.63**	1	
Grass Biomass[4]	-0.20	-0.26	-0.09	0.36	0.57	1

[1] measured in %
[2] measured in %, log transformed
[3] measured in $kgha^{-1}$ square root transformed
[4] measured in $kgha^{-1}$, log transformed

Table 2.3. Untransformed mean, minimum, maximum and standard deviations (SD) associated with the forage metrics collected from pastures through the grazing season. Forage metrics from 30 quadrats per pasture were averaged together by soil type to create the summary data.

	All Pastures (n = 13)				Native Pastures only (n = 8)			
Variable	Min	Max	Mean	SD	Min	Max	Mean	SD
Herbage biomass[1]	332	4781	2159	1081	332	4781	1783	1018
Herbage crude protein[2]	2.3	24.2	8.7	4.2	2.3	11.4	6.7	2.7
Herbage ADF[2]	9.7	64.24	38.2	9.4	9.7	48.2	36.1	9.5
Grass biomass[1]	332	3960	1718	884	332	3187	1445	734
Grass protein	4.1	24.2	9.1	3.5	4.1	10.8	7.5	1.9
Grass ADF[2]	36.1	56.8	42.5	4.8	37.2	55.2	43.6	4.6
Forb biomass[1]	0	2930	441.1	609	0.0	1596	338	389
Forb crude protein[2]	5.5	16.4	12.2	2.8	5.5	16.0	11.5	3.0
Forb ADF[2]	19.5	71.6	39.5	11.7	19.5	59.5	37.1	9.9

Herbage crude protein and fiber are weighted averages.
[1] Measured in kg ha^{-1}
[2] Measured in %

Table 2.4. Results of the ANOVA evaluating variation in lying bout frequency, proportion of total time spent lying down, and movement rates by standing cattle in native pastures only (n = 8), in relation to RFI grouping, season of grazing, and their interaction. Pasture size was included as a covariate in the model.

			Lying Time (%)		Lying Bout (# hr^{-1} total time)		Movement Rate (steps hr^{-1} of standing time)[1]	
Model Factor	Num df	Den df	F-Stat	P-Value	F-Stat	P-Value	F-Stat	P-Value
Pasture Size	1	140	26.80	**<0.0001**	0.53	0.46	0.85	0.36
RFI Group	1	140	0.03	0.87	0.0006	0.97	1.46	0.23
Time of Grazing (early, mid, late)	2	140	5.33	**0.004**	0.35	0.70	21.13	**<0.0001**
Time of Grazing x RFI Group	2	140	0.10	0.90	0.79	0.45	0.83	0.44

[1] Movement rate analysis was based on square root transformed data.

Table 2.5. Results of the ANOVA evaluating variation in lying bout frequency, the proportion of time spent lying down, and movement rates by standing cattle, in relation to RFI group, all pasture types (n = 13), season of grazing (early and mid-growing season only), and all interactions thereof. Pasture size was included as a covariate in the model.

			Lying Time (%)		Lying Bout (# hr^{-1} total time)		Movement Rate (steps hr^{-1} of standing time)[1]	
Model Factor	Num df	Den df	F-Stat	P-Value	F-Stat	P-Value	F-Stat	P-Value
Pasture Size	1	191	4.33	**0.04**	2.09	0.15	0.17	0.68
RFI Group	1	191	0.09	0.76	0.54	0.46	0.72	0.40
Pasture Type (Native /Tame/Cultivated)	2	191	3.28	**0.04**	7.76	**0.0004**	4.93	**0.007**
Time of Grazing (early, mid, late)	1	191	2.19	0.14	7.68	**0.006**	33.03	**<0.0001**
Pasture Type x RFI Group	2	191	0.29	0.75	0.50	0.61	1.58	0.21
Time of Grazing x RFI Group	1	191	0.002	0.96	2.20	0.14	0.56	0.45
Pasture Type x Time of Grazing	2	191	2.07	0.13	0.35	0.70	7.85	**0.0004**
Pasture Type x RFI Group x Time of Grazing	2	191	2.43	0.09	0.34	0.71	0.01	0.99

[1] Movement rate analysis was based on square root transformed data.

Table 2.6. Significance (P-value) results of the ANOVA evaluating variation in native pasture forage metrics in relation to time of grazing (early, mid and late season), topographic/soil type (upland, midland, lowland) and their interaction. Pasture was included as a random effect in the models.

		Acid Detergent Fiber (%)		Crude Protein (%)		Biomass (kg ha^{-1})		Crude Protein Yield		Crude Fiber Yield	
Covariate	df	Grass[1]	Forb	Grass[1]	Forb	Grass[2]	Forb[3]	Grass[3]	Forb[3]	Grass[3]	Forb[3]
Season of Grazing	2	0.44	**<0.0001**	0.12	0.24	0.54	**0.004**	0.34	**0.008**	0.58	**0.02**
Soil Grouping	2	0.15	0.87	0.52	**0.008**	0.42	0.74	0.07	0.75	0.34	0.45
Season x Soil Grouping	4	0.53	0.15	0.75	**0.03**	0.78	0.77	0.58	0.56	0.78	0.99

[1] Data were log(x+1) transformed
[2] Data were log transformed
[3] Data were square root transformed

Table 2.7. Adjusted R^2, F-statistics and P-values of the multiple regression models relating movement rate (square root transformed), lying time and lying bout frequency, to the leading forage metrics models[1]. Independent response data are from all native pastures grazed within the 2015 grazing season. Stepwise regression was used to determine the dominant uncorrelated covariates brought forward for regression.

	Lying Time			Lying Bout Frequency			Movement Rate		
Model	R^2	F-Stat	P-value	R^2	F-Stat	P-value	R^2	F-Stat	P-value
Forage model[1]	0.32	47.82	**<0.0001**	0.02	4.23	**0.02**	0.14	13.6	**<0.0001**

[1] Lying Time model: grass fiber (log transformed), forb protein, forb biomass, grass biomass (log transformed)
Lying Bout Duration model: forb protein, forb biomass
Movement rate model: forb fiber, grass fiber (log transformed), forb protein, forb biomass, grass biomass (log transformed)

Table 2.8. Multiple linear regression model summary statistics predicting square root transformed cow movement rate (# hr^{-1} of standing time) relative to the main forage metrics tested within native pastures over the grazing season. Stepwise regression was used to determine what variables were the dominant uncorrelated covariates brought forward for regression. Total R^2 for this model was 13%.

Model	Beta	Standard Error	t-stat	Partial R^2	P-value
Forb Fiber[1]	0.04	0.02	2.21	0.01	**0.03**
Grass Fiber[2]	3.76	1.97	1.91	0.009	0.06
Forb Protein[2]	0.14	0.06	2.45	0.02	**0.01**
Forb Biomass[3]	0.002	0.0004	5.76	0.08	**<0.0001**
Grass Biomass[4]	-2.33	0.47	-5.00	0.06	**<0.0001**

[1] Measured in %, log transformed
[2] Measured in %
[3] Measured in kg ha^{-1}
[4] Measured in kg ha^{-1} , log transformed

Table 2.9. Multiple linear regression model summary statistics predicting lying bout frequency (# hr^{-1} of total time) relative to the main forage metrics tested within native pastures over the grazing season. Stepwise regression was used to determine what variables were the dominant uncorrelated covariates brought forward for regression. Total R^2 for this model was 2%.

Model	Beta	Standard Error	t-Stat	Partial R^2	Significance
Forb Protein[1]	-0.004	0.002	-1.58	0.15	0.11
Forb Biomass[1]	0.00004	0.00002	2.56	0.02	**0.01**

[1] Measured in %

Table 2.10. Multiple linear regression model summary statistics predicting time spent lying down (%) relative to the main forage metrics tested within native pastures over the grazing season. Stepwise regression was used to determine what variables were the dominant uncorrelated covariates brought forward for regression. Total R^2 explained was 32%.

Model	Beta	Standard Error	t-Stat	Partial R^2	Significance
Grass Fiber[1]	-15.12	8.65	-1.76	0.008	0.08
Forb Protein[2]	2.04	0.25	8.07	0.25	**<0.0001**
Forb Biomass[3]	-0.02	0.002	-11.74	0.26	**<0.0001**
Grass Biomass[4]	16.16	2.0	8.06	0.14	**<0.0001**

[1] Measured in %, log transformed
[2] Measured in %
[3] Measured in kg ha^{-1}
[4] Measured in kg ha^{-1}, log transformed

Table 2.11. Adjusted R^2, F-statistics and P-values of the linear model regression evaluating variation in cow weight gain, cow backfat gain, and calf weaning weight as a percentage of final cow weight, with cattle activity budgets over the entire grazing season (n = 27 cows).

	Cow Gain (kg)			Cow Back Fat Gain (mm)			Calf Weaning weight (% final dam weight)		
Model	R^2	F-Stat	P-value	R^2	F-Stat	P-Value	R^2	F-Stat	P-Value
Movement Rate[1]	-0.04	0.05	0.83	-0.04	0.007	0.93	0.01	1.27	0.27
Lying Bout Frequency[2]	0.02	1.42	0.25	0.003	1.06	0.31	-0.04	0.0009	0.98
Lying Time[3]	0.06	2.66	0.12	0.05	2.20	0.15	0.003	1.05	0.32

[1] Measured in steps hr^{-1} of standing time
[2] Measured in number of times hr^{-1} of lying time
[3] Measured in % of total activity budget

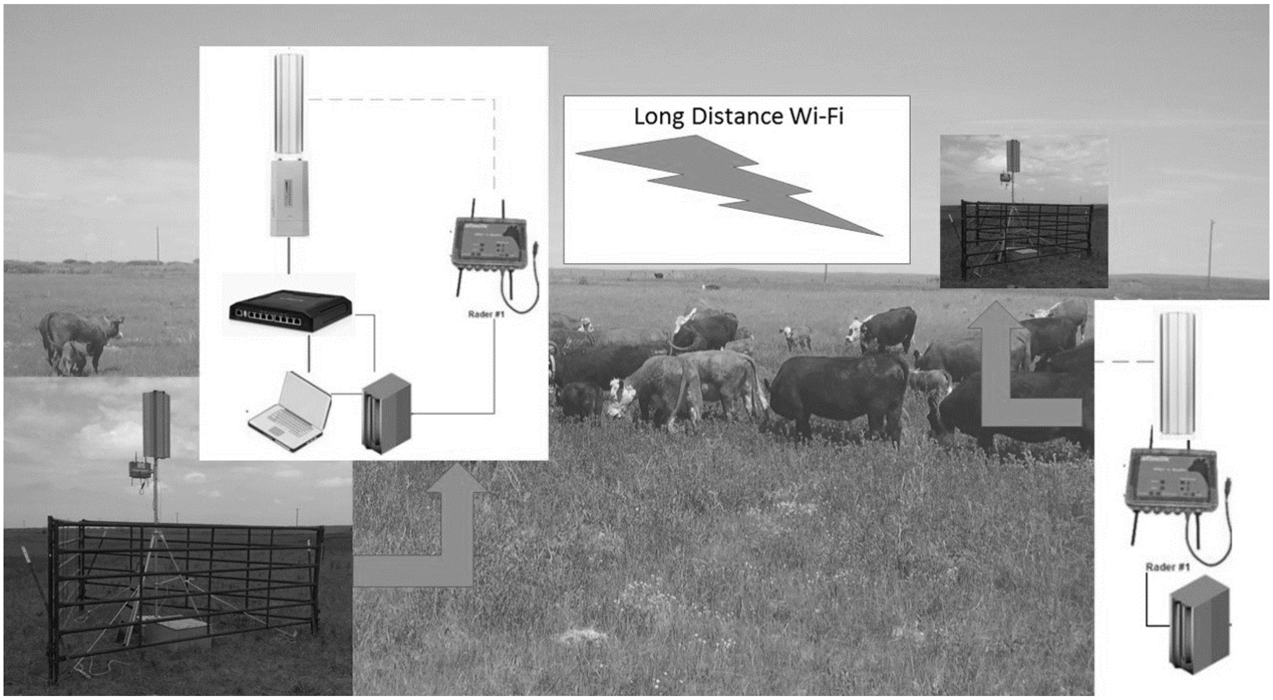

Figure 2.1. Schematic of the in-field pedometer reader system used to collect data on cattle activity during the summer of 2015. The main reader (left) contained the laptop recording pedometer information. The secondary reader (right) collected information from another area of the pasture and transmitted it to the main reader via Wi-Fi. The two stations were strategically placed to capture as much data as possible from nearby cows.

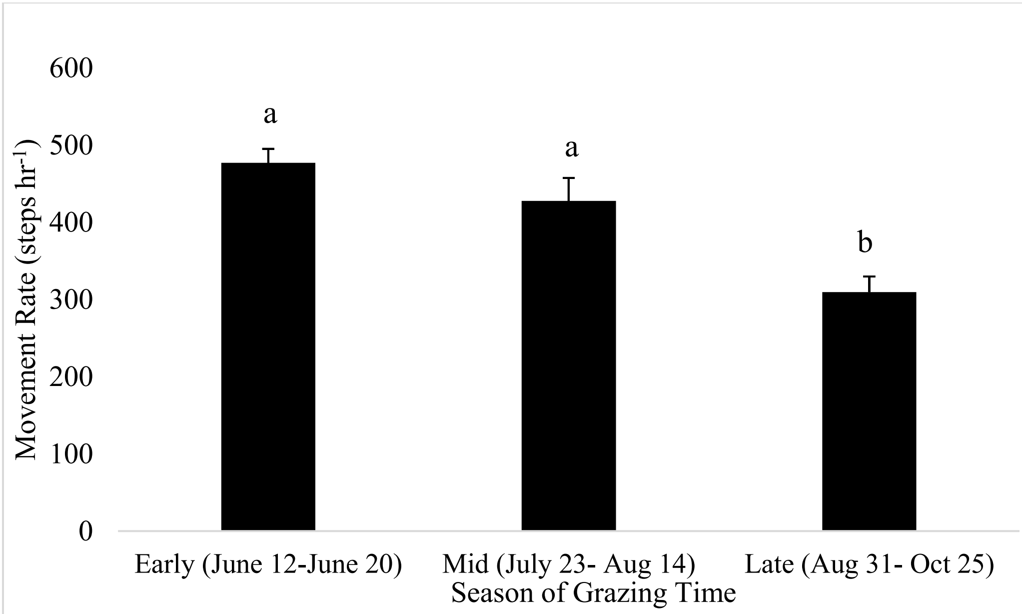

Figure 2.2. Analysis of variance comparing mean (± 20.8, 29.0, and 18.3 SE for early, mid, and late season grazing, respectively) movement rate (steps hr^{-1} of standing time) for 27 cattle grazing in three different seasons of native pasture use (early, mid, late season). Data presented are untransformed, p-values are based on square root transformed data. Means with different letters are significantly different ($P \leq 0.002$).

