THESIS

PREDICTING CATTLE GRAZING DISTRIBUTIONS:

AN AGENT-BASED MODELING APPROACH

Submitted by

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ABSTRACT

PREDICTING CATTLE GRAZING DISTRIBUTIONS:

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An agent-based model was designed which simulates foraging of yearling steers grazing in the short grass steppe region of Colorado, USA. Eleven hypotheses were analyzed that address different aspects of foraging behavior. Models tracked the grazing distributions of simulated steers, as well as their time spent grazing and amount of forage consumed. Model output was validated against grazing distributions and time spent grazing of real steers, observed using GPS-collars. Results indicate that in pastures containing sufficient heterogeneity, steers exhibit selective grazing behaviors in response to forage concentration and slope, as well as use reference memory to return to higher quality patches. In relatively homogenous pastures, cattle graze evenly, and over the course of multiple grazing seasons do not exhibit the selective foraging behaviors tested in this model. Future uses of this model include applying it to other range management scenarios to address differences in steer foraging behavior and pairing the agent-based model with a more elaborate ecosystem model to analyze relationships between steers and vegetation.

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1. INTRODUCTION

Rangelands compose approximately 25% of the Earth's land area, are some of the most species-rich ecosystems, and account for 10% of global meat supply through livestock farming (Alkemade et al., 2010). In the United States, rangelands compose 61% of all land surface (Fuhlendorf and Engle, 2001). Conversion of natural habitats to food production causes a loss of ecosystem services and biodiversity (Tillman et al., 2001). Heterogeneity of rangelands is needed to both promote biodiversity directly through variation of plant species, and indirectly, as animals native to rangelands often are adapted to a diverse suite of habitat types that were present before European settlement (Fuhlendorf and Engle, 2001).

A key driver of heterogeneity in rangelands (or lack thereof) is grazing distribution of livestock. In addition to plant composition and productivity (Milchunas and Lauenroth, 1993; Augustine and McNaughton, 1998), distribution of cattle in rangeland systems impacts several processes, such as fire regimes (Fuhlendorf et al., 2009), edaphic and hydrological processes (Ludwig et al., 2005; Popp et al., 2009), and livestock-wildlife interactions (Fuhlendorf et al., 2006). Grazing distribution has been well studied (e.g., Bailey et al., 1996), and is affected by several abiotic and biotic factors. Abiotic factors include distance to water, slope, and topography (Gersie et al., 2019). Biotic factors include forage quantity and quality, nutrient content of plants, and presence or absence of toxins (Senft et al., 1987; Bailey et al., 1996; Launchbaugh and Howery, 2005). Cattle respond to a combination of both abiotic and biotic factors when making decisions about where to graze (Allred et al., 2013). Cattle also have spatial memory, which influences decisions about movements and bite rates within patches of a landscape (Provenza and Balph, 1987; Bailey et al., 1996). Cattle are social animals who respond to the structure and mechanisms of their social environment (Lazo, 1993). Understanding how these abiotic and biotic factors, along with social mechanisms, influence cattle grazing behavior and distribution can help guide management of rangelands for desired outcomes (Rinella et al., 2011).

Cattle make grazing decisions at a variety of spatial and temporal scales, ranging from an individual bite lasting a few seconds, to a feeding station lasting approximately a minute, to a patch lasting up to 30 minutes, a feeding site lasting a few hours, a camp lasting a few weeks, and a home range which lasts months to years (Bailey et al., 1996). Large-scale foraging patterns are the aggregate results of many individual small-scale grazing decisions. Cattle tend to allocate the time they spend in specific areas of a pasture based on the resources found there, attempting to balance intake of maximum quality and adequate quantity (Senft et al., 1987). There is a trade-off for herbivores in selecting biomass swards for either quality or quantity. Nutritional quality is an inverse function of biomass abundance, and herbivores often sacrifice intake (quantity) for nutritional quality (Wilmshurst et al., 2000). Quantity is limited by body size, gut capacity, ability to crop forage, and available feeding time (Senft et al., 1987). Large herbivores may use momentary maximization to find a balance between quality and quantity. Momentary maximization is the sequential acceptance of the most palatable items encountered at a feeding location until palatability decreases to some threshold level. This threshold level is likely based on experience and can change depending on recent experiences and satiation level (Senft et al., 1987). Once the threshold is met, the animal changes its location until the array of plants available changes. At the patch level, an herbivore may decide to enter a new patch based on the rate of intake at the present patch, expected rate at other patches, and cost of moving to a new patch. If intake falls to a threshold level, the herbivore will likely move to a new patch. As the threshold is met more quickly in a poor patch, less time is spent in poor patches than in rich patches. At broader landscape levels, such as the camp and home range scale, grazing distribution is likely a result of herbivores moving from patch to patch, and moving more slowly through rich patches and more quickly through poor patches (Senft et al., 1987).

