FORAGING ECOLOGY & MANAGEMENT OF BEEF CATTLE WINTERING IN THE CENTRAL ROCKY MOUNTAINS

by

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DEDICATION

To Duke and Lettie

“We can judge the heart of a man by his treatment of animals”

–Immanuel Kant

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ABSTRACT

Winter is the most challenging period to manage livestock grazing. Unpredictable environmental extremes bring severe cold, snow, and wind. The nutritional content of forage is low and can be difficult to access due to drifting snow. Providing livestock with a supplement is the most commonly recommended strategy for dealing with these challenges, however, the success of supplementation is based upon a series of poorly understood factors. While it is broadly understood that forage is low-quality during the winter, the exact nutritional content and the variation thereof are poorly understood. Further, understanding the way livestock interact with the forage and the landscape has not been well developed, either independently, or in response to supplementation. Therefore, to bring clarity to these problems, we established two lines of research at Montana State University’s Red Bluff Research Ranch in Norris, Montana. First, we evaluated the winter temporal variation in forage quality and the environmental changes associated with it. Second, we completed three subsequent two-year studies evaluating the foraging behavior and resource use of beef cattle throughout the winter in response to various protein supplementation treatments. Over two years of biweekly sampling the forage quality of the top two graminoids at Red Bluff, we detected dynamic, at times rapid shifts in crude protein (1.9–4.0%) and acid detergent fiber (37–42%) associated with changes in temperature. Using a circular moving window, vegetation and topography covariates were scaled between 30 m and 2550 m. Over the course of all six years, patch-level (30 m) cattle resource use patterns were most strongly explained by intermediate (570–1650 m) and coarse (2370–2550 m) scale covariates. When provided on alternate days, the act of providing a protein supplement shifted cattle behavior immediately afterward but otherwise the effects on activity were minimal. When evaluating the amount provided, protein supplementation decreases the intensity and duration of foraging activity, expands the total area used, and increases the use of areas at higher elevations and further from water. Overall, our research provides insight into the complex interplay between the spatial and temporal dimensions of forage quality and cattle foraging behavior.

CHAPTER ONE

INTRODUCTION & LITERATURE REVIEW

Typical winter management of beef cattle in the western North America involves feeding harvested forages at a level intended to meet animal nutrient requirements. Often cited reasons for doing so include the low-quality or quantity of available forage, high animal nutrient requirements, severe cold and snow, and the difficulty of managing grazing in an unpredictable environment (Fig. 1.1). Feeding full rations is an effective way to avoid these issues, but represents a major cost and limitation to profitability (Putnam and DelCurto, 2020).

Figure 1.1. Cattle grazing during the winter face many challenges including extreme and often unpredictable weather. Grazing through February snow at −20 °C, these cows wear collars equipped with GPS sensors and accelerometers used to monitor their location and activity.

As the rise in production costs continues to outpace the rise in commodity prices (American Farm Bureau Federation, 2022), beef cattle producers are evaluating ways to reduce inputs. A clear choice is management systems that reduce the amount of harvested forages fed.

This requires a commensurate increase in reliance on grazing and addressing the challenges raised above. While there has been research evaluating aspects of winter nutritional management (Brandyberry, 1994; DelCurto et al., 1991; Larson et al., 2009) and environmental impacts on cattle (Adams et al., 1986; Olson and Wallander, 2002; Wyffels et al., 2021), there is still a need for clarity in understanding cattle foraging behavior during the winter.

History of Livestock Foraging Ecology

Foraging ecology is the study of the interaction between animals, their environment, and their acquisition of resources from it (Schoener, 1971). Although foraging ecology as a scientific discipline is relatively young, the roots of it extend far back into the history of man. As long as man has been interacting with wild and domestic herbivores he has been observing and manipulating their behavior. Across the world, prehistoric man memorialized the animals he relied upon for resources in carved figurines cave paintings. The relationship was so close with some species that he transitioned from hunting to herding them. The earliest chapters of the Hebrew Bible in the Book of Genesis describe the movement of sheep and goats in relation to forage and water conditions. Aristotle's History of Animals contains early descriptions of zoology and animal ecology. Virgil's Georgic III describes foraging behavior of cattle, sheep, and goats in the ancient Mediterranean. The enlightenment and eventual progression of the industrial revolution led to developments in the classification and organization of species and an interest in a more thorough understanding of animal management (du Monceau, 1761; Sinclair, 1814). Qualitative descriptions of livestock behavior by nineteenth century stockman (Roosevelt, 1885) transitioned into organized assessments of grazing lands and the impact of herbivores on them by naturalists and scientists in the early twentieth century (Clements, 1920; Griffiths et al., 1902;

Roth and Agriculture, 1901; Thornber, 1910), paving the way for the quantitative science that has developed over the last century.

Animal behavior is a complex series of processes that take place over a range of spatial and temporal scales, thus, quantifying it in a meaningful way has remained a challenge for scientists. Direct, visual observations of animal behavior formed the foundation of the methodology (Adams, 1985; Beaver and Olson, 1997; Hatfield et al., 1990; Houseal and Olson, 1995; Malechek and Smith, 1976; Marlow and Pogacnik, 1986; Senft et al., 1984, 1985) and has remained in use even in more recent research (Clark et al., 2013; Kluth et al., 2025; Porath et al., 2002). In the absence of direct measurements, several indirect measures have been employed. Tracks have long been used as a method to estimate space use for intractable or nocturnal wildlife populations (Bider, 1968; Kuzyakin and Lomanov, 1986; Pringle and Landsberg, 2004; Sun et al., 2020). Others such as utilization measurements (Miller and Krueger, 1976; Miller et al., 1981) or dung pellet counts have been used as a proxy for grazing intensity (Johnstone-Wallace and Kennedy, 1944; Julander, 1955; Miller et al., 1981; Mueggler, 1965; Porath et al., 2002; Senft et al., 1983), and are still used in some broad-scale herbivore studies today (Eldridge et al., 2025; Kimuyu et al., 2017; Maestre et al., 2022).

Technological developments introduced the ability to remotely capture animal behavior at times and locations that would otherwise be impossible or inconvenient to do so. Vibracorders and grazing clocks were employed to estimate time spent grazing (Adams et al., 1986; DelCurto et al., 1990; Jones and Cowper, 1975; Mosley et al., 1987; Stobbs, 1970). Photography and film have been used to assess animal feeding patterns and behavior (Fuentes et al., 2020; Gillen et al., 1985; Nyamuryekung'e et al., 2016). Land-based radio telemetry networks allowed the regular collection of animal location data spurring research evaluating animal interactions and space use (Coe et al., 2001; Long et al., 2008; Pinchak et al., 1991; Stewart et al., 2002; Walburger et al., 2009). The advent of the public availability of the Global Positioning System (GPS) and others like it brought about the ability for the collection of high accuracy tracking data anywhere in the world and has largely eclipsed the use of telemetry systems. Today, the standard equipment in livestock foraging behavior studies often includes paired use of a GPS receiver with auxiliary sensors such as accelerometers or gyroscopes (e.g. Fig. 1.1; Clark et al., 2017; Sprinkle et al., 2021; Wyffels et al., 2020). Often, the combination of sensors is used to predict behavior (Augustine and Derner, 2013; Brennan et al., 2021; Lipinski et al., 2025) resulting in data that can be used to evaluate the spatio-temporal distribution of use partitioned by animal activity.

Behavioral Scaling

Ecological processes occur in neighborhoods of discrete spatial and temporal scales of influence (Addicott et al., 1987; Wiens, 1989). Animal behaviors are the aggregate of individual movements and can be categorized according to the spatial and temporal scales over which they occur. Most often, this takes the form of either a series of behavioral levels (Bailey et al., 1996; Owen-Smith et al., 2010; Senft et al., 1987) or selection orders (Johnson, 1980; Meyer and Thuiller, 2006). Fourth order selection is bite and feeding station-level diet selection from within habitat patches. Third order selection is food patch and foraging area-level selection from within an individual's home range. Second order selection is the selection of an individual's home range from within its species range and first order selection is the collective selection of a species range.

Although behaviors intrinsically occur at discrete scales, they are influenced by processes occurring at both coarser and finer scales (Nash et al., 2014). Behavior is hierarchically nested, and decisions made at one level both constrain the available choices at finer levels and contribute to the decisions made at coarser levels. For example, the decision to begin foraging in a particular area limits diet selection to the plants available there. Likewise, the pattern of sequential movement between feeding stations determines the size and shape of the realized foraging area. The exact mechanisms driving movement at each behavioral level have been debated, but, broadly it has been proposed that animals have a set of physiological and psychological needs and a drive to fulfil them (Bailey et al., 1996; Mueller and Fagan, 2008; Nathan et al., 2008). Animals attempt to fulfil these needs by responding to the conditions in their immediate environment (e.g. forage quality or dietary options; Parsons and Dumont, 2003; WallisDeVries et al., 1999) and their perceived environment, formed from a combination of sensory cues (e.g. visual, auditory, or olfactory; Laca et al., 2010; Palmer et al., 2022), social cues (Provenza and Balph, 1988), and spatial memory (Bailey et al., 1989; Edwards et al., 1996). Consequently, the scales that drive movement may correspond to the physical or temporal extent of information used to make decisions or the inherent scale of environmental heterogeneity.

The importance of scale has received much attention in movement ecology over the last 30 years (Mayor et al., 2009; McGarigal et al., 2016; Meyer and Thuiller, 2006). Research has illustrated that the scales shaping animal behavior vary by behavioral level (DeCesare et al., 2012), habitat component (Heit et al., 2023; Ranglack et al., 2022), animal species (Laca et al., 2010), sex (de Knegt et al., 2011), body size (Laca et al., 2010; Mech and Zollner, 2002), season (de Knegt et al., 2011; Stephens et al., 2024), home range size (Heit et al., 2023) and habitat characteristics (Anderson et al., 2005; Hysen et al., 2025; Ranglack et al., 2022). Consequently, there can be considerable variation between and within populations (Heit et al., 2023; Kuemmerle et al., 2018; Ranglack et al., 2022).

Diet Selection

There have been numerous proposed frameworks that describe potential mechanisms controlling herbivore diet selection. Optimal foraging theory suggests that animal diets are driven by the spatial distribution of forage quality and quantity (Pyke, 1984). Animals are assumed to accurately perceive the nutritional value of forage and "optimize" their intake by maximizing intake rate of a particular nutrient (e.g. energy or protein; Schoener, 1971; Westoby, 1974). While it can be a useful heuristic, optimal foraging theory's assumptions are invalid and it fails to account for the nuances of real-world foraging and thus has received significant criticism (Pierce and Ollason, 1987).

Senft et al. (1987) described two hypothetical frameworks that control herbivore diet selection at the plant community level: the momentary maximization and feeding station hypotheses. A feeding station is defined as the forage available to an animal when the front feet are stationary (Goddard, 1968). Within the momentary maximization framework, an animal searches an area larger than the feeding station and sequentially consumes the most palatable plants in that area. There is some threshold of palatability acceptance that is adjusted by a moving window of recent encountered plant quality. Once the best available plant is no longer within the feeding station, the animal moves to consume that plant, thus establishing a new feeding station and search area.

An alternative hypothesis is the feeding station hypothesis where the search area and feeding station are the same. Diet selection within the feeding station proceeds as per momentary maximization, but since the search area is constrained to the feeding station, the animal is not aware of specific forage options outside of the feeding station. Thus, the decision to leave the feeding station is determined by a "giving-up rule," that is driven by some threshold of plant quality or diminishing return of intake rate (McNair, 1982).

Others have invoked the momentary maximization hypothesis (Bailey et al., 1996; Mládek et al., 2013; Nota et al., 2024), however, their descriptions of it have conflated the momentary maximization and feeding station hypotheses. I would propose a third alternative hypothesis, closely related to momentary maximization, with some important distinctions. First, the decision to consume or not consume a particular plant is determined by a dynamically updated threshold determined by not only recently encountered plant quality (Senft et al., 1987), but also nutrient-specific hunger (Gregorini et al., 2007; Provenza, 1996), competition (Fortin et al., 2004; Jorns et al., 2024), and perceived forage availability (Black and Kenney, 1984; Dumont et al., 2002; Poli et al., 2006). Rather than a single search area that is either the size of the feeding station or somewhat larger than it, there is a "zone of awareness" that is the entire area perceived by the animal. Perceptual resolution within the zone of awareness decreases with distance from the animal (Olden et al., 2004). In nearby areas, individual plants are perceived whereas in further areas, only plant communities or landscape positions are perceived. Search occurs within a focal region that expands or shrinks based on the perceived plant quality within it. Perceived plant quality is also adjusted based on the distance from the animal's mouth representing the energy required to prehend it. Thus, certain plants or species that would otherwise not be selected may have a higher probability of being consumed if they are within the same feeding station or adjacent to a higher quality plant. To transition between feeding stations, rather than invoking a giving-up rule, we can follow the same logic. As mean plant quality within a feeding station declines, the focal area expands until the animal identifies a new location with sufficient plant quality which it then moves to and establishes a new feeding station. This same logic can then be extended to allow for the transition not only between feeding stations within the same patch but across patches and foraging areas.

Though related, perceived plant quality by an animal is distinct from the chemical nutrient composition of a plant as evaluated by a nutritionist. Plant quality is determined by a combination of plant characteristics including size (Ganskopp and Rose, 1992; Silva et al., 2020), maturity (Ganskopp et al., 1997), smell (Provenza, 1995), texture, presence of prior growth (Ganskopp et al., 1992), taste (Yearsley et al., 2006), and the distinct combination of the characteristics into discernable types (e.g. individual species) (Ganskopp and Cruz, 1999; Ganskopp et al., 1997) based on post-ingestive characteristics (Provenza, 1995), and the relative abundance of those groups (Dumont et al., 2002; Poli et al., 2006). Different herbivore species perceive quality differentially based on body size, digestive morphology, and the physical ability to discriminate between plants and plant parts (Daskin et al., 2023; Grant et al., 1985). Quality is modified by animal physiological state and recent experience including overall hunger (Gregorini et al., 2007; Provenza, 1995), nutrient specific hunger (Critchley and Rolls, 1996; Wang and Provenza, 1996), the specific composition of recent diets (Newman et al., 1992; Parsons et al., 1994), and foraging experience in similar plant communities (Distel and Provenza, 1991; Ganskopp and Cruz, 1999; Provenza et al., 2003).

Herbivore plant identification and novel plant quality assessment are primarily visual processes, although taste and smell are involved. In the winter, when snow is deep enough to visually obscure plants, I have observed cattle to engage in one of two foraging patterns. First, animals may engage in active search behavior, brushing snow away from the ground with their noses then using their prehensile organs (e.g. lips, tongue) to first feel for the presence of a plant, briefly assess its physical characteristics, then consume it or move on, presumably based on assessed quality relative to the acceptance threshold. Second, animals may forage in a passive search pattern, walking and spending little time in any given location or not stopping at all. The snow is not brushed and only the plant material above the snow is consumed.

Quantifying Habitat Selection

Behavioral ecology assumes that amount of time an animal spends in a particular location is related to the habitat quality of that location, and by evaluating the assemblage of resources there, we can infer certain things about that animal and make predictions about future habitat use. This is known as a habitat selection analysis (HSA) and is defined as any spatially-explicit, quantitative analysis that relates the use of a resource to its availability (Northrup et al., 2022). Habitat selection analyses can evaluate resource use at any behavioral level, but are most commonly applied to capture second or third order selection. Broadly, HSAs include the families of resource selection functions (RSFs) and resource utilization functions (RUFs). The former includes point selection functions, step selection functions, and path selection functions (Zeller et al., 2012). Given that it is easier to know locations an animal has used than locations it has not used, most RSFs employ a used-available framework where known animal locations are compared to resources at a subset of “available” locations (Boyce et al., 2002; Manly et al., 2002). Determining what is available can be a challenge and is often demarcated as anything within the next highest behavioral level or selection order (Meyer and Thuiller, 2006). For example, to evaluate home range selection for an individual, used locations within that individual's home range are compared to a sample within the collective range of all individuals in the same population. Each type of RSF has distinct differences in defining availability, but all evaluate selection.

In contrast, RUFs add an additional level of detail to the analysis and evaluate not only if locations were used, but also how intensely (Marzluff et al., 2004). To accomplish this, RUFs employ a two-stage analysis. The first stage creates a utilizations distribution (UD) that estimates the intensity of use in a gridded area over a period of time (Millspaugh et al., 2006). Early UDs relied on kernel smoothing to interpolate use between all locations simultaneously (e.g. Fig 1.2; Jennrich and Turner, 1969) and have been criticized for introducing error (Hooten et al., 2013).

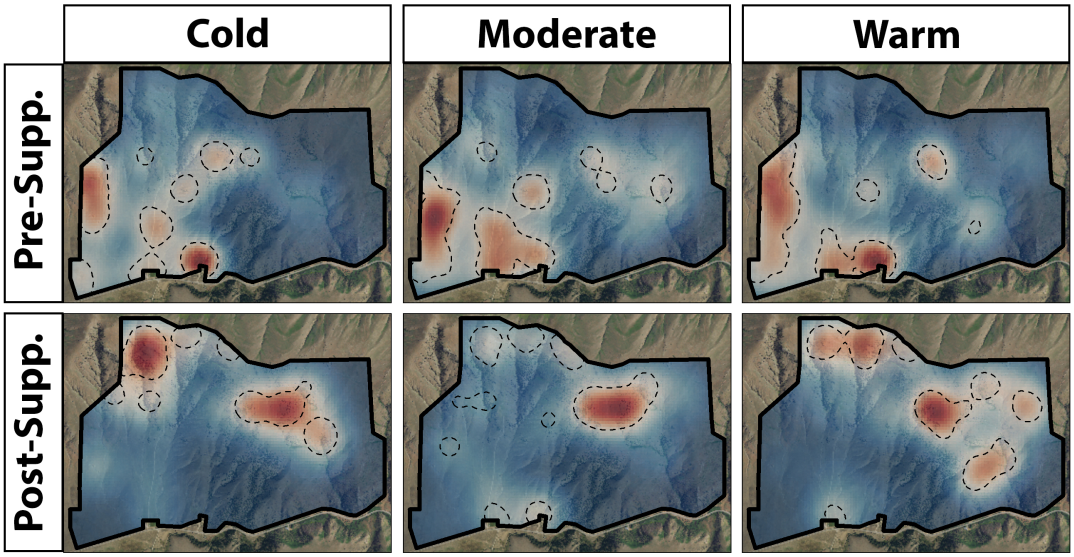

Figure 1.2. Utilization distributions (UDs) can be used to qualitatively and quantitatively assess animal space use patterns. In this example, UDs developed with kernel smoothing are used to compare the change in grazing distribution before and after supplementation relative to temperature.

More recent methods use the sequential, autocorrelated nature of a movement track to estimate the probability of use between subsequent locations based on movement models such as Brownian motion (Byrne et al., 2014; Horne et al., 2007; Kranstauber et al., 2012). With increasingly fine temporal resolution tracking data, the spatial distance between subsequent fixes will render interpolation unnecessary and UDs can be created simply using the proportion of locations in each cell (e.g. Raynor et al., 2021). The second stage of the RUF analysis regresses the UD against gridded resource data covering the same area.

While the differences between RSFs and RUFs may seem subtle, there are several important distinctions to be made between them. Resource selection functions quantify selection—a binary decision made at a discrete point in time. Resource utilization functions quantify intensity of use. The pattern of use observed in a UD is the accumulated result of repeated selection decisions. While similar, the aggregate pattern of selection may be somewhat different than the sum of all selection decisions. Accordingly, the fundamental unit of analysis for an RSF is the point whereas for an RUF is the grid cell. Resource selection functions are fundamentally animal focused and RUFs are fundamentally land focused. This distinction becomes more apparent with track-focused RSFs, such as step selection functions.

Summary

Foraging behavior is the primary link between grazing management, vegetation impact, and the productivity of grazing animals. Therefore, effective grazing management requires an understanding of foraging behavior itself. However, foraging is a complex, hierarchical series of connected processes. There has been substantial progress in the understanding of wildlife ecology by incorporating these concepts (McGarigal et al., 2016). Livestock research has traditionally focused on fine-scale behavioral processes such as diet selection (Dumont et al., 2002; Utsumi et al., 2009) and has lagged in the advancement of coarse-scale behavioral analyses (Laca, 2009).

Recent developments in GPS and other sensor technologies allow for the collection of unprecedented amounts of data that provide for detailed insight into animal behavior (Nathan et al., 2022). Coupled with parallel developments in remote sensing technology (Allred et al., 2025), these tools provide the opportunity for improved understanding animal-habitat interactions.

Despite growing adoption, these technologies are often not being used to their full potential. The volume of data can be overwhelming and even basic questions such as, “What is important?” or “What should be asked?” remain unclear. Study design and analysis often employ implicit assumptions driven by logistical convenience or an anthropocentric view of ecological processes. Instead, research must be guided by a conceptualization of the environment from the target species’ perspective (Searle et al., 2007; Wiens, 1976). Research questions should be clearly framed in terms of the behavioral levels of interest and the spatial and temporal scale of the responses.

Our research addresses some of the current shortfalls in understanding animal behavior and the challenges in managing grazing during the winter. In Chapter 2, we evaluate the winter temporal variation in the forage quality of two widespread graminoids and assess how environmental change is associated with it. In Chapter 3, we consider the behavioral variation in response to alternate day protein supplementation. In Chapter 4, we examine the spatial scaling of patch-level resource use and evaluate how it varies between individuals, pastures, and resources. In Chapter 5, we evaluate the response to graded levels of a protein supplement across a broad array of behavioral metrics. In Chapter 6, we provide an overview of our findings and draw several conclusions.

CHAPTER TWO

INFLUENCE OF TEMPERATURE AND PRECIPITATION ON THE FORAGE QUALITY OF BLUEBUNCH WHEATGRASS AND IDAHO FESCUE DURING THE DORMANT SEASON

Contribution of Authors and Co-Authors

Manuscript in Chapter 3

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Contributions: Conceptualization, methodology, software, validation, formal analysis, investigation, data curation, original draft preparation, writing—review and editing, visualization, project administration

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Contributions: Conceptualization, methodology, review and editing

Co-Author: Timothy DelCurto

Contributions: Conceptualization, methodology, resources, review and editing, supervision, project administration, funding acquisition

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Abstract

Dormant forage is generally understood to be low-quality, but, how and why it changes over the dormant season have not been well studied. Therefore, this study evaluated the changes in the forage quality of bluebunch wheatgrass (*Pseudoroegneria spicata*) and Idaho fescue (*Festuca idahoensis*) over the course of the dormant season and in response to concurrent environmental conditions. We collected forage samples every 14 days in southwestern Montana, USA for two consecutive winters. Samples were analyzed for crude protein (CP), acid detergent fiber (ADF), and neutral detergent fiber (NDF). A suite of environmental metrics was derived from PRISM weather data. Data were analyzed with a linear mixed model and the STATICO ordination method. Crude protein and ADF varied throughout the winter across both years, with CP ranging from 1.9-4.0% and ADF from 37-42%. The differences between species were more pronounced and more consistent in CP. The differences between years were more pronounced in ADF and NDF. Relative temperature explained the most variation in forage quality. Crude protein is positively correlated with short-term warmer temperatures whereas NDF is positively correlated with longer-term warmer temperatures. This demonstrates that forage quality can change over the dormant season and is influenced by winter weather events.

Introduction

Understanding the dynamics of native forage is key to successfully managing livestock grazing on rangelands. Characterizing rangeland forage quality was a focus of early rangeland livestock research in western North America (Green, 1934; Knight and Nelson, 1905; McCall, 1939) and has continued to be an area of interest today (Davis et al., 2025a; Larsen et al., 2021;

Tolleson et al., 2020). Most research has focused on documenting changes in forage quality during the growing season, which coincides with most livestock grazing and is when changes in forage quality are most pronounced. In an effort to reduce overhead costs by minimizing reliance on harvested feeds, some livestock producers continue grazing into the dormant season—the period during fall and winter when plants are not actively growing (DelCurto et al., 2023). This shift necessitates the use of low-quality, dormant forage (Putnam and DelCurto, 2020). To compensate for this, producers often provide high-quality supplemental feedstuffs (DelCurto et al., 2000), however, decisions about the kind and amount of supplementation are frequently based on professional judgement or anecdotal evidence. This highlights the need for robust data to inform these decisions. Despite this, how and why forage quality changes over the dormant season have not been thoroughly studied. Most of the studies that have reported on this are limited in temporal or spatial scale (Abouguendia, 1998; Ganskopp et al., 2007; Ganskopp and Bohnert, 2001; Houseal and Olson, 1996; Jensen et al., 2002; Waldron et al., 2006).

Bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] Á. Löve) and Idaho fescue (*Festuca idahoensis* Elmer) are two important forage species in the sagebrush steppe, mixed-grass prairie, and Palouse prairie rangelands of western North America (Holechek et al., 1989; Rosiere, 2018; USDA, 1937). Similar to rangeland forage as a whole, the growing season forage quality of Idaho fescue and bluebunch wheatgrass has been well-documented (Ganskopp and Bohnert, 2001; Johnston and Bezeau, 1961; McLean and Tisdale, 1960; Skovlin, 1967), however, changes in dormant season forage quality have been poorly tested in scope or sampling frequency. Additionally, while the influence of growing season environmental conditions is largely understood (Bates et al., 2023; Mainetti et al., 2023; Peek, 2014; Tolleson et al., 2020), there has been little to no research on the influence of winter environmental conditions on forage quality. Therefore, this study sought to characterize the changes in the forage quality of bluebunch wheatgrass and Idaho fescue over the course of the dormant season and in response to concurrent environmental conditions. We hypothesized that forage quality would fluctuate over the course of the dormant season and that these changes would be correlated with variations in temperature and precipitation.