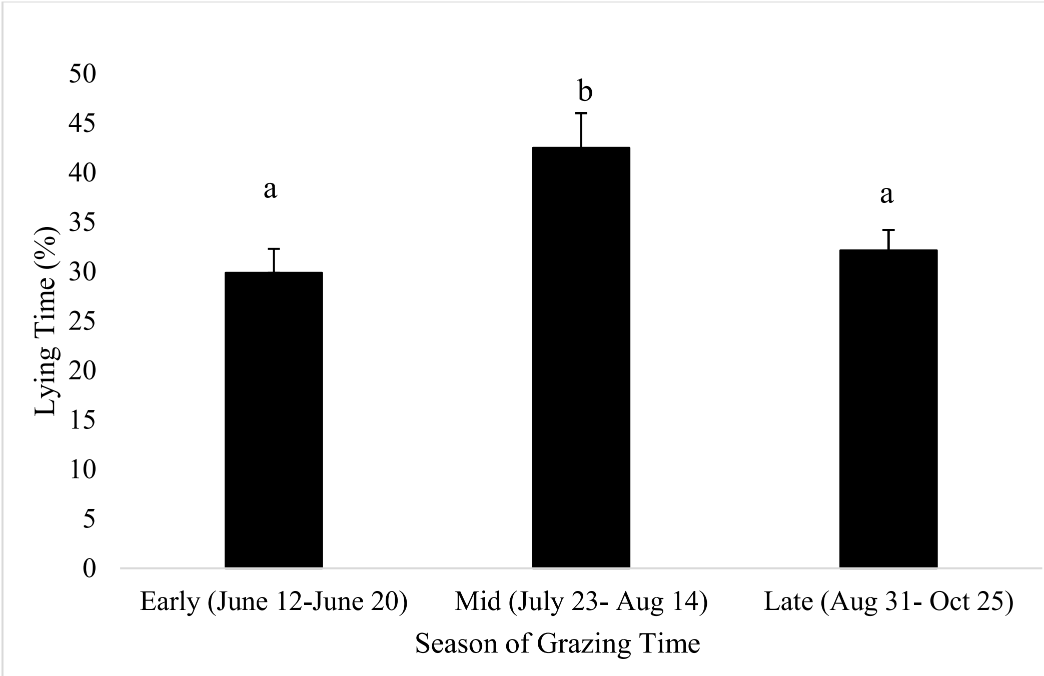

Figure 2.3. Analysis of variance comparing mean (± 2.4, 3.5, and 2.1 SE for early, mid, and late season grazing, respectively) lying time (%) of 27 cattle during each of three different seasons while grazing on native pasture (early, mid and late season). Means with the same letters are not significantly different ($P \geq 0.05$).

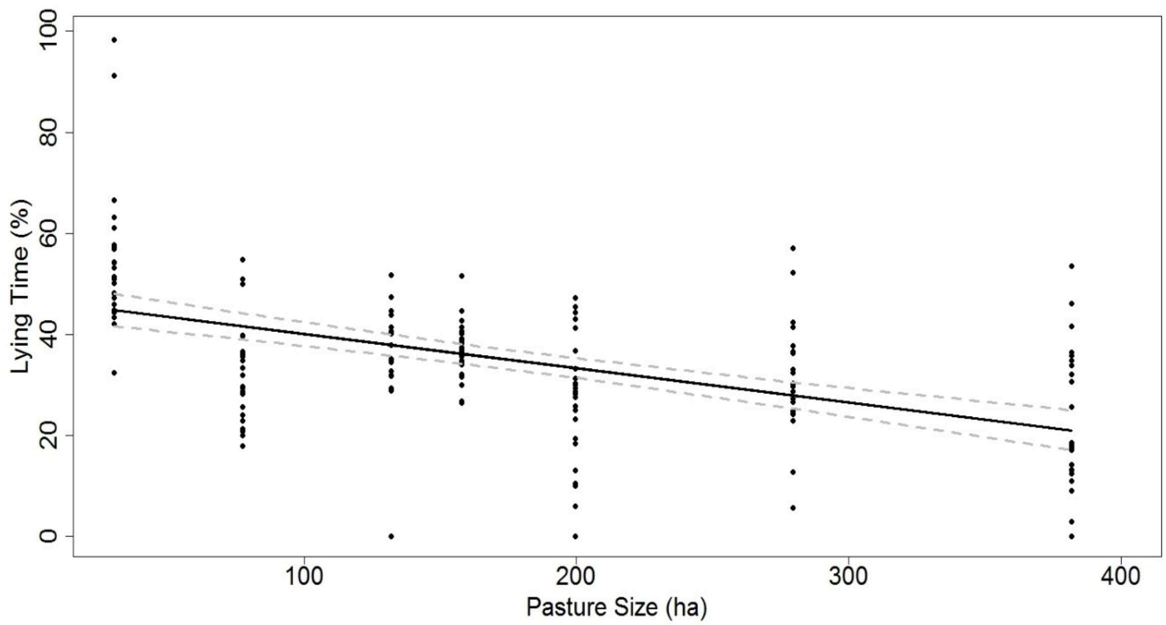

Figure 2.4. The relationship between mean (± 95% fitted confidence intervals) lying time (% of total time) and the size of 8 native Dry Mixedgrass pastures for 27 cattle across all times of grazing (early, mid, and late season). Lying time decreased with increasing pasture size (LT = 46.3 - 0.06PS: Adj. R^2= 0.20; $P < 0.001$).

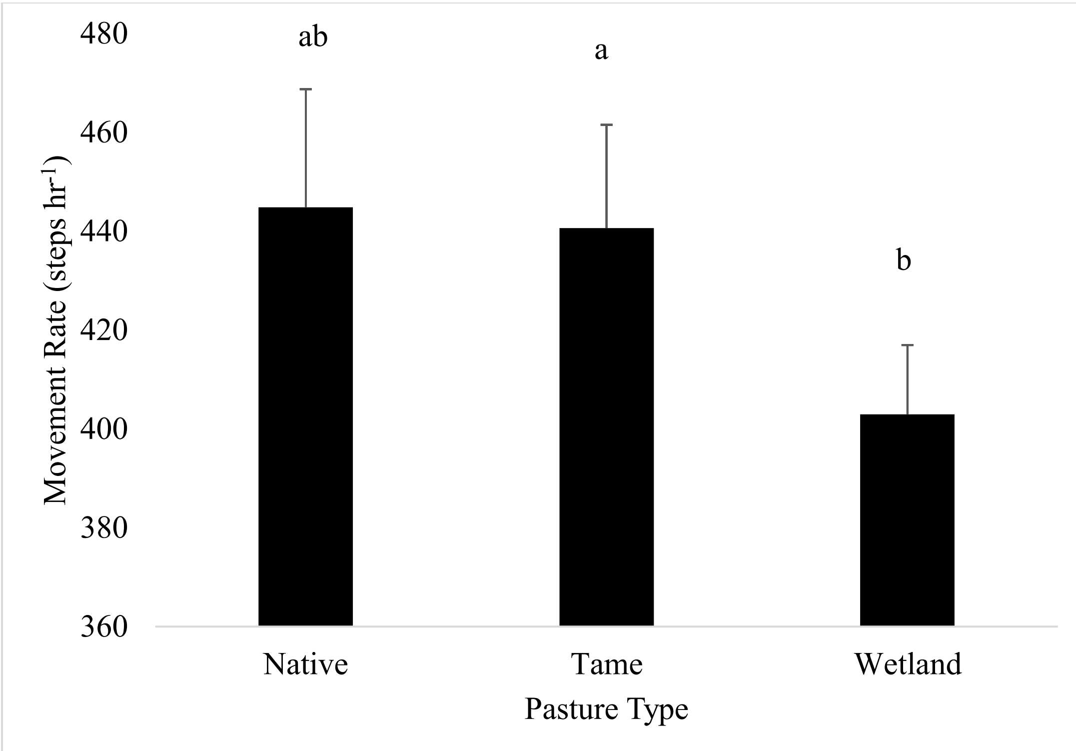

Figure 2.5. Analysis of variance comparing mean (± 23.7, 20.9, and 14.0 SE for native, tame, and wetland pasture types, respectively) movement rate (steps hr^{-1} of standing time) for 27 cattle grazing in different pasture types within the early and mid- grazing seasons. Data are averaged over times of grazing and RFI groups. Data presented are untransformed, but analysis is based on square root transformed data. Means with different letters are significantly different ($P \leq 0.05$).

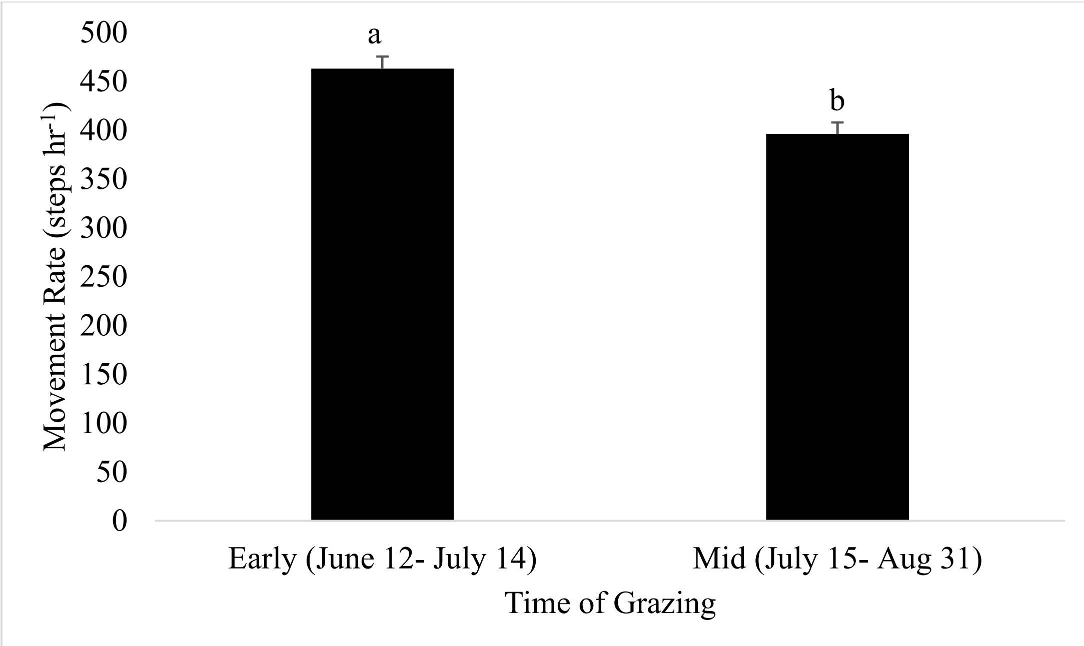

Figure 2.6. Analysis of variance comparing mean (± 12.5 and 11.8 SE for early and mid- season grazing, respectively) movement rate (steps hr^{-1} of standing time) for 27 cattle during the early and mid-summer grazing seasons within all pasture types. Data are averaged over pasture types and RFI groups. Data presented are untransformed, but analysis is based on square root transformed data. Means with different letters are significantly different ($P \leq 0.0001$).

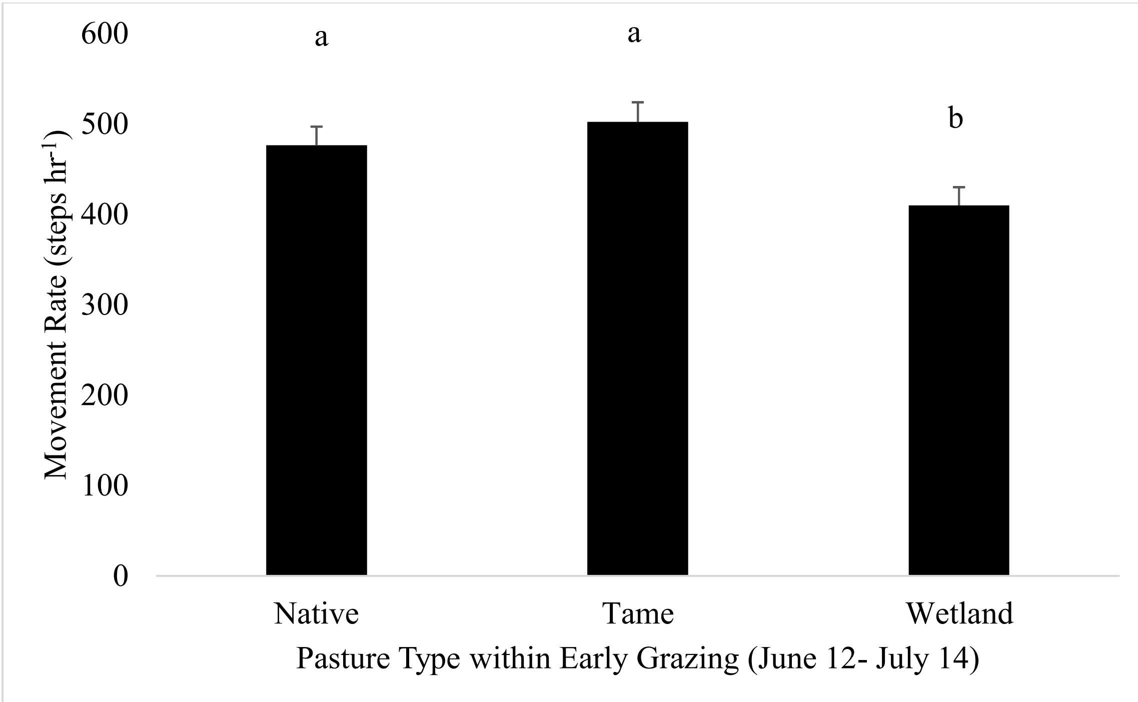

Figure 2.7. Analysis of variance comparing mean (± 20.5, 21.8, 19.9 SE for Native, Tame and Wetland respectively) movement rate (steps hr^{-1} of standing time) for 27 cattle in different pasture types within the early grazing season. Data are averaged over RFI groups. Data presented are untransformed, but analysis is based on square root transformed data. Means with different letters are significantly different ($P \leq 0.02$).