Areas close to water are generally grazed more heavily than areas further away and changing the location of water sources in a pasture can dramatically alter grazing distribution (Ganskopp, 2001). Topography is another key factor, as cattle often avoid steep slopes (Ganskopp and Vavra, 1987) and high elevations (Bailey et al., 2015). In relatively gentle terrain, cattle still show uneven grazing patterns, especially later in the grazing season when vegetation is sparser, preferring lowlands and avoiding uplands (Gersie et al., 2019). Additionally, fences are an abiotic influence on cattle grazing distribution, as cattle tend to travel next to and graze more frequently in proximity to fences (Augustine and Derner, 2014).

Finally, social interactions in herds affect grazing distribution, and cattle often form stable social subgroups that share a common home range (Lazo, 1994). Howery et al. (1996) found that in Idaho, 78% of the cows in a herd showed high consistency in home ranges. Within herds, individuals may fill roles of leaders, followers, and independents (Sato, 1982). Leaders are individuals that tend to initiate changes in behavior, such as moving toward or away from grazing areas or water, and the rest of the group may follow. Independent cattle tend to have a further distance to their herdmates than other cattle (Sato, 1982). The social behavior of cattle has an influence on the grazing distribution of cattle and can be manipulated by managers to achieve desired outcomes (Sowell et al., 2000).

Herbivore foraging systems are considered complex because herbivores are making decisions about foraging based on several variables at multiple spatial and temporal scales. Due to this complex nature, herbivore foraging systems are difficult to model with traditional mathematical models, and isolating variables to test through real-world experimentation is impossible. A better understanding of the factors influencing cattle grazing distribution may come through the development of an agent-based model (ABM). Agent-based models are computational simulation tools in which a system is modeled as a collection of autonomous decision-making entities called agents who assess the environment and agents around them to make decisions based on a set of programmed rules (Bonabeau, 2002). ABMs may be particularly useful for modeling group foraging by herbivores, as they can be used to simulate the complexity of animal spatial interactions and behavior (Dumont and Hill, 2003). Dumont and Hill (2003) also note that ABMs would be particularly useful in scenarios in which experimentation is impractical, or where different management strategies are being compared. ABMs are also useful in gaining a better understanding of the ways that parts make up the whole of a system, as ABMs are able to capture emergent behaviors (Bonabeau, 2002). In this context, an ABM can be used to both better understand the underlying decisions cattle are making in determining their grazing behavior, intensity, and distribution, and in running experiments to analyze the outcomes of management decisions impacting grazing distributions (Coughenour, 1991; Jablonski et al., 2018).

I developed a spatially explicit ABM to gain a deeper understanding of the factors contributing to the grazing distribution of cattle. I parameterized the model through both relevant literature and through analyses of movement rates of grazing steers equipped with GPS-collars, grazing in the shortgrass steppe of Colorado, USA. The ABM uses remotely-sensed measures of spatial heterogeneity in forage availability and slope at 1 m^2 resolution to simulate three ~130 hectare pastures. Rules guiding the behavior of the simulated steers were adjusted to test a series of hypotheses, each sequentially increasing in complexity, regarding the behavioral rules driving grazing distribution. Hypotheses were tested by comparing the predicted grazing distributions with real-world grazing distributions captured from steers equipped with GPS-collars. My overarching goal was to evaluate the degree to which specific behavioral rules are likely to contribute to real-world grazing distributions. A longer-term goal is to evaluate the potential for an ABM such as this to be coupled with an ecosystem-level process model of forage growth, to simulate cattle grazing in response to changing environmental variables.