Materials and Methods

Study Area

This study was conducted in a 1064-ha management unit at Montana State University's Red Bluff Research Ranch in Norris, MT at 45°35'N, 111°38'W. The area has a cold semi-arid climate (Köppen-Geiger Climate BSk; Kottek et al., 2006) with long, cold winters and warm summers. Mean annual temperature is 6.9 °C and mean annual precipitation is 418 mm, with 55% coming during the growing season months of May-September (PRISM Climate Group, 2024). The elevation of the management unit ranges from 1,415 to 1,715 m in a combination of gently sloping alluvial fans, steep slopes, and broad ridges. Most of the soils in the study area are classified as mollisols or inceptisols (Soil Survey Staff, 2024).

The vegetation is characteristic of the region, dominated by grassland accompanied by scattered woodlands of Rocky Mountain juniper (*Juniperus scopulorum* Sarg.) and limber pine (*Pinus flexilis* James) on the slopes and ridges. Idaho fescue and bluebunch wheatgrass are the dominant grasses. Subdominant grasses are needle-and-thread (*Hesperostipa comata* [Trin. & Rupr.] Barkworth), and prairie Junegrass (*Koeleria macrantha* [Ledeb.] Schult.). Dominant forbs include fringed sagewort (*Artemsia frigida* Willd.), cudweed sagewort (*Artemisia ludoviciana*

Nutt.), and lupine (*Lupinus* spp.). There are few shrubs in the management unit, but those that are present include scattered individuals of rubber rabbitbrush (*Ericameria nauseosa* [Pall. ex Pursh] G.L. Nesom & Baird) and skunkbush sumac (*Rhus trilobata* Nutt.), localized patches of antelope bitterbrush (*Purshia tridentata* [Pursh] DC.), and populations of mountain big sagebrush (*Artemesia tridentata* Nutt. ssp. *vaseyana* [Rydb.] Beetle) above 1,550 m.

Field and Laboratory Methods

Idaho fescue and bluebunch wheatgrass were selected for investigation because they are the dominant forage species and constitute a large component of livestock diets in the study area (Davis, 2018; Kluth et al., 2025; Kluth et al., 2024). Five sites were selected within the management unit that were representative of the vegetation and topography of the area and contained both species. Beginning October 17th, 2018, and continuing every fourteen days until February 6th, 2019, we used step transects to collect seven to ten ungrazed individuals of Idaho fescue and bluebunch wheatgrass by clipping to a 1 cm stubble height. This was repeated for the winter of 2019–2020.

Samples were collected in paper bags in the field and transported to the Oscar Thomas Nutrition Center in Bozeman, MT. They were subsequently dried at 55 °C in a forced-air oven for 48 hours, ground to pass a 1-mm screen and stored in plastic bags at room temperature for subsequent chemical analysis. Samples were analyzed for crude protein content (CP) using a LECO 828 Series analyzer (LECO Corp., St. Joseph, Michigan, USA; AOAC, 1990). Acid detergent fiber (ADF) and neutral detergent fiber (NDF) were analyzed using an ANKOM 200 Fiber Analyzer (ANKOM Technology, Macedon, NY, USA; Goering and Van Soest, 1970).

Results are reported on a dry matter basis. All samples were run in duplicate and any sample whose coefficient of variation was greater than 5% was reanalyzed.

Environmental Data

Daily mean temperature and precipitation data for the study area were obtained from PRISM (PRISM Climate Group, 2024). Monthly precipitation for the 2018 and 2019 water years is shown in Figure 2.1. The water year is defined as period from October 1st of the preceding year to September 30th of the named year (U.S. Geological Survey, 2016). Year one had a wet spring but a dry summer whereas year two had a dry spring but a wet summer. Overall, both years were somewhat wetter than normal. Temperature and precipitation over the study period are shown in Figure 2.2. Both winters were typical for the study area.

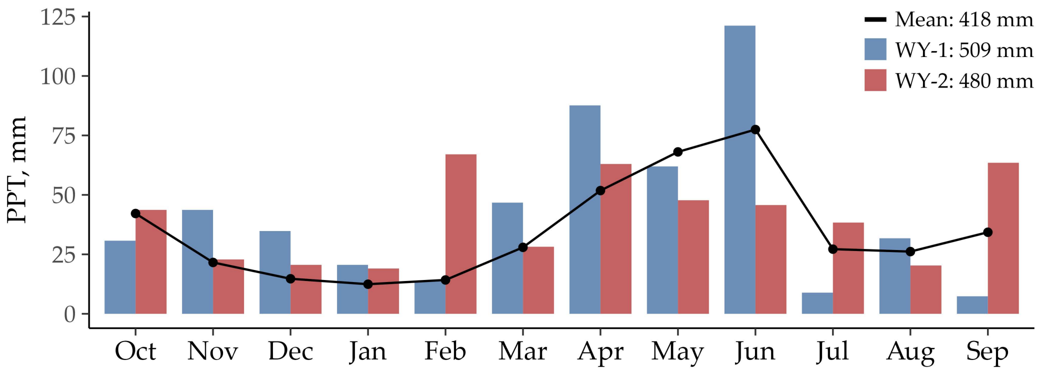

Figure 2.1. Monthly and total precipitation for the 2018 and 2019 water years (WY; ending September 30th of the named year) at the study site in southwestern Montana, USA. The black line indicates the 30-year mean. Year one received 137% of mean spring precipitation (April–June) but only received 55% of mean summer precipitation (July–September). In contrast, year two received 79% of mean spring precipitation but received 139% of mean summer precipitation.

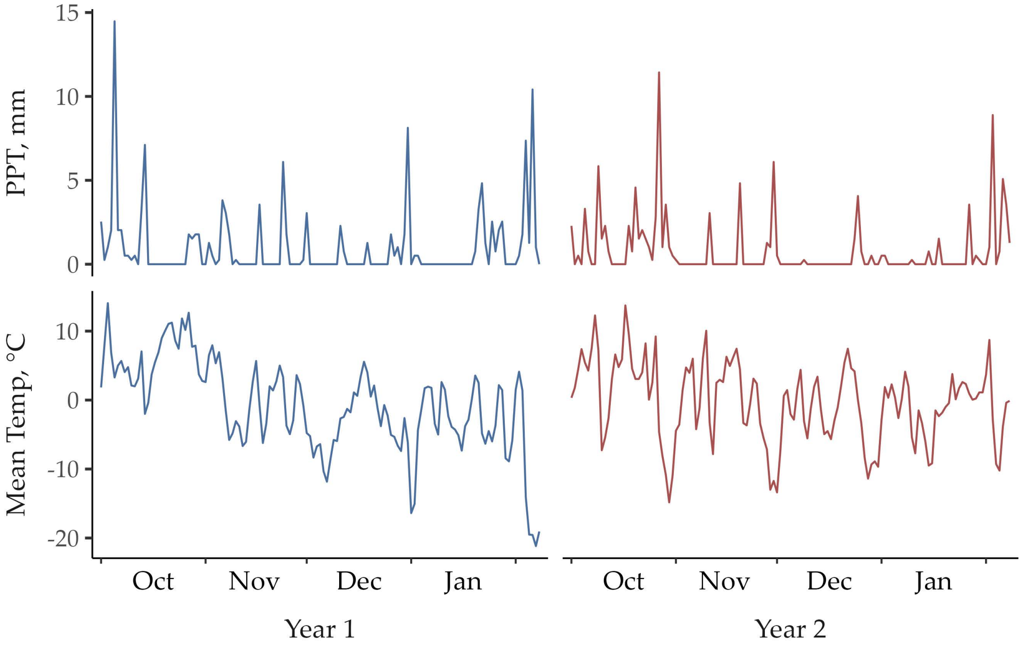

Figure 2.2. Daily precipitation and mean temperature over the winters of 2018–2019 (Year 1) and 2019–2020 (Year 2) at the study site in southwestern Montana, USA. Both winters were typical for the area. Over the study period in years one and two, total precipitation was 91 and 74 mm, respectively; mean weekly maximum temperature was 8.3 and 9.1° C, respectively; mean weekly minimum temperature was -16.2 and -18.0° C, respectively; and overall mean temperature was -1.3 and -1.0° C, respectively.

Daily temperature and precipitation data were used to derive environmental metrics for each of the sampling dates (Table 2.1). Growing degree day (GDD) is a conceptual tool that quantifies heat accumulation above plant-specific growth thresholds (McMaster and Wilhelm, 1997). It is routinely used to estimate plant (Frank and Hofmann, 1989; Zavalloni et al., 2006) and has been extended to predict forage quality (Peratoner et al., 2020; Tolleson et al., 2020). For each sampling date, the number of GDD were calculated as:

$$GDD_i = T_{mean} - T_{base} \tag{1}$$

where:

- GDD_i is the accumulated number of GDD on day *i*,

- T_{mean} is the mean temperature on day i, and
- T_{base} is the threshold temperature above which plants are able to initiate growth.

We set T_{base} at 0° C as that is the temperature above which cool-season grasses are theoretically capable of growth (Moot et al., 2000; Nagelmüller et al., 2016).

Table 2.1. Environmental metrics derived from daily temperature and precipitation data used in the study. See Equations (1)-(6) for mathematical descriptions of the calculations. See Results for the use of the listed codes.

	Code	Description
Growing degree day		
	gdd_5	5-day sum
	gdd_10	10-day sum
	gdd_15	15-day sum
Precipitation		
	ppt_5	5-day sum
	ppt_10	10-day sum
	ppt_15	15-day sum
Absolute temperature		
	temp_5	5-day mean
	temp_10	10-day mean
	temp_15	15-day mean
Short-term thermal stress		
	stts5_5	Difference of the 5-day mean from the previous 5-day mean
	stts5_10	Difference of the 5-day mean from the previous 10-day mean
	stts5_15	Difference of the 5-day mean from the previous 15-day mean
	stts5_20	Difference of the 5-day mean from the previous 20-day mean
	stts10_10	Difference of the 10-day mean from the previous 10-day mean
	stts10_20	Difference of the 10-day mean from the previous 20-day mean
	stts10_30	Difference of the 10-day mean from the previous 30-day mean

To derive metrics used in the analysis, we calculated the 5-, 10-, and 15-day sums for GDD and precipitation as:

$$Metric_i = \sum_{j=0}^{n-1} V_{(i-j)} \tag{2}$$

And we calculated the 5-, 10-, and 15-day means for mean daily temperature as:

$$Metric_i = \frac{1}{n}\sum_{j=0}^{n-1} V_{(i-j)} \tag{3}$$

where:

- $Metric_i$ is the calculated mean for day i,
- n is the number of days in the summation window, and
- $V_{(i-j)}$ is the daily value for the variable of interest on day $i-j$.

Finally, we calculated short-term thermal stress (STTS), a metric that quantifies relative temperature. We adapted Senft and Rittenhouse's STTS model (Senft and Rittenhouse, 1985) to apply to plants. Senft and Rittenhouse modeled thermal acclimation in cattle (*Bos taurus*), calculating the difference between the mean temperature for a given day, *i,* and a rolling mean of previous days' temperatures. Since plants respond more slowly to changes in temperature compared to mammals, we adjusted the calculation to account for this lag. Specifically, we calculated the difference between the stimulus temperature, defined as the 5- and 10-day mean temperatures preceding day *i*, and the acclimated temperature, calculated as the 5- to 30-day mean temperatures prior to the stimulus temperature. For each sampling date, STTS was calculated as:

$$STTS_i = T_{stim} - T_{accl} \tag{4}$$

where:

- $STTS_i$ is the STTS for day i,
- T_{stim} is the stimulus temperature, and
- T_{accl} is the acclimated temperature.

Stimulus and acclimated temperatures were calculated as:

$$T_{stim} = \frac{1}{N}\sum_{j=1}^{N} T_{(i-j)} \tag{5}$$

$$T_{accl} = \frac{1}{M}\sum_{k=1}^{N+M} T_{[i-(N+k)]} \tag{6}$$

where:

- N is the number of days in the calculation of the stimulus temperature on day i,
- M is the number of days in the calculation of the acclimated temperature, and
- $T_{(i-j)}$ and $T_{[i-(N+k)]}$ are the mean daily temperatures on days $i-j$ and $i-(N+k)$, respectively.

See Table 2.1 for the values of N and M used in calculating the STTS metrics.

Statistical Analysis

Influence of Sampling Date: This analysis was split into two parts. To quantify how forage quality changed over the course of the study period, we used a linear mixed model. The analysis treated the study as a repeated measures completely randomized design with five replications of three factors (species, n = 2; year, n = 2; and sampling date, n = 9). Species-site-sampling date was the experimental unit and CP, ADF, and NDF were the response variables. Data were analyzed in R 4.3.1 (R Core Team, 2023) with the lmerTest (Kuznetsova et al., 2017) and lme4 (Bates et al., 2015) packages using a mixed-effects model that included all factors and up to all two-way interactions with site as a random intercept. For significant effects of sampling date, we tested linear, quadratic, and cubic orthogonal contrasts with the Kenward-Roger method using the emmeans package (Lenth, 2024).

To test for differences in the coefficient of variation (CV) of CP, ADF, and NDF between Idaho fescue and bluebunch wheatgrass, we implemented the Feltz–Miller CV equality test (Feltz and Miller, 1996) using the cvequality package (Marwick and Krishnamoorthy, 2019) in R. Statistical significance was accepted at $P \leq 0.05$ and tendencies were considered at $0.05 < P \leq 0.10$.

Influence of Environment: To evaluate how changes in forage quality were related to concurrent environmental conditions, we implemented the STATICO method (Simier et al., 1999; Thioulouse et al., 2004) using the ade4 package (Thioulouse et al., 2018) in R. STATICO assesses the relationship between paired series of ecological tables using co-inertia analysis on each pair of tables then partial triadic analysis on the resulting series of cross tables. This method produces two relevant outputs: the compromise and the intrastructure. Though primarily used in community ecology (Certain et al., 2011; Kraus et al., 2021), STATICO and, more broadly, ordination analysis have precedent in forage nutrition (Andueza et al., 2016; Locke et al., 2021; Mainetti et al., 2023; Scasta, 2017)

In our case, the two series of tables were: 1) environmental metrics at every sampling date, and 2) forage quality metrics (CP, ADF, and NDF) for both species at every sampling date. The compromise, the primary final product of STATICO, represents the stable relationships between environmental metrics and forage quality across the two species. This provides a broad overview of how environmental conditions consistently influence the forage quality of both species. The intrastructure maps the relationship between environmental and forage quality metrics for each species back onto the compromise. This step describes how each species is influenced by environmental conditions and enables comparisons between them.

As the environmental metrics are at the scale of the study area, the experimental unit was the species-sampling date, so, we used the species-level means of the forage quality metrics, averaged across the sites. All data were standardized before analysis.

Results

Influence of Sampling Date

Crude protein was influenced by the main effect of species ($P < 0.01$) and the sampling date × year interaction ($P = 0.02$). Idaho fescue had a greater concentration of CP than bluebunch wheatgrass (3.14 ± 0.14% vs. 2.41 ± 0.14%, respectively; $P < 0.01$; Table 2.2), however, Idaho fescue also had a greater CV than bluebunch wheatgrass ($P < 0.01$; Table 2.3). In year one, we detected no trends in CP across sampling dates ($P \geq 0.11$), however, in year two, there was a positive linear trend ($P = 0.05$) and a tendency for quadratic and cubic trends ($P = 0.07$; Figure 2.3, Table 2.4).

Table 2.2. Influence of species and year on the crude protein (CP), acid detergent fiber (ADF), and neutral detergent fiber (NDF) of Idaho fescue and bluebunch wheatgrass sampled over 9 two-week intervals over two winters in southwestern Montana, USA.

	Idaho Fescue		**Bluebunch wheatgrass**		**SEM**[1]	***P*-values**[2]		
	Year 1	Year 2	Year 1	Year 2		**Y**	**S**	**Y×S**
CP, %	2.83	3.45	2.36	2.46	0.19	0.04	< 0.01	0.13
ADF, %	40.70^{a}	39.90^{b}	38.90^{b}	41.70^{a}	0.66	0.10	0.98	< 0.01
NDF, %	62.20	68.70	62.80	69.70	1.31	< 0.01	0.50	0.87

[1] Pooled standard error of the mean

[2] *P*-values for main effects and the interaction between year (Y) and species (S)

[a-b] Within year, means in a row that do not share a common superscript differ ($P \leq 0.05$)

Table 2.3. Results of the Feltz–Miller coefficient of variation equality test for crude protein (CP), acid detergent fiber (ADF), and neutral detergent fiber (NDF) of Idaho fescue and bluebunch wheatgrass sampled over 9 two-week intervals over two winters in southwestern Montana, USA. The coefficient of variation represents variability in forage quality between sites, reflecting the spatial consistency in nutritive value available at each site relative to the area-level mean.

	Idaho Fescue	**Bluebunch wheatgrass**	***P*-value**
	Coefficient of Variation		
CP, %	52.7	35.7	< 0.01
ADF, %	10.0	12.8	0.02
NDF, %	15.0	12.8	0.15

Acid detergent fiber was influenced by the species × year ($P < 0.01$) and sampling date × year ($P < 0.01$) interactions. In year one, Idaho fescue had 1.8 percentage points more ADF than bluebunch wheatgrass ($P = 0.05$), however in year two, Idaho fescue had 1.8 percentage points less ADF than bluebunch wheatgrass ($P = 0.04$; Table 2.2). Across years, the CV for bluebunch wheatgrass ADF was greater than the CV for Idaho fescue ($P = 0.02$; Table 2.3). In year one, ADF exhibited a cubic trend across sampling dates ($P = 0.05$), whereas in year two there was a tendency for a quadratic trend ($P = 0.06$; Table 2.4).

Neutral detergent fiber was only influenced by the main effect of year ($P < 0.01$), where NDF was lower in year one than in year two (62.5 ± 0.90% vs. 69.3 ± 0.92%, respectively; $P < 0.01$). We detected no difference in the CV of NDF between Idaho fescue and bluebunch wheatgrass ($P = 0.15$; Table 2.3).

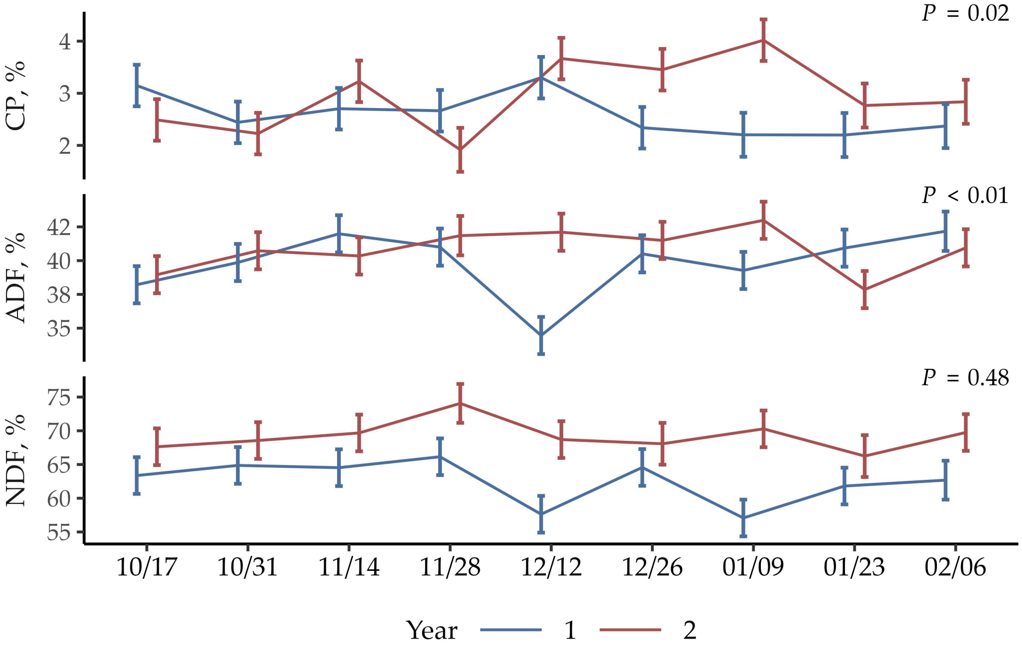

Figure 2.3. Influence of sampling date and year on the crude protein (CP), acid detergent fiber (ADF), and neutral detergent fiber (NDF) of Idaho fescue and bluebunch wheatgrass sampled over 9 two-week intervals over two winters in southwestern Montana, USA. The *P*-values for the sampling date × year interactions are shown in the top right portion of each panel. The *P*-values for polynomial orthogonal contrasts of the significant interactions are shown in Table 2.4.

Table 2.4. Results for polynomial orthogonal contrasts of crude protein (CP) and acid detergent fiber (ADF) of Idaho fescue and bluebunch wheatgrass sampled over 9 two-week intervals over two winters in southwestern Montana, USA.

	Orthogonal Contrast *P*-values		
	Linear	**Quadratic**	**Cubic**
CP			
Year 1	0.11	0.87	0.99
Year 2	0.05	0.07	0.07
ADF			
Year 1	0.23	0.22	0.05
Year 2	0.69	0.06	0.70

Influence of Environment

For each species, the relationships between forage quality and concurrent environmental conditions are visualized in the intrastructure biplots (Figure 2.4). The $\cos^2$ values quantify how well the species-specific relationships align with the overall compromise structure, which represents the shared patterns between the two species. While the compromise captures the information for both species well, it aligns more strongly with Idaho fescue ($\cos^2 = 0.93$) than bluebunch wheatgrass ($\cos^2 = 0.89$). This suggests that Idaho fescue exhibited a slightly more consistent relationship between environmental and forage quality metrics than bluebunch wheatgrass.

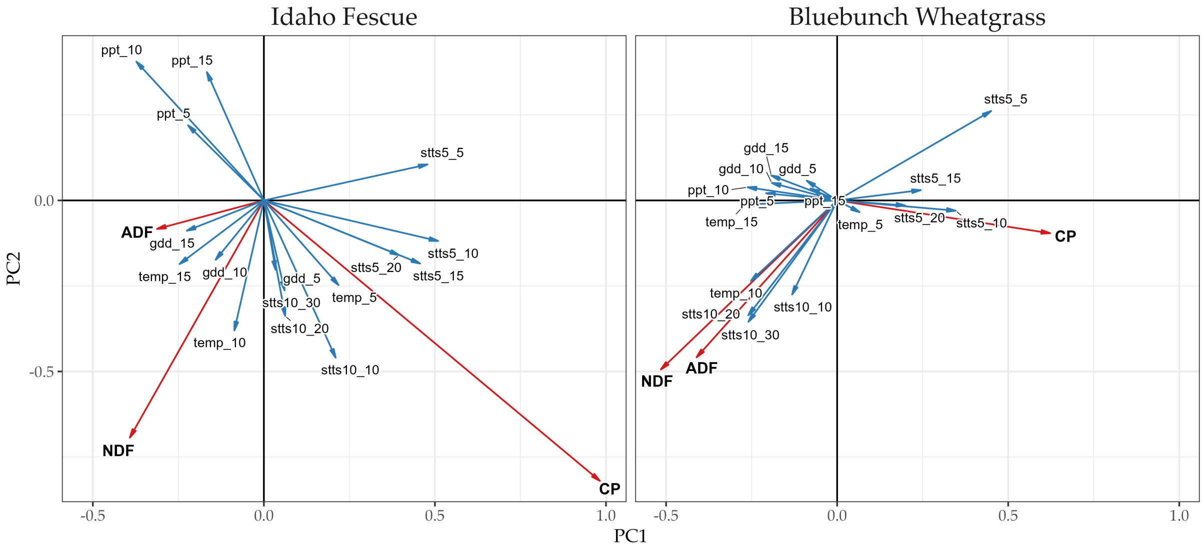

Figure 2.4. Relationships between winter forage quality metrics (crude protein, CP; acid detergent fiber, ADF; and neutral detergent fiber, NDF) and environmental metrics (see Table 2.1 for environmental metric codes) for Idaho fescue and bluebunch wheatgrass sampled over 9 two-week intervals over two winters in southwestern Montana, USA. The first (PC1) and second (PC2) principal components represent the primary gradients of variability, where PC1 is characterized by short-term temperature changes and PC2 is characterized by longer-term temperature changes. Distance from the origin indicates variability of each metric, and the angle between metrics indicates their correlation.

Inertia represents the total variability of the data captured by the components of the model. The proportion of the inertia contained by each component or variable indicates how well it explains variability in the data. In the compromise, the first axis (PC1) contains 57% of the overall inertia while the second axis (PC2) contains 35%. The first axis is primarily characterized by short-term temperature changes with warmer temperatures on the right. Five-day STTS metrics contain 62% of PC1 inertia. The second axis is characterized by longer-term temperature changes with warmer temperatures in the lower part of the plot. Ten-day STTS metrics contain 54% of PC2 inertia.

At our study site, winter precipitation events are generally in the context of a winter storm from a passing cold front followed by a decrease in temperature. Precipitation metrics load in the second quadrant, correlated with both short- and longer-term cold temperatures. Precipitation metrics contain 16% of PC1 inertia and 17% of PC2 inertia. Growing degree day metrics contain little overall inertia, only containing 7.3% of PC1 inertia and 1.4% of PC2 inertia, all loading on the left. Ten-day mean absolute temperature contained 15% of PC2 inertia, otherwise individual absolute temperature metrics contained less than 7% of PC1 or PC2 inertia, all loading in the lower part of the plot.