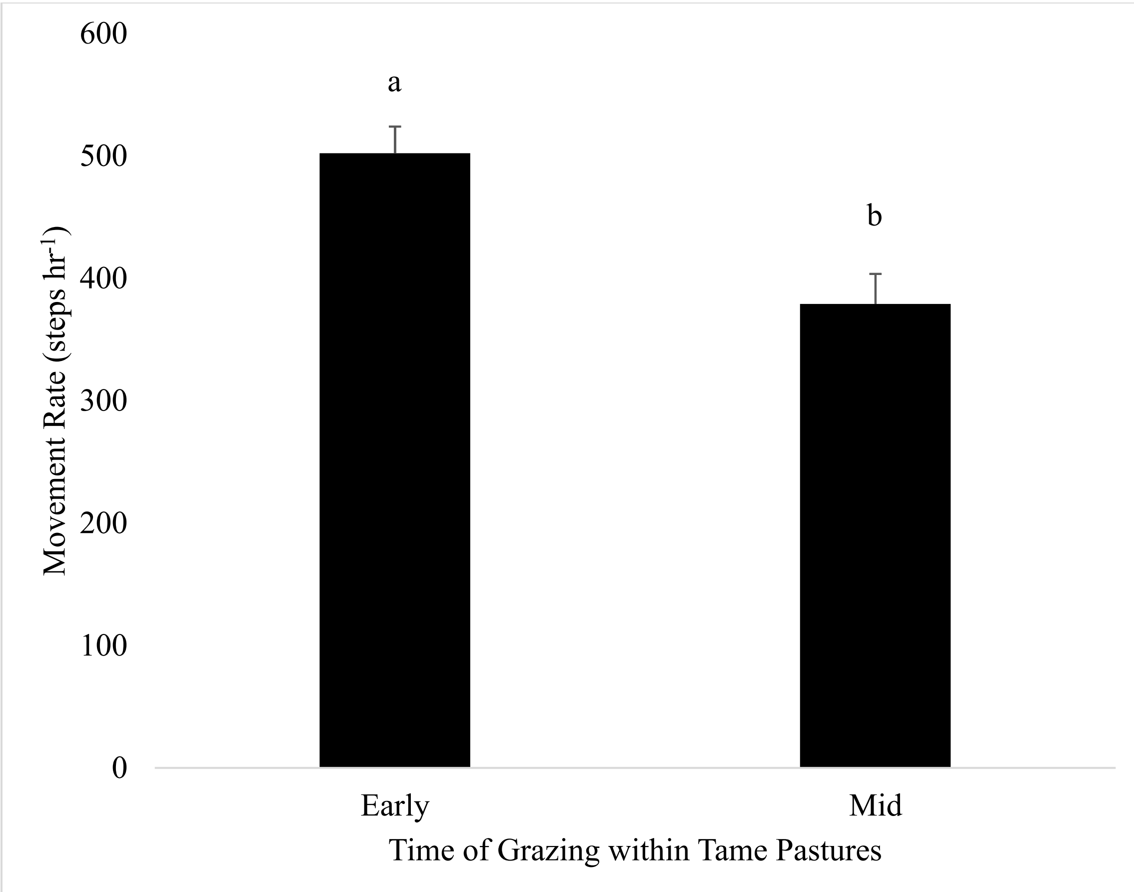

Figure 2.8. Analysis of variance comparing mean (± 21.8 and 24.5 SE for early and mid- season grazing, respectively) movement rate (steps hr^{-1} of standing time) for 27 cattle during the early and mid-summer grazing seasons within the tame pasture type. Data are averaged over RFI groups. Data presented are untransformed, but analysis is based on square root transformed data. Means with different letters are significantly different ($P \leq 0.0001$).

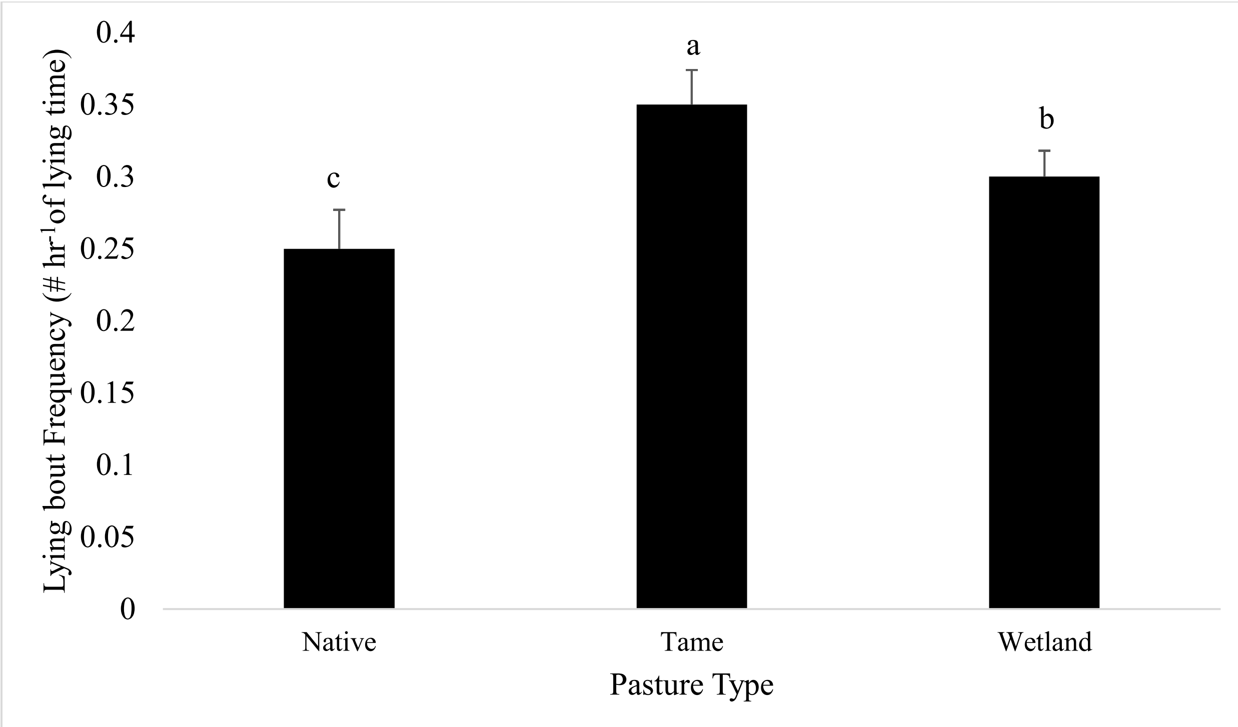

Figure 2.9. Analysis of variance comparing mean (± 0.03, 0.02, and 0.02 for native, tame and wetland pastures, respectively) lying bout frequency (# times hr^{-1} of total time) of 27 cattle over three pasture types. Data are averaged over two time periods of grazing [early (June 12- July 14) and mid-season (July 15- August 31) grazing]. Means with different letters are significantly different ($P \leq 0.05$).

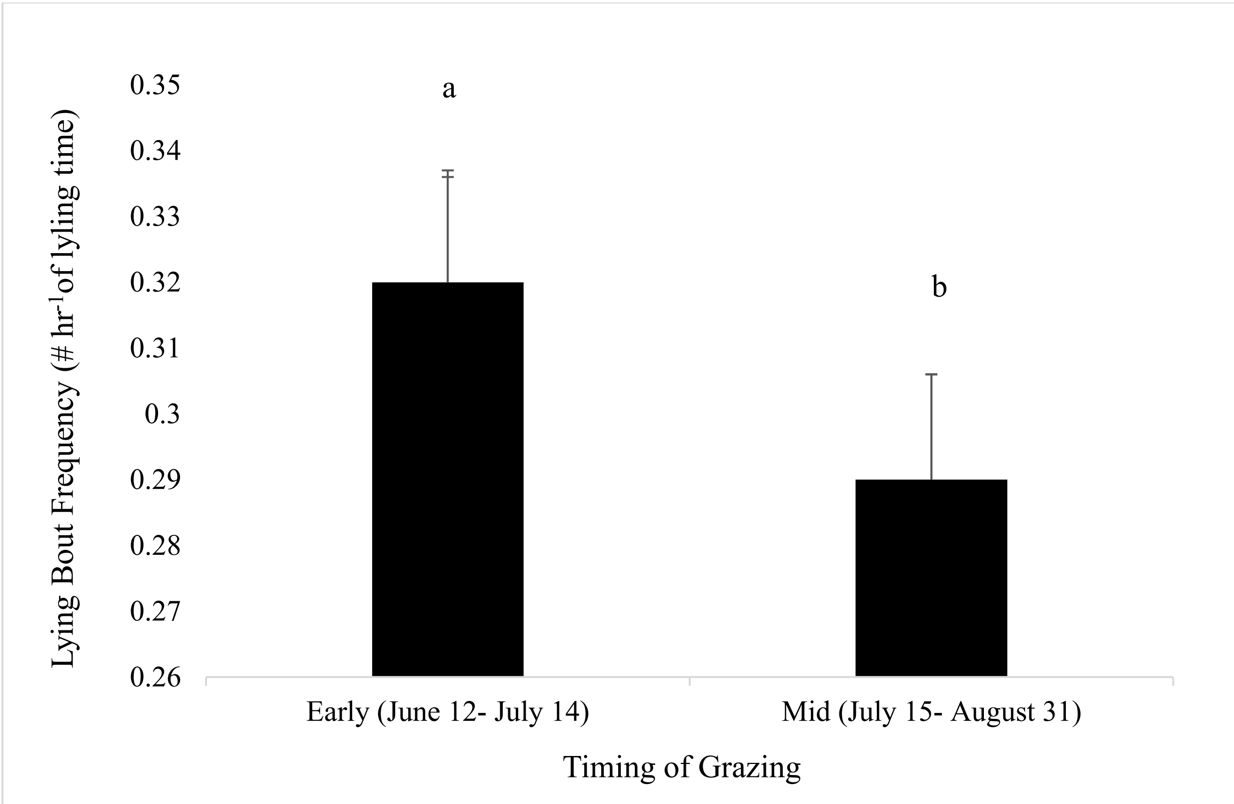

Figure 2.10. Analysis of variance comparing mean (± 0.02) lying bout frequency (# times hr^{-1} of total time) for 27 cattle within two periods of grazing. Data are averaged over three different pasture types (native, tame, and wetland) and both RFI groups. Means with different letters are significantly different ($P \leq 0.006$).

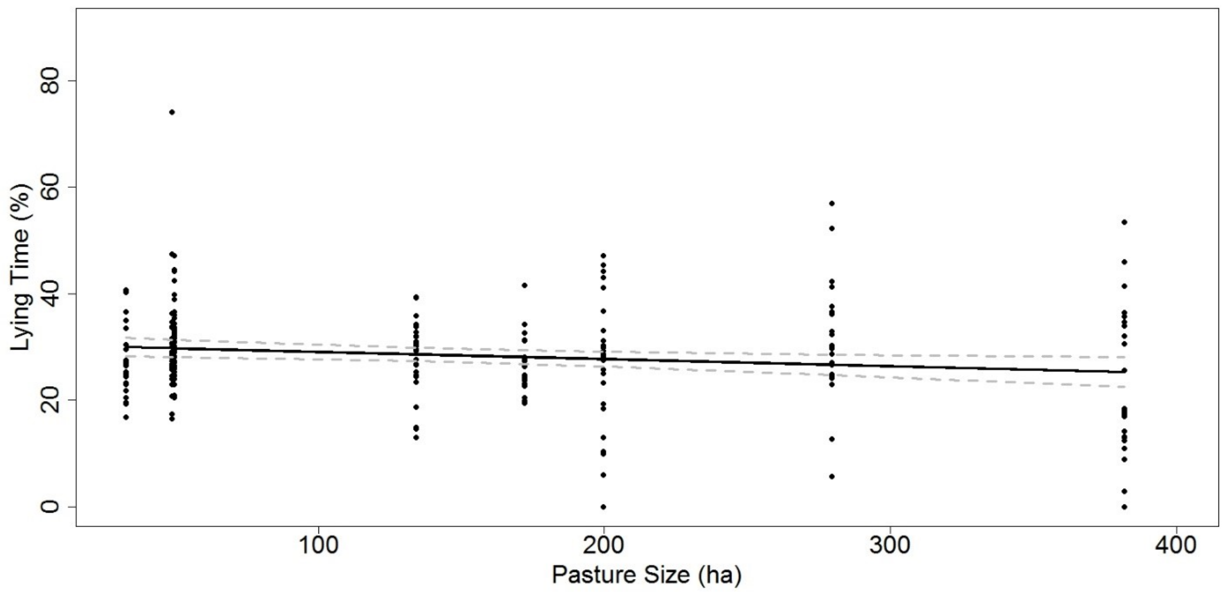

Figure 2.11. The relationship between mean (± 95% fitted confidence intervals) lying time (% of total activity time) of 27 cattle and the size of 13 pastures (native, tame and wetland types) across two grazing times (early and mid-season). Lying time decreased with increasing pasture size ($LT = 30.45 - 0.01PS$: Adj. $R^2 = 0.02$; $P < 0.05$).

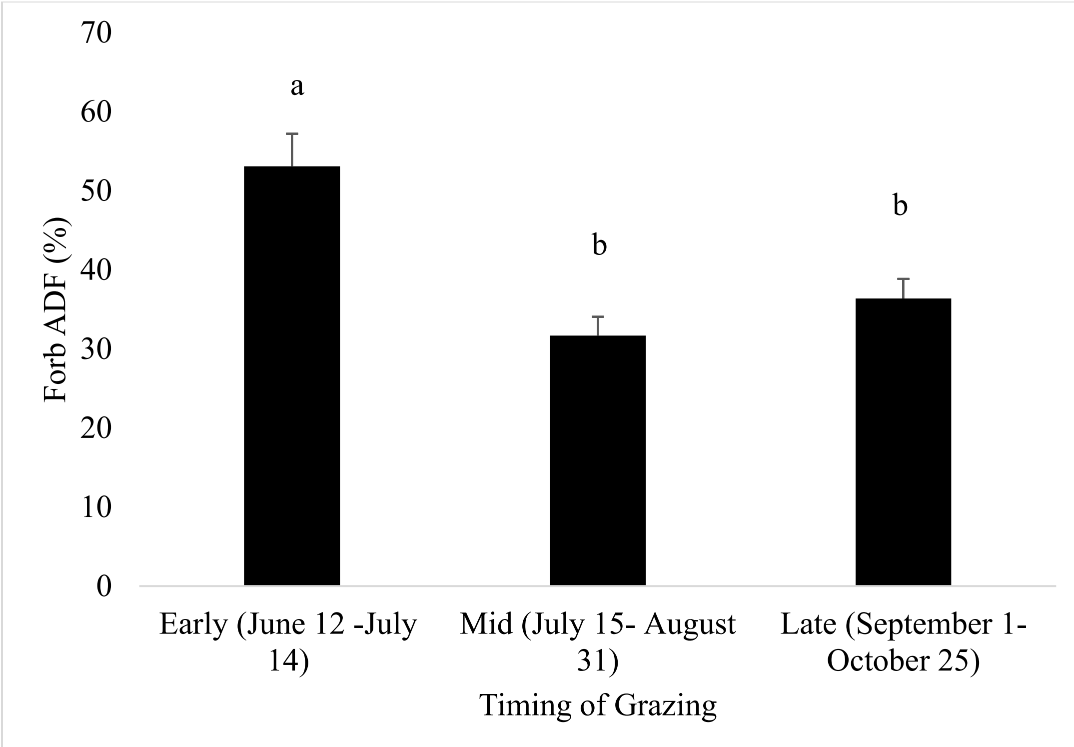

Figure 2.12. Analysis of variance comparing mean (± 4.1, 2.4, 2.5 SE for early, mid, and late season of grazing, respectively) forb fiber concentrations (%) over different times of grazing. Data are averaged over topographic/soil types (upland, midland, lowland types). Means with different letters are significantly different ($P \leq 0.02$).