2. METHODS

A series of hypotheses were tested using the ABM created regarding cattle grazing behavior at different spatial scales. These scales were defined from Bailey et al. (1996) and range from the smallest spatial scale of a feeding station, to the largest, the feeding site. The feeding station is defined as the plants available to a steer without moving its front feet. The patch level is an animal's reorientation to a new location, or a break in the foraging sequence. The feeding site is defined as a collection of patches in a contiguous area that animals graze in a foraging bout and may consist of more than one plant community. This spatially explicit ABM defines a feeding station as a 1 m^2 pixel, a patch as pixels within a circle with a 20 m radius, and a feeding site as the entire simulated pasture. Table 1 provides the hypotheses being analyzed using the ABM and defines the forage selection and memory rules followed by simulated steers, occurring at each spatial scale for each hypothesis. These hypotheses are defined further in Section 2.4.

Table 1: List of hypotheses tested using the ABM.

Hypothesis	**Scale**	**Description**
Null	Feeding Station	Steers select pixels at random.
	Patch	Patch level selection not present.
	Feeding Site	Feeding site level selection not present.
1	Feeding Station	Steers select pixels with the most biomass.
	Patch	Patch level selection not present.
	Feeding Site	Feeding site level selection not present.
2	Feeding Station	Steers select pixels at random.
	Patch	Steers adjust rate of movement through patch based on patch's forage quantity (biomass).
	Feeding Site	Entire pasture is used to define patch selection.

3	Feeding Station	Select pixels with the most biomass.
	Patch	Steers adjust rate of movement through patch based on patch's forage quantity (biomass).
	Feeding Site	Entire pasture is used to define patch selection.
4	Feeding Station	Steers select pixels with intermediate biomass (quality).
	Patch	Steers adjust rate of movement through patch based on patch's forage quality, defined here as patches with intermediate amounts of biomass (Bailey et al., 1996; Wilmshurst, 2000).
	Feeding Site	Entire pasture is used to define patch selection.
5	Feeding Station	Steers select for pixels with least amount of slope.
	Patch	Steers adjust rate of movement through patch based on patch's accessibility, defined here as patches with the least amount of slope.
	Feeding Site	Entire pasture is used to define patch selection.
6	Feeding Station	Steers select for pixels based on best outcome from Hypotheses 3 or 4, combined with least slope.
	Patch	Steers adjust rate of movement through patch based on patch's forage quality, based on the best outcome of Hypotheses 3 and 4, combined with least slope.
	Feeding Site	Entire pasture is used to define patch selection.
7	Feeding Station	Steers select for pixels based on best outcome of Hypotheses 3 and 4, combined with least slope.
	Patch	Steers adjust rate of movement through patch based on patch's forage quality, based on the best outcome of Hypotheses 3 and 4, combined with least slope.
	Feeding Site	Set of remembered patches is used to define patch selection. Steers use reference memory to return to good quality patches after visiting water.
8	Feeding Station	Steers select for pixels based on best outcome of Hypotheses 3 and 4, combined with least slope.
	Patch	Steers adjust rate of movement through patch based on patch's forage quality, based on the best outcome of Hypotheses 3 and 4, combined with least slope.
	Feeding Site	Entire pasture is used to define patch selection. Steers use episodic memory to leave bad quality patches.

9	Feeding Station	Steers select for pixels based on best outcome of Hypotheses 3 and 4, combined with least slope.
	Patch	Steers adjust rate of movement through patch based on patch's forage quality, based on the best outcome of Hypotheses 3 and 4, combined with least slope.
	Feeding Site	Set of remembered patches is used to define patch selection. Steers use episodic memory to leave bad quality patches. Steers use reference memory to return to good quality patches after visiting water and when leaving bad quality patches.
10	Feeding Station	Steers select for pixels based on best outcome of Hypotheses 3 and 4, combined with least slope.
	Patch	Steers adjust rate of movement through patch based on patch's forage quality, based on the best outcome of Hypotheses 3 and 4, combined with least slope.
	Feeding Site	Set of remembered patches is used to define patch selection. Steers use episodic memory to leave bad quality patches and use reference memory to return to good quality patches after visiting water and when leaving bad quality patches. Steers are limited in time spent grazing by reaching thresholds of either indigestible or digestible organic matter consumed.