Of the three forage quality metrics, CP exhibited the strongest structure, containing 49% of the overall inertia. Crude protein loaded into the fourth quadrant, with PC1 containing 75% of its inertia and PC2 containing 25% of its inertia. Both NDF and ADF loaded into the third quadrant. Neutral detergent fiber contained 34% of the overall inertia, with PC1 containing 35% of its inertia of NDF and PC2 containing 60% of its inertia. Acid detergent fiber had the weakest structure, only containing 18% of the overall inertia, with PC1 containing 42% of its inertia and PC2 containing 24% of its inertia.

Discussion

It has been well-documented that forage quality declines over the growing season (Davis et al., 2025a; Ganskopp and Bohnert, 2001; Jensen et al., 2017; Smart et al., 2006), however, there are conflicting reports on how forage quality changes over the dormant season (Clark et al., 2000; Jensen et al., 2002; Wagner and Peek, 2006; Waldron et al., 2006). Most previous studies that collected data during the dormant season sampled with a relatively coarse temporal resolution (1x/month to 1x/season). Therefore, they may not have been able to adequately characterize the change in forage quality. In contrast, we sampled every two weeks, a frequency that has scarcely been reported over the dormant season (McCall, 1939), allowing us to detect changes that may otherwise have been missed. Our results show that forage quality is relatively stable but can be dynamic within a narrower range of values than during the growing season. In year one, we did not detect any changes in CP whereas in year two CP fluctuated over the winter, at one point increasing by two percentage points (a 110% increase), over the course of six weeks. In both years, ADF followed either a cubic or quadratic pattern, fluctuating by over five percentage points.

The differences between species were more pronounced and consistent in CP, with Idaho fescue containing greater levels of CP than bluebunch wheatgrass. In contrast, ADF and NDF varied more between years and showed less consistent or no differences between species. The range of values and relationships between the species in our results are broadly consistent with previously published data. For example, in the salt desert shrubland of Utah, bluebunch wheatgrass had 2.8-3.4% CP during winter (Cook and Harris, 1950, 1968; Cook et al., 1954). Similarly, in the sagebrush steppe of southeastern Oregon, bluebunch wheatgrass had 2.3% CP and 57.1% ADF during winter (McInnis and Vavra, 1987). In southwestern Montana, bluebunch wheatgrass had 3.0% CP, 48.9% ADF, and 73.7% NDF during winter (Wambolt et al., 1997). In contrast, in eastern Washington, Idaho fescue CP fluctuated between 3.6-5.8% with a mean of

4.6%, during late fall and winter (McCall, 1939). In the mountains of northeastern Nevada, Idaho fescue contained more CP than bluebunch wheatgrass in the early fall (5.6 vs. 4.0% CP, respectively) (Beck and Peek, 2005). Likewise, in the Palouse prairie of eastern Washington, Idaho fescue contained more CP and less crude fiber (CF) than bluebunch wheatgrass (4.62 vs. 2.94% CP and 27.2 vs. 33.4% CF, respectively) during the late fall and early winter (McCall, 1940).

Idaho fescue is preferentially consumed over bluebunch wheatgrass during the dormant season by elk (*Cervus canadensis*; Dragt and Havstad, 1987; Frisina et al., 2008), domestic sheep (*Ovis aries*; Franco Urcos, 2024), and cattle (Holechek et al., 1982; Houseal and Olson, 1996; Kluth et al., 2025). Idaho fescue responds to fall precipitation by generating new vegetative growth (Ganskopp and Bohnert, 2001; McCall, 1939) and does so more readily than bluebunch wheatgrass (Houseal and Olson, 1996). This fall growth retains its nutritional quality through the winter; in one study, it was reported at a mean of 15.8% CP, 26.5% ADF, and 53.3% NDF between October and February (Houseal and Olson, 1996). Livestock are selective foragers and are capable of consuming higher quality diets than samples obtained by clipping (Clark et al., 2013; Cruz and Ganskopp, 1998; Hart et al., 1983). Over the course of two winters at our study site, ewes and yearling heifers were able to select diets that contained 7.0 and 4.3% CP, respectively (Van Dyne et al., 1964). Livestock consuming a diet dominated by Idaho fescue may be able to exploit its greater variation in CP and select a proportionately higher quality diet compared to livestock consuming a diet dominated by bluebunch wheatgrass. Combined with Idaho fescue's greater mean CP, this may partially explain why Idaho fescue is preferentially consumed over bluebunch wheatgrass during the dormant season.

The influence of growing season environmental conditions on forage quality is well understood and has been modeled (Mainetti et al., 2023; Peek, 2014; Tolleson et al., 2020). Our results indicate that dormant season environmental conditions are also associated with patterns of forage quality. While several authors who measured forage quality during the dormant season have postulated the influence of environmental conditions on forage quality (Clark et al., 2000; Ganskopp and Bohnert, 2001; Ganskopp and Bohnert, 2003), to our knowledge, this is the first study to formally analyze this relationship.

A common modus operandi among range and livestock managers working on northern rangelands is to assume that between fall quiescence and spring green-up, cool-season perennial plants remain in an unresponsive, dormant state. However, this may not be the case. In contrast to spring annuals, which avoid harsh temperatures by not maintaining live tissue during the winter, fall annuals and perennials retain live tissue over the winter and must undergo physiological changes to protect their tissues from frost damage by avoiding or tolerating freezing (Smallwood and Bowles, 2002). Rather than a binary state, cold tolerance is a dynamic characteristic achieved through acclimatization, a process of adaptation in response to successively lower temperatures (Źróbek-Sokolnik, 2012). This process continues even below 0 °C (Bykova and Sage, 2012; Yu et al., 2020). The reverse process, deacclimatization, occurs in response to successively warmer temperatures (Hoffman et al., 2014). Thus, a plant's degree of cold tolerance is actively matched to its acclimated thermal environment.

In our study, relative temperature (STTS) accounted for the most variation in forage quality, surpassing both absolute temperature and GDD. This suggests that plants responded more to relative temperature change rather than to absolute temperature. Additionally, the minimal variation explained by GDD metrics indicates that plants responded to the full range of temperatures over the winter rather than exclusively temperatures above freezing.

In northern Idaho, Daubenmire reported slow, intermittent development of Idaho fescue and bluebunch wheatgrass over the course of the winter during periods of weather above freezing (Daubenmire, 1968). Although temperatures in southwestern Montana are typically colder than northern Idaho, this illustrates that both species are capable of acclimatization and deacclimatization throughout the winter. In the STATICO analysis, Idaho fescue contained a more coherent data structure which may imply that environmental factors have a more consistent influence on its forage quality than that of bluebunch wheatgrass. Idaho fescue has a larger proportion of its roots in the upper portions of the soil profile than bluebunch wheatgrass (Goodwin et al., 1996; Spence, 1937; Weaver, 1982). Relative to deeper horizons, soil temperatures of surface horizons are more dynamic and closely reflect changes in air temperature (Smith et al., 1964). Consequently, Idaho fescue may be more sensitive and responsive to changes in air temperature than bluebunch wheatgrass.

While this study did not seek to identify the mechanisms behind the changes in forage quality, we can make some inferences. Rather than a progressive decline in quality that could be attributed to an external factor such as nutrient leeching or tissue decay, we observed fluctuations in forage quality throughout the winter. These fluctuations may reflect internal, physiological changes, such as the translocation of phytochemicals during successive acclimatization and deacclimatization in response to temperature changes.

Conclusions

Our results show fine scale, at times rapid changes in winter forage quality associated with environmental conditions. Livestock managers in the region can use this information to estimate baseline forage quality for pastures dominated by Idaho fescue and/or bluebunch wheatgrass.

Despite some differences, Idaho fescue and bluebunch wheatgrass shared many of the same patterns in forage quality. Although our study focused on specific conditions in southwestern Montana, the relationship between forage quality and environmental conditions is likely comparable in other cool-season perennial grasses found in similar rangelands across the globe.

In this study, we used modeled air temperature and precipitation data at the scale of the entire study area; however, the conditions experienced by plants are at the site scale and include ambient air and soil temperature. Future studies investigating this topic could improve data quality by measuring environmental conditions in the field at each site. Higher quality data may allow investigators to move from relational analyses (ordination) to predictive analyses (regression). This would allow the development of tools to predict changes in forage quality in real time as the winter progresses. Livestock managers would be able to use these tools to adjust management in response to changing conditions.

CHAPTER THREE

INFLUENCE OF THREE TIMES WEEKLY ALFALFA SUPPLEMENTATION ON THE BEHAVIOR OF BEEF COWS GRAZING DORMANT MONTANA RANGELAND

Contribution of Authors and Co-Authors

Manuscript in Chapter 3

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Contributions: Conceptualization, methodology, software, validation, formal analysis, investigation, data curation, original draft preparation, review and editing, visualization, project administration

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Contributions: Conceptualization, methodology, software, data curation, review and editing

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Contributions: Data curation, review and editing

Co-Author: Timothy DelCurto

Contributions: Conceptualization, methodology, investigation, data curation, resources, review and editing, supervision, project administration, funding acquisition

Manuscript Information

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Abstract

The objectives of this research were to determine how daily and hourly distance travelled, grazing time, and resting time of beef cows are influenced relative to the timing of supplementation. Over two winters, a herd of commercial Angus cows grazed in a 645-ha Montana foothill rangeland pasture for 56 days between December and February each year. At 1300 every Monday, Wednesday and Friday, all cows were gathered and taken to a central location in the pasture where 3.18 $kg \cdot hd^{-1}$ of alfalfa pellets (17% CP) were immediately delivered. Each year, 18 cows were randomly assigned a global positioning system (GPS) collar. Using the GPS collar data, distance traveled, grazing time, and resting time were estimated for each hour and day for each cow. Activity was grouped into the 24-h period pre-supplementation and 24-h period post-supplementation. Cows travelled 1.7 km further and grazed for 0.7 h less per day post-supplementation ($P < 0.01$). Daily resting time was similar pre- and post-supplementation ($P = 0.07$). Post-supplementation, cows travelled further in the afternoon and morning and reduced grazing in the afternoon and at night ($P < 0.05$). Cows rested less in the morning pre-supplementation and in the afternoon post-supplementation ($P < 0.03$). Results indicate that three times weekly supplementation alters cow activity, though differences are mostly associated with the time surrounding when supplement is delivered.

Introduction

Supplementation is a popular management strategy among livestock producers in western North America. Conventionally, supplementation has been used to bridge the gap between livestock nutrient requirements and the nutrient content of low-quality forage. More recently, there has been interest in using supplementation as a tool to improve livestock distribution on heterogeneous landscapes (Bailey et al., 2019; Bohnert and Stephenson, 2016).

Protein supplements are often the best choice for use with low-quality forages because they improve digestion and increase basal forage intake (DelCurto et al., 2000; Moore et al., 1999). Though commonly fed daily, hand-fed protein supplements can be delivered as infrequently as once-weekly to decrease labor costs while maintaining the same level of performance (Klein et al., 2014; Kunkle et al., 2000).

While there is information describing the influence of supplementation on cow behavior (Bailey, 2004; Bohnert and Stephenson, 2016), there is little information describing the behavior of cattle supplemented infrequently (Brandyberry et al., 1992; Schauer et al., 2005), or comparing behavior between days cattle were supplemented and those they were not (Dunn et al., 1988; Sprinkle et al., 2019).

Reducing the frequency of protein supplementation has no effect on performance, however, it may alter grazing behavior. Many livestock producers strive to maximize use of the basal forage resource in large rangeland pastures. So, it is important to understand how infrequent supplementation influences grazing behavior. Therefore, the objective of this research is to evaluate differences in grazing behavior of cows supplemented three times weekly on supplemented vs non-supplemented days. We hypothesize that cattle grazing behavior is influenced by timing/day of supplementation.

Materials and Methods

The care and use of cattle in this study was approved by the Institutional Animal Care and Use Committee of Montana State University (ACUP #2018-AA14).

This study was conducted in a 645-ha pasture at Montana State University's Red Bluff Research Ranch in Norris, MT (45°35'N, 111°38'W). Mean annual precipitation is 406 mm, 60% of which comes during the growing season (May through September). Topography of the pasture is a combination of gently sloping alluvial fans, steep hillslopes, and broad ridges. Pasture elevation ranges from 1415 to 1715 m. The vegetation is primarily a grassland with an open woodland of Rocky Mountain juniper (*Juniperus scopulorum*) and limber pine (*Pinus flexilis*) on the hillslopes. Dominant herbaceous species are bluebunch wheatgrass (*Pseudoroegneria spicata*), Idaho fescue (*Festuca idahoensis*), needle-and-thread (*Hesperostipa comata*), and isolated patches of cheatgrass (*Bromus tectorum*).

Over two winters, a herd of commercial, March-calving, multiparous Angus cows (n = 139 in year one and 143 in year two) grazed in the pasture for 56 days each year (December 14, 2018 to February 8, 2019 and December 12, 2019 to February 6, 2020). The stocking rate was considered light to moderate for the area (2.63 $\text{ha}\cdot\text{AUM}^{-1}$). On days 0 and 56, all cows were weighed and ranked by body condition score (BCS; 1-9 scale; NASEM, 2016) following a 16-h shrink (Table 3.1). At 1300 every Monday, Wednesday and Friday, all cows were gathered and taken to a central location in the upland region of the pasture. All cows reached the supplement site, between 1400 and 1500, where 3.18 kg·hd^{-1} of alfalfa pellets (17% CP) were delivered on the ground via a truck-mounted cake feeder.

Each year, 18 cows were randomly assigned a global positioning system (GPS) collar (LiteTrack 420; Lotek Wireless, Newmarket, Ontario, Canada). Each collar contained a GPS receiver and 3-axis accelerometer. Collars were programmed to take GPS location readings at 5-min intervals and accelerometer readings at 1-min intervals for the entirety of the study. Distance traveled and rate of travel were estimated between successive points for each location reading (Ganskopp, 2001).

Table 3.1. Forage availability, weather conditions, and cow performance for beef cows grazing between December and February over two years in Norris, MT.

	Year One	Year Two
Standing crop, kg·ha^{-1}	1425	592
Temperature, °C		
Mean	-3.12	-1.32
Min	-25.60	-16.90
Wind speed, m·s^{-1}		
Mean	4.75	6.30
Max	16.60	20.10
Snow depth, cm		
Mean	5.70	2.97
Max	35.60	20.30
Body weight, kg		
Initial	599	604
Final	602	599
Body condition score, 1-9*		
Initial	5.0	5.4
Final	5.0	5.1

*NASEM, 2016

In year one, each collared cow was observed for 3 ± 1 h and its dominant activity was recorded every minute. Grazing, resting, and travelling made up over 99% of observations, therefore these were the only activities considered. A behavior prediction model was developed via a random decision forest using the randomForest package in R to estimate grazing and resting time (Liaw and Wiener, 2002; R Core Team, 2019). The dependent variable was activity and the independent variables were the X, Y and Z axes from the accelerometer data and the rate of travel from the location data. To validate accuracy, only 80% of the observations were used for training the model. The model was then used to predict activity of the remaining 20% of the observations using the location and accelerometer data. The actual and predicted activities were compared, resulting in a model accuracy of 88.7%.

Activity was classified relative to the timing of supplementation. All activity 24 h after gathering the cows for supplementation was considered “post-supplementation”. All activity 24 h prior to gathering the cows for supplementation was considered “pre-supplementation”. Hereafter, this classification will be referred to as the “24-h period”. Data from 1300 Saturday to 1259 Sunday does not fall into either category and was excluded from analysis. We developed two datasets from our data. The first summed distance travelled, grazing time, and resting time for each cow over each 24-h period of the study. The second summed distance travelled, grazing time, and resting time for each cow over each hour of the study.

Temperature and wind speed readings were collected on a 5-min interval using a HOBO U30 weather station (Onset, Bourne, MA) deployed in a central location in the study pasture (Table 3.1). Snow depth was manually measured and recorded daily (Table 3.1). Standing crop was estimated by clipping 0.25 m^2 plots at 10 random sites in the pasture at the start of the study each year (Table 3.1).

All data were analyzed in R with the lmerTest (Kuznetsova et al., 2017) and lme4 (Bates et al., 2015) packages using a generalized linear mixed model. Each collared cow was considered an experimental unit. The 24-h period dataset was analyzed using a model that included 24-h period and year with a random intercept of individual cow. The hour-level dataset was analyzed using a model that included hour, 24-h period, and the hour by 24-h period interaction as fixed effects with a random intercept of individual cow. Means were separated with the emmeans package (Lenth, 2019) using the Tukey method. Statistical significance was accepted at $P < 0.05$.

Results

Daily activity data are presented in Table 3.2. Cows travelled 1.7 km further and grazed for 0.7 h less per day post-supplementation ($P < 0.01$). Resting time was similar pre- and post-supplementation (9.29 ± 0.25 $h \cdot d^{-1}$; $P = 0.07$). There were no effects of year on daily activity ($P > 0.30$).

Table 3.2. Effect of three times weekly protein supplementation on the daily activity for the 24-h period pre-supplementation and 24-h period post-supplementation of beef cattle grazing native foothill rangeland between December and February over two years in Norris, MT.

	24-h[*]			Year[†]			*P*-value	
	Pre-supp.	Post-supp.	SEM	Year One	Year Two	SEM	24-h	Year
Distance travelled, $km \cdot d^{-1}$	5.18	6.90	0.69	6.07	6.02	0.82	< 0.01	0.67
Grazing time, $h \cdot d^{-1}$	12.90	12.20	0.21	12.70	12.30	0.28	< 0.01	0.30
Resting time, $h \cdot d^{-1}$	9.14	9.44	0.25	9.06	9.52	0.33	0.07	0.34

[*] 24-h = 24-h period pre-supplementation (Pre-supp.) vs. 24-h period post-supplementation (Post-supp.)
[†] Year = Year One vs. Year Two

Distance travelled, grazing time, and resting time displayed an hour by 24-h period interaction ($P < 0.01$; Fig. 3.1). Cows travelled further the afternoon and morning hours post-supplementation ($P < 0.02$). Cows grazed less the afternoon and night post-supplementation ($P < 0.05$). Cows rested less the morning pre-supplementation and afternoon post-supplementation ($P < 0.03$). Cows also rested more at night post-supplementation ($P < 0.05$).

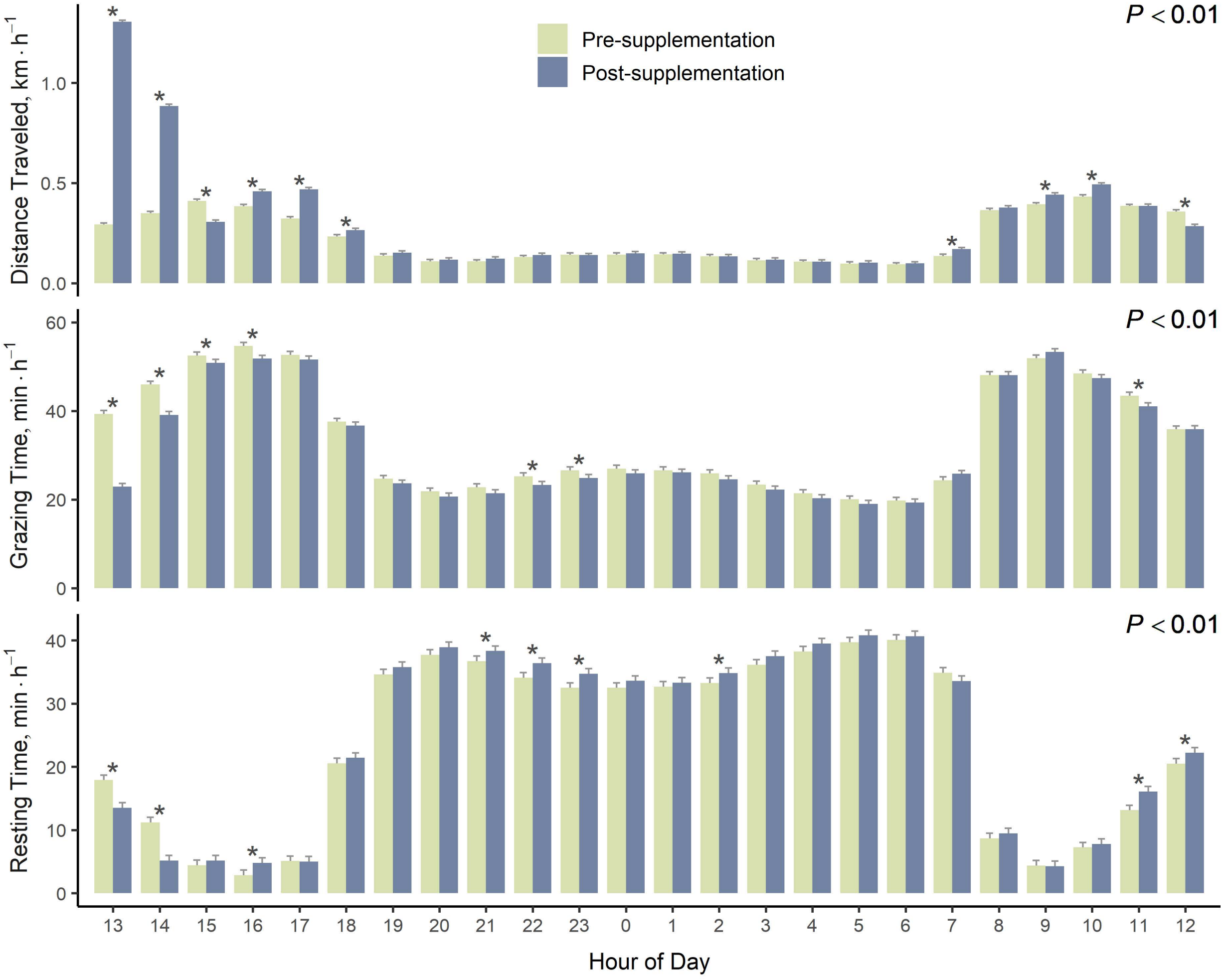

Figure 3.1. Hourly activity for the 24-h period pre-supplementation and 24-h period post-supplementation of beef cattle supplemented at 1300 three times weekly, grazing native foothill rangeland between December and February over two years in Norris, MT. Means are displayed with standard error bars. Asterisks above paired bars indicates a significant difference ($P < 0.05$) in the activity for that hour of the day. The *P*-value for each hour by 24-h supplementation period interaction was < 0.01.

Discussion

Year one was coldest, received the most snow accumulation, and had over twice the amount of available forage compared to year two. The mean daily temperature was less than 0°C for 37 days in year one and 30 days in year two. There was measurable snow coverage for 38 days in year one and 14 days in year two. Despite the differences in weather conditions and forage availability, there was no main effect of year on daily distance travelled nor grazing and resting time.

Mean grazing time across years and supplementation periods was 12.5 $h \cdot day^{-1}$, which is higher than 6-9 h as has been reported for cattle grazing dormant vegetation (Adams et al., 1986; Prescott et al., 1994; Wyffels et al., 2019). This may be due to differences in the classification of grazing, resting, and travelling during activity observation. Despite this difference, the pattern of grazing throughout the day was similar to previous studies, where most grazing occurs in the morning and afternoon (Ganskopp, 2001; Ganskopp and Bohnert, 2006; Schoenbaum et al., 2017). Therefore, relative differences between groups should remain consistent.

Most of the differences in distance travelled and grazing time between pre- and post-supplementation periods occurred in the hours immediately after the cows were supplemented. Ninety percent of the 1.7 km increase in distance travelled and 65% of the 0.7 h decrease in grazing time occurred within five hours of supplementation. Similarly, others have noted cattle reduced grazing after they received supplement. Steers grazing Russian wildrye reduced grazing time for four hours after they received supplement (Adams, 1985). Cows grazing winter rangeland in Idaho, receiving protein supplement once weekly, often reduced grazing time the day of or the day after supplement was delivered (Sprinkle et al., 2019). Conversely, in Montana, cows provided a protein supplement on alternate days increased grazing time in the 24-h period after supplementation (Dunn et al., 1988), however, the amount of supplement delivered in this study was 3.5 times less than in our study and was individually fed, which may have altered behavior. In our case, it is possible that feeding a larger quantity of a high-fiber protein supplement could have increased gut fill, reducing grazing post-supplementation.

Our results indicate that, for beef cows supplemented three times weekly, both daily activity and the hourly partitioning of activities differ pre- and post-supplementation. Most differences in daily activity are around the time when supplement is delivered; the remainder of the 24 h post-supplementation is largely the same as pre-supplementation. Therefore, infrequent protein supplementation as a tool to use low-quality forage and improve livestock distribution, may result in minor changes to cow grazing behavior between supplemented and non-supplemented days. Continued research evaluating supplement delivery strategies that optimize use of low-quality forages on extensive rangeland environments are needed for western beef cattle production systems.

CHAPTER FOUR

EVALUATING THE SPATIAL SCALE OF RESOURCE USE BY BEEF COWS ON WINTER RANGE

Contribution of Authors and Co-Authors

Manuscript in Chapter 4

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Manuscript Information

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Abstract

The importance of spatial scale in ecological processes is widely recognized, however, it has yet to be quantitatively incorporated into analyses of livestock habitat selection. We evaluated the spatial scaling of patch-level (third order) resource use by beef cattle (*Bos taurus taurus*) grazing dormant rangeland in southwestern Montana, USA across individuals, diel intervals, pastures, and habitat covariates. Using data collected from 381 GPS collar deployments over six winters, estimated cattle space use was related to six topographic and eleven vegetation covariates across 15 spatial scales ranging between 30–2550 m. We modeled resource use with resource utilization functions implemented by serial univariate beta regression. The scale of effect, defined as the scale that minimized relative AIC, varied between covariates, pastures, and individuals. Among covariates, the effect of scale was weakest at fine scales (≤ 390 m) and the scale of effect peaked at either intermediate (n = 11; 570–1650 m) or coarse scales (n = 5; ≥ 2370 m). There was more variation among pastures where covariates were variably selected for or against, however, the scale of effect generally remained within a similar range of values. Within pasture, diel interval modified the strength of selection, but the scale of effect largely remained the same. Among individuals, variation was substantial; all scales were the scale of effect for a portion of the population. Our results illustrate the scale-dependence of resource use in beef cattle. We encourage future livestock habitat selection research to carefully consider the spatial scale of the evaluated covariates.