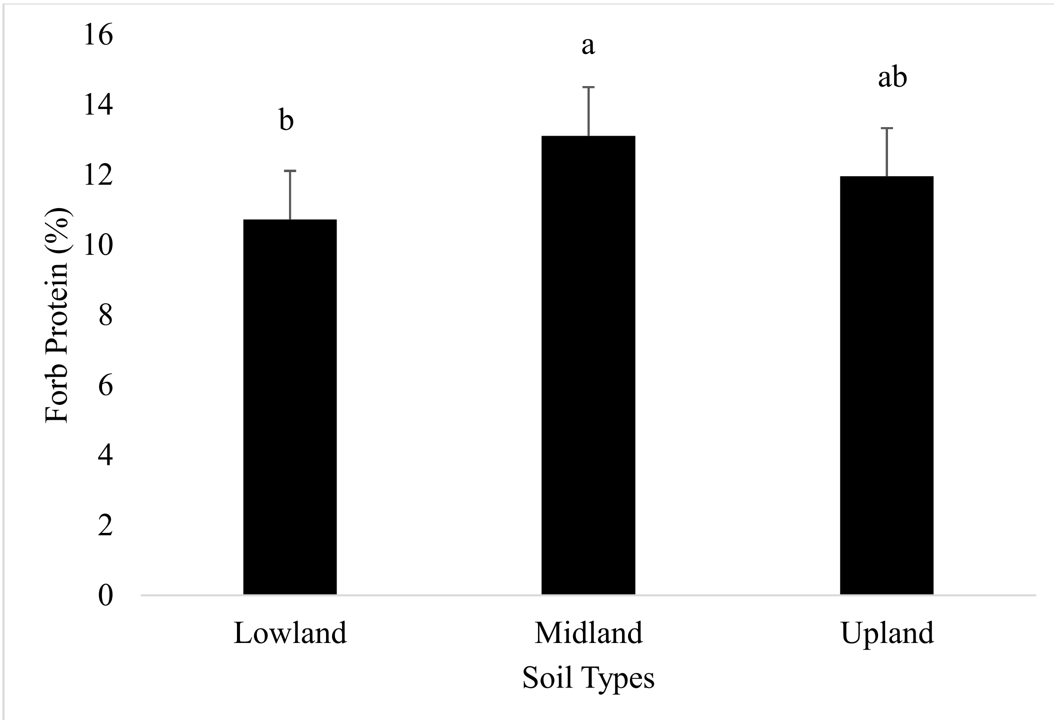

Figure 2.13. Analysis of variance comparing mean (± 1.4 SE) forb protein concentrations among different topographic/soil types. Data are averaged over times of grazing (early, mid, and late season grazing). Means with different letters are significantly different ($P \leq 0.05$).

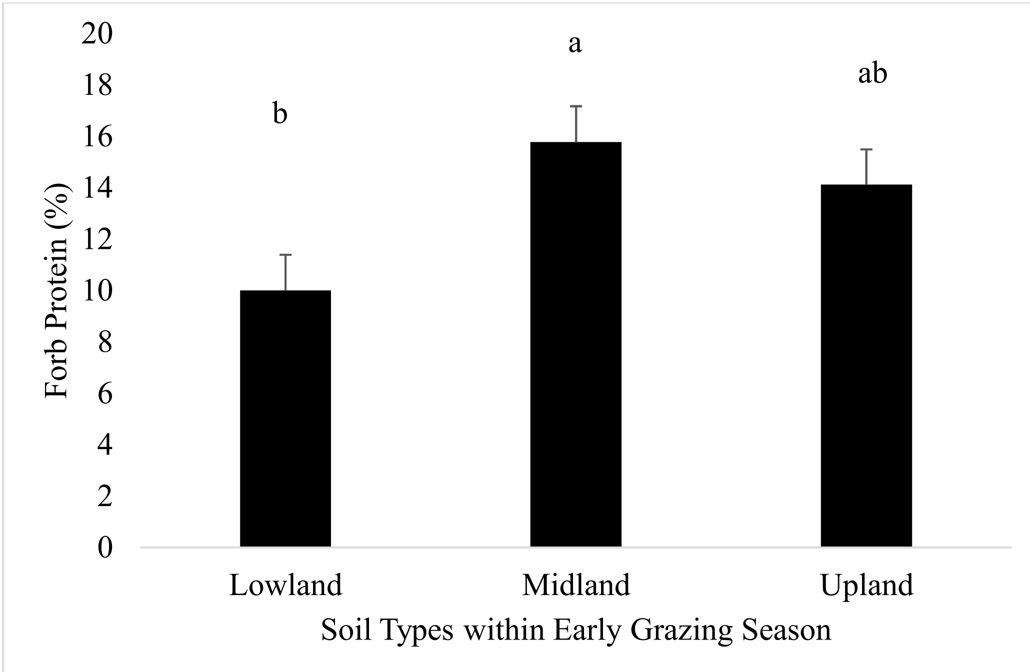

Figure 2.14. Analysis of variance comparing mean (± 3.3 SE) forb protein concentrations among different topographic/soil types, during the early season of grazing (June 12- July 14). Means with different letters are significantly different ($P \leq 0.05$).

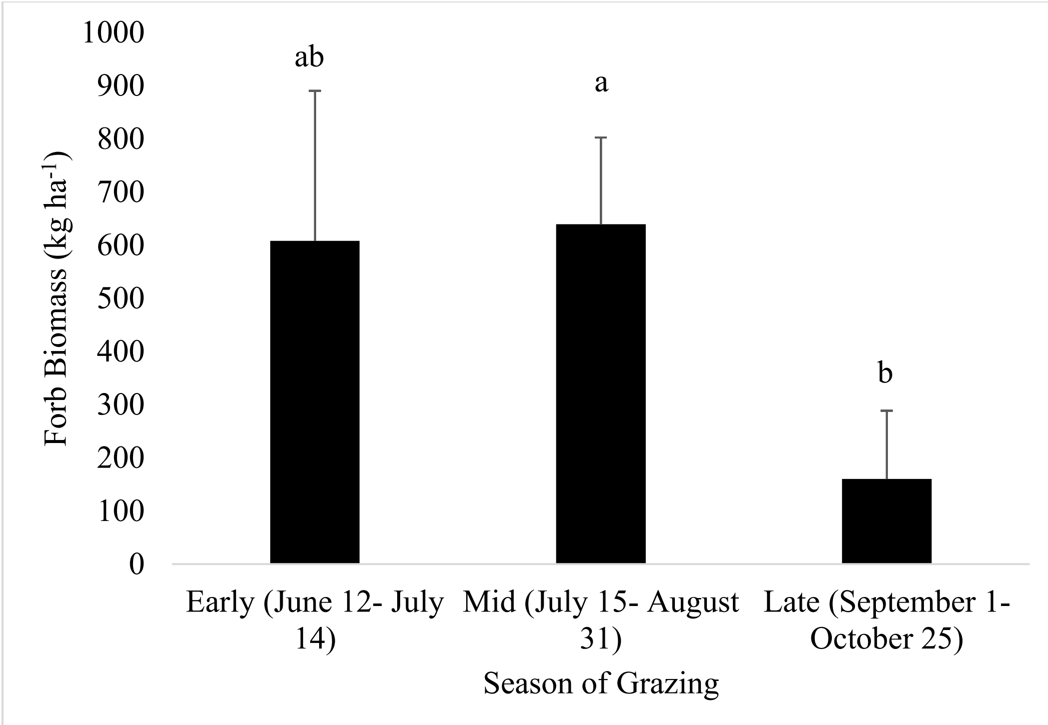

Figure 2.15. Analysis of variance comparing mean (± 282.1, 162.9, 128.6 SE for early, mid, and late season grazing, respectively) forb biomass over seasons of grazing. Data are averaged over topographic/soil type (upland, midland, lowland types). Data and SE presented are untransformed, but analysis is based on square root transformed data. Means with different letters are significantly different ($P \leq 0.05$).

Chapter 3. Resource Selection Analysis of Rangeland Cattle with Divergent Molecular Breeding Values for Residual Feed Intake

3.1 Introduction

Feed consumed, digested and absorbed by animals contributes to either maintenance or production, the latter of which includes growth and/or the rearing of young. Up to 75% of total dietary energy cost is used for maintenance (Basarab et al. 2003), creating high feed costs for producers to simply maintain their herd. Residual feed intake (RFI) is the difference between metabolizable energy of intake and the metabolizable energy required for maintenance and gain, and is independent of growth and maturity patterns (Okine et al. 2004). RFI is a moderately heritable trait (Berry and Crowley 2013) that producers can use to help identify animals in their herds that divert lower amounts of energy towards maintenance and instead use higher amounts of their feed to achieve growth and lactation. Selection for these animals (i.e. with lower RFI) can either be done through direct testing of growth and feed intake in controlled pen feeding trials (Basarab et al. 2003; Basarab et al. 2007; Wang et al. 2006), or alternatively can be done through the use of molecular breeding values (MBVs), which are established with scientifically tested associations between multiple markers on the bovine genome and the animal's actual residual feed intake (Moore et al. 2009). Selection for greater feed efficiency could result in a 9 to 10% reduction in maintenance costs for the cow herd (Moore et al. 2009), so selecting for RFI has important implications for cattle producers.

Past research on RFI has mostly been done in a drylot situation, where there is close proximity to high quality water, and a readily available and standardized good quality feed. In addition, confined spatial areas greatly limit animal movement due to the lack of need to travel about in their search and consumption of food and water. Controlled drylot environments have been integral for creating the conditions necessary for exploring the fundamental association between animal production and their genetic constitution for feed efficiency (i.e. RFI). Even within a drylot setting, Richardson and Herd (2004) found that cattle feeding patterns and activity (feeding session length and number, time standing) still explained 2 and 10% of the variation in RFI, respectively.

Relative to feedlot conditions, livestock that are foraging within a pasture environment must deal with much greater complexities in resource availability. Pastures can be expansive in size with few water sources of varying quality. Moreover, forage resources are likely to differ in quantity, quality, and accessibility, both spatially across the landscape and temporally throughout the grazing season (Bailey et al. 1996; Coughenhour 1991; Senft et al. 1987). Biomass availability progressively increases through peak growth times, then declines with ongoing senescence. In contrast, forage quality is initially high, then declines with advancing vegetation development.

There is an entire body of research that quantifies cattle grazing behaviour in response to these terrain factors, plant toxins and nutrients, distance to water and changing environmental conditions (e.g., heat, rain, wind, insects, and predators). This in turn, has led to a greater understanding of how the spatial arrangement of vegetation and where the animal was raised collectively affect foraging choices, and how memory plays a part in their use of the landscape and plant communities (Galyean and Gunter 2016; Bailey et al. 1996; Provenza 1995; Coughenour 1991). Although there have been scientific efforts to quantify the energetic costs of these additional activities (Di Marco and Aello 2001; Osuji 1974), there is still no answer as to how cattle feed efficiency (i.e. RFI) is affected by the use of landscapes with varying environmental characteristics like forage quantity and quality, as well as water availability.

Effectively quantifying movement and habitat use of livestock on pasture is a challenging process on its own. Using non-automated methods requires observers to follow individual animals, potentially introducing observation bias and requiring significant manpower commitment. With the advent of global positioning system (GPS) collars, however, research on cattle behaviour (at least on habitat use) has become much easier and scientifically rigorous, enabling the continuous tracking of animal locations over an extended period of time (Handcock et al. 2009). GPS collars have been used on livestock to determine distances of travel (Bailey et al. 2010; Bailey et al. 2006), terrain and landscape use (Bailey et al. 2015; Kaufmann et al. 2013b; Ganskopp and Bohnert 2009), as well as pasture activity (Ungar et al. 2005). To our knowledge, collars have not been used in the next vital step to associate habitat use with animal performance and corresponding MBVs for RFI. Doing so is important so producers are able to both ensure that the landscape is used sustainably and predict and manage livestock performance based on the habitat they use.

One objective of this study was to use GPS collars to determine if there are differences in open-range habitat selection between cattle with MBVs for high or low RFI. We hypothesized that cows with lower MBV's for RFI (i.e. increased efficiency) will occupy habitats with greater forage mass and improved quality metrics, and/or prefer to occupy areas closer to water, compared to cows with high MBV's for RFI (i.e. less efficient). These hypotheses are formulated with the logic that efficient animals will be more likely to find and occupy habitat with optimal forage quantity and quality, as well as access to water, while minimizing the energy spent travelling, searching and using less suitable habitats. In theory, selecting high quality forage should make it easier for an animal to meet its energetic requirements, and staying close to water would prevent the animal from wasting excess energy travelling to it, thereby leading to greater cow summer weight gain and calf weaning weight.

The second study objective was to explore whether variation in cattle production metrics (weight gain, fat gain, calf gain) was better predicted by the average use of environmental variables (forage conditions, environment, or landscape features), MBV for RFI, or an interaction of these factors. This question will help us determine how animal genetics and their habitat selection interact to affect beef cattle production.

3.2 Materials and Methods

3.2.1 Study Area

The Mattheis Research Ranch is situated within the Dry Mixedgrass natural subregion of Alberta and has an abundance of both C_3 (cool-season) and C_4 (warm-season) plants. Common grasses at the ranch include *Hesperostipa comata*, *Pascopyrum smithi*, *Bouteloua gracilis*, *Calamovilfa longifolia*, *Koeleria macrantha*, and various *Poa* species, among others. Rose and sage species with some chenopods dominate the rest of the vegetative component, although there is a large diversity of other native forbs. Although the cattle actually grazed 21 different pastures total over the grazing season, only fourteen different pastures were considered in our study, because the other pastures were smaller than 13 hectares and so cows spent no more than two days in these pastures at very high stocking densities (over 50 head ha^{-1}) compared to other study pastures. Nine of the 14 pastures (1453 ha) used in this study were comprised of native upland grasslands. The Ranch also has 98 ha of improved (tame) pastures with irrigation pivots and seeded forage that were grazed during this study. Additionally, several pastures (339 ha) are strongly influenced by water addition and associated sub-irrigation arising from an influx of overflow irrigation water into a series of Ducks Unlimited-created wetlands. The resulting landscape contains open wetlands, surrounding riparian areas, interspersed shrublands, and an abundance of hygric and mesic plants like sedges, wetland grasses and forbs. *Shepherdia argentea* is a native shrub that is encroaching into sub-hygric areas of the landscape, and the irrigation canals are a potential invasion mechanism for weed seeds such as *Sonchus arvensis*, *Cirsium arvense*, *Crepis tectorum*, and *Arctium minus*, among others, markedly increasing the diversity of vegetation within these pastures.