2.1 Study Area

The ABM has been developed to simulate real-world pastures present at the USDA-Agricultural Research Service's Central Plains Experimental Range (CPER) in Nunn, Colorado (40 50' N, 104 43' W). Mean annual precipitation is 340 mm with mean elevation of 1640 m. CPER is within the shortgrass steppe eco-region, which occupies approximately 3.4 x 10^5 km^2 in the semiarid, south-western portion of the Great Plains (Lauenroth et al., 1999). Cattle production is a major land use of this region, and cattle account for 97% of grazing pressure by large herbivores (Hart and Derner, 2008). An ongoing experiment, the Collaborative Adaptive Rangeland Management Project, is designed to compare the livestock grazing behavior and weight gains under adaptive vs. traditional rangeland management (Wilmer et al., 2018), among other goals. Here, I focus on development of an ABM for cattle in the traditional rangeland management treatment. Three of the traditionally managed pastures, which differ in the distribution of soil types, vegetation communities, and topographic complexity, were chosen for inclusion in the ABM to represent different suites of environmental conditions occurring at CPER (Table 2). These pastures were grazed by 20 – 22 yearling steers in 2014 and 22 – 24 yearling steers in 2016 from mid-May to early October, which corresponds to a stocking rate of 0.64 animal unit months (AUM) ha^{-1} in 2014 and 0.68 AUM ha^{-1} in 2016.

Table 2: Environmental variables from the three pasture replicates.

Variable	**Replicate 1**	**Replicate 2**	**Replicate 3**
Pasture area (m^2)	1,330,634	1,262,336	1,286,346
NDVI (index)	Min: 0 Max: 0.5851 Mean: 0.2664	Min: 0.0559 Max: 0.5314 Mean: 0.3007	Min: 0 Max: 0.8831 Mean: 0.3073
Slope (degrees)	Min: 0 Max: 27.7 Mean: 2.9	Min: 0 Max: 20.9 Mean: 2.9	Min: 0.1 Max: 41.0 Mean: 3.9
Standing Biomass (g m^{-2})	Min: 0 Max: 127.86 Mean: 58.19	Min: 0 Max: 124.54 Mean: 70.47	Min: 0 Max: 211.44 Mean: 73.55
Number of water locations	2	1	2

2.2 Collar Data

Cattle distribution was measured by placing GPS collars (Lotek collars; Lotek Engineering, Newmarket, ON, Canada), which recorded positions at 5-min intervals, on two randomly selected steers in each pasture. Previous studies (Gersie et al., 2019; Augustine and Derner, 2014) indicate that the two replicate steers adequately represent the distribution patterns of the entire herd. Collars contained an activity sensor that recorded movements of the neck along the X- and Y- axes and the estimated percent of each 5-min interval in which the neck angle indicated the animal's head was down. We used the calibration of Augustine and Derner (2014) to predict whether each animal was grazing or not grazing for each 5-min tracking interval. In some cases where the activity sensors did not function correctly in 2016, we used the methods described by Gersie et al. (2019) to predict grazing vs. non-grazing intervals based only on the movement rate calculated from sequential GPS locations. This method increased the proportion of nongrazing locations that are misclassified as grazing locations, but still gave a reasonable estimate of where and when cattle were grazing each day (Gersie et al., 2019). Data were combined for the two collared steers in each pasture and year to generate one data set that represents two steers grazing over the course of two grazing seasons. By using two grazing seasons in this analysis, a more general measure of grazing distribution is obtained, as inter- and intra-annual weather variation influences the grazing distribution of cattle (Gersie et al., 2019). Only fixes categorized as grazing fixes were used in analysis. I note that GPS collar data were also used to parameterize some aspects of the model, as described below.