Introduction

A fundamental focus of grazing ecology is understanding how animals interact with their environment. As animals move through space and time, they make discrete decisions to use particular units of space at each subsequent time step. These decisions can be aggregated into a nested hierarchy of spatio-temporal behavioral levels ranging from the acquisition of dietary components from a feeding station to the emergence of a home range within a landscape (Bailey et al., 1996; Owen-Smith et al., 2010; Senft et al., 1987). These levels are often expressed in simplified form as Johnson's four orders of selection (Johnson, 1980; Meyer and Thuiller, 2006). Fourth order selection is bite and feeding station-level diet selection from within habitat patches. Third order selection is food patch and foraging area-level selection from within an individual's home range. Second order selection is the selection of an individual's home range from within its species range and first order selection is the collective selection of a species range.

Driven by different needs, each behavioral level is expressed within its own "ecological neighborhood" at distinct spatial and temporal scales (Addicott et al., 1987; Wiens, 1989), however, none of these levels are independent of one another, rather they form a series of nested feedback loops where decisions at coarser behavioral levels limit the available options at finer levels and cumulative decisions at finer levels inform and influence coarser-level decisions (Nash et al., 2014; Senft et al., 1987).

Accordingly, animal selection for habitat features varies both with the behavioral level being evaluated and the spatial scale of the habitat feature itself. The scale of effect is defined as the spatial scale of a habitat variable that elicits the greatest selection for a particular behavior.

All animal movements occur as a response to either environmental features or animal perception (Bailey et al., 1996; Mueller and Fagan, 2008; Nathan et al., 2008). Environmental features, such as habitat heterogeneity, forage quality, or patch size determine animal ability to express selectivity (Parsons and Dumont, 2003; WallisDeVries et al., 1999) and alter movement dynamics (Benhamou and Bovet, 1989; Kerby, 2002). Animal perception is a result of the combination of current sensory input (e.g. visual or auditory; Laca et al., 2010; Mech and Zollner, 2002) and spatial memory (Bailey et al., 1989; Edwards et al., 1996; Quail and Fraser, 2025).

Consequently, any change in environment or perception can shift patterns in animal behavior. For instance, the scale of effect has been reported to vary by habitat covariate (Ranglack et al., 2022), sex (de Knegt et al., 2011), season (Leblond et al., 2011), home range size (Heit et al., 2023), and habitat characteristics (Anderson et al., 2005). Thus, there is no single best scale of effect, and the scale used in an analysis should be carefully considered for each habitat covariate. In some cases, a covariate may be selected for, against, or not at all depending on the scale evaluated (Heit et al., 2023). Therefore, analyses conducted without regard for spatial scaling may lead to spurious or even opposite conclusions (de Knegt et al., 2010).

This concept has received much attention in wildlife research (Mayor et al., 2009; McGarigal et al., 2016; Meyer and Thuiller, 2006) and has been incorporated into quantitative habitat selection analyses (Hysen et al., 2025; McNew et al., 2013; Ranglack et al., 2022). In contrast, while there has been some attention given to scale in livestock foraging research (Dumont et al., 2002; Laca et al., 2010; Larson-Praplan et al., 2015; Utsumi et al., 2009), most has focused on assessments of feed acquisition at fine behavioral levels. Current livestock habitat selection analyses typically use a single a priori scale, typically between 20−100 m (Clark et al., 2014; Nyamuryekung'e et al., 2022; Raynor et al., 2017; Roever et al., 2015). If livestock habitat selection is most strongly expressed at different scales than are evaluated, research may not fully capture animal behavior. To better understand livestock foraging ecology, there is a need to evaluate and incorporate scale into livestock habitat selection analyses.

Herbivore behavior is structured in regular diel cycles (Ager et al., 2003; Gregorini, 2012) that correspond with patterns of resource selection (Padilla et al., 2024; Roberts et al., 2017). Differences in individual behavioral (Heit et al., 2023) and seasonal movement (Stephens et al., 2024) have been shown to influence the scale of resource selection, however, it is unknown how the scale of resource selection varies across the diel cycle.

Here, we clarify our use of three related terms that are variously used elsewhere. Resolution refers to the level of spatial detail in data and is often used as a general descriptor encompassing both grain and scale. Grain is the smallest mapping unit in a dataset (e.g. pixel size) whereas scale is the spatial extent over which a variable or process is quantified.

We evaluated the spatial scaling of patch-level (third order) diel resource use by beef cattle (*Bos taurus taurus*) grazing winter range in five pastures on one ranch. We hypothesized that the selection response would vary across covariates and diel intervals, but that consistent patterns would emerge across pastures. Our approach used a pseudo-optimized multi-scale spatial and multi-level temporal modeling framework implemented with a series of resource utilization functions (RUFs).

Methods

Study Area

This study was conducted at Montana State University’s Red Bluff Research Ranch (45°35′ N, 111°38′ W). Red Bluff is a 4961 ha ranch situated along the Madison River in the foothills between the Tobacco Root Mountains and the Madison Range in southwestern MT, USA. Elevation of the ranch ranges between 1370–1980 m. The climate is characterized as cold semi-arid (Kottek et al., 2006) and mean annual precipitation is 418 mm (PRISM Climate Group, 2024). The rangelands are dominated by Central Rocky Mountain foothill grassland (NRCS, 2025; Olson et al., 2001) with Rocky Mountain juniper (*Juniperus scopulorum* Sarg.)-limber pine (*Pinus flexilis* James) woodland on the upper slopes and ridges and sporadic patches of either mountain big sagebrush (*Artemesia tridentata* Nutt. ssp. *vaseyana* [Rydb.] Beetle) or antelope bitterbrush (*Purshia tridentata* [Pursh] DC) shrubland. The grasslands are dominated by cool season perennial bunchgrasses including bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] Á. Löve), Idaho fescue (*Festuca idahoensis* Elmer), prairie Junegrass (*Koeleria macrantha* [Ledeb.] Schult.), and needle-and-thread (*Hesperostipa comata* [Trin. & Rupr.] Barkworth) (Mueggler and Stewart, 1980). This study used a subset of six pastures ranging in size from 236-565 ha (Fig. 4.1; Table 4.1). FF-16M is a combination of two pastures whose gates were left open and managed as one pasture over the duration of its use. First Feeder is the west half of FF-16M and was used separately from the broader FF-16M. The ranch maintains a herd of 200 crossbred Angus-based commercial and purebred Angus beef cows that graze on rangeland for most of the year.

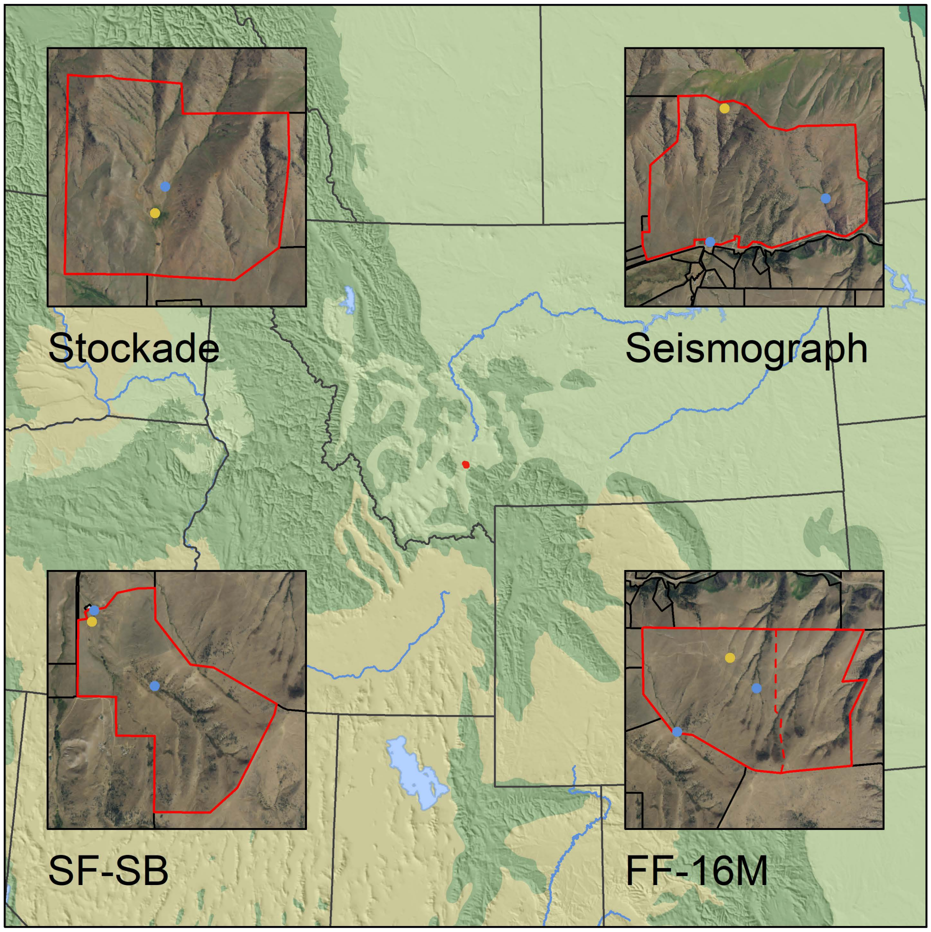

Figure 4.1. Reference map of the study area (red dot) in southwestern Montana, USA. The pastures used in the study are indicated in the inset maps. Solid red lines indicate perimeter fences of each pasture. The dashed line in FF-16M indicates the internal fence separating First Feeder (left side) from the remainder of FF-16M. Yellow dots indicate supplement delivery locations and blue dots indicate water sources. Within the background map, temperate grassland and shrubland, desert and xeric shrubland, and temperate coniferous forests are indicated by the light green, beige, and dark green colors, respectively (Olson et al., 2001).

GPS Data

Between December of 2018 and March of 2024 we deployed Lotek GPS collars (Newmarket, ON, Canada) on 13 groups of cattle for a total of 381 individual collar deployments (Table 4.1). All GPS collars were programmed to record GPS locations every 5 minutes. This study was overlaid with a series of supplementation studies. Every year, all cows were gathered every Monday, Wednesday, and Friday and herded to a location in the pasture where they were provided a hand-fed protein supplement treatment. In four of the six years, there was a treatment group that did not receive any protein supplement, however, those cows were still gathered and brought to the corrals with the remainder of the herd. Additionally, all cows were moved to a corral and weighed every 28 days. To remove locations directly influenced by human activity, all GPS data were removed on any day cows were handled or fed. To remove potentially erroneous data, all GPS locations outside of the pasture boundaries and all locations with an estimated rate of travel of over 1.5 m · s^{-1} between both the preceding and subsequent locations were removed. After filtering all GPS data, we were left with 2,381,617 GPS locations.

Table 4.1. Pasture, date range, and Lotek GPS collar specifications for beef cattle grazing rangeland over six winters at Red Bluff Research Ranch in Norris, MT, USA. Data completeness is the post-cleaning percentage of expected records given continuous 5-min fixes over the duration of the collar deployment.

Pasture	Area (ha)	Year	Dates	Dur.	GPS Collars		
					Model	Num.	Data Completeness (%)
Seismograph	565	1	Dec-Feb	56d	Lite Track 420	17	96.0
Seismograph	565	2	Dec-Feb	56d	Lite Track 420	17	96.4
Seismograph	565	2	Dec-Feb	56d	Lite Track 800	18	98.7
First Feeder	236	3	Dec-Jan	28d	Lite Track 800	17	98.8
First Feeder	236	3	Dec-Jan	28d	LR3300	27	56.6
FF-16M	394	3	Jan-Mar	56d	Lite Track 800	17	99.5
FF-16M	394	3	Jan-Mar	56d	LR3300	26	57.6
First Feeder	236	4	Dec-Jan	28d	Lite Track 800	43	98.8
FF-16M	394	4	Jan-Mar	56d	Lite Track 800	43	99.0
Stockade	376	5	Jan-Mar	56d	Lite Track 800	38	88.4
SF-SB	256	5	Mar-Apr	28d	Lite Track 800	38	93.2
Stockade	376	6	Jan-Mar	56d	Lite Track 800	40	98.6
SF-SB	256	6	Mar-Apr	28d	Lite Track 800	40	93.1

Diel Intervals

To meet their daily requirements, cattle engage in a cyclical series of behaviors that include grazing, traveling, and resting (Bailey, 1995; Gregorini, 2012; Kilgour, 2012). Among these, grazing is a major disturbance in ecosystems (Milchunas and Lauenroth, 1993; Pringle et al., 2023), thus understanding the location and intensity of grazing has been a central focus of ecological research (Brock and Owensby, 2000; Maestre et al., 2022; Mueggler, 1965; Senft et al., 1984).

Although algorithms have been developed to predict animal behavioral state based on telemetry or wearable sensor data (Augustine and Derner, 2013; Brennan et al., 2021; Lipinski et al., 2025), these are often specific to the technology they were developed on, and are either incompatible or perform poorly with other sensor models. Because our dataset contains three different models of GPS collar, behavioral predictions would be confounded with collar model. Therefore, instead of using behavioral states directly, we partitioned our data into diel intervals that broadly correspond with distinct behavioral phases.

To define the diel intervals, we examined the activity patterns in our dataset (Davis et al., 2020; Lipinski et al., 2025; Chapter 5) and identified four natural breaks: morning, midday, evening, and night. Morning was defined as the period between sunrise and two hours prior to solar noon; midday as the four-hour period centered on solar noon; evening as the period from two hours post solar noon to sunset; and night as the period between sunset and sunrise. These intervals broadly correspond to the morning grazing period, midday rest, evening grazing period, and nighttime rest and rumination (Gregorini et al., 2006). The time of sunrise, solar noon, and sunset was calculated separately for each day in the dataset using the R package “suncalc”

(Thieurmel and Elmarhraoui, 2022). Each individual collar deployment, subdivided by diel interval is hereafter referred to as a sub-individual.

Utilization Distributions

Utilization distributions (UDs) quantify relative use of a spatial area over a defined period of time (Calhoun and Casby, 1958; Jennrich and Turner, 1969). All portions of every pasture were visited by cattle, thus we defined pasture as the de facto home range (Howery et al., 1999) and used it as the spatial extent to quantify UDs over. We developed a UD for each sub-individual using Brownian bridge movement models (BBMMs; Horne et al., 2007). BBMMs estimate the probability of occurrence between two locations conditioned on the distance and elapsed time between them. Using the R Package "BBMM" (Nielson et al., 2013), we calculated BBMMs between all relocations occurring within 30 minutes of each other, then rasterized the resulting probability density over the pasture at a 30-m resolution. Within each resulting UD, potential values range from zero to one, and all values sum to one. The UD value in each cell represents the relative intensity of use for that location (Horne et al., 2007; Millspaugh et al., 2006).

Covariates

We selected an a priori set of 17 habitat covariates we hypothesized may contribute to resource use and are widely available through remote sensing (Table 4.2; Roever et al., 2015; Senft et al., 1983; Wyffels et al., 2020). We derived topographical covariates from a 1 arc-second (30-m resolution) digital elevation model of the study area (USGS, 2019) using the R package "terra" (Hijams, 2025). Slope and aspect were calculated using a cell and its eight neighbors following Horn (1981). Aspect was separated into N–S and E–W components by calculating the cosine and sine of the aspect, respectively (Wilson et al., 2007). Ruggedness is a measure of the local variability in topography and was calculated using the Terrain Ruggedness Index following Wilson et al. (2007). Topographic Position Index (TPI) is a quantification of landform position calculated as the difference between a cell and its eight neighbors (Wilson et al., 2007). A high TPI indicates that a cell is on a ridge or peak whereas a low value indicates that a cell is in a valley or other depression. We used Google Earth Engine (Gorelick et al., 2017) to derive Rangeland Analysis Platform-generated estimates for 30-m resolution fractional cover (Allred et al., 2021) and plant biomass (Jones et al., 2021) for the growing season prior to the winter of each study year.

Table 4.2. Source and description of covariates used in resource use analysis of beef cattle grazing dormant rangeland.

Category	Covariates	Resolution	Source
Topography	Elevation, slope, Terrain Ruggedness Index, Topographic Position Index, N–S aspect, E–W aspect	30-m	Digital elevation model (USGS, 2019)
Cover	Annual, perennial, shrub, tree, bare ground, litter	30-m	Rangeland Analysis Platform (Allred et al., 2021)
Biomass	Annual, perennial, shrub, tree	30-m	Rangeland Analysis Platform (Jones et al., 2021)

All covariates are natively available at 30-m resolution. We increased the spatial scale while maintaining the same 30-m grain using a circular moving window mean. For each covariate, we developed a set of 15 scaled rasters with scales ranging from 30-m to 2550-m where scale is expressed as the diameter of the moving window. Livestock are bound by pasture fences and are only capable of using the space within those fences. For locations near the pasture boundaries, the moving window covered locations inside and outside of the pasture. Rather than exclude values outside of the pasture, covariate values outside the pasture were included in the mean. We assumed that animals may still use information from areas not directly accessible to them in making foraging decisions. The largest scale considered corresponds with the spatial extent of the next largest selection order, the home range (second order; Heit et al., 2023; Kuemmerle et al., 2018; Meyer and Thuiller, 2006). The largest scale represents an area of 510 ha whereas the finest scale represents an area just under 0.1 ha.

Resource Utilization Functions

Our approach to evaluate the scaling of resource use followed what McGarigal et al. (2016) describe as a pseudo-optimized multi-scale analysis where the effect of scale was determined by the marginal explanatory power of a univariate analysis of each covariate (Fig. 4.2). We used RUFs to link each UD to the scaled covariates. In contrast to the more common resource selection functions that model use as a binary response using a sample of locations in the area of interest (Boyce et al., 2002; Manly et al., 2002), RUFs model use as a continuous response across the entire area of interest (Marzluff et al., 2004; Millspaugh et al., 2006). Resource utilization functions have been criticized for being a two-stage procedure that introduce error in the first stage with the estimation of the response variable (i.e. the UD), that is unaccounted for in the second stage (i.e. the regression; Hooten et al., 2013). However, with fine temporal resolution location data and time-explicit utilization estimation methods (e.g. BBMMs vs kernel methods), the error introduced in the first stage is minimized.

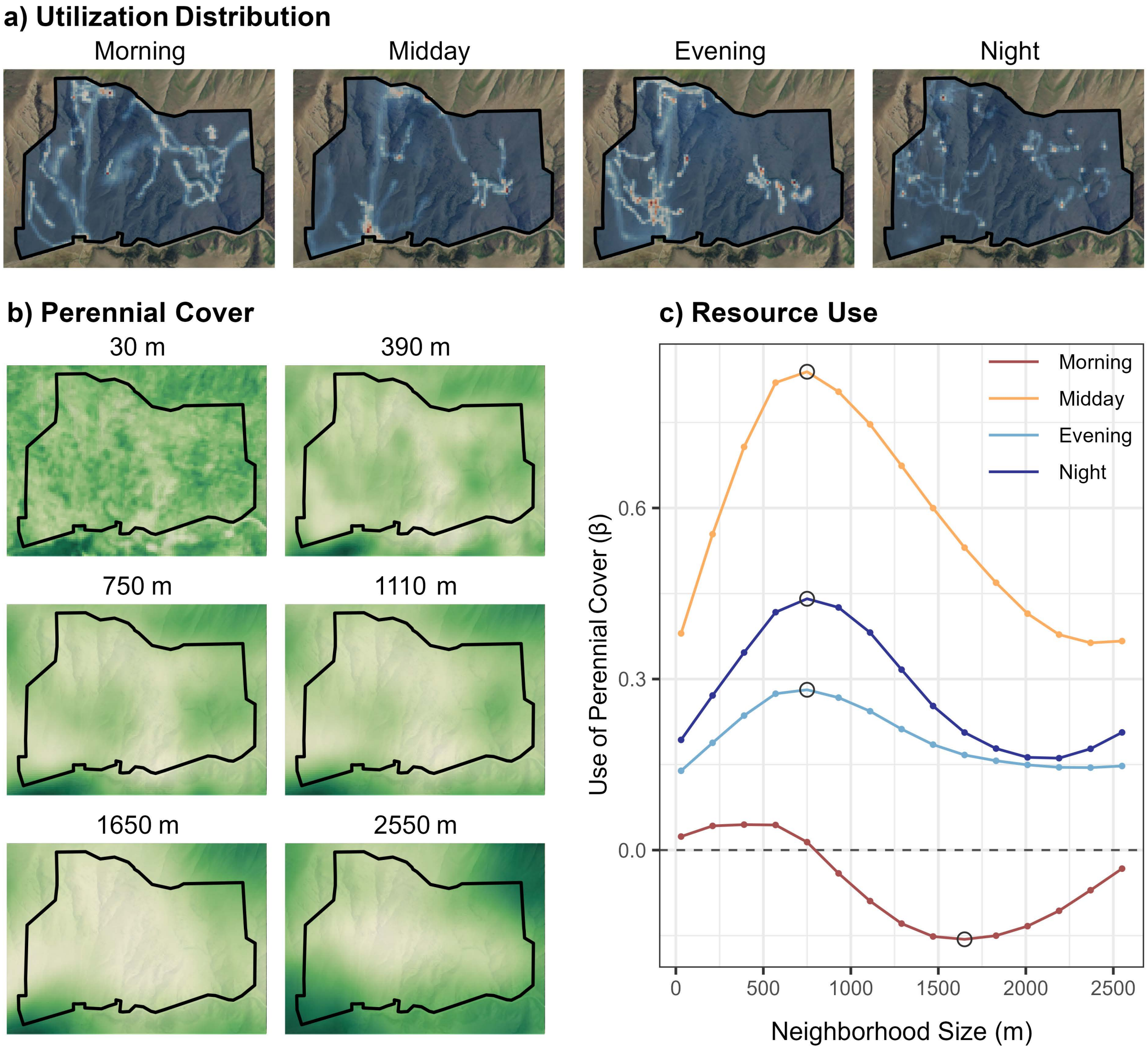

Figure 4.2. Overview of multi-scale resource use evaluation. a) Animal GPS data are subdivided into four diel intervals to develop a utilization distribution for each. b) A circular focal mean produces gridded covariate data at scales between 30 m and 2550 m. c) Resource utilization functions regress each utilization distribution against each scaled covariate. Each model within the set produces an estimate for the strength and direction of resource use (β coefficient) and model parsimony (AIC). In most cases, the scale with the largest absolute β coefficient corresponds to the scale with the most parsimonious model (open black circles).

For each UD and covariate, we built a model set containing 15 univariate beta regressions (Ferrari and Cribari-Neto, 2004; Geissinger et al., 2022), each linking the UD to one scaled covariate using the “glmmTMB” package in R (Brooks et al., 2017). For each model, we extracted the slope coefficient (β) and AIC (Burnham and Anderson, 2002). At the individual level, we defined the scale of effect for each covariate as the scale with the minimum AIC (Heit et al., 2023; Laforge et al., 2015). To compare the effect of scale between individuals and across covariates, we z-scored the AIC values for all models within each model set. This provided a normalized index to evaluate mean relative AIC support. All data processing and analyses were completed in R 4.3.1 (R Core Team, 2023).

Results

Subdividing data from 381 collar deployments into 1524 sub-individuals, we analyzed a total of 365,760 RUF models. Among individuals, the scale of effect was variable within and across pastures (Fig. 4.3). Across covariates, the finest scale (30 m) was the scale of effect for 1.7% of sub-individuals (range: 0.0-24.1%) whereas the largest scale (2550 m) was the scale of effect for 29.7% of sub-individuals (range: 16.4-60.2%). Many covariates exhibited bimodal distribution of individual-level scale of effect with a peak near the largest scale and another at an intermediate scale between 390 m and 1110 m.