The elevation of the study area ranges from 700 to 723 meters above sea level, although the typical relief within a pasture is limited (1-5 m). The general topography of the landscape is quite flat, but there are areas with vegetated rolling sand hills creating barren hill tops and moist depressions. Soils are primarily Brown Chernozems on more loamy soils, with stabilized sandy grasslands containing Humic Regosols; wetlands are likely to be gleyed. Average growing season temperatures range from 11.4°C in May to 19.2°C in July. The total growing season precipitation reported in 2015 was 259 mm, slightly above the 30-year average for this period (248 mm), and the average monthly temperatures from April to October in 2015 were similar to long-term norms for the period that ranged from 4 - 20 °C.

3.2.2 Cattle Herd and Collection of Production Metrics

This study used 27 animals selected from a commercial herd of 450 head of predominantly Hereford/Angus cross cattle grazing on 2750 hectares of pasture at the Mattheis Research Ranch in SE Alberta. These animals were the same used in Chapter 2 for the assessment of activity budgets using pedometers. The whole herd was assigned MBVs for RFI using genomic best linear unbiased prediction (GBLUP) of genotyped (BovineSNP50 Beadchip; Illumina Inc., San Diego, CA) ear tissue samples collected using Typifix (Gene Check, Inc., Greely, CO) ear tags from cattle in 2014 (Lansink 2017). From all animals assessed, 12 of the highest and 15 of the lowest predicted RFI scoring animals were selected for behavioral monitoring. The unbalanced number in groups was due to the random order of cattle coming through the chute, and the RFID reader not identifying potential project animals early in the collaring day. The resulting range of MBVs for the high RFI group was from 0.007 to 0.364 with a mean of 0.088 (SD ± 0.11). The low RFI group ranged from -0.149 to -0.081 with a mean of -0.102 (SD ± 0.11). The predicted accuracy of MBVs was 0.33-0.50.

Cows used in this study were owned by the Gemstone Cattle Company, a local producer whose cattle are custom grazed on University of Alberta land. Calving of this herd starts in mid-April and ends in late May. Calves are then processed (vaccinated, etc.) in early June prior to being moved out to pasture with their dams for the rest of the grazing season. From early June through late October the herd was managed as a single large group and rotated through a series of 15 pastures ranging from 32-381 ha in size using a primarily once-over rotational grazing system; cows spent 5-12 days in each pasture (Appendix 1). All handling of animals during the project conformed to animal care guidelines and approvals from the University of Alberta Animal Care and Use committee (AUP #00001284).

Production metrics collected for analysis included cow weight gain, cow back fat gain, and calf weight gain over the grazing season. Initial cow weight and back fat thickness using a chute scale and ultrasound, respectively, were collected during animal processing on June 11, 2015. All animals were assessed for any health concerns and these were addressed as needed. Comments were recorded on these animals. Throughout the summer, the animals were monitored on at least a weekly basis for any health issues like foot rot or general sickness. These animals were treated as needed and their herd tag recorded. A fall cow weight and back fat ultrasound measurement were taken in a chute scale on October 28, 2015.

Data collection for calf weight gain was initiated April 25, 2015 and continued through the rest of the calving season for the project cows until June 8, 2015. Cows were checked daily for new calves. After calving, the dam of the calf was identified by herd tag number and the calf weighed with a fish scale and a duffel bag, sexed, and given a herd ID ear tag. If the cow was uncooperative with allowing us to weigh the calf in the bag, the weight was estimated by the cattle's owner or hired hand. Both cows and calves were assessed visually for general health and treated for any ailments if needed, with comments recorded. All information was recorded in a book while in the field and transferred to a computer file at the end of the day. Fall calf weights were collected in a squeeze chute immediately after weaning. Steers and heifers were weighed in groups on separate days, with the heifers weighed first.

3.2.3 GPS Collar Data Acquisition

On June 11, 2015, Lotek 3300 LR GPS collars were attached to 27 cows, with 15 placed on low RFI cows (MBVp = -0.149 to -0.081) and 12 on high RFI cows (MBVp = +0.007 to +0.364). Each GPS collar was initially loosened to its largest circumference, then tightened sufficiently to leave approximately 2 cm of space to ensure fit and comfort for the animal.

Collars needed no extra operational equipment outside of the store-on-board computer and batteries within the pack at the bottom of the collar. Collars were set to a more frequent 15 minute fix interval from 0400 hrs to 2200 hrs during daytime and an hourly fix rate from 2201 hrs to 0359 hrs during night-time. Data collected from the collar included the time of GPS fix, temperature, latitude and longitude of the fix point, and head movement sensor data. Fit for collars was checked throughout the summer. If issues were noticed (too tight, too loose, collar falling off) the animal was brought in and the collar adjusted. The occasional collar came off during the summer. Once these collars were located, the previous data were downloaded, the collar was reinitialized, and then the collar promptly reinstalled on the cow. Throughout the grazing season, a VHF antenna was used to confirm collars were in working order at least once a month. Collars collected data until the fall processing of animals on October 27, 2015. At that time collars were removed and all data were downloaded onto a personal computer.

3.2.4 Forage Quality and Quantity

Forage conditions were assessed within each of the study pastures throughout the summer at the time cattle were present. A soils and vegetation geodatabase (Becker 2013) of the ranch in ArcMap was used to select 30 random points that were stratified by the proportional area of all soil types within each pasture (n = 480 quadrats in total for the entire grazing season). Soil types were used as they effectively distinguished between upland and lowland sites within each pasture, and therefore accounted for the majority of variation in spatial distribution of primary plant communities (Becker 2013). In the field, each point was located using a handheld GPS, and a 50 cm by 50 cm quadrat of vegetation assessed for canopy composition to the nearest 5%, and then clipped to 2 cm height. Harvested vegetation was separated into grasses and grass-likes (hereafter called 'grasses'), and forbs. Where encountered, the current annual growth of palatable shrubs (estimated at < 1% total composition) was included in the forb component. Biomass was dried in an oven at 45°C until constant mass was attained, and then weighed.

To assess forage quality, each of the samples (480 plots x all growth forms – grasses/forbs) were first ground using a Wiley Mill to 1 mm size, then assessed for fiber and nitrogen (N) concentration. To evaluate fiber content, the ANKOM 200 (ANKOM Technology, Macedon, NY, USA) filter bag technique was used for grasses and forbs, which is a proxy for digestibility for cattle. For each quadrat, an ANKOM mesh bag was weighed. After the scale was tared with the empty mesh bag on it, a 0.45-0.5 gram sample of ground vegetation was weighed into this mesh bag, sealed with a heat sealer, then agitated in an ANKOM analysis machine with an 8% sulphuric acidic detergent for 1 hr at 100°C. Mesh bags were rinsed 3 times, for 5 minutes each, with hot water in the ANKOM fiber analyzer machine. Next, they were washed in acetone for 5 minutes in a beaker to remove all water, then air dried on racks for at least 24 hr. Dried bags were subsequently reweighed and weights recorded to derive final fiber concentrations (in %). A blank mesh bag was also weighed and washed as a control and for the formulation of a correction factor. The initial and final weights of the mesh bag, along with a correction factor, were used in the following formula to determine non-digestible fiber content:

$$\%\text{ADF (as received basis)} = \frac{(\text{W3} - (\text{W1} \times \text{C1}))}{\text{W2}} \times 100$$

Where: W1 = Bag tare weight (empty bag weight)

W2 = Sample weight

W3 = Dried weight of bag with fiber after extraction process

C1 = Blank bag correction (running average of final dried weight divided by the original blank bag weight)

Crude protein concentrations were derived using a standard protocol for a LECO TruSpec CN elemental analyzer (LECO Corporation, St. Joseph, MI, USA). Drift calibrations were measured using commercial standards every 10^{th} sample, that spanned the range of expected nitrogen (N) levels within all forage samples to ensure the LECO readings were precise and accurate. Following any adjustments for the standards, all N values were converted to crude protein by multiplying N values by the conversion factor of 6.25.

To prepare the resulting data for analysis, each quadrat's fiber, protein and biomass metrics were matched back to the soil type they occurred on. Herbage biomass was created by summing forb and grass biomass. Herbage protein was calculated by summing grass and forb protein values weighted by the biomass contribution of each growth form in the quadrat, and herbage fiber was calculated similarly. Protein, insoluble (ADF) and soluble fiber yields were calculated for grass, forb and herbage. These metrics at the quadrat level were then averaged together by soil type, within each pasture, in preparation for analysis.

3.2.5. Collar Data Preparation and Statistical Analysis

Raw data from GPS collars were screened for quality and necessary cleaning prior to analysis. GPS fixes for all animals that occurred during the first 6 days (June 10-16) were excluded from analysis to account for the time between initialization and actual collar attachment, the time animals spent standing in the processing pens before being released, and a 5-day buffer period to allow animals time to settle into their normal grazing pattern. Vegetation information was also not collected in this first pasture. The same was done for the last 3 days of data (October 26, 27, 28) to account for the 2 days that cows had calves weaned before collars were removed. Fixes from the specific times of each pasture move plus one hour afterward were removed for all animals to eliminate bias associated with the interruption of normal cattle behaviour. Data from collars that came off and were reattached at some point during the summer were visually inspected to determine when the collar came off and fixes from the first point at which the collar was not on an animal until an hour after the collar was reattached were removed from analysis. The dates June 12 12:01 AM to July 12 7:00 AM were also removed for collars 4383, 4394 and 4385, because these animals were not with the rest of the herd during this time. Data from pastures smaller than 13 ha (2 of 18 pastures) were removed because cows spent at the most only two days in these pastures, and particularly high stocking densities (over 50 head ha^{-1})

within these pastures may have led to different selection patterns compared to the other pastures. GPS collar data within the daily times of 400-1000 hrs and 1600-2200 hrs were used for analysis; previous studies have shown that these times coincide with peak grazing activity in cattle (Ganskopp and Bohnert 2006; Ganskopp 2001; Lofgreen et al. 1957). After all exclusions, 153,999 telemetry fixes remained for analysis.

All fixes from the 27 cattle were then related to all habitat information available. These data were averaged over the entire grazing season to determine 1) if there were any differences in mean habitat attributes used between low and high RFI groups, 2) effects of environmental exposure on subsequent cattle production metrics, and 3) to explore if MBV for RFI were associated with cow and/or calf performance alone, or interactively with environment. All habitat information available in native pastures only was also averaged for this analysis to isolate native pasture effects on cattle production.

Independent variables explored in habitat use included average ADF, protein and biomass for herbage, grass and forbs, the average distance of animal locations to water (Euclidean distance), the ratio of time spent within 200 meters of water, ambient temperature (from collars), topographic position occupied, and average distance of animal locations to shrub (Euclidean distance) (Table 3.). If any variables were found to be collinear ($r \geq 0.6$), they were not included in the same model (see Table 3.2, Table 3.3). The uncorrelated variables used in the analysis of all pastures over the grazing season were grass biomass, forb protein, topographic position index and ratio of time spent within 200 meters of water. The uncorrelated variables used during the analysis of native pastures only were grass biomass and forb fiber, and the ratio (i.e. proportion) of time cattle spent within 200 meters of water. In the second stage of the analysis, uncorrelated habitat use variables were related to cow/calf production metrics (cow weight and back fat gain, as well as calf weight at weaning as a % of mature dam weight).

A multiple analysis of variance (MANOVA) was used to explore differences in the habitat attributes used by high and low RFI groups of cows. Multiple linear regression models were also used to explore the effects of habitat use on animal performance within 1) subcategories of forage variables only, 2) landscape variables only, and 3) environment (forage + landscape together). Finally, MBVs for RFI were added as another fixed effect to the three habitat models from the previous step to determine if RFI had any additive effects in explaining the beef cattle production metrics.

3.3 Results

3.3.1 Characteristics of Habitat Used

Mean herbage mass in the areas used by cattle (based on GPS locations and field sampling data) across all pastures was 2007 kg ha^{-1}, and 320 kg ha^{-1} less than this on native areas (Table 3.4). The majority of biomass available to cattle was comprised of grasses and sedges (about 80%). Mean protein levels across all pastures that cattle used were 10.2%, but just over 8% on native pastures, and forbs had higher protein than grasses in both cases (Table 3.4). Fiber concentrations were similar between all and native only pastures. Notably, cattle spent around half of their time within 200 m of water. Cattle utilized areas at an average distance of 347 meters from shrub in all pastures, 45 meters closer than that typically used in native pastures alone. Distances to shrub and water were found to be correlated (Table 3.2, Table 3.3). Cattle were generally exposed to mean temperatures about 2 °C lower in native pastures compared to all pastures combined (Table 3.4).

3.3.2 Production Metrics and Environmental Use

Cow weight gain, nor calf weaning weight as a proportion of dam weight, were not significantly related to forage, landscape or environmental models that included the selected habitat characteristics (see section 3.2.5) used across all pastures over the grazing season ($P \geq 0.20$, Table 3.5). Cow back fat gain was significantly predicted by the landscape model comprised of the ratio of time spent close to water and topography used (Table 3.5), with 18% of the variation in fat gain explained. Further exploration of the landscape model revealed that as the proportion of time spent within 200 meters of water increased, fat gain decreased (Table 3.6). When we examined use patterns from strictly native pastures, only the landscape model (ratio of time spent near water) significantly predicted the ratio of calf weaned weight to cow weight ($P = 0.05$, Table 3.7). As cows spent proportionally more time within 200 m of water, calf weaning weight was reduced ($\beta = -0.28 \pm 0.14$ SE). None of the other two production metrics (cow gain, back fat gain) were significantly predicted by any forage, landscape, or environmental model ($P \geq 0.15$, Table 3.7).

3.3.3 RFI and Relationships with Habitat Use and Production Metrics

No differences existed in the collective average habitat characteristics used by the study cows across all pastures during the entire grazing season relative to RFI grouping based on a MANOVA; this pattern occurred for both forage metrics, landscape metrics, and their combination ($P \geq 0.51$; Table 3.8). A similar result was found when examined only across native pastures ($P \geq 0.63$) for all 3 combinations of habitat use metrics (Table 3.8). The addition of MBVs for RFI to the habitat use models evaluating associated cow/calf production metrics within all pastures failed to improve the predictive fit for cow gain, calf weaning weight or back fat gain ($P \geq 0.11$, Table 3.9); the same was true when cow/calf production was related only to native pastures ($P \geq 0.14$, Table 3.10).