2.3 Overview, Design Concepts, and Details

A description of the ABM is provided which follows the Overview, Design Concepts, and Details (ODD) protocol, an accepted method for standardizing published descriptions of ABMs (Grimm et al., 2010).

2.3.1 Purpose

This model was developed to test hypotheses about behavioral rules guiding the grazing behavior and distribution of cattle grazing in the short grass steppe ecosystem. Through *in silico* experimentation (Peck, 2004), hypotheses can be assessed by enabling or disabling behavioral rules programmed in the model (Railsback and Grimm, 2012). *In silico* experimentation, when applied to cattle grazing behavior, can provide management-relevant insight into the fine-scale decisions cattle are making when grazing, which coalesce to form larger-scale patterns of grazing distributions. The model was developed with the goal of yielding the best fitting model resembling the real-world patterns of cattle grazing distribution observed at CPER. Additionally, this model can provide a baseline for the development of a more intricate ABM of cattle grazing that could be combined with an ecosystem model of vegetation growth to model the interactions between cattle and vegetation, and to predict the outcomes of different grazing management systems in terms of cattle and vegetation growth. NetLogo 6.0.4 (Wilensky, 1999) was used for model development and execution.

2.3.2 Entities, state variables, and scales

The entities in this model include agents representing yearling steers, and pixels representing 1 m^2 patches of land. The patches form a model landscape that attempts to replicate one of the three pastures chosen from CPER. The model has been made spatially explicit by incorporating three sets of geographic data. Remotely sensed data from the National Ecological Observatory Network (NEON) Aerial Observation Platform (AOP), taken in May 2017, provided a map of the Normalized Difference Vegetation Index (NDVI) at 1 m^2 resolution for each of the replicate pastures. The raster of NDVI was clipped to the digitized fence lines of each pasture. Pixels outside of the pasture boundaries are included in the model but are inaccessible to the agent steers. A digital elevation model (DEM) at 1 m^2 spatial scale, also obtained from the NEON AOP, was used to generate a slope layer for each of the three pastures. The resulting slope layer was aligned with the previous NDVI layer and clipped to the digitized fence lines of each pasture. For each pasture replicate, the center of each permanent water source was digitized using aerial imagery, and the center point was buffered by 10 m. The resulting polygon was then rasterized and snapped to the NDVI raster, and these pixels were assigned the role of a water location. All processing of GIS layers was performed using ArcGIS 10.6 (ERSI, Redlands, CA).

The number of steers (agents) in all simulations was held constant at 24 steers per pasture, achieving a stocking rate of approximately 0.65 AUMs ha^{-1} which emulates the real stocking rate of the replicate pastures at CPER. Steers are assigned a starting weight of 281 kg, which is the approximate average weight of yearling steers at the beginning of the grazing season at CPER (J.D. Derner, unpublished data). Steers are assigned roles, with 5% assigned the role of leader, 10% as independent, and the remaining 85% as followers (Sato, 1982; Jablonski et al., 2018). Leaders remain in the center of the herd and function differently from the followers and independents in that they make some decisions for the entire herd. Depending on the hypothesis being tested, leaders have knowledge of the forage in either the entire pasture, or in certain locations of the pasture. Leaders use this knowledge to compare forage quantity or quality in their current site with the forage quantity or quality available at the feeding site level. Independents differ from followers only in that they can access pixels further from the herd leader on any given timestep. Global variables, as well as state variables belonging to steers and pixels, are described in Table 3.

Table 3: Global and state variables used in the ABM.

Entity	Variable	Description
Pixels	NDVI	Normalized Difference Vegetation Index of pixel, taken from NEON AOP remotely sensed data. Remains constant throughout a simulation (unitless).
	Slope	Slope (degree) derived from DEM taken from NEON AOP remotely sensed data. Remains constant throughout a simulation.
	Fence	Fence status is assigned a positive value for pixels outside the pasture boundary. These pixels are inaccessible to steers.
	Biomass	Amount of forage (g m^{-2}) present in the pixel. Initially determined by the pixels' NDVI