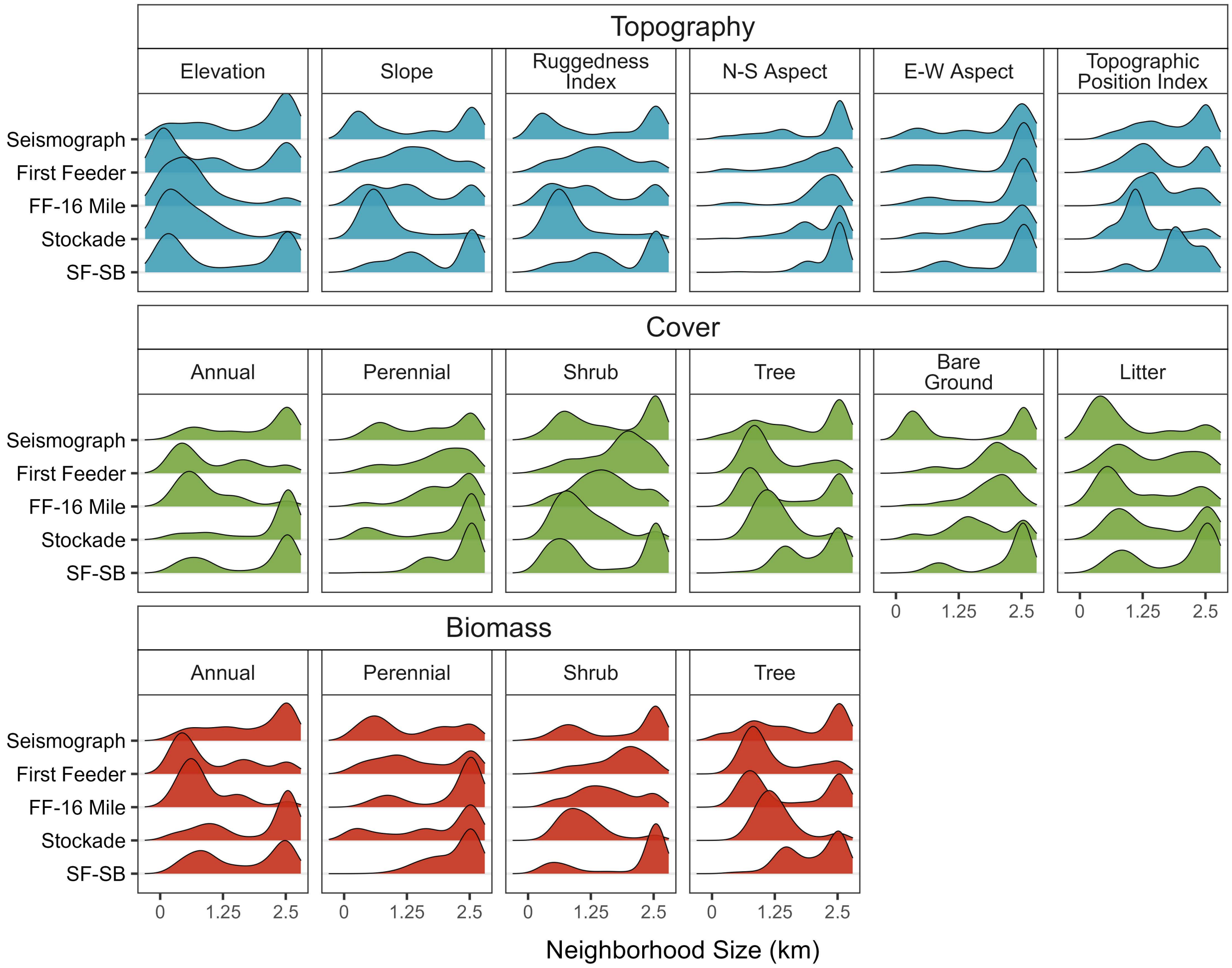

Figure 4.3. Density plot of individual-level scale of effect for resource use across 15 spatial scales (30–2550 m) for beef cattle grazing dormant foothill rangeland in southwestern Montana, USA.

At the overall population level, relative AIC support generally increased with scale (Fig. 4.4). For most of the covariates, support was weakest at the finest scales, increased rapidly to intermediate scales (390–930 m), then slightly declined or oscillated at coarser scales. For both components of aspect and perennial cover, support generally increased linearly, peaking at or near the coarsest scale (2550 m). Elevation was the only variable where support was stronger at finer scales than coarser scales, peaking at 570 m. At the pasture level, the response was more variable. Support remained weakest at the finest scales but varied across intermediate and coarse scales, generally peaking between 570 m and 2550 m. Within pasture, diel interval modified the magnitude of relative AIC support but, generally, the shape of the relationship was similar, and maximum support was near the same scale.

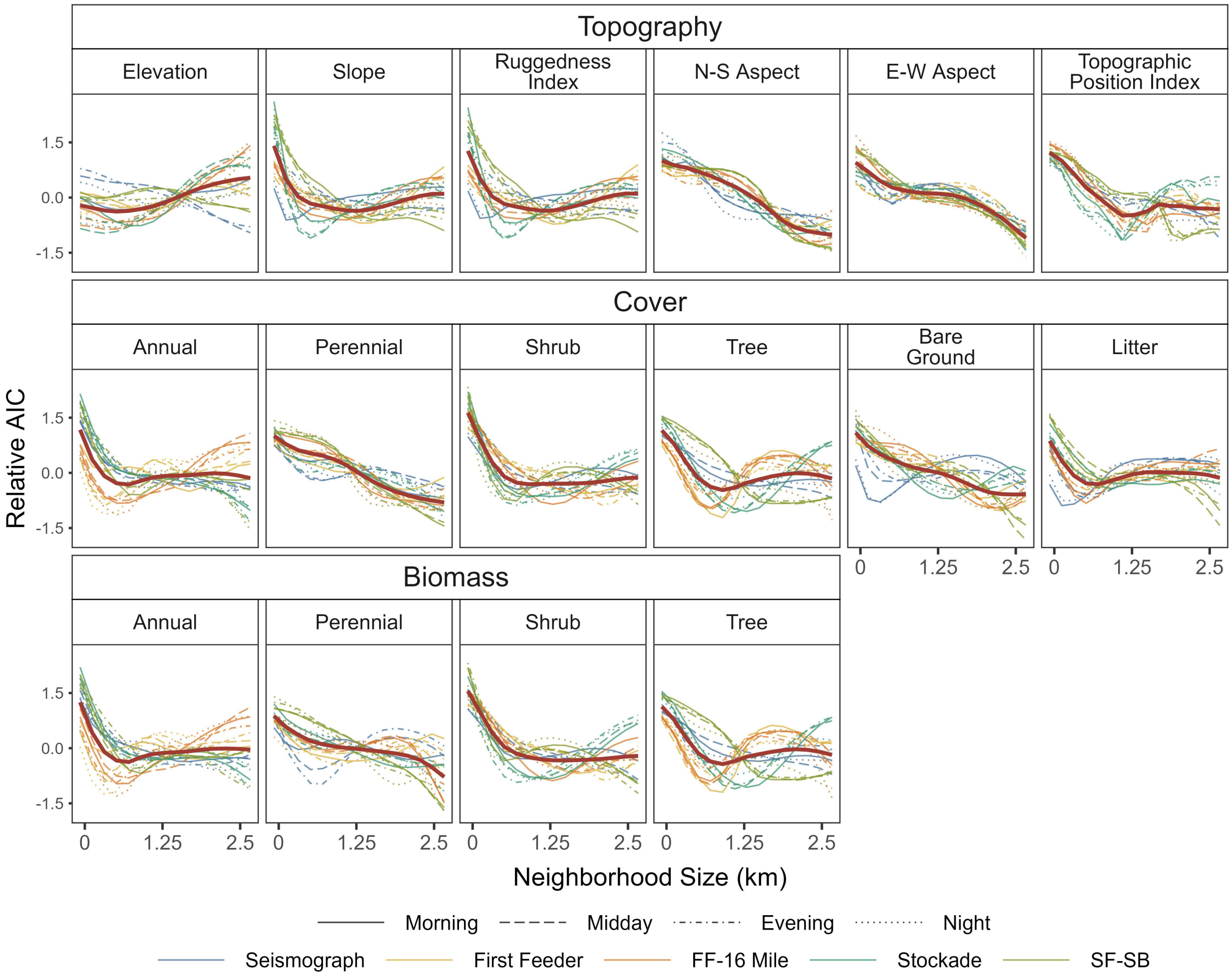

Figure 4.4. Relative AIC support for population, pasture, and diel-level resource use across 15 spatial scales (30–2550 m) for beef cattle grazing dormant foothill rangeland in southwestern Montana, USA. The dark red line indicates the overall covariate mean.

Patterns in β coefficients generally paralleled those observed in relative AIC support (Fig. 4.5). Within each pasture, scales with the largest absolute β coefficients broadly concorded with those with the greatest relative AIC support. Coefficients for elevation, slope, and terrain ruggedness index were relatively consistent across scales and pastures, whereas other covariates varied more substantially. For most covariates, selection was weak at fine scales and strengthened at coarser scales, following linear, quadratic, or irregular trends. Some covariates, such as shrub cover and annual biomass, exhibited consistent directional selection across all pastures, whereas others, such as north aspect and perennial cover, varied in direction between pastures. Despite this, the scales with the strongest selection largely remained within a similar range. In several instances, the direction of selection shifted as scale was increased. In a few cases, such as perennial cover in Seismograph, the direction of selection shifted between years, but generally, selection patterns were consistent across years. Similarly, diel interval altered the magnitude of selection, but the overall patterns remained consistent within each pasture.

Discussion

Resource use differed between pastures and across scales, however, consistent patterns emerged. In moderate to large pastures (236–565 ha), our results indicated that pasture-level animal utilization is most strongly driven by intermediate to coarse scale (~500–2500 m) resource patterns. For 15 of the 16 evaluated covariates, relative support increased with scale. Ten of these exhibited a saturating trend where support was considerably weaker at fine scales (< 400 m) but stabilized at intermediate and coarse scales (> 500 m). Likewise, other studies that have evaluated ungulate resource selection across a similar range of scales (min: 30–120 m; max: 2040–4000 m) report strongest support for intermediate (800–1900 m) or coarse scale covariates (4000 m; Heit et al., 2023; Kuemmerle et al., 2018; Sun et al., 2020).

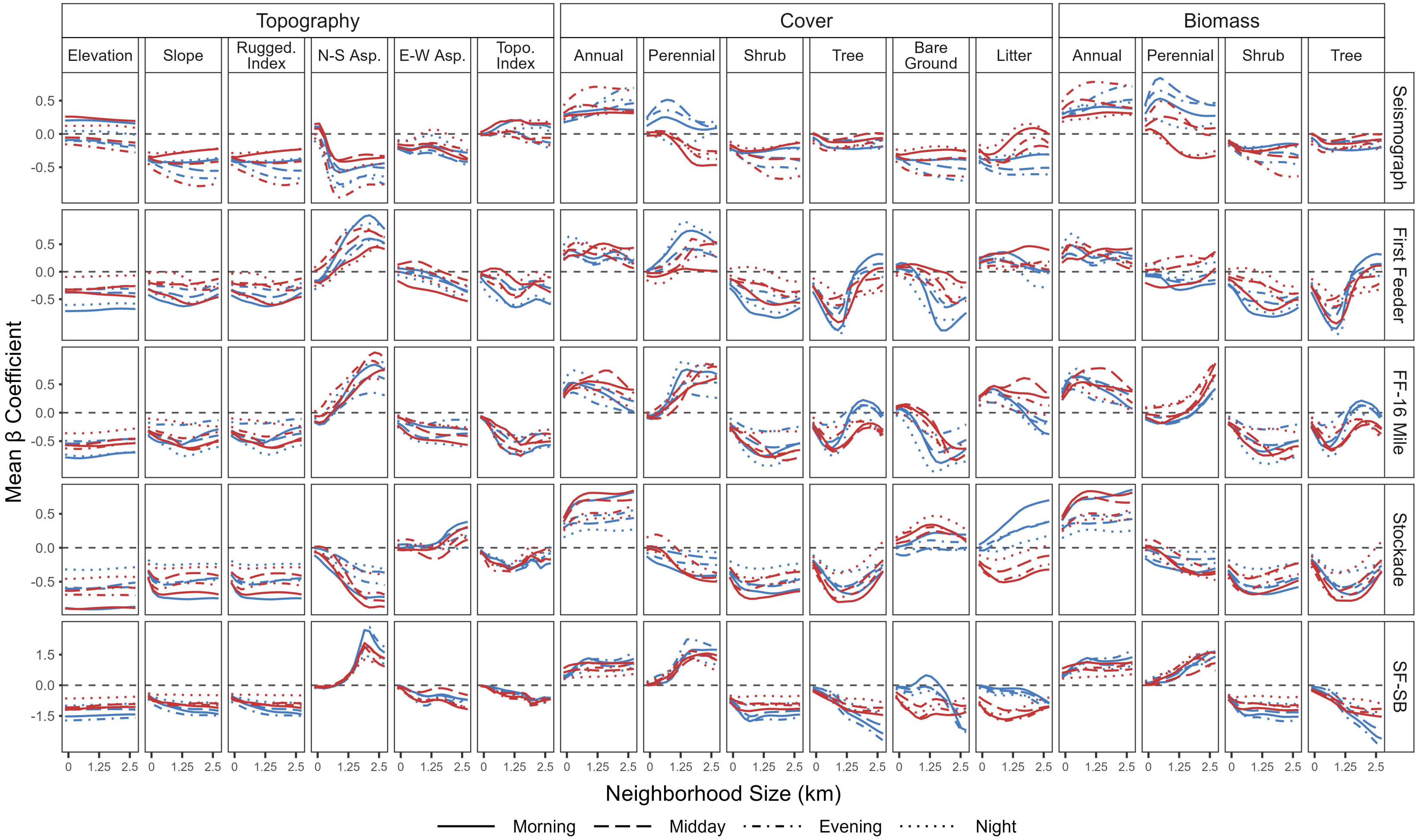

Figure 4.5. Resource use across spatial scales for beef cattle grazing dormant foothill rangeland in southwestern Montana, USA. Panels illustrate resource use (β coefficients) within a pasture across 15 spatial scales (30–2550 m). Lines represent population-level use partitioned into four diel intervals over two years of consecutive grazing within each pasture (red and blue lines). Positive and negative coefficients indicate selection for or against a covariate, respectively. Data are from 381 collar deployments across six winters.

These results underscore the importance of evaluating and justifying the methodology used in habitat selection analyses. As previously cautioned, an analysis of the same data using resources at different scales could result in different or even opposite conclusions (de Knegt et al., 2010; Heit et al., 2023). We used 30 m covariate data as it has been widely used in prior analyses (Nyamuryekung'e et al., 2022; Parsons et al., 2021; Wyffels et al., 2019) and readily available to the public (Allred et al., 2021). This same data provider recently released an updated version of the data available at 10 m resolution (Allred et al., 2025). The use of the data, as natively available, may not prove to be more informative for evaluating or predicting patch-level resource use, however, heterogeneity can be an important factor in animal behavior and space use (Laca, 2009; Laforge et al., 2015; WallisDeVries et al., 1999), which this product could prove useful for evaluating.

This also brings into question the adequate temporal fix resolution for third order habitat selection analyses. If patch-level use is driven by moderate to large scale patches, there may be a diminishing return for higher frequency, finer temporal resolution animal location data. Scaling across space and time are linked through the intrinsic scale ecological processes take place over (Owen-Smith et al., 2010; Wiens, 1989). Evaluating the temporal aspect of scaling has been encouraged (Mayor et al., 2009; McGarigal et al., 2016), however, it has received less attention than spatial scaling.

We evaluated scaled resources; however, this is an abstraction used to compare between covariates. Rather, animals interact with the physical structure and quantity of resources. The selection of a resource is based upon its own absolute abundance and its relative abundance compared to other resources in what is known as a “functional response” (Matthiopoulos et al., 2011; Mysterud and Ims, 1998). The relationship between the abundance of a resource and the use of it is often non-linear (Holbrook et al., 2019; Senft et al., 1987). For example, a resource such as water may be quantitatively selected for when it is scarce but against when it is abundant. This may be reflected in the use patterns of perennial cover. Of the four vegetation cover metrics, perennial cover relative AIC support broadly linearly increased with scale whereas annual, shrub, and tree cover peaked at an intermediate scale and roughly plateaued at coarser scales. This could be tied to the physiognomy of the pastures. All five pastures are dominated by perennial grassland interspersed with patches of annuals, shrubs, and trees. Beef cattle are generalist herbivores, and their diets are dominated by perennial herbaceous species (Holechek et al., 1982; Kluth et al., 2025). The annual herbaceous species at the study site, such as cheatgrass (*Bromus tectorum* L.), are winter annuals and can be used as a protein source in the fall and winter months (Van Dyne et al., 1964). At the study site, trees and shrubs are associated with lower understory herbaceous biomass but can act as a windbreak and provide thermal cover (Rubio et al., 2008). Animals may not need to discriminate for perennials at fine or intermediate scales. As long as they are broadly within the portion of the pasture where perennials are abundant, they will be able to find sufficient forage. In contrast, due to the more patchy, sporadic occurrence of the other functional groups, animals may need to discriminate for their use at finer scales.

Similarly, the scale of effect for various resources has been reported to vary between herbivore herds in different locations (Kuemmerle et al., 2018; Ranglack et al., 2022). Our results indicate that the scale of effect varies within the same herd, even between adjacent pastures. These differences may be partially reconciled through the incorporation of the concept of functional response by quantitatively evaluating the absolute and relative availability of resources across scales (Northrup et al., 2022).

Within pasture, we found few differences in the scale of effect between diels intervals. Diel intervals broadly correspond to daily behavioral cycles but are not explicitly linked to specific behaviors. Periods of resting occur in most diel intervals. Resting sites are heavily weighted in a UD and skew results to those locations. An additional multi-scale evaluation using behaviorally categorized and partitioned data could help uncover behavior specific selection patterns.

As noted before, animal movements occur as a response to environmental features and animal perception (Bailey et al., 1996; Mueller and Fagan, 2008). Thus, the scale of effect may be tied to the intrinsic scale of the underlying landscape processes driving patch size and landscape heterogeneity such as topography, soils, and vegetation (de Knegt et al., 2010; Johnson et al., 2005; Newman et al., 2019; Zhang et al., 2019). Increasing the scale of covariates results in a smoothing effect, the biggest changes of which are realized in our study area at fine scales (< 500 m). Likewise, a major component of animal perception is spatial memory. Most pastures used in this study are grazed annually, consequently all but the youngest animals in this study (3-year-olds) had used these pastures before. Older, more experienced animals may have better mental models of the pastures and therefore could have a larger, more consistent scale of effect.

The scale of effect varied between individuals, pastures, and covariates. For many individuals within each pasture, some pastures within each covariate, and some covariates across all pastures, the scale of effect was the coarsest scale evaluated. This can be interpreted to mean that the true scale of effect was still larger (Jackson and Fahrig, 2015), however, our largest scale matched the extent of the next largest selection order—the home range. Including larger scales would confound second and third order selection (Meyer and Thuiller, 2006); and second order selection was already constrained by pasture boundaries. Instead, support for coarse scales of effect may indicate selection for another, correlated variable (e.g. SF-SB water and supplement) or may indicate patch level selection is washed out by coarser level selection.

For example, SF-SB is a relatively narrow pasture; a water source and the supplement site are located at the bottom of a drainage on one end of the pasture. Moving away from the corrals, the pasture follows the drainage up a slope, ending on a ridge. While there is heterogeneity at fine scales, most covariates follow the elevational gradient at coarse scales. Elevation, distance to water, and distance to supplement are known as three of the strongest drivers of livestock distribution (Bailey et al., 1996). Selection for any of those would obscure the scale of selection for other covariates.

Additionally, our analysis evaluated patch-level (third order) selection within the animals' home range. This is a common approach (Heit et al., 2023; Kuemmerle et al., 2018; Meyer and Thuiller, 2006), however, there are several behavioral levels between the patch and home range-levels. Decisions made at the patch-level are constrained by decisions made at the grazing bout-level and so on. A coarse scale of effect may indicate that a much coarser behavioral process (e.g. daily movement) is masking the scale of effect at the patch-level.

Both issues are recognized weaknesses of the analytical approach used in this paper (McGarigal et al., 2016; Meyer and Thuiller, 2006). Rather than our pseudo-optimized univariate approach, others have used multivariate single level approaches (Ranglack et al., 2022) or hierarchical multilevel approaches (DeCesare et al., 2012). Parallel methodology could be applied to livestock data. Fine temporal resolution, behaviorally labelled animal location data could be categorized into each distinct behavioral level within third order selection and used to develop a multivariate hierarchically nested multilevel model. This could alleviate both issues discussed above and would allow for powerful insights into the dynamics of animal behavior across behavioral levels (Stahl et al., 2025).

Implications

This study demonstrates the scale-dependent nature of resource use in beef cattle. Future research evaluating livestock habitat selection should carefully consider research objectives to determine the appropriate behavioral level and scale of the habitat covariates evaluated. Analyses using an a priori scale that report no or few differences in selection or seem to contradict existing literature should consider if the scale used was appropriate and the results accurately characterize the evaluated relationships, or if they may reflect a scale mismatch and a different response was captured.

As illustrated here, the scale response is dependent on the specific characteristics of the area being evaluated. Even adjacent pastures may have a different scale of effect. Because of this, we would caution future researchers in using the scales of effect reported here in their own analyses and would encourage them to include some form of multi-scale or scale optimization specific to the conditions of their research.

These results also have direct implications for livestock management. The selection response to most vegetation covariates at fine scales was relatively weak. If not providing an otherwise scarce, high-value resource (e.g. water or high quality feed; Villalba, 2025), any attempt to modify or improve livestock habitat may have little impact on livestock distribution unless it modifies some threshold area (~10-25 ha).

CHAPTER FIVE

RESOURCE USE AND FORAGING BEHAVIOR OF BEEF COWS GRAZING DORMANT RANGELAND FED INCREASING SUPPLEMENTAL PROTEIN

Contribution of Authors and Co-Authors

Manuscript in Chapter 5

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Contributions: Conceptualization, methodology, software, validation, formal analysis, investigation, data curation, original draft preparation, review and editing, visualization

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Contributions: Conceptualization, methodology, investigation, data curation, resources, review and editing

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Manuscript Information

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Abstract

On northern rangelands, grazing during the winter reduces feed costs and shifts the period of plant impact out of the growing season. To make up for nutrient-deficient, dormant forage, livestock are often provided with a supplement. While the impact of supplementation on animal performance has received attention, there has been limited research on its impact on animal behavior. This study evaluated the influence of increasing levels of supplemental protein on the foraging behavior and resource use of beef cows grazing dormant rangeland. Over the course of two winters in southwest Montana, a herd of May-calving, Angus-based beef cows were assigned to one of three supplementation treatments: a non-supplemented control, 0.2% BW · day^{-1}, or 0.4% BW · day^{-1} of a 30% crude protein, canola-based pellet. All cows grazed in the same pasture and were gathered and hand-fed three times per week. Over the course of both years, 60 cows were equipped with Global Positioning System (GPS) collars. We derived a suite of behavioral metrics from the GPS collar data and estimated grazing resource use using resource utilization functions. Non-supplemented cows grazed longer, along more sinuous paths, and in smaller areas, while using larger overall areas. In contrast, supplemented cows rested longer, spent more time at the supplement site, and grazed for less time along less sinuous paths, while using smaller overall areas. These patterns reflect a decrease in intensive, selective search and grazing behavior associated with protein supplementation that we hypothesize may be attributed to the expression of protein-specific hunger and satiety.

Introduction

Outside of a short growing season, rangeland forage is largely low-quality (Abouguendia, 1998; Davis et al., 2025a; Ganskopp and Bohnert, 2001) and livestock managers and animal scientists have long recognized the benefit of supplementation (Smith, 1906). The kind and amount of supplement to feed has received much attention (Bowman and Sowell, 1997; DelCurto et al., 2000; Kunkle et al., 2000), and, when forage is not limiting, protein supplementation has been found to elicit the most beneficial response (Moore et al., 1999).

Animal nutrient intake is a function of diet quality and total intake. When diet quality falls below 6–8% crude protein (CP), rumen microbial activity slows to the point that intake becomes limiting by digestion and passage rate. Thus, ruminants become incapable of consuming enough quantity to meet their nutrient requirements. In addition to directly providing nutrients to the ruminant animal, supplemental protein first passes through the rumen, stimulating microbial activity and accelerating digestion. This can increase digestion rate and stimulate forage intake (Moore et al., 1999), thus compounding the nutritional impact of protein supplementation (Krysl and Hess, 1993). Beyond this, the form, frequency, and physical location of supplementation on animal foraging behavior has been reported (George et al., 2008; Wyffels et al., 2020; Wyffels et al., 2019). However, how the quantity of supplement provided influences foraging behavior remains poorly understood. Most prior studies reporting animal behavior have only evaluated one level of supplement against a non-supplemented control and have been limited in their ability to quantify animal behavior, reporting a limited number of metrics derived from an early technology (e.g. vibracorders) or visual observations (Barton et al., 1992; Hess et al., 1994; Schauer et al., 2005).

Given recent advances in animal behavioral monitoring, we have the ability to track animals at fine temporal and spatial resolutions. Therefore, we evaluated the impact of graded levels of a protein supplement on a broad range of behavioral measures. We considered three possible mechanistic drivers for differences in the behavioral response to protein supplementation.

First, within the framework of classic optimal foraging theory, animal diets are driven by the spatial distribution of forage quality and quantity (Pyke, 1984). Animals are assumed to select a diet that maximizes the intake of a particular nutritional currency (e.g. energy or protein) and minimizes the time required to find and consume it (Schoener, 1971; Westoby, 1974). Under these assumptions, animals will select optimized diets, regardless of the amount of supplement provided, therefore, supplementation will have no effect on animal foraging behavior.

Alternatively, if, as expected, supplementation increases intake (Moore et al., 1999), we may expect to observe changes in foraging behavior. Total forage intake is determined by time spent grazing and intake rate (Provenza et al., 2007). Thus animals may increase forage intake by either increasing time spent grazing, or increasing intake rate (Hess et al., 1994).

Lastly, rather than shifting the amount of forage consumed, supplementation may shift the kind of forage consumed. All feeds have specific combinations of physical and chemical properties that before, during, and after ingestion stimulate sensory and visceral neurons (Hill et al., 2009; Provenza et al., 2007) that influence overall and nutrient-specific satiety (Critchley and Rolls, 1996; Provenza, 1995) and subsequent selection for specific feedstuffs (Newman et al., 1992; Villalba et al., 2011; Wang and Provenza, 1996). Thus, protein supplementation may shift hunger away from protein-rich forages and shifting selectivity (Villalba and Provenza, 1999).