3.4 Discussion

3.4.1 Characteristics of Habitat Use

The mean habitat attributes selected by cattle tended to differ based on whether tame pasture and wetlands were included together with native pasture. Previous work by Dahl (2014) at the Mattheis ranch supports our finding that native pastures tended to have lower biomass than tame and wetland pastures. This would be expected given the water limited nature of native mixedgrass communities in this environment (Bork et al. 2017) and the benefit of water for growth in wetland pastures, as well as irrigation in tame pastures. Native pasture generally had lower crude protein values compared to other areas (Chapter 2). While the specific cause of these differences is unknown, variation in plant species composition and phenology, again arising from differences in moisture availability, may be the cause. Wetland pastures in particular had a high presence of introduced 'weedy' plant species, which could have added both to total biomass availability, as well as herbage protein values, particularly early in the year as abundant moisture would allow this vegetation to remain actively growing for an extended period throughout the summer. In contrast, native grasslands were generally comprised of early growing, short-statured mixedgrass herbage, and is likely to be exemplified by vegetation with a reduced stem:leaf ratio.

The reduced presence of water also coincided with a trend for cattle to occupy increased mean distances from water within native pastures. This pattern is not surprising if we consider the abundance of water in the wetland pastures and the smaller size of the tame pastures (Appendix 1, Appendix 3); that is, animals had shorter distances to travel to water when these pasture types were included (i.e., across all pastures) compared to the native pastures. Notably, the lower temperatures experienced by cattle in native pastures were unexpected as shrublands are capable of providing shade from high summer temperatures. Instead, native pastures with limited shrub cover may experience cooler nighttime temperatures, and the lack of shrub cover may also lead to increased wind, which in combination, could subject cattle to cooler conditions in native grassland.

3.4.2 Production Metrics and Environment Use

It was important to average the habitat use data over the entire grazing season for this portion of the analysis because our production metrics were derived from measurements collected at the beginning and end of the grazing season. The absence of intra and inter-pasture variation in production metrics (and therefore among pasture averaging) may explain the non-significant results for the analysis of overall production metrics within native pasture, and cow gain and calf weight gain across all pastures. The two metrics demonstrating relationships with performance were cow fat gain and calf weaning weight as a percentage of cow weight. Both metrics decreased as cows spent a greater proportion of their time close to water. This may have occurred because animals that were unwilling to move further from water may have limited their diet during foraging to areas that were either markedly depleted of biomass due to heavy use (i.e. the piosphere effect; (Thrash and Derry 1999)), or had diet qualities that were lower in forage quality (i.e. see Chapter 2). The latter is supported by habitat use data for the entire grazing season, which showed a trend for herbage crude protein concentrations to be higher on the whole landscape compared to areas within 200 meters of water. In contrast however, grass biomass was generally higher in areas close to water. These findings speak to the complexity of rangeland ecosystems and indicate cattle production cannot be managed by focusing on only one metric of the forage resource. Notably, when forage metrics were added to the landscape model, it decreased model fit (Table 3.5, Table 3.7), suggesting foraging conditions had less influence than landscape factors in regulating cattle use and production. Alternatively, water availability is likely at least partly indicative of foraging conditions, particularly in a semi-arid environment where water limits plant growth, suggesting at least some redundancy between forage availability and landscape factors within the analysis.

3.4.3 RFI and Relationships with Habitat Use and Production Metrics

Our hypotheses of differing habitat use between RFI groups were rejected. The lack of differences in environmental use between RFI groups could be due to several reasons. MBV's for RFI tended to be relatively low in accuracy (0.334 - 0.498 for this population), and with the two groups of animals in this study, the predicted RFI scores overlapped (SD ± 0.11). In addition to the challenges of genetic accuracy, Wood et al. (2014) found that determining phenotypic RFI on forage based diets, and while an animal is pregnant, is difficult because of the greater variation these conditions impose on an animal's feed efficiency (forage quality and conceptus growth as respective examples). Conditions in the previous study (gestating cows on a forage-based diet) were similar to our project animals, with our cows likely exposed to even greater variation in the quality of forage available (native prairie vs. hay, silage and straw diets in the cited trials). Even if our cows had very accurate genetic breeding values for RFI, the complexity of environmental variables may have had a strong effect on our animal's efficiency and their subsequent performance (weight gain, etc.), thereby creating too much variation to express true differences in habitat use between RFI groups.

Other factors that affect animal responses to environmental variables are social dynamics and dominance. The selection of certain foraging areas may be influenced by one or two individuals leading the group (Bailey 1995), and environmental conditions (availability of forage, temperature regulation) influence how closely group members stay together (Harris et al. 2007). Stephenson et al. (2016) found that in larger herd sizes (53 - 240 cows), associations between animals were not random but remained low, and may have been so because of a preference for a particular pasture area. Physical characteristics of the pastures (size, water sources, etc.) and associated management of cattle do appear to be significant factors within subgroups forming strong associations between grazing animals (Stephenson and Bailey 2017). Thus, these factors should be considered when determining whether a small number of individuals can be collared without creating biased results (Stephenson and Bailey 2017). In comparing the large pastures rotationally grazed at the Mattheis Ranch and the management conditions (animals kept in one large herd the entire year with little other disturbance) to the various study ranches examined by Stephenson and Bailey (2017), we propose that our study (collared) animals could have strong associations with others. To be conclusive, association patterns would have to be explored through further analysis (Stephenson and Bailey 2017; Stephenson et al. 2016; Harris et al. 2007; Bailey 1995). As we did no prior study of social dominance within our cattle herd, we may have collared subdominant animals, and if so, the habitat use we reported may have been affected by other dominant animals, in turn impacting the behavior and performance metrics independent of predicted RFI. Although studying social dominance alone did not provide clear relationships with grazing behaviour and performance elsewhere (Sato 1982), when attempting to account for all variation in the pasture environment to attempt to predict RFI, it would appear to be an important consideration.

Social interactions aside, simply more animals may need to be collared to fully quantify variation within the herd or even relevant subgroup. Being financially limited by the number of cattle we could collar introduced errors into the accuracy of what habitats animals of differing

RFI groups used. Turner (2000) found that collaring 4 out of 5 animals studied introduced 10% error in their location and subsequent habitat use, and 40% error with 1 of 5 cows collared. There were 45 animals categorized as high RFI and 46 animals categorized as low RFI in our project. Extending the logic from Turner (2000), we could consider that because we collared 26% (12/45) and 33% (15/46) of our RFI groups, we may not have evaluated enough animals from each RFI group to effectively encompass the natural variation in habitat use among animals, resulting low statistical power in detecting differences in habitat use.

3.5 Conclusion

No differences in habitat use were found between low and high RFI groups in this study, with little relationship to animal production. These results are still important contributions to our currently limited understanding of cattle habitat use and its relationship to both performance and RFI on our Western Canadian prairies. As one of the first studies to link GPS collar data to RFI marker-tested cattle on Mixedgrass prairie in Alberta, our research identifies several aspects of studying RFI in these conditions for future research to improve upon. Our results show that more research needs to be done on validating predicted RFI values within pasture-based systems. This would first involve more conclusive work in accurately determine animal feed efficiency while grazing on rangelands and during pregnancy. This would be the basis for creating the ability for further research on marker testing that more accurately predicts RFI in these (extensive cow/calf) production systems.

GPS collar studies done in Alberta previously with cattle (Kaufmann et al. 2013a; Kaufmann et al. 2013b) and wildlife (Girard et al. 2013; Nielsen et al. 2010; Hebblewhite et al. 2007) have focused on determining and predicting land use patterns (see Chapter 1). Our study took the next step forward and focused more on answering the question of how do habitat use patterns affect animal production. The latter is what beef producers are most concerned about, as it directly affects profitability. Cows that spent more time near water were found to have reduced fat gain and smaller calves, results that support the large body of research already existing that says cattle prefer to be close to water. These findings have implications to producer management and subsequent profitability. By adding water sources in large pastures, producers could potentially increase the overall utilization of their landscapes and provide more opportunities for cattle to be exposed to a greater variation of good quality forages, which could improve animal performance through the grazing season.

3.6 Literature Cited

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Table 3.1. Covariates used for examining habitat use of 15 low and 12 high RFI animals (based on MBV) within the Dry Mixedgrass prairie of SE Alberta.

Variable	Description
Forb biomass[1]	Biomass of forbs calculated from $0.25m^2$ quadrats
Grass biomass[1]	Biomass of grasses calculated from $0.25m^2$ quadrats
Forb crude protein[2]	Protein concentration (%) of forbs from biomass collected in $0.25m^2$ quadrats
Grass crude protein[2]	Protein concentration (%) of grasses from biomass collected in $0.25m^2$ quadrats
Forb acid detergent fibre[2]	Non-digestible forb biomass (%) collected in $0.25m^2$ quadrats
Grass acid detergent fibre[2]	Non-digestible grass biomass (%) collected in $0.25m^2$ quadrats
Herbage biomass[1]	Total biomass of grasses and forbs within and scaled up from $0.25m^2$ quadrat
Herbage crude protein[2]	Protein concentration of grasses and forbs (%) weighted by composition within and scaled up from $0.25m^2$ quadrat
Herbage acid detergent fiber[2]	Non-digestible herbage biomass (%) of grasses and forbs weighted by composition within and scaled up from a $0.25m^2$ quadrat
Temperature[3]	Temperature logged by GPS collar at each fix interval
Distance to water[4]	Euclidean distance to the nearest body of water
Distance to shrub[4]	Euclidean distance to the nearest shrubland
Topographic position[5]	Index describing topography based on elevation. Grid cell size was 5 m, and scale used was 31 cells. Most negative values denote a depression, most positive are hilltops.
Time spent within 200 m of water	Proportion of points (%) each animal was present in an area of 200 meters or less to water (out of entire dataset)

[1] Expressed kg ha^{-1}
[2] Expressed in %
[3] Expressed in °C
[4] Expressed in meters
[5] Index from -1.1 to 1.6
[6] Ratio from 0- 1

Table 3.2. Pearson correlation matrix associated with the environmental values within all pastures used by 27 collared cattle during the grazing season on mixedgrass prairie. Bolded values within the matrix indicate correlation over the assigned threshold of 0.6. Underlined variables indicate those that were used in the respective habitat models for analysis.

	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.	14.
1.Herbage biomass[1]	1													
2. Herbage crude protein[2]	**0.73**	1												
3. Herbage ADF[2]	**0.74**	0.31	1											
4. Grass biomass[1]	**0.95**	0.61	**0.69**	1										
5. Grass protein[2]	**0.66**	**0.99**	0.25	0.54	1									
6. Grass ADf[2]	**-0.84**	**-0.93**	-0.41	**-0.79**	**-0.90**	1								
7. Forb biomass[1]	**0.70**	**0.71**	0.54	0.44	**0.68**	-0.59	1							
8. Forb crude protein[2]	**0.71**	**0.98**	0.36	0.54	**0.97**	**-0.86**	**0.83**	1						
9. Forb ADF[2]	-0.34	**-0.80**	-0.12	-0.11	**-0.84**	0.56	**-0.75**	**-0.88**	1					
10. *Temperature*[3]	**0.71**	**0.86**	0.55	0.51	**0.83**	**-0.75**	**0.88**	**0.91**	**-0.83**	1				
11. *Distance to shrub*[4]	-0.26	-0.54	-0.36	-0.07	-0.56	0.38	**-0.62**	**-0.64**	**0.75**	**-0.74**	1			
12. *Distance to water*[4]	-0.26	-0.27	-0.45	-0.16	-0.26	0.18	-0.37	-0.34	0.39	-0.45	**0.72**	1		
13. *Topographic position index*[5]	-0.01	0.33	-0.08	-0.09	0.38	-0.24	0.18	0.32	-0.43	0.29	-0.32	-0.18	1	
14. *Time spent near water*[6]	0.33	0.22	0.54	0.24	0.20	-0.16	0.41	0.30	-0.31	0.46	**-0.68**	**-0.89**	0.13	1

[1] expressed kg ha-1 [2] expressed in % [3] expressed in °C [4] expressed in meters [5] index from -1.1 to 1.6, most positive numbers being hilltops, most negative numbers being valley bottoms [6] ratio of points animal was present in an area of 200 meters or less to water (out of entire dataset)

Table 3.3. Pearson correlation matrix associated with the environmental values within <u>native pastures</u> used by 27 collared cattle during the grazing season on mixedgrass prairie. Bolded values within the matrix indicate correlation over the assigned threshold of 0.6. Underlined variables indicate those that were used in the respective habitat models for analysis.

	1.	2.	3.	4.	5.	6.	7.	8.	9.	10.	11.	12.	13.	14.
1.Herbage biomass[1]	1													
2. Herbage crude protein[2]	**0.96**	1												
3. Herbage ADF[2]	**0.90**	**0.79**	1											
4. <u>Grass biomass[1]</u>	**0.92**	**0.82**	**0.81**	1										
5. Grass protein[2]	**0.86**	**0.94**	**0.71**	**0.60**	1									
6. Grass ADf[2]	**-0.82**	**-0.85**	**-0.73**	**-0.79**	**-0.71**	1								
7. Forb biomass[1]	**0.95**	**0.95**	**0.86**	**0.74**	**0.96**	**-0.74**	1							
8. Forb crude protein[2]	**0.94**	**0.99**	**0.80**	**0.75**	**0.98**	**-0.80**	**0.98**	1						
9. <u>Forb ADF[2]</u>	**-0.80**	**-0.88**	**-0.65**	-0.51	**-0.97**	0.56	**-0.93**	**-0.93**	1					
10. *Temperature*[3]	**0.94**	**0.87**	**0.92**	**0.91**	**0.72**	**-0.83**	**0.85**	**0.84**	**-0.65**	1				
11. *Distance to shrub*[4]	**-0.63**	-0.58	**-0.71**	**-0.65**	-0.45	**0.69**	-0.54	-0.53	0.32	**-0.74**	1			
12. *Distance to water*[4]	-0.21	-0.001	-0.35	-0.48	0.24	0.19	0.04	0.09	-0.32	-0.36	0.57	1		
13. *Topographic position index*[5]	0.05	0.20	-0.01	-0.26	0.45	0.03	0.30	0.30	-0.48	-0.11	0.13	**0.63**	1	
14. <u>*Time spent near water*[6]</u>	0.31	0.11	0.44	0.57	-0.13	-0.26	0.07	0.02	0.20	0.46	**-0.62**	**-0.95**	**-0.61**	1

[1] expressed kg ha-1 [2] expressed in % [3] expressed in °C [4] expressed in meters [5] index from -1.1 to 1.6, most positive numbers being hilltops, most negative numbers being valley bottoms [6] ratio of points animal was present in an area of 200 meters or less to water (out of entire dataset)

Table 3.4. Mean, minimum (Min), maximum (Max) and standard deviation (SD) of the average environmental variables used by 27 collared cattle in the mixed grass prairie. Habitat use was initially collected across each pasture, then averaged per animal over the entire grazing season (Average Use in All Pastures) as well as averaged over native pastures only (Average Use in Native Pastures Only). Summary statistics shown below are of these two secondary datasets.