Therefore, we may expect non-supplemented animals that are protein deficient to search for and select relatively protein-rich forages (Davis et al., 2025b) that would be reflected in their broader foraging behavior.

Furthermore, prior studies have reported broad behavioral variation among individuals (Wyffels et al., 2019) sometimes with a high degree of consistency (Creamer and Horback, 2024; Toscano et al., 2016). Therefore, we evaluated behavioral consistency within each grouping variable or pasture level. Our objectives were to (1) characterize beef cow foraging behavior and resource use on dormant rangeland, (2) quantify the impact of increasing levels of supplemental protein on these metrics, and (3) assess how variation in behavioral responses is structured among individuals through space and time.

Methods

Study Area

This study was conducted at Montana State University's Red Bluff Research Ranch in Norris, MT (45°35′ N, 111°38′ W). Red Bluff is a 4961 ha ranch situated along the Madison River in the foothills between the Tobacco Root Mountains and the Madison Range. Elevation of the ranch ranges between 1370–1980 m and mean annual precipitation is 418 mm (PRISM Climate Group, 2024). This study took place over the winters of 2020–2021 and 2021–2022, both of which were typical (Table 5.1). This study used two adjacent pastures: First Feeder (236 ha) and Sixteen Mile (158 ha). Together, these pastures cover a strath terrace remnant dissected by three north-draining draws. The south portion of the pastures rise to a ridge crest along which the southern fenceline sits. The pastures are characterized as Central Rocky Mountain Foothill Grassland (NRCS, 2025; Olson et al., 2001) dominated by Idaho fescue (*Festuca* *idahoensis* Elmer) and bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh] Á. Löve; Mueggler and Stewart, 1980). Rocky mountain juniper (*Juniperus scopulorum* Sarg.) occurs along the margins of the draws and in several small, open woodlands. The bottoms of the draws support narrow strips of riparian vegetation including Kentucky bluegrass (*Poa pratensis* L.), sedges (*Carex* spp.), willows (*Salix* spp.), and snowberry (*Symphoricarpos albus* L.).

Table 5.1. Mean temperature and wind speed during three periods over two winters in Norris, MT.

	Temperature (°C)				**Wind Speed**
	Maximum	**Daily Maximum**	**Daily Minimum**	**Minimum**	**(km · h^{-1})**
2020–2021					
Period One	7.54	2.64	−6.05	−14.8	15.3
Period Two	9.83	−2.31	−11.50	−27.1	13.7
Period Three	15.10	7.25	−3.43	−10.2	12.8
2021–2022					
Period One	9.37	4.84	−4.43	−12.0	20.1
Period Two	11.90	3.22	−7.31	−28.8	18.8
Period Three	17.70	4.48	−6.06	−21.7	19.0

Treatments

Between December and March of both winters, a herd of Angus-based beef cows (n = 105 in year one and n = 75 in year two; Table 5.2) grazed both pastures. Cows were stratified by shrunk body weight (BW), body condition score, and age and randomly assigned to one of three protein supplement treatments: a non-supplemented control, 0.2% BW · day^{-1} (low), or 0.4% BW · day^{-1} (moderate) of a 30% crude protein (CP), canola meal-based pellet. Supplement was delivered three times per week and fed by hand. At mean body weight (616 kg), the low and moderate treatments received 2.87 and 5.75 kg of supplement per delivery, which provided the equivalent of 0.37 and 0.74 kg of CP per day, respectively. All cows were managed in one herd, gathered every Monday, Wednesday, and Friday, and brought to a centrally located set of corrals within the pasture where they were sorted and hand-fed their supplement treatment.

Table 5.2. Mean shrunk body weight and body condition score for cattle grazing dormant rangeland over two winters in Norris, MT.

	Body Weight (kg)		Body Condition Score (1–9)	
	Year 1	**Year 2**	**Year 1**	**Year 2**
Period One	621.5	611.5	5.34	5.23
Period Two	606.6	623.0	5.27	5.23
Period Three	600.0	624.7	5.01	5.08

The study lasted 84 days and was segmented into three, 28-day periods (Table A1). For period one, the herd grazed in First Feeder, after which the gates to Sixteen Mile were opened and the two were managed as one pasture, hereafter referred to as FF-16M (394 ha). In periods two and three, the herd grazed in FF-16M. The corrals and water sources were located in First Feeder. Grazing management was typical, and the stocking rates were considered moderate for the area (Table 5.3).

Table 5.3. Pasture size, available forage upon entry and stocking rate for pastures grazed over two winters in Norris, MT. After the first 28 days of the study each year, the gates to a pasture adjacent to First Feeder were opened and managed together (FF-16M). The stocking rate for FF-16M includes cumulative use from the first 28 days spent in First Feeder.

Year	Dates	Dur.	Pasture	Area (ha)	Total Head	Biomass ($kg \cdot ha^{-1}$)	Stocking Rate ($kg \cdot ha^{-1}$)
2020–2021	Dec–Jan	28 d	First Feeder	236	108	1182	156.48
	Jan–Mar	56 d	FF-16M	394	108	2345	281.20
2021–2022	Dec–Jan	28 d	First Feeder	236	75	1224	110.01
	Jan–Mar	56 d	FF-16M	394	75	2347	197.69

GPS Data

Within treatment and feeding group, we randomly assigned Lotek Lite Track 800 (Lotek, Newmarket, ON, Canada) GPS collars to 18 cows in year one and 45 cows in year two. Collars were programmed to record GPS locations every 5 minutes, and a three-axis accelerometer fix every one minute. To remove locations directly influenced by human activity, all GPS data were removed on any day cows were handled or fed. To remove potentially erroneous data, all GPS locations outside of the pasture boundaries and all locations with an estimated rate of travel of over 1.5 $m \cdot s^{-1}$ between both the preceding and subsequent locations were removed. After filtering, there remained 692,225 total GPS locations collected over 45 days per year with 99.0% expected data completeness (Table A1). To classify animal behavior, we used the hidden Markov algorithm developed by Lipinski et al. (2025) to estimate the probability of grazing, resting, or traveling at each GPS location, then selected the behavior with the highest probability and assigned that as the behavioral state for that 5-min period.

Using the assigned behavioral states, we created two datasets. The overall dataset included all GPS locations regardless of behavioral state. The grazing dataset included all GPS locations occurring within a grazing bout and a grazing bout was defined as a series of a minimum of three consecutive locations assigned as grazing (i.e. at least 15 minutes grazing; Augustine et al., 2022; Orr et al., 2001).

Response Variables

We next developed a set of 47 response variables (Table 5.4). As period was our fundamental unit of management, all response variables were summarized over each 28-d period. We calculated daily activity budgets by determining the daily proportion of grazing, resting, and traveling locations. Distance traveled was calculated as the sum of the planar Euclidean distances between subsequent relocations. For both datasets, mean turning angle was calculated as the absolute value of the change in angular heading between subsequent relocations. Turning angle indicates movement path tortuosity where values near 0° indicate straighter paths and values near 180° indicate direction reversal. At a 5-minute temporal resolution, turning angle is a strong predictor of behavioral state (Homburger et al., 2014; Lipinski et al., 2025) and within behavior is associated with animal density, stocking rate, and foraging behavior (Augustine et al., 2023; Larson-Praplan et al., 2015).

Table 5.4. Description of covariates used in analysis of beef cattle grazing dormant rangeland over two winters in Norris, MT. Parenthetical values following resource utilization covariates indicate the spatial scale of the covariate.

Category	**Covariates**
Behavior	
Time Budget	Time Spent Grazing, Time Spent Resting, Time Spent Traveling, Time at Supplement Site
Movement & Foraging	Daily Distance Traveled, Turn Angle, Grazing Turn Angle, Grazing Velocity, Grazing Bouts per Day, Grazing Bout Duration
Core Range Size	Daily Grazing Range, Weekly Grazing Range, Period Grazing Range, Daily Range, Weekly Range, Period Range
Full Range Size	Daily Grazing Range, Weekly Grazing Range, Period Grazing Range, Daily Range, Weekly Range, Period Range
Core Range Ratio	Daily Grazing Ratio, Weekly Grazing Ratio, Period Grazing Ratio, Daily Ratio, Weekly Ratio, Period Ratio
Temporal Range Overlap	Daily-Weekly Grazing Range, Daily-Period Grazing Range, Weekly-Period Grazing Range, Daily-Weekly Full Range, Daily-Period Full Range, Weekly-Period Full Range
Resource Utilization	
Topography	Distance to Water (30 m), Distance to Supplement (30 m), Elevation (330 m), Slope (1290 m), N–S aspect (2550 m), E–W aspect (2550 m), Topographic Position Index (1350 m)
Cover	Annual (510 m), Perennial (2490 m), Shrub (1890 m), Tree (810 m), Bare Ground (2190 m), Litter (750 m)

Grazing velocity was calculated as the mean displacement rate within grazing bouts. Grazing bouts per day was calculated as the number of distinct grazing bouts per day. Many of the cows used the area surrounding the supplement delivery site as a loafing area. We calculated time spent at supplement site using the number of locations within 150 m of the corrals.

Next, we derived a series of space use metrics using utilization distributions (UDs). Utilization distributions quantify relative use of a spatial area and are often used to delineate home ranges and other estimates of space use (Calhoun and Casby, 1958; Jennrich and Turner, 1969; Millspaugh et al., 2006). We developed UDs for every animal for every day, week, and period. Using the R Package “BBMM” (Nielson et al., 2013), we built Brownian bridge movement models (BBMMs; Horne et al., 2007) between all relocations occurring within 30 minutes of each other, then rasterized the resulting probability density over the pasture at a 30-m resolution. All space use metrics were calculated for both datasets.

First, we calculated range sizes. For every UD, we calculated the full range size using the 95% contour and the core range size using the 50% contour. Full range is an estimation of the size of the total area covered by an animal in a given period whereas core range is an estimation of the area used most intensively (Parsons et al., 2021). We then calculated the core range ratio, defined as the proportion of the area of the core range to the full range. High values indicate even distribution of use and lower values indicate more intense, localized or patchy use.

Lastly, we quantified temporal consistency in space use. For every week and period, we calculated the ratio of the mean daily or mean weekly full range sizes to the full range size of the corresponding longer interval. We defined this as temporal range overlap and refer to each as the daily–weekly (D–W), daily–period (D–P), and weekly–period (W–P) ranges. Similar to the concept of range stability (Roshier and Reid, 2003), high values indicate high site fidelity and consistent space use whereas low values indicate less consistent, possibly exploratory space use (Fieberg and Kochanny, 2005).

Resource Utilization Functions

Next, we estimated resource use using resource utilization functions (RUFs; (Marzluff et al., 2004; Millspaugh et al., 2006). We developed an a priori set of 13 scale-optimized covariates including seven derived from a digital elevation model (USGS, 2019) and six derived from rangeland analysis platform vegetation cover estimates (Allred et al., 2021; Table 5.4). For a more detailed description of the covariates and the scale optimization process see Chapter 4. For each period-level UD, we built a beta regression (Ferrari and Cribari-Neto, 2004; Geissinger et al., 2022) modeling the response of use to the covariate set using the R package "glmmTMB" (Brooks et al., 2017) and extracted the slope coefficient for each covariate. Coefficients represent the strength of resource use over the modeled period (Marzluff et al., 2004).

Statistical Analysis

The analysis for this study was split into two parts. First, we built a series of linear mixed models to evaluate the impact of protein supplementation on each response variable. Then we ran a variance partitioning analysis to evaluate how each level of the grouping structure of the data influenced the variance in each response variable. All data were analyzed at the period-level with individual animal as the experimental unit using R version 4.3.1 (R Core Team, 2023).

Influence of Protein: We hypothesized that the response to protein supplementation may take one of three functional forms: linear, saturation (square root), or quadratic, and that the response may vary by year, period, and the strength of the response may vary by period. We developed a candidate set of 17 models to reflect these hypotheses (Table 5.5). To account for repeated measures, each model included random intercepts for individual animal and pasture. Models were built using the R package "lmerTest" (Bates et al., 2015; Kuznetsova et al., 2017) and were ranked by second-order Akaike's information criterion (AICc) as calculated by the R package "AICcmodavg" (Mazerolle, 2023).

Variance Partitioning: To evaluate how the variation in each response variable was accounted for by the grouping structure of the data, we calculated intraclass correlation coefficients (ICCs; Nakagawa and Schielzeth, 2010) using linear mixed models. For each response variable, we built a model that included the fixed effect of protein supplementation using the functional form in the top-ranked model from the first analysis. Random effects were specified using a maximal complexity approach (Barr et al., 2013). First, we included random intercepts for individual animal and for period nested within pasture nested within year. The model was then tested for singularity (tolerance = 1×10^{-5}), and if failing, the term with the smallest ICC was removed and the model was iteratively refit until non-singular. Marginal R^2 and group-level ICCs were calculated using the R package "performance" (Lüdecke et al., 2021) according to Nakagawa et al. (2017).

Table 5.5. Candidate list for linear mixed models evaluating the response of cattle behavior and resource use to graded levels of a protein supplement while grazing dormant foothill rangeland across three consecutive periods during two winters in Norris, Montana, USA. All models included random intercepts for individual animal and pasture.

Model	**Fixed Effects**
Null and Covariates Only	
1	**Random effects only*
2	Suppl.
3	Period
4	Year
5	Period + Year
Linear	
6	Suppl. + Period
7	Suppl. × Period
8	Suppl. + Period + Year
9	Suppl. × Period + Year
Square Root	
10	$\sqrt{}$Suppl. + Period
11	$\sqrt{}$Suppl. × Period
12	$\sqrt{}$Suppl. + Period + Year
13	$\sqrt{}$Suppl. × Period + Year
Quadratic	
14	Suppl.^{2} + Period
15	Suppl.^{2} × Period
16	Suppl.^{2} + Period + Year
17	Suppl.^{2} × Period + Year

Results

Protein supplementation influenced cow time budgets, movement, foraging behavior, and space use (Figs. 5.1, A1). Specifically, non-supplemented animals had higher intensity of use measures related to grazing activity. Supplementation alone explained little variation in behavior or resource use ($R^2_m \leq 0.11$) and was often eclipsed by variation between individuals, periods, or pastures (Fig 5.2; Table A2). Of the top models for each response variable, 59% contained an effect of protein supplementation, 94% contained an effect of period, and 62% contained an effect of year (Table A3).

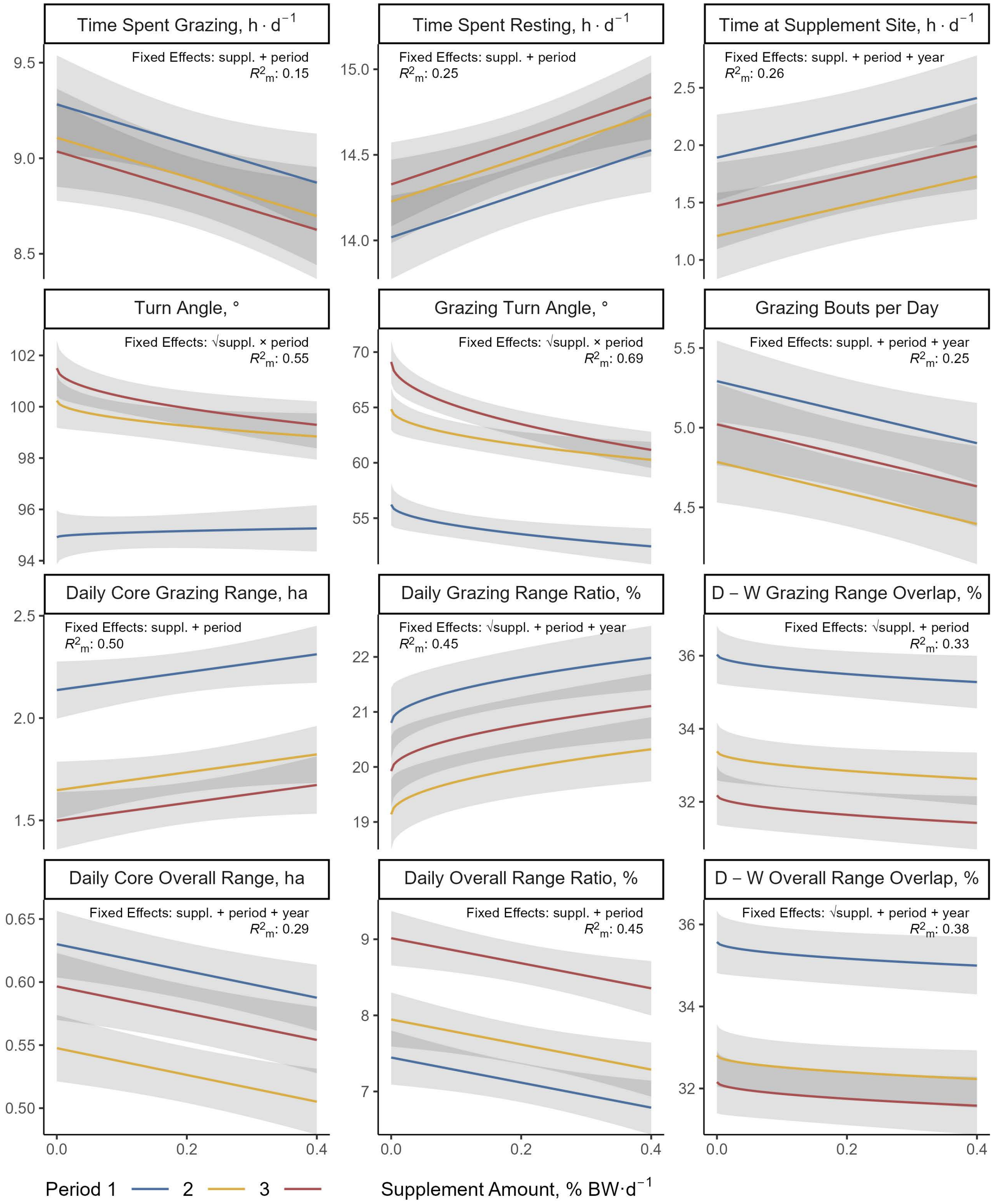

Figure 5.1. Relationship between animal behavior metrics and protein supplementation (± 95% confidence intervals) for beef cows grazing dormant foothill rangeland across three consecutive periods during the winters of 2020–2021 and 2021–2022 in Norris, Montana, USA. Each panel lists the fixed effects and marginal R^2 of the best-supported model. See also Fig. A1.

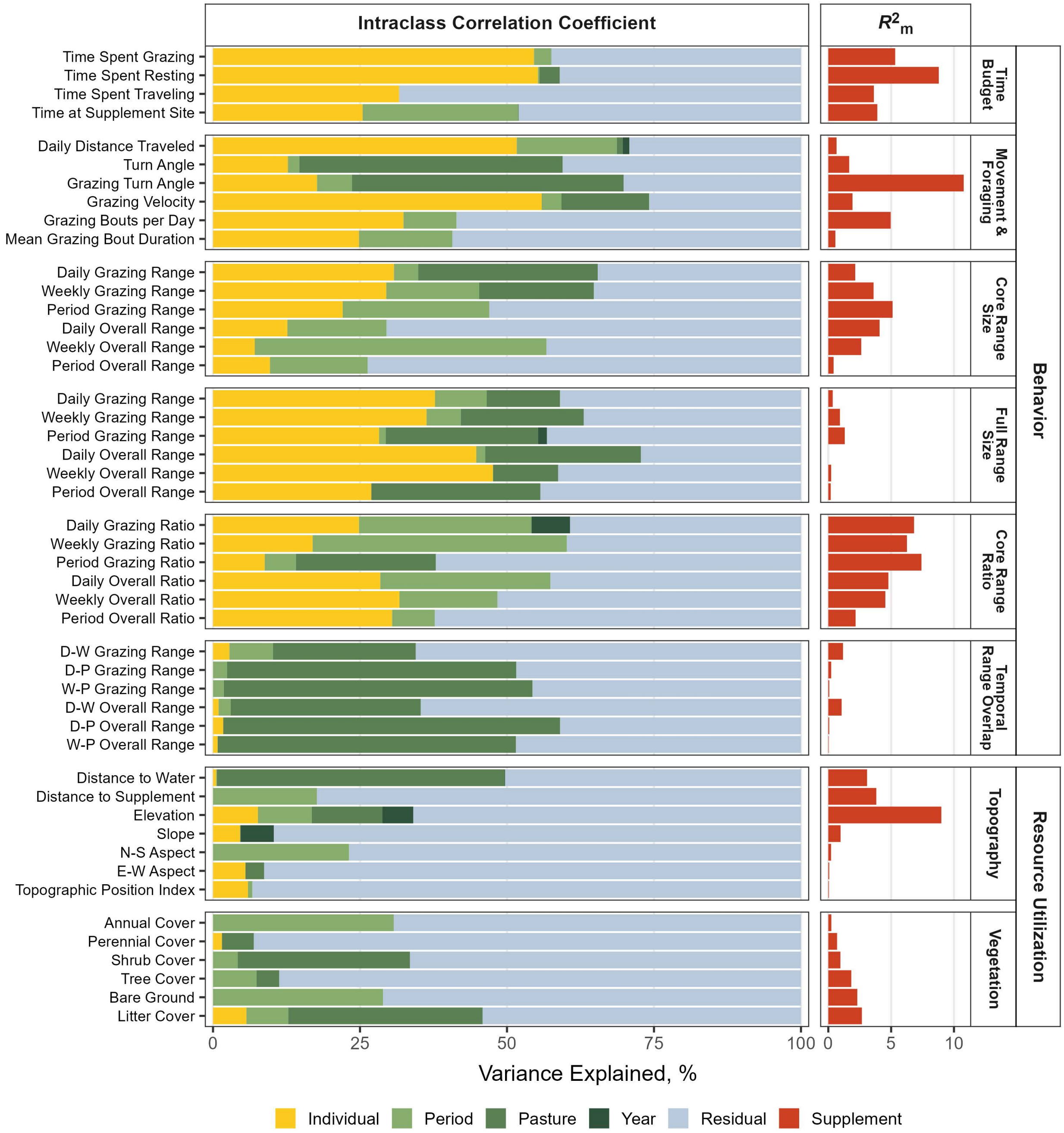

Figure 5.2. Intraclass correlation coefficients and marginal R^2 for the behavior and resource use response of beef cows receiving graded levels of a protein supplement grazing dormant foothill rangeland across three consecutive periods during two winters in Norris, Montana, USA.

Animal Behavior

Time Budget: Cows spent an average of 8.9 h · d^{-1} grazing and 14.4 h · d^{-1} resting. Supplementation reduced time spent grazing by 0.41 h · d^{-1} (R^2_m = 0.05) and increased time spent resting by 0.52 h (R^2_m = 0.09). Supplementation reduced time spent travelling, however it explained little variance (R^2_m = 0.04) and had little support over the null model (ΔAICc = 1.8, evidence ratio = 2.4). Supplemented cows also spent more time at the supplement delivery location (R^2_m = 0.04), increasing from 1.5 h · d^{-1} to 2.0 h · d^{-1}. Most variation in time spent grazing and resting was explained by differences between individuals (ICC = 0.55). Time spent at the supplement site was explained by differences between individuals (ICC = 0.25) and periods (ICC = 0.26).

Movement & Foraging: Despite altering daily time budget, supplementation did not influence daily distance traveled ($\bar{x}$ = 5.0 km · d^{-1}), of which most variation was attributed to differences between individuals (ICC = 0.52) and periods (ICC = 0.17). On average, cows grazed in 4.8 bouts per day each lasting 2.1 h. Supplementation decreased the number of grazing bouts by 0.4 per day (R^2_m = 0.05) but did not alter bout length or grazing velocity ($\bar{x}$ = 4.7 m · min^{-1}).

Supplementation influenced both turning angle metrics, and the response differed across periods. The top models for both supported square root transformations of supplementation indicating a saturating effect where the two supplemented groups were more similar to one another than to the non-supplemented group. Supplemented cows grazed in straighter paths in all three periods (P = 0.02) and moved in straighter paths during all activities in periods two and three (P = 0.02). The magnitude of the response to supplementation increased as the study progressed. In period one, supplementation altered overall turn angle and grazing turn angle by

0.4% and 6.7%, respectively, whereas in period three the magnitude of the response increased to 2.2% and 11.5%, respectively. For both metrics, most variation was attributed to differences between pastures (ICC = 0.45–0.46) and individuals (ICC = 0.13–0.18). Supplementation explained more variation in grazing turn angle ($R^2_m = 0.11$) than overall turn angle ($R^2_m = 0.02$).

Range Size: Supplementation expanded core grazing ranges, the magnitude of which increased with temporal scale. Daily, weekly, and period core grazing ranges expanded 10.2%, 13.3%, and 18.5%, respectively ($R^2_m = 0.02$–0.05). In contrast, supplementation contracted core overall ranges at the daily and weekly scales by a mean of 7.3% ($R^2_m = 0.04$–0.05). All full range size metrics had strongest support for models containing only the effects of period or period and year. Additionally, full range size metrics were better explained ($ICC_{Residual} = 0.27$–0.44) than core range size metrics ($ICC_{Residual} = 0.35$–0.74). In particular, differences between individuals captured more of the variation in full range size (ICC = 0.27–0.48) than in core range size (ICC = 0.07–0.31).

Core Range Ratio: Of all space use metrics, core range ratios were most consistently explained by supplementation. Across temporal scales, supplementation increased grazing range ratios by 5.9–10.2% ($R^2_m = 0.06$–0.07) and decreased overall range ratios by 7.4–9.5% ($R^2_m = 0.02$–0.05). This indicates that supplementation increased the evenness of space use while grazing but decreased the evenness of overall space use. All core range ratio metrics had mixed support and high uncertainty for linear and root-transformed models. While inconsistent, the variation in range ratios were largely attributed to differences between individuals (ICC = 0.09–0.32) and periods (ICC = 0.05–0.43).

Temporal Range Overlap: Temporal range overlap varied little between individuals (ICC = 0.0–0.03) or periods (ICC = 0.0–0.07) and was primarily driven by differences between pastures (ICC = 0.24–0.57). Although supplementation was included in the top model for both D–W grazing and D–W overall range overlap, it explained little variation ($R^2_m = 0.01$) and only reduced overlap by 1.7–2.2%.

Resource Utilization

Overall, use was most strongly driven by selection against slope ($\beta = -0.56$), north aspect ($\beta = -0.49$), and elevation ($\beta = -0.49$), and selection for shrub cover ($\beta = 0.40$) and locations near the supplement site ($\beta = -0.35$; Fig. 5.3). In general, coefficients were highly variable and poorly explained by any of our grouping variables ($ICC_{Residual} = 0.50\text{-}0.93$). Supplementation increased the use of areas further from water ($R^2_m = 0.03$), closer to the supplement site ($R^2_m = 0.04$), and reduced the magnitude of selection against elevation ($R^2_m = 0.09$; Fig. 5.4). Supplementation had a variable effect on the use of tree cover ($R^2_m = 0.02$) and decreased the use of bare ground ($R^2_m = 0.02$). Litter cover is the only variable that supported a quadratic effect of supplementation, where the moderate treatment increased use relative to the other treatments ($R^2_m = 0.03$).

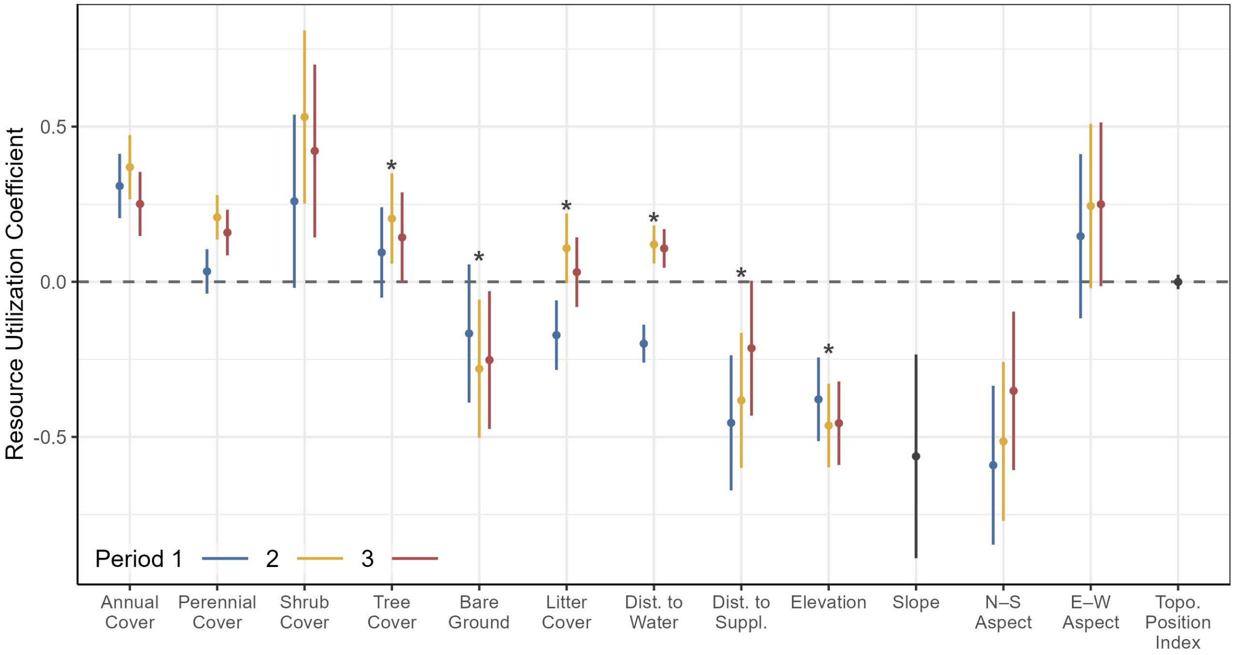

Figure 5.3. Resource utilization coefficients (± 95% confidence intervals) of beef cows grazing dormant foothill rangeland fed three levels of a protein supplement across three consecutive periods during the winters of 2020-21 and 2021-22. All response variables except for slope and topographic position index supported a model that contained a period effect. Variables with an asterisk indicate support for an effect of protein supplementation (See Figure 5.4 for more details). Negative coefficients for distance to water and distance to supplement indicates use of areas closer to the source. Positive coefficients for N–S and E–W aspect indicate use of areas with north and east aspects, respectively.

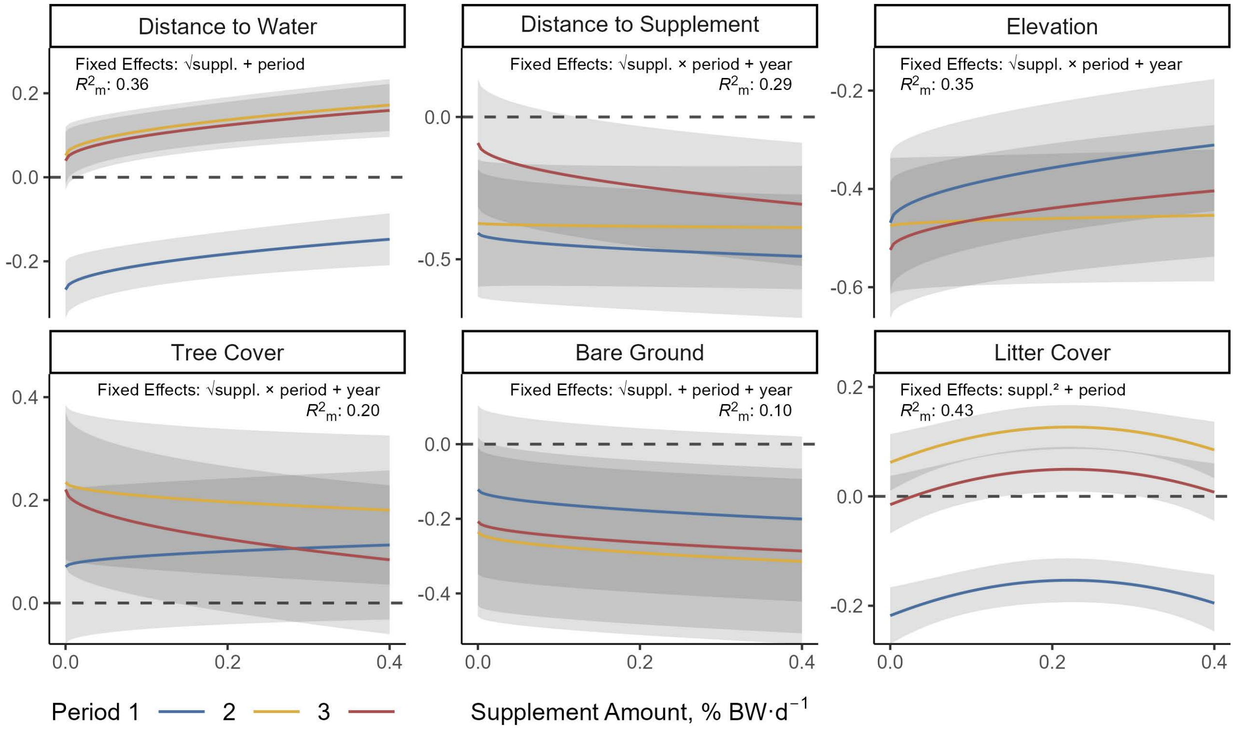

Figure 5.4. Relationship between resource utilization coefficients and protein supplementation (± 95% confidence intervals) for beef cows grazing dormant foothill rangeland across three consecutive periods during the winters of 2020–2021 and 2021–2022 in Norris, Montana, USA. Each panel lists the fixed effects and marginal R^2 of the best-supported model.

Discussion

Using animal tracking data, we found consistent differences in foraging behavior, space use, and resource utilization of cows provided different amounts of protein supplement. While the total amount of variation explained by supplementation was modest, our results broadly support our third hypothesis that non-supplemented animals forage more intensively than supplemented animals. Non-supplemented cows grazed for longer, along more sinuous paths, and in smaller areas, while using larger overall areas. In contrast, supplemented cows rested longer, spent more time at the supplement site, and grazed for less time along less sinuous paths, while using smaller overall areas. These patterns reflect a decrease in intensive, selective search and grazing behavior with protein supplementation.

Our first hypothesis predicted that supplementation would have no impact on behavior. Optimal foraging theory predicts that the environment drives animal behavior; therefore, given that all animals were managed in one herd and had access to the same environment, supplementation would be irrelevant. However, our results do not align with this prediction. Over half the response variables were influenced by protein supplementation, indicating a physiological effect of supplementation.

Our second hypothesis predicted that supplementation would alter behavior by increasing forage intake. Previous studies in similar conditions have reported supplementation to reduce time spent grazing (Wyffels et al., 2020) while increasing intake rate apparently enough to maintain or increase overall intake (Barton et al., 1992; Hess et al., 1994; Schauer et al., 2005). Although we did not measure forage intake, the behavioral patterns we observed are consistent with this.

Our third hypothesis predicted that supplementation would shift nutrient-specific hunger, thus altering foraging selectivity. Protein supplementation should partially satiate protein-specific hunger, reducing selection for protein rich feeds (Provenza, 1996; Villalba and Provenza, 1999; Wang and Provenza, 1996). In dormant cool-season grasslands, energy is relatively abundant whereas CP is low and highly variable across the landscape. High-CP forages are tied to specific plant communities (Davis et al., 2025b; Van Dyne et al., 1964) or topoedaphic features (Ganskopp and Bohnert, 2009).

The two treatments were designed to meet a portion of the cows' protein requirements. If supplementation induced partial satiation of protein-specific hunger, it would shift selection away from scarce, protein-rich feeds, reducing overall selectivity. This would be expected to lower the acceptance threshold and increase the proportion of acceptable plants (Bailey et al., 1996; Senft et al., 1987). As more plants are deemed acceptable, the number of bites at each feeding station would increase. Given no change in grazing velocity, this would increase intake rate, and animals would reach gut fill more quickly, thus reducing time spent grazing. This would also be consistent with the mechanism described in hypothesis two.

Grazing is an energetically expensive activity, especially in rugged terrain (Brosh et al., 2010; NASEM, 2016). If supplemented cattle can graze less selectively, or make strategic use of terrain while still meeting their nutrient requirements, they may be able to lower their energy expenditure (Krysl and Hess, 1993).

This can also be considered from the perspective of the non-supplemented cows. An increase in protein-specific hunger could increase selectivity across behavioral levels. Non-supplemented cows may search over a larger area to locate high-CP plant communities, and once there, spend more time foraging in them. Given the scarcity of these locations, they would be expected to return to them. Our results are consistent with these predictions. Non-supplemented cows grazed more intensively and selectively. Additionally, while the effect size was modest, non-supplemented cows had higher temporal range overlap, indicating higher site fidelity.

Overall, most of the differences associated with supplementation related to behaviors reflected in foraging activity and space use intensity. Five-minute resolution GPS data is limited in its ability to capture fine-scale behaviors within the foraging bout. While we were able to detect differences, that may indicate that differences between treatments were more strongly expressed at finer scales than we measured.

We detected some numerically large responses to supplementation, however, the amount of variation explained by it was relatively minor. Cattle are hierarchical social animals and prefer to stay with other animals (Sowell et al., 1999), sometimes at their own expense (Bica et al., 2020). Given that treatments were randomly assigned, social groups contained cows from all three treatments. As a result, behavioral responses were not independent, and were conditioned upon the treatment assignment of other, especially lead cows, in the social group (Bailey, 1995; Harris et al., 2007). That may have diluted the magnitude or the consistency in the treatment response.

Many behavioral metrics also exhibited large individual-level ICCs, indicating a large degree of consistent individual behavior (Creamer and Horback, 2024; Réale et al., 2007; Toscano et al., 2016). This may reflect individual phenotypic differences (e.g. breed, weight, reticulo-ruminal volume; Demment and Van Soest, 1985; Nyamuryekung'e et al., 2022) or experience (e.g. age, location of development; Bailey et al., 1996; Flores et al., 1989).

Implications

The use of supplementation goes beyond its immediate nutritional impact or use as a locational attractant. Our results illustrate that protein supplementation altered space use, coarse-scale resource use, and fine-scale movement patterns. Supplementation may improve consistency in overall pasture use. Supplemented cows grazed more evenly across a larger area, at higher elevations, and further from water.

However, the effect of supplementation was often exceeded by individual, period, and pasture-level variation. Individual differences may reflect measurable, heritable traits that could be incorporated into selection decisions. Period effects may be tied to differences between pastures, environmental conditions, or the progressive depletion of forage. Pasture differences may be linked to size or the specific makeup of resources within them. Grazing managers must understand and balance supplementation decisions with the complex impacts these factors.

Our study did not evaluate the behavioral response to environmental conditions nor the interplay between supplementation, nutritional condition, and behavior. Furthermore, our ability to understand fine-scale behavior was limited. Future research should evaluate these relationships and incorporate methods that allow finer-scale behavioral monitoring. Research quantifying diet selection and behavior within the foraging bout would also clarify the link between the mechanisms invoked in our hypotheses and our observations. Furthermore, given the large between-group variation, research at additional locations under different conditions is needed to understand the generality of our results.

CHAPTER SIX

CONCLUSIONS

On northern ranges, the winter period is often perceived as the most challenging time to manage livestock grazing due to low-quality forage, harsh and unpredictable weather, and complexity in nutritional management. Often, supplementation is a recommended tool to address these challenges (DelCurto et al., 2000; Kunkle et al., 2000). Supplementation directly provides nutrients lacking in the basal diet, can be used to either stimulate or depress intake, and can be a physical attractant to improve grazing distribution (Bailey, 2004; Bohnert and Stephenson, 2016; Moore et al., 1999). Its successful use relies on understanding and predictably modifying responses to winter conditions, however, the current understanding of winter forage quality and the behavioral response to supplementation remains limited. Our research was designed to address that (Fig. 6.1).

Figure 6.1. Managing livestock grazing during the winter is challenging. Our research answered several important questions related to winter forage quality and animal behavior, but there is still much work to be done.

In Chapter 2, we illustrated high variation and dynamic, sometimes rapid changes in the forage quality of two major rangeland forage species. We quantitatively associated those changes with changes in environmental conditions, particularly short-term relative temperature. This opens questions into the traditional understanding of plant dormancy and may indicate these species are more sensitive during the winter than previously thought. Typically, dormant rangelands are perceived as being more tolerant of grazing. However, if plants respond to changes in temperature, can they sense or respond to defoliation? Further, if quality is also highly spatially variable, grazing management may be able to take advantage of that. If stocking rates are lowered during the winter and animals are allowed to graze more selectively, can the amount of supplement fed be reduced?

In Chapter 3, we explained the development of a behavior classification algorithm and employed it to assess the diel response to alternate day alfalfa supplementation. While there were differences in time budgets and distance traveled on the days supplement was provided, those differences were primarily restricted to the hours immediately following supplement delivery. This indicates that cattle are capable of adapting their behavior to large, infrequent ingestion of a high-fiber supplement.

In Chapter 4, we illustrated that patch-level (30 m) winter resource use at Red Bluff Research Ranch was most strongly driven by intermediate (570–1650 m) to coarse (2370–2550 m) scale patterns in vegetation and topography. Current similar livestock habitat selection analyses have only assessed covariates at fine scales (25–100 m), some of which reported non-significant results. For most covariates in our analysis, resource use was weakest at fine scales and strongest at intermediate or coarse scales, potentially explaining discrepancies between studies. This indicates that at the patch-level, the lens with which cows view the landscape may be coarser than conventionally presumed. However, there was considerable variation and even in adjacent pastures, the effect of scale varied. We encourage future research to carefully consider scaling effects and we provide a framework to incorporate it into their study design and analysis.

In Chapter 5, we determined the effect of the amount of supplemental protein on an array of behavioral metrics. Most prior supplementation behavior research has either evaluated the effect of supplement placement, free-choice intake, or one level against a non-supplemented control. We demonstrated a consistent response where supplementation decreased intensive search activity. Given low mean forage quality, cattle typically select for higher quality sites and diets in the winter (Van Dyne et al., 1964; Wyffels et al., 2019). We hypothesized that the decrease in search intensity was related to a partial protein satiation and a decrease in the magnitude of the selection for higher quality forage. Interestingly, supplementation also resulted in an expansion of the area and increase in the evenness of use across the pasture, including use at higher elevations and further from water.

Our results also revealed some methodological challenges that could be addressed by future research. The results from Chapter 4 bring into question the adequacy of the temporal and spatial resolution of data for similar analyses. If patch-level use is driven by intermediate or coarse-scale resource patterns, there is likely a diminishing return for higher resolution, high frequency animal location data. Similarly, higher resolution spatial data (e.g. 10 m) may not prove to be more informative than what we used. Higher resolution data may be useful if the design is updated to capture and assess a finer behavioral level. While we found minimal support for cattle selection of 30 m scale spatial data, this should not be interpreted to mean that cattle do not use the spatial information represented by 30 m data, indeed, they clearly interact with resources at that and much finer scales (Holechek et al., 1982; Larson-Praplan et al., 2015; Simmons et al., 2025). Instead, our results should be interpreted to mean that the behavioral process captured with 5-min resolution GPS data, when gridded at 30-m resolution, is most strongly linked to coarser scale information. We interpreted our response to characterize the aggregate patterns of 5-min selection over the course of each 28-d period, representing patch-level selection, however, that link is not clearly established either.

This research also highlights one of the perennial difficulties in grazing animal research: achieving independence and replication in a heterogeneous environment (Brown and Waller, 1986; Giesbrecht, 1989). In Chapter 5 we managed all treatments together and considered individual as the experimental unit. However, given the social nature of cattle, none in a herd can truly be considered independent, and the herd would be the proper experimental unit. But, if strictly followed and treatments were separated by period or pasture, we would introduce major confounding, and it would be difficult to separate the effects of each.

Truly addressing these issues requires long-term, repeated observations of the same individuals across different pastures over time. This presents a major financial and logistical challenge and historically would have been impossible. However, by integrating long-term research with standard ranch operating procedures and strategically deploying low-cost, emerging technologies, this can be accomplished.

Lastly, while my research relied heavily on technology, I offer a word of caution. While it has greatly advanced scientific progress in many ways, technology can easily begin to dictate research rather than help complete it (Hebblewhite and Haydon, 2010). As the volume of data collected increases, there is the risk that technology will be used as a substitute for a field-based understanding rather than a complement to it. Technology can provide quantitative detail but only in narrow dimensions. Fieldwork forces interaction with the system and provides nuanced understanding that technology cannot capture.

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APPENDIX

SUPPLEMENTARY INFORMATION FOR CHAPTER FIVE

Table A1. Date range and GPS collar specifications for beef cattle grazing dormant rangeland over two winters in Norris, MT.

Year	Period	Dates	Pasture	Area (ha)	Data Completeness	Observations	Days	Collars
1	1	12/31/2020 – 01/27/2021	First Feeder	236	99.5	73,046	15	17
	2	01/28/2021 – 02/24/2021	FF-16M	394	98.9	72,655	15	17
	3	02/25/2021 – 03/24/2021	FF-16M	394	98.7	72,521	15	17
2	1	12/30/2021 – 01/26/2022	First Feeder	236	98.8	116,926	15	43
	2	01/27/2021 – 02/23/2021	FF-16M	394	99.1	181,833	15	43
	3	02/24/2021 – 03/23/2021	FF-16M	394	98.9	175,244	15	41

Table A2. Model parameters for variance partitioning analysis for the behavior and resource use response of beef cows receiving graded levels of a protein supplement grazing dormant foothill rangeland across three consecutive periods during two winters in Norris, Montana, USA. Intraclass correlation coefficient terms with no value were removed in model development to achieve non-singular fit. See the Chapter 5 text for full details.

	R^2 Supplement		**Intraclass Correlation Coefficient**					**Grand Mean**	**IQR**
	Conditional	**Marginal**	**Individual**	**Period**	**Pasture**	**Year**	**Residual**		
Behavior									
Time Budget									
Time Spent Grazing, $h \cdot d^{-1}$	0.60	0.05	0.55	0.03	0.00	0.00	0.42	8.94	0.96
Time Spent Resting, $h \cdot d^{-1}$	0.63	0.09	0.55	0.00	0.03	0.00	0.41	14.44	0.95
Time Spent Traveling, $h \cdot d^{-1}$	0.34	0.04	0.32	-	-	-	0.68	0.67	0.27
Time at Supplement Site, $h \cdot d^{-1}$	0.54	0.04	0.25	0.26	0.00	0.00	0.48	1.64	1.42
Movement & Foraging									
Daily Distance Traveled, km	0.71	0.01	0.52	0.17	0.01	0.01	0.29	4.97	0.64
Turn Angle, °	0.60	0.02	0.13	0.02	0.45	-	0.41	98.24	4.44
Grazing Turn Angle, °	0.73	0.11	0.18	0.06	0.46	-	0.3	60.28	8.93
Grazing Velocity, $m \cdot min^{-1}$	0.75	0.02	0.56	0.03	0.15	0.00	0.26	4.72	0.73
Grazing Bouts per Day	0.44	0.05	0.32	0.09	-	-	0.59	4.77	0.93
Mean Grazing Bout Duration, h	0.41	0.01	0.25	0.16	0.00	0.00	0.59	2.08	0.44
Core Range Size									
Daily Core Grazing Range, ha	0.66	0.02	0.31	0.04	0.31	-	0.35	1.85	0.56
Weekly Core Grazing Range, ha	0.66	0.04	0.29	0.16	0.19	0.00	0.35	5.38	1.58
Period Core Grazing Range, ha	0.50	0.05	0.22	0.25	0.00	0.00	0.53	15.51	6.76
Daily Core Overall Range, ha	0.32	0.04	0.13	0.17	0.00	-	0.70	0.56	0.11
Weekly Core Overall Range, ha	0.58	0.03	0.07	0.50	-	0.00	0.43	1.42	0.35
Period Core Overall Range, ha	0.27	0.00	0.10	0.17	-	-	0.74	3.75	1.44
Full Range Size									
Daily Full Grazing Range, ha	0.59	0.00	0.38	0.09	0.12	-	0.41	9.43	3.13
Weekly Full Grazing Range, ha	0.63	0.01	0.36	0.06	0.21	0.00	0.37	28.07	8.55
Period Full Grazing Range, ha	0.57	0.01	0.28	0.01	0.26	0.02	0.43	79.02	24.32
Daily Full Overall Range, ha	0.73	0.00	0.45	0.02	0.26	-	0.27	7.76	1.83
Weekly Full Overall Range, ha	0.59	0.00	0.48	-	0.11	-	0.41	23.22	4.53
Period Full Overall Range, ha	0.56	0.00	0.27	-	0.29	0.00	0.44	64.35	14.95

Table A2 Continued.

	R^2 Supplement		Intraclass Correlation Coefficient					Grand Mean	IQR
	Conditional	Marginal	Individual	Period	Pasture	Year	Residual		
Core Range Ratio									
Daily Grazing Range Ratio, %	0.63	0.07	0.25	0.29	-	0.07	0.39	20.95	2.17
Weekly Grazing Range Ratio, %	0.63	0.06	0.17	0.43	0.00	0.00	0.40	19.39	2.66
Period Grazing Range Ratio, %	0.42	0.07	0.09	0.05	0.24	-	0.62	19.70	3.21
Daily Overall Range Ratio, %	0.59	0.05	0.28	0.29	-	-	0.43	7.79	1.58
Weekly Overall Range Ratio, %	0.51	0.05	0.32	0.17	-	-	0.52	6.33	1.53
Period Overall Range Ratio, %	0.39	0.02	0.30	0.07	-	-	0.62	5.91	1.64
Temporal Range Overlap									
D–W Grazing Range Overlap, %	0.35	0.01	0.03	0.07	0.24	-	0.66	33.45	4.02
D–P Grazing Range Overlap, %	0.52	0.00	0.00	0.02	0.49	-	0.48	12.58	3.14
W–P Grazing Range Overlap, %	0.54	0.00	-	0.02	0.53	-	0.46	36.97	6.54
D–W Overall Range Overlap, %	0.36	0.01	0.01	0.02	0.32	-	0.65	33.44	2.63
D–P Overall Range Overlap, %	0.59	0.00	0.02	0.00	0.57	0.00	0.41	12.77	2.20
W–P Overall Range Overlap, %	0.52	0.00	0.01	-	0.51	-	0.48	37.58	5.37
Resource Utilization									
Topography									
Distance to Water	0.51	0.03	0.01	0.00	0.49	0.00	0.50	0.01	0.39
Distance to Supplement	0.21	0.04	-	0.18	-	-	0.82	0.01	0.29
Elevation	0.40	0.09	0.08	0.09	0.12	0.05	0.66	-0.09	0.16
Slope	0.11	0.01	0.05	-	0.00	0.06	0.90	-0.04	0.39
N-S Aspect	0.23	0.00	-	0.23	-	0.00	0.77	-0.03	0.36
E-W Aspect	0.09	0.00	0.06	-	0.03	-	0.91	0.00	0.19
Topographic Position Index	0.07	0.00	0.06	0.01	-	-	0.93	0.00	0.14
Vegetation									
Annual Cover	0.31	0.00	-	0.31	0.00	0.00	0.69	0.08	0.17
Perennial Cover	0.08	0.01	0.02	-	0.05	-	0.93	0.13	0.38
Shrub Cover	0.34	0.01	-	0.04	0.29	0.00	0.66	-0.03	0.38
Tree Cover	0.13	0.02	0.00	0.07	0.04	0.00	0.89	-0.07	0.17
Bare Ground	0.31	0.02	-	0.29	-	0.00	0.71	-0.03	0.27
Litter Cover	0.47	0.03	0.06	0.07	0.33	-	0.54	-0.01	0.23

Table A3. Model selection for linear mixed models evaluating the response of cattle behavior and resource use to graded levels of a protein supplement while grazing dormant foothill rangeland across three consecutive periods during two winters in Norris, Montana, USA. All models included random intercepts for individual animal and pasture. All models with ΔAICc < 2 are presented.