	Average Use in All Pastures				Averaged Use in Native Pastures only			
Variable	Min	Max	Mean	SD	Min	Max	Mean	SD
Herbage biomass[1]	1814	2410	2007	137	1444	2103	1687	137
Herbage crude protein[2]	9.0	13.8	10.2	1.0	7.5	9.7	8.2	0.5
Herbage ADF[2]	37.7	40.1	38.9	0.4	37.5	39.8	38.4	0.4
Grass biomass	1370	1963	1605	110	1271	1606	1391	65
Grass protein	8.3	13.4	9.6	1.1	6.8	8.4	7.4	0.4
Grass ADF[2]	39.6	41.4	41.0	0.3	41.1	42.0	41.7	0.2
Forb biomass	347	561	402	46	148	540	296	82
Forb crude protein[2]	11.1	14.6	12.1	0.9	9.2	12.6	10.4	0.7
Forb ADF	31.2	40.1	38.1	1.8	33.7	42.2	38.7	1.9
Temp[3]	17.3	22.4	19.1	1.5	13.9	23.0	17.3	1.9
Distance to shrub[4]	194	405	347	44.0	295	489	392	41
Distance to water[4]	199	291	239	21.6	204	487	269	54
Topographic Position Index(TPI)[5]	-0.06	0.09	0.01	0.03	-0.07	0.30	0.03	0.07
Time spent within 200 m of water[6]	0.39	0.59	0.51	0.05	0.08	0.61	0.47	0.1

[1] Expressed kg ha^{-1}
[2] Expressed in %
[3] Expressed in °C
[4] Expressed in meters
[5] Index from -1.1 to 1.6
[6] Ratio from 0- 1

Table 3.5. Adjusted R^2, F-statistics and P-values relating leading beef cow habitat use models with various cow/calf production metrics (cow weight gain, percent weaning weight of calf, and cow back fat gain) through multiple regression. Independent response data are from all pastures grazed within the 2015 grazing season.

Model	Cow Gain			Percent Wean Weight			Cow Fat Gain		
	R^2	F-Stat	P-value	R^2	F-Stat	P-value	R^2	F-Stat	P-value
Forage model[1]	-0.09	0.30	0.97	0.06	1.75	0.20	-0.07	0.29	0.75
Landscape model[2]	-0.08	0.15	0.86	-0.07	0.31	0.74	**0.18**	**3.51**	**0.05**
Environmental model[3]	-0.19	0.08	0.98	0.02	1.12	0.38	0.12	1.78	0.17

[1] Forage model included grass biomass and forb protein variables
[2] Landscape model included topographic position index and ratio of time spent close to water variables
[3] Environmental model includes all forage and landscape variables combined

Table 3.6. Multiple linear regression model summary statistics predicting cow back fat gain relative to the main landscape metrics observed within all pastures over the grazing season. Total model R^2 is 18%.

Habitat Use Model	Beta	Standard Error	t-Stat	Partial R^2	Significance
Time spent within 200 m of water[1]	**-0.82**	0.34	-2.44	**0.22**	**0.02**
Topographic position index[2]	0.65	0.46	1.43	0.09	0.16

[1] Measured as a ratio from 0-1
[2] Relative index from -1.1 (valley bottom) to 1.6 (hill top)

Table 3.7. Adjusted R^2, F-statistics and P-values relating leading beef cow habitat use models with various cow/calf production metrics (cow weight gain, percent weaning weight of calf, and cow back fat gain) through multiple regression. Independent response data are for the native pastures only within the 2015 grazing season, which comprised 59% of the time spent grazing.

	Cow Gain			Percent Wean Weight			Cow Fat Gain		
Independent Model	R^2	F-Stat	P-value	R^2	F-Stat	P-value	R^2	F-Stat	P-value
Forage model	-0.09	0.04	0.96	-0.07	0.37	0.69	-0.07	0.30	0.75
Landscape model	-0.05	0.02	0.90	**0.14**	**4.22**	**0.05**	-0.04	0.16	0.70
Environmental model	-0.14	0.08	0.97	0.13	1.98	0.15	-0.10	0.35	0.79

[1] Forage model included grass biomass and forb fiber variables
[2] Landscape model included ratio of time spent close to water variables
[3] Environmental model included all forage and landscape variables combined

Table 3.8. Results of the MANOVA evaluating variation in the characteristics of habitat used between RFI groups of beef cows, which were made up of 15 low RFI animals and 12 high RFI cows grazing mixedgrass prairie. RFI groups did not differ in their use of any environmental variables within all pastures across the grazing season.

		RFI Group Test for All Pastures					RFI Group Test for Native Pastures				
Response Model	df	Pillai score	F-value	Num df	Den df	P-value	Pillai score	F-value	Num df	Den df	P-value
Forage only[1]	1	0.06	0.79	2	23	0.47	0.07	0.41	2	22	0.67
Landscape only[2]	1	0.01	0.15	2	23	0.86	0.01	0.16	2	22	0.85*
Environmental model[3]	1	0.07	0.39	4	21	0.82	0.04	0.29	3	21	0.83

[1] Included forage based variables, (all pastures: grass biomass and forb crude protein; native: grass biomass and forb fiber)
[2] Included landscape based variables, (all pastures: topographic position index and ratio of time spent close to water; native pastures: ratio of time spent close to water)
[3] Included both forage and landscape based variables, as listed above.
* Denotes t-test as this is based on 2 variables only.

Table 3.9. Adjusted R^2, F-statistics and P-values reporting results for the multiple regression of various cow/calf production metrics (cow weight gain, percent weaning weight of calf, and cow fat gain) against habitat and pRFI MBV (as independent variables). Data are for all pastures within the grazing season.

	Cow Gain			Percent Wean Weight			Cow Fat Gain		
Independent Model	R^2	F-Stat	P-value	R^2	F-Stat	P-value	R^2	F-Stat	P-value
Forage + RFI[1]	-0.06	0.54	0.66	0.05	1.37	0.28	-0.12	0.18	0.91
Landscape + RFI[2]	-0.07	0.52	0.68	-0.08	0.50	0.69	0.14	2.28	0.11
Environment + RFI[3]	-0.17	0.33	0.89	-0.003	0.99	0.46	0.09	1.44	0.26

[1] Forage model included grass biomass and forb protein variables
[2] Landscape model included topographic position index and ratio of time spent close to water variables
[3] Environmental model included all forage and landscape variables combined

Table 3.10. Adjusted R^2, F-statistics and P-values reporting results for the multiple regression of various cow/calf production metrics (cow weight gain, percent weaning weight of calf, and cow fat gain) against habitat and pRFI MBV (as independent variables). Data are for native pastures within the grazing season, which comprised 59% of the total time spent grazing.

	Cow Gain			Percent Wean Weight			Cow Fat Gain		
Independent Model	R^2	F-Stat	P-value	R^2	F-Stat	P-value	R^2	F-Stat	P-value
Forage + RFI[1]	-0.07	0.54	0.66	-0.11	0.35	0.79	-0.11	0.27	0.84
Landscape + RFI[2]	-0.01	0.84	0.45	0.10	2.17	0.14	-0.07	0.21	0.81
Environment + RFI[3]	-0.11	0.44	0.78	0.09	1.50	0.25	-0.14	0.32	0.86

[1] Forage model included grass biomass and forb fiber variables
[2] Landscape model included and ratio of time spent close to water variables
[3] Environmental model included all forage and landscape variables combined

Chapter 4. Synthesis

4.1 Research Summary

Predicting feed efficiency through RFI while accounting for activity expenditures, and cattle grazing behaviour in pasture and its effects on performance, have both been extensively explored, but always in isolation of each other. This project was one of the first in Western Canada to attempt to bring these concepts together to explore both the pasture selection patterns of beef cows with contrasting predicted RFI scores, and the subsequent performance of these animals. Selection patterns included investigations into animal activity (e.g. resting and rates of movement) as well as habitat used by cows in relation to changing forage metrics through the grazing season, including the role of pasture type and season of grazing. Performance measurements of the animals included cow weight and back fat gain over the grazing season, and end of season calf weaning weight.

Chapter 2 explored cattle movement rate, lying time, lying bout frequency, and how genetic and environmental factors influenced cow activity and performance throughout the grazing season. The initial hypotheses for this chapter were that low RFI MBV cattle would spend more time resting and have lower movement rates than high RFI cows, and that animals would spend more time lying down when pastures were smaller or when forage was abundant and of better quality. MBVs for RFI did not affect cow movement rates, the proportion of time cows spent lying down, nor the number of times cows got up and down during the whole grazing season. Pasture type (native, tame, wetland) and season of grazing (early, mid, or late season) were the drivers of cattle activity. Lying time decreased as pasture size went up, as predicted. Cows generally had the highest level of activity in the early growing season, with high movement rates and less time spent lying down. Forage metrics were found to affect cattle movement, lying time and the frequency that cows lay down and got up, but the complexity of scale within which cows select habitat on pasture throughout a grazing season creates some uncertainty on how these metrics and subsequent cattle activity affect their production performance.

Exploration of cattle habitat use through GPS collars in Chapter 3 was hypothesized to find that as cattle were genetically predicted to be more efficient, they would choose to spend their time in areas of greater forage mass and quality, and prefer areas closer to water, and that this would help them be more successful in their production performance. Again, our study found no significant differences between animals predicted to be inefficient and efficient. Distances from water that cattle used were found to be a significant predictor of the animals' fat gain and calf weaning weight over the season, but in the opposite way expected. Both back fat gain and calf weaning weight as a percentage of cow weight were found to be lower as cattle spent proportionally more time near water. Because of the scale of measurement for the production metrics (integrated from the beginning to the end of the grazing season), the fine resolution of data collected for forage metrics had to be averaged across the grazing season. This may explain why the forage metric models did not perform well in predicting calf growth or cow condition recovery. A lack of any other significant differences in both Chapter 2 and 3 may have also been due to the predicted RFI scores of our animals not being different enough, or the animals' social dominance structures or other behaviours more strongly driving activity, pasture use, and performance.

4.2 Management Implications

Rangeland managers have the complex goal of achieving an even distribution of animals on the landscape to ensure that all areas are used to a level that the plant community and soil can be sustained. This goal is challenging because of inherited and learned behaviours in cattle, such as repeated and/or excessive use of key areas (watering or salting areas, valley bottoms) with little use elsewhere in the pasture. As reviewed in Chapter 1, there is a significant body of research that provides both management tools and genetic selection of animals for range managers to use for controlling cattle landscape use. Selectively breeding (and culling) for animals accustomed to achieving more even use by utilizing hilly topography or travelling longer distances to water would potentially help managers improve rangeland sustainability. The insignificant differences in habitat use and activity by cattle in my study may indicate that further adding selection for low residual feed intake into trait selection indices would not further complicate the work of achieving even rangeland use.

Another important reason for livestock managers to control the use of their landscape is to ensure favorable performance of animals while grazing on pasture. Changes in forage quality and availability are shown in the literature to be key factors regulating weight gain in grazing cattle (Collins et al. 2001). Changes of forage metrics across different locations and time scales were found to influence cattle activity, but changes in those activities in turn, did not affect cattle performance in our study.

When considering habitat use and relationships to cattle performance, we found that cows spending more time within 200 m of water were likely to accumulate less back fat over the grazing season. Although fat is energetically expensive to create (Berry and Crowley 2013), it is essential to lower feeding costs, and helps maintain cow health and pregnancy over winter. Research by Bailey (1996) discusses how managers have the ability to alter the path, feeding sites, and camp selection of their animals, but finer scales of selection such as feeding station are much more difficult to assess because it is difficult to identify them all and create management strategies that suit those fine scales. Watering sites are easy to identify and managers can prevent animals from camping at water bodies through salt use or fencing to ensure even use of the land and that animals are exposed to a greater variety of forage quality and quantity.

4.3 Future Research

Many considerations for future research are possible on the topic of validating how genetic selection may affect animal grazing behaviour and performance. For the pedometers, we are still unsure of how close the cattle had to be to the reader station in order for activity data to be downloaded. With the simultaneous collection of GPS collar location, future analysis within the confines of the pedometer data collection radius would be able to create a dataset that we can use to create correlations between habitat selection and cattle activity. With these correlations, we may be able to expand animal activity by habitat to similar landscapes, providing that there was significant variation of habitat within the pedometer collection radius. Maintaining fine resolution forage metrics and landscape properties would allow researchers to create quantifiable connections between these activities and the conditions the animal is exposed to on a pasture-by-pasture level. Further, use patterns may differ between individual animals of differing RFI molecular breeding values or between low or high RFI groups. Cow and calf weight gain should also be metrics included in this area of study, as this would have a great operational benefit for producers.

Our GPS collar research results showed that the potential interaction and stand-alone effects of forage and landscape metrics regulated habitat use, cattle activity, and cattle performance more than an animal's predicted RFI score. Further exploration of this result is warranted as ranch management strategies, physical characteristics of pastures (water sources, pasture size), and social dominance may have also played key roles in habitat use for individual animals (Bailey et al. 1996; Stephenson and Bailey 2017), and account for the variation reported in performance in pasture.

Teasing out the effect of environment from an individual's genetic potential on performance requires long term and high data resolution studies, the most costly of all research. Past studies of performance in relationship to RFI were mostly done in feedlot and therefore can only accurately predict performance in that setting. My study contributes to the body of research beginning to identify how genetic and environmental influences affect cattle performance, and can provide a good stepping stone for future research to expand upon. Using predicted RFI scores with greater accuracy may allow researchers to more easily focus on the effects of environment when testing RFI and cattle performance on pasture, although the feedlot conditions that these predictions are based upon are still very different than those in extensive pastures. By focusing further research on quantifying the variation of cattle responses to environmental factors, development and prediction of phenotypic RFI scores may be possible and lead to the development of predictive genetic RFI scoring for pasture based systems. Regardless of the success of genetic advances though, understanding cattle responses to environmental factors and their effect on performance remains an integral piece of knowledge for beef producers that this and future research should continue to provide. With this knowledge, producers can proactively manage their herds to optimize their performance and profitability, all while being sustainable stewards of our rangelands.