	Model	**AICc**[a]	**ΔAICc**[b]	**AICc Weight**		**K**[e]	**R^2_m**[f]	***P*-values**[g]			
				Ind.[c]	**Cum.**[d]			**Suppl.**	**Period**	**Sup:Per**	**Year**
Behavior											
Time Budget											
Time Spent Grazing	suppl. + period	338.2	0.0	0.187	0.187	7	0.15	0.03	0.02	-	-
	√suppl. + period	338.3	0.2	0.172	0.359	7	0.15	0.04	0.02	-	-
	suppl.	338.3	0.2	0.172	0.531	5	0.05	0.03	-	-	-
	suppl. + period + year	339.8	1.7	0.081	0.612	8	0.16	0.03	0.02	-	0.48
	√suppl. + period + year	340.0	1.8	0.075	0.687	8	0.16	0.03	0.02	-	0.47
Time Spent Resting	suppl. + period	313.2	0.0	0.225	0.225	7	0.25	< 0.01	< 0.01	-	-
Time Spent Resting	√suppl. + period	313.2	0.0	0.224	0.449	7	0.25	< 0.01	< 0.01	-	-
	√suppl. + period + year	314.7	1.5	0.109	0.558	8	0.26	< 0.01	< 0.01	-	0.39
	suppl. + period + year	314.7	1.5	0.107	0.664	8	0.26	< 0.01	< 0.01	-	0.40
	suppl.	315.1	1.9	0.085	0.749	5	0.09	< 0.01	-	-	-
Time Spent Traveling	suppl.	-69.7	0.0	0.375	0.375	5	0.05	0.05	-	-	-
	**Random effects only*	-67.9	1.8	0.155	0.531	4	0	-	-	-	-
Time at Supplement Site	suppl. + period + year	483.2	0.0	0.277	0.277	8	0.26	0.02	< 0.01	-	< 0.01
	√suppl. + period + year	483.5	0.3	0.238	0.515	8	0.26	0.02	< 0.01	-	< 0.01
	√suppl. × period + year	484.2	1.1	0.164	0.679	10	0.27	0.02	< 0.01	0.15	< 0.01
	suppl. × period + year	484.3	1.1	0.16	0.838	10	0.27	0.02	< 0.01	0.18	< 0.01
Movement & Foraging											
Daily Distance Traveled	period + year	189.4	0.0	0.42	0.420	7	0.34	-	< 0.01	-	< 0.01
	√suppl. + period + year	190.9	1.5	0.2	0.620	8	0.35	0.40	< 0.01	-	< 0.01
	suppl. + period + year	191.0	1.6	0.188	0.808	8	0.35	0.44	< 0.01	-	< 0.01
Turn Angle	√suppl. × period	821.2	0.0	0.334	0.334	9	0.55	0.05	< 0.01	0.02	-
	suppl. × period	822.4	1.2	0.18	0.514	9	0.55	0.09	< 0.01	0.03	-
Grazing Turn Angle	√suppl. × period	1012.1	0.0	0.462	0.462	9	0.69	< 0.01	< 0.01	0.02	-

Table A3 Continued.

	Model	**AICc**[a]	**ΔAICc**[b]	**AICc Weight**		**K**[e]	**R^2_m**[f]	***P*-values**[g]			
				Ind.[c]	**Cum.**[d]			**Suppl.**	**Period**	**Sup:Per**	**Year**
Grazing Velocity	period + year	-1211.4	0.0	0.185	0.185	7	0.36	-	< 0.01	-	0.10
	suppl. + period + year	-1211.0	0.4	0.148	0.333	8	0.38	0.19	< 0.01	-	0.10
	period	-1210.8	0.6	0.134	0.468	6	0.30	-	< 0.01	-	-
	√suppl. + period + year	-1210.8	0.6	0.134	0.602	8	0.38	0.21	< 0.01	-	0.10
	suppl. + period	-1210.5	0.9	0.116	0.718	7	0.34	0.17	< 0.01	-	-
	√suppl. + period	-1210.3	1.1	0.107	0.825	7	0.34	0.19	< 0.01	-	-
Grazing Bouts per Day	suppl. + period + year	329.3	0.0	0.32	0.320	8	0.25	< 0.01	< 0.01	-	0.02
	√suppl. + period + year	330.2	0.8	0.212	0.532	8	0.25	0.02	< 0.01	-	0.02
Mean Grazing Bout Duration	period + year	83.2	0.0	0.255	0.255	7	0.14	-	< 0.01	-	0.08
	period	84.0	0.9	0.166	0.421	6	0.12	-	< 0.01	-	-
	suppl. + period + year	84.6	1.4	0.127	0.548	8	0.15	0.37	< 0.01	-	0.07
	√suppl. + period + year	84.7	1.6	0.117	0.665	8	0.15	0.43	< 0.01	-	0.07
Core Range Size											
Daily Core Grazing Range	suppl. + period	146.3	0.0	0.172	0.172	7	0.50	0.08	< 0.01	-	-
	√suppl. + period	146.5	0.2	0.155	0.327	7	0.50	0.10	< 0.01	-	-
	suppl. × period	146.7	0.4	0.138	0.466	9	0.51	0.08	< 0.01	0.14	-
	period	147.1	0.8	0.113	0.579	6	0.48	-	< 0.01	-	-
	√suppl. × period	148.1	1.8	0.071	0.649	9	0.51	0.09	< 0.01	0.24	-
	suppl. + period + year	148.1	1.9	0.068	0.718	8	0.50	0.09	< 0.01	-	0.56
Weekly Core Grazing Range	suppl. + period	541.3	0.0	0.229	0.229	7	0.35	0.02	< 0.01	-	-
	√suppl. + period	541.7	0.4	0.185	0.414	7	0.35	0.03	< 0.01	-	-
	suppl. + period + year	542.6	1.3	0.117	0.531	8	0.36	0.02	< 0.01	-	0.35
	√suppl. + period + year	543.1	1.8	0.094	0.625	8	0.36	0.03	< 0.01	-	0.36
Period Core Grazing Range	suppl.	1014.8	0.0	0.429	0.429	5	0.07	< 0.01	-	-	-
Daily Core Overall Range	suppl. + period + year	-417.8	0.0	0.367	0.367	8	0.29	< 0.01	< 0.01	-	< 0.01
	√suppl. + period + year	-417.5	0.3	0.311	0.679	8	0.28	< 0.01	< 0.01	-	< 0.01
Weekly Core Overall Range	suppl. + period + year	-23.0	0.0	0.375	0.375	8	0.26	< 0.01	< 0.01	-	< 0.01
	√suppl. + period + year	-23.0	0.0	0.372	0.747	8	0.26	< 0.01	< 0.01	-	< 0.01

Table A3 Continued.

	Model	AICc[a]	ΔAICc[b]	AICc Weight		K[e]	R^2_m[f]	*P*-values[g]			
				Ind.[c]	Cum.[d]			Suppl.	Period	Sup:Per	Year
Period Core Overall Range	period + year	468.0	0.0	0.349	0.349	7	0.27	-	< 0.01	-	< 0.01
	√suppl. + period + year	468.7	0.7	0.252	0.602	8	0.28	0.22	< 0.01	-	< 0.01
	suppl. + period + year	468.8	0.7	0.243	0.844	8	0.28	0.23	< 0.01	-	< 0.01
Full Range Size											
Daily Full Grazing Range	period + year	764.6	0.0	0.24	0.240	7	0.37	-	< 0.01	-	0.04
	suppl. × period + year	765.2	0.6	0.175	0.415	10	0.40	0.55	< 0.01	0.06	0.04
	√suppl. × period + year	766.2	1.6	0.107	0.521	10	0.39	0.65	< 0.01	0.09	0.04
	suppl. + period + year	766.5	1.9	0.094	0.615	8	0.37	0.57	< 0.01	-	0.04
	√suppl. + period + year	766.6	2.0	0.088	0.703	8	0.37	0.67	< 0.01	-	0.04
Weekly Full Grazing Range	period + year	1112.9	0.0	0.237	0.237	7	0.28	-	< 0.01	-	< 0.01
	suppl. × period + year	1113.0	0.1	0.22	0.457	10	0.32	0.28	< 0.01	0.07	0.01
	suppl. + period + year	1114.0	1.1	0.137	0.594	8	0.29	0.29	< 0.01	-	0.01
	√suppl. × period + year	1114.1	1.2	0.129	0.723	10	0.31	0.34	< 0.01	0.10	0.01
	√suppl. + period + year	1114.2	1.3	0.122	0.844	8	0.29	0.35	< 0.01	-	0.01
Period Full Grazing Range	period + year	1519.4	0.0	0.26	0.260	7	0.21	-	< 0.01	-	< 0.01
	suppl. + period + year	1519.7	0.4	0.217	0.477	8	0.23	0.18	< 0.01	-	< 0.01
	√suppl. + period + year	1519.9	0.5	0.199	0.677	8	0.23	0.20	< 0.01	-	< 0.01
Daily Full Overall Range	period	535.4	0.0	0.324	0.324	6	0.48	-	< 0.01	-	-
	period + year	536.4	1.0	0.195	0.519	7	0.49	-	< 0.01	-	0.29
Weekly Full Overall Range	period + year	937.8	0.0	0.349	0.349	7	0.26	-	< 0.01	-	0.04
	suppl. + period + year	939.8	2.0	0.126	0.475	8	0.26	0.70	< 0.01	-	0.04
Period Full Overall Range	period + year	1405.7	0.0	0.422	0.422	7	0.22	-	< 0.01	-	< 0.01
	suppl. + period + year	1407.6	1.9	0.161	0.584	8	0.22	0.60	< 0.01	-	< 0.01
	√suppl. + period + year	1407.6	1.9	0.16	0.744	8	0.22	0.61	< 0.01	-	< 0.01
Core Range Ratio											
Daily Grazing Range Ratio	√suppl. + period + year	635.9	0.0	0.474	0.474	8	0.45	< 0.01	< 0.01	-	< 0.01
	suppl. + period + year	637.2	1.3	0.251	0.725	8	0.44	< 0.01	< 0.01	-	< 0.01
	$suppl.^2$ + period + year	637.9	2.0	0.172	0.897	9	0.45	< 0.01	< 0.01	-	< 0.01

Table A3 Continued.

	Model	**AICc**[a]	**ΔAICc**[b]	**AICc Weight**		**K**[e]	**R^2_m**[f]	***P*-values**[g]			
				Ind.[c]	**Cum.**[d]			**Suppl.**	**Period**	**Sup:Per**	**Year**
Weekly Grazing Range Ratio	√suppl. + period + year	709.3	0.0	0.447	0.447	8	0.38	< 0.01	< 0.01	-	< 0.01
	suppl. + period + year	710.0	0.7	0.31	0.757	8	0.38	< 0.01	< 0.01	-	< 0.01
Period Grazing Range Ratio	suppl. + period + year	773.8	0.0	0.342	0.342	8	0.40	< 0.01	< 0.01	-	< 0.01
	√suppl. + period + year	773.9	0.1	0.331	0.673	8	0.40	< 0.01	< 0.01	-	< 0.01
	suppl.^{2} + period + year	775.8	2.0	0.128	0.800	9	0.40	< 0.01	< 0.01	-	< 0.01
Daily Overall Range Ratio	suppl. + period	490.0	0.0	0.191	0.191	7	0.45	0.01	< 0.01	-	-
	suppl. × period	490.4	0.4	0.159	0.350	9	0.46	< 0.01	< 0.01	0.13	-
	√suppl. + period	490.6	0.6	0.142	0.492	7	0.45	0.01	< 0.01	-	-
	√suppl. × period	491.4	1.4	0.097	0.590	9	0.46	0.01	< 0.01	0.16	-
	suppl. + period + year	491.7	1.7	0.083	0.673	8	0.45	< 0.01	< 0.01	-	0.47
Weekly Overall Range Ratio	suppl. + period	515.0	0.0	0.214	0.214	7	0.30	0.02	< 0.01	-	-
	√suppl. + period	515.1	0.1	0.208	0.422	7	0.30	0.02	< 0.01	-	-
	suppl. + period + year	516.3	1.3	0.113	0.535	8	0.31	0.02	< 0.01	-	0.34
	√suppl. + period + year	516.3	1.3	0.112	0.647	8	0.31	0.02	< 0.01	-	0.33
Period Overall Range Ratio	√suppl. + period	567.6	0.0	0.195	0.195	7	0.14	0.11	< 0.01	-	-
	suppl. + period	567.7	0.1	0.183	0.377	7	0.10	0.12	< 0.01	-	-
	period	567.9	0.3	0.164	0.541	6	0.11	-	< 0.01	-	-
	√suppl. + period + year	568.8	1.2	0.108	0.649	8	0.15	0.10	< 0.01	-	0.32
	suppl. + period + year	568.9	1.3	0.099	0.748	8	0.15	0.11	< 0.01	-	0.32
	period + year	569.3	1.7	0.083	0.831	7	0.12	-	< 0.01	-	0.37
Temporal Range Overlap											
D–W Grazing Range Overlap	√suppl. + period	817.4	0.0	0.198	0.198	7	0.33	0.10	< 0.01	-	-
	suppl. + period	818.0	0.6	0.148	0.346	7	0.33	0.14	< 0.01	-	-
	period	818.0	0.6	0.147	0.493	6	0.32	-	< 0.01	-	-
	√suppl. + period + year	818.5	1.0	0.118	0.611	8	0.33	0.11	< 0.01	-	0.28
	period + year	818.9	1.5	0.095	0.706	7	0.32	-	< 0.01	-	0.26
	suppl. + period + year	819.0	1.6	0.09	0.796	8	0.33	0.15	< 0.01	-	0.28
	suppl.^{2} + period	819.2	1.8	0.08	0.876	8	0.33	0.21	< 0.01	-	-

Table A3 Continued.

	Model	AICc[a]	ΔAICc[b]	AICc Weight		K[e]	R^2_m[f]	*P*-values[g]			
				Ind.[c]	**Cum.[d]**			**Suppl.**	**Period**	**Sup:Per**	**Year**
D–P Grazing Range Overlap	period + year	896.1	0.0	0.437	0.437	7	0.52	-	< 0.01	-	< 0.01
	√suppl. + period + year	897.7	1.6	0.198	0.636	8	0.52	0.43	< 0.01	-	< 0.01
	suppl. + period + year	897.9	1.8	0.178	0.814	8	0.52	0.53	< 0.01	-	< 0.01
W–P Grazing Range Overlap	period + year	1158.9	0.0	0.492	0.492	7	0.55	-	< 0.01	-	< 0.01
	√suppl. + period + year	1161.0	2.0	0.178	0.670	8	0.55	0.69	< 0.01	-	< 0.01
D–W Overall Range Overlap	√suppl. + period + year	763.6	0.0	0.287	0.287	8	0.38	0.12	< 0.01	-	< 0.01
	suppl. + period + year	763.7	0.1	0.269	0.557	8	0.38	0.13	< 0.01	-	< 0.01
	period + year	763.8	0.3	0.252	0.809	7	0.37	-	< 0.01	-	< 0.01
D–P Overall Range Overlap	period + year	899.0	0.0	0.502	0.502	7	0.50	-	< 0.01	-	< 0.01
	√suppl. + period + year	900.9	1.9	0.191	0.694	8	0.50	0.61	< 0.01	-	< 0.01
	suppl. + period + year	901.0	2.0	0.187	0.881	8	0.50	0.64	< 0.01	-	< 0.01
W–P Overall Range Overlap	period + year	1159.1	0.0	0.525	0.525	7	0.52	-	< 0.01	-	< 0.01
Resource Utilization											
Topography											
Distance to Water	√suppl. + period	-36.1	0.0	0.342	0.342	7	0.36	< 0.01	< 0.01	-	-
	suppl.² + period	-34.9	1.2	0.184	0.526	8	0.36	< 0.01	< 0.01	-	-
	suppl. + period	-34.2	1.9	0.132	0.659	7	0.35	< 0.01	< 0.01	-	-
Distance to Supplement	√suppl. × period + year	-52.5	0.0	0.376	0.376	10	0.29	< 0.01	< 0.01	0.07	< 0.01
	√suppl. + period + year	-51.5	1.0	0.232	0.608	8	0.27	< 0.01	< 0.01	-	< 0.01
Elevation	√suppl. × period + year	-254.1	0.0	0.665	0.665	10	0.35	< 0.01	0.19	0.01	< 0.01
Slope	year	83.3	0.0	0.541	0.541	5	0.06	-	-	-	< 0.01
N-S Aspect	period + year	8.4	0.0	0.468	0.468	7	0.20	-	< 0.01	-	< 0.01
	√suppl. + period + year	10.0	1.7	0.205	0.673	8	0.20	0.46	< 0.01	-	< 0.01
	suppl. + period + year	10.0	1.7	0.205	0.878	8	0.20	0.46	< 0.01	-	< 0.01

Table A3 Continued.

	Model	**AICc^a**	**ΔAICc^b**	**AICc Weight**		**K^e**	**R^2_m^{f}**	***P*-values^g**			
				Ind.^{c}	**Cum.^{d}**			**Suppl.**	**Period**	**Sup:Per**	**Year**
E-W Aspect	period + year	6.0	0.0	0.174	0.174	7	0.06	-	0.03	-	0.12
	year	6.4	0.3	0.148	0.322	5	0.01	-	-	-	0.12
	period	6.4	0.3	0.148	0.47	6	0.04	-	0.03	-	-
	**Random effects only*	6.7	0.7	0.123	0.593	4	0.00	-	-	-	-
	√suppl. + period + year	8.1	2.0	0.064	0.657	8	0.06	0.66	0.03	-	0.11
Topographic Position Index	**Random effects only*	-285.2	0.0	0.261	0.261	4	0.00	-	-	-	-
	period	-284.6	0.6	0.196	0.457	6	0.02	-	0.12	-	-
	year	-283.2	2.0	0.094	0.552	5	0.00	-	-	-	0.77
	suppl.	-283.1	2.0	0.094	0.646	5	0.00	0.79	-	-	-
Vegetation											
Annual Cover	period + year	-311.9	0.0	0.462	0.462	7	0.26	-	< 0.01	-	< 0.01
	√suppl. + period + year	-310.3	1.6	0.206	0.668	8	0.27	0.45	< 0.01	-	< 0.01
	suppl. + period + year	-310.1	1.8	0.187	0.856	8	0.27	0.53	< 0.01	-	< 0.01
Perennial Cover	period	67.9	0.0	0.182	0.182	6	0.07	-	< 0.01	-	-
	suppl. × period	68.5	0.6	0.136	0.318	9	0.10	0.24	< 0.01	0.09	-
	suppl. + period	68.8	0.9	0.116	0.434	7	0.07	0.26	< 0.01	-	-
	√suppl. + period	69.2	1.2	0.099	0.533	7	0.07	0.33	< 0.01	-	-
	period + year	70.0	2.0	0.066	0.599	7	0.07	-	< 0.01	-	0.72
Shrub Cover	suppl. + period + year	37.5	0.0	0.264	0.264	8	0.21	0.12	< 0.01	-	< 0.01
	√suppl. + period + year	37.6	0.1	0.246	0.511	8	0.21	0.13	< 0.01	-	< 0.01
	period + year	37.6	0.2	0.24	0.750	7	0.20	-	< 0.01	-	< 0.01
Tree Cover	√suppl. × period + year	-195.0	0.0	0.531	0.531	10	0.20	0.04	< 0.01	< 0.01	< 0.01
	suppl. × period + year	-193.8	1.2	0.293	0.824	10	0.19	0.06	< 0.01	0.01	< 0.01
Bare Ground	√suppl. + period + year	-42.8	0.0	0.212	0.212	8	0.10	0.03	< 0.01	-	0.07
	suppl. + period + year	-42.3	0.5	0.164	0.376	8	0.09	0.04	< 0.01	-	0.06
	√suppl. + period	-41.6	1.2	0.116	0.492	7	0.08	0.03	< 0.01	-	-
	suppl. + period	-41.1	1.8	0.088	0.580	7	0.07	0.04	< 0.01	-	-
Litter Cover	suppl.^{2} + period	-158.2	0.0	0.292	0.292	8	0.43	0.04	< 0.01	-	-
	suppl.^{2} + period + year	-157.8	0.5	0.232	0.524	9	0.44	0.03	< 0.01	-	0.19

Table A3 Continued.

[a] Second order Akaike's Information Criterion

[b] Difference in AICc relative to best model in set

[c] AICc weight

[d] Cumulative sum of AICc weights between this and the best model

[e] Number of parameters

[f] Marginal R^2

[g] *P*-values for the main effects of supplement, period, and year, and the interaction of supplement and period

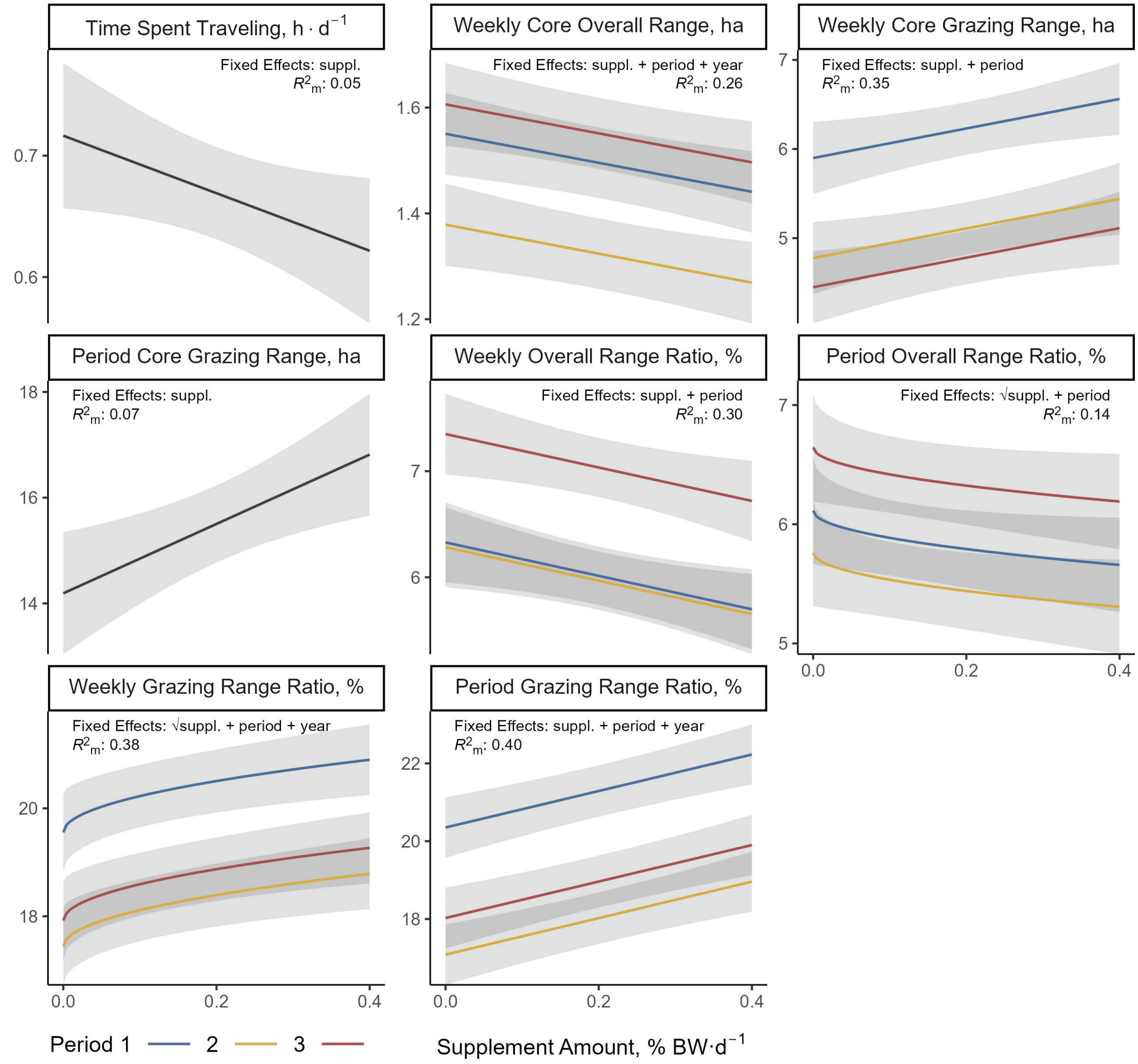

Figure A1. Additional variables for the relationship between animal behavior metrics and protein supplementation (± 95% confidence intervals) for beef cows grazing dormant foothill rangeland across three consecutive periods during the winters of 2020–2021 and 2021–2022 in Norris, Montana, USA. Each panel lists the fixed effects and marginal R^2 of the best-supported model.