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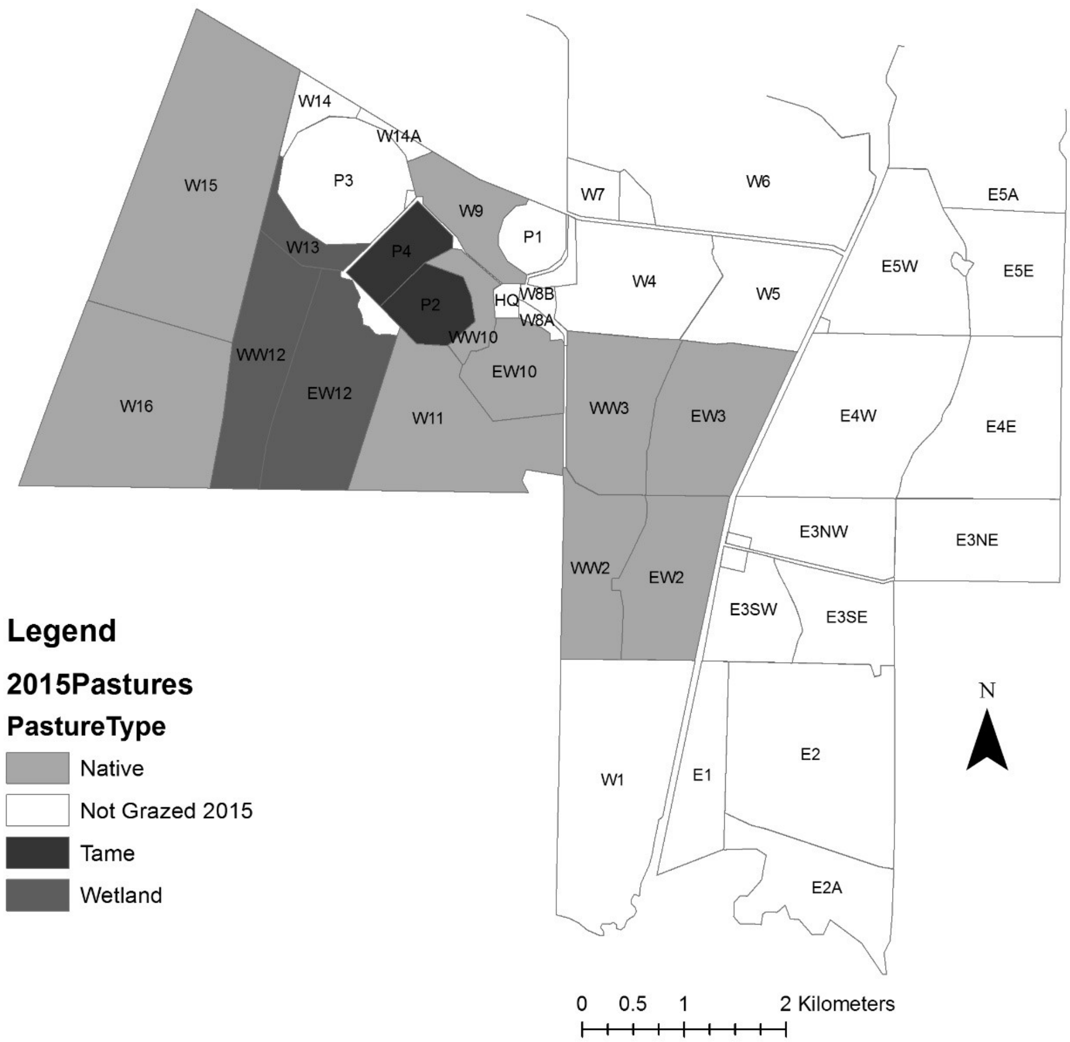
Appendices

Appendix 1. Map of the Mattheis Research Ranch and the different pasture types examined during the 2015 summer and fall grazing season. The total number of pastures used in Chapter 2 or Chapter 3 for analysis may be different due to technical breakdowns (i.e. Chapter 2- W9 was not included in analysis due to equipment failure)

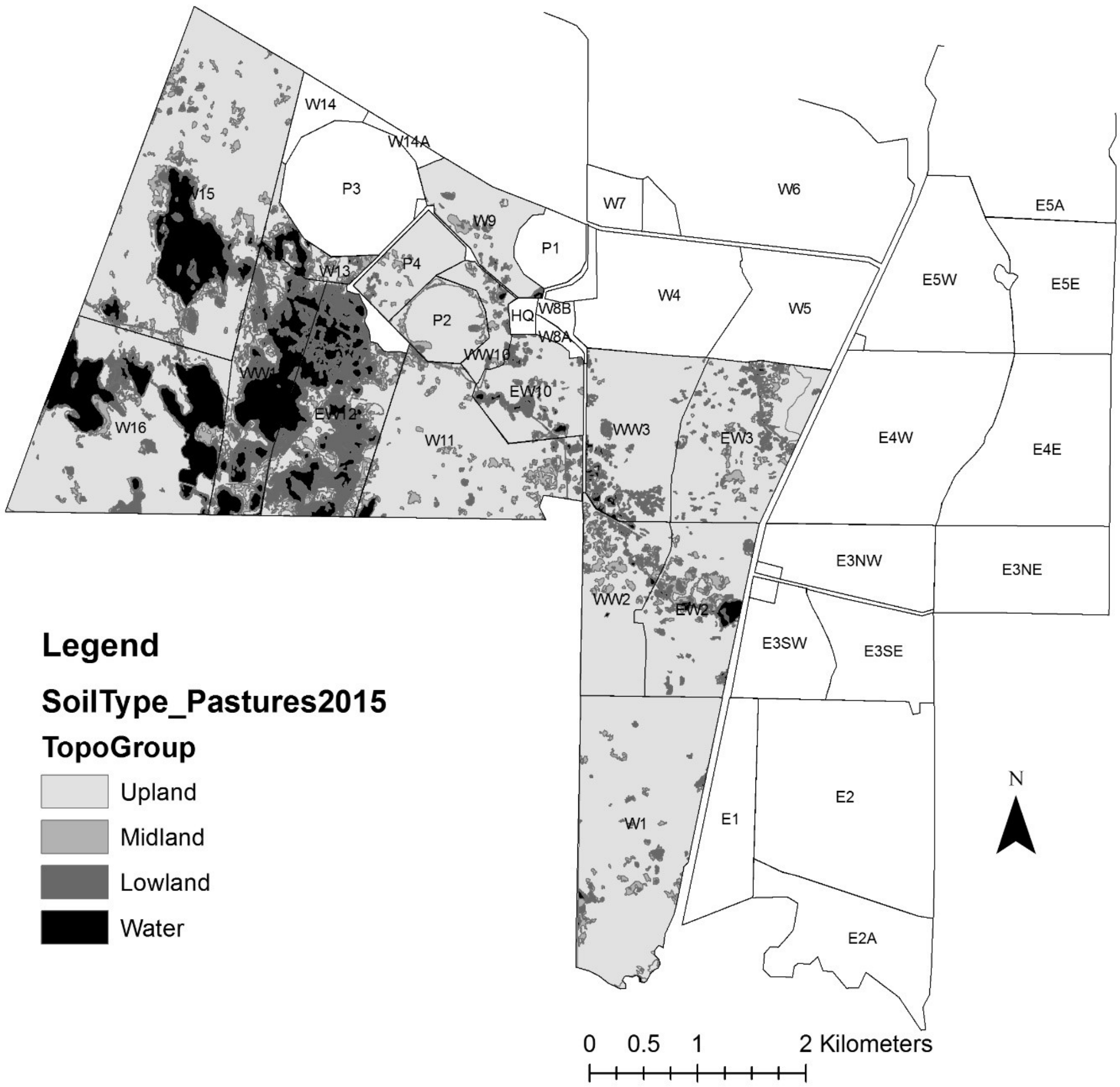


Appendix 2. Order of pasture rotation for the 2015 grazing season. This list includes some pastures that were not included in the analysis (underlined) for reasons described in relevant methods in Chapters 2 and 3.

Pasture to Pasture	Move Date (yyyy-mm-dd)
W2-W11	2015-06-11
W11- EW12	2015-06-16
EW12-P2	2015-06-20
P2-P4	2016-06-26
P4- W13	2015-07-06
W13-WW12	2015-07-12
WW12-W16	2015-07-14
W16-W15	2015-07-19
W15-W9[1]	2015-07-23
W9[1]-Road	2015-07-30
Road-P4	2015-08-05
P4-P2	2015-08-14
P2-WW10	2015-08-15
WW10-EW10	2015-08-23
EW10-Shop Yard	2015-08-31
Shop yard-W10E	2015-09-07
W10E-W8A	2015-09-13
W8A-Yard + Lane	2015-09-15
Yard + Lane- South Road	2015-09-18
South Road/W6B-WW3	2015-09-19
WW3-EW3	2015-09-21
EW3-EW2	2015-09-22

[1]W9 was not included in the Chapter 2 pedometer analysis as there was a pedometer reader equipment malfunction due to rain damage.

Appendix 3. Mattheis Ranch soil types of the pastures grazed during the 2015 season, grouped into topographic/soil moisture regimes.



Appendix 4. Mean and coefficient of variation of forage metrics. These descriptive statistics were performed on a dataset in which forage metrics were averaged by soil type within pasture, then further averaged by topographically similar soil types. This dataset was used for the pedometer analysis. Values of NA indicate there were not multiple soil types to take descriptive statistics on.

		Forb Fiber[1]		Grass Fiber[2]		Forb Protein[1]		Grass Protein[2]		Forb Biomass[3]		Grass Biomass[4]	
Pasture	Type	Mean	CV	Mean	CV	Mean	CV	Mean	CV	Mean	CV	Mean	CV
EW10	Native	36.97	0.03	3.78	0.05	8.86	0.18	2.12	0.01	20.47	0.18	7.76	0.03
EW12	Wetland	29.16	0.05	3.75	0.00	13.94	0.25	2.42	0.03	14.16	0.16	7.32	0.03
EW2	Native	NA	NA	4.00	0.01	NA	NA	1.81	0.06	2.31	1.73	6.94	0.07
WW3	Native	39.11	0.60	3.82	0.01	7.47	0.39	1.86	0.06	4.91	1.14	6.41	0.09
P2-1	Tame	32.59	NA	3.71	0.01	14.54	0.14	2.70	0.03	41.14	0.39	7.18	0.02
P2-2	Tame	42.15	0.09	3.73	0.02	14.02	0.13	2.63	0.05	31.96	0.76	7.34	0.10
P4-1	Tame	29.57	NA	3.63	0.01	16.21	NA	3.09	0.06	5.46	1.41	7.52	0.09
W11	Native	53.08	0.11	3.76	0.01	13.30	0.22	2.32	0.01	24.63	0.06	7.10	0.02
W13	Wetland	58.56	0.12	3.70	0.00	11.00	0.04	2.28	0.02	19.25	0.25	7.72	0.02
W15	Native	34.67	0.05	3.73	0.01	11.95	0.08	2.28	0.03	31.90	0.36	7.57	0.07
W16	Native	25.86	0.21	3.83	0.01	12.35	0.05	2.30	0.07	18.64	0.29	7.10	0.03
W9	Native	34.51	0.13	3.72	0.01	13.21	0.10	2.22	0.05	20.42	0.33	7.64	0.02
WW10	Native	34.51	0.03	3.73	0.01	15.42	0.05	2.37	0.02	16.03	0.36	7.53	0.05
WW12	Wetland	48.23	0.08	3.78	0.03	12.32	0.12	2.32	0.01	19.29	0.41	7.92	0.05
WW2	Native	NA	NA	3.81	0.01	NA	NA	1.83	0.15	0.00	NA	6.66	0.03
EW3	Native	41.18	NA	3.75	0.01	7.79	NA	1.98	0.06	3.89	0.60	7.04	0.02

[1]Measured in % [2]Measured in %, log transformed [3]Measured in $kgha^{-1}$, square root transformed
[4]Measured in $kgha^{-1}$, log transformed

Appendix 5. Mean and coefficient of variation of forage metrics. These descriptive statistics were performed on a dataset that had forage metrics averaged by soil type, within pasture. This dataset was used for the GPS collar analysis. Values of NA indicate there were not multiple soil types to take descriptive statistics on.

		Forb Fiber[1]		Grass Fiber[1]		Forb Protein[1]		Grass Protein[1]		Forb Biomass[2]		Grass Biomass[2]	
Pasture	Type	Mean	CV	Mean	CV	Mean	CV	Mean	CV	Mean	CV	Mean	CV
EW10	Native	36.97	0.03	43.18	0.21	8.86	0.18	7.36	0.02	428.47	0.34	2398.13	0.29
EW12	Wetland	28.80	0.05	41.62	0.08	13.94	0.25	10.22	0.08	223.31	0.51	1493.27	0.22
EW2	Native	NA	NA	53.35	0.03	NA	NA	5.15	0.14	16.00	1.73	1124.53	0.51
WW3	Native	39.11	0.60	44.20	0.05	7.47	0.39	5.67	0.13	34.42	1.83	624.42	0.62
P2-1	Tame	32.59	NA	39.80	0.04	14.54	0.14	13.95	0.10	1818.86	0.72	1320.21	0.11
P2-2	Tame	42.15	0.09	40.79	0.10	14.02	0.13	13.00	0.13	1414.67	1.03	1814.36	0.68
P4-1	Tame	29.57	NA	36.69	0.02	16.21	NA	21.15	0.21	59.71	1.41	2042.86	0.61
W11	Native	53.08	0.11	41.78	0.03	12.47	0.24	9.21	0.03	593.80	0.12	1245.65	0.11
W13	Wetland	57.35	0.28	39.36	0.07	11.08	0.10	8.93	0.05	349.61	0.60	2315.88	0.31
W15	Native	34.67	0.05	40.90	0.05	11.95	0.08	8.83	0.09	1104.98	0.60	2106.00	0.49
W16	Native	25.86	0.21	44.89	0.03	12.35	0.05	9.03	0.17	366.92	0.55	1224.50	0.19
W9	Native	34.51	0.13	40.36	0.03	13.21	0.10	8.25	0.12	447.06	0.56	2107.00	0.16
WW10	Native	34.51	0.03	40.74	0.03	15.42	0.05	9.66	0.04	279.52	0.60	1923.67	0.31
WW12	Wetland	47.67	0.08	43.19	0.18	12.60	0.13	9.14	0.04	345.39	0.90	3083.65	0.26
WW2	Native	NA	NA	44.31	0.04	NA	NA	5.38	0.35	0.00	NA	788.99	0.21
EW3	Native	41.18	NA	41.53	0.06	7.79	NA	6.28	0.14	17.88	1.02	1147.27	0.17

[1]Measured in % [2]Measured in $kghha^{-1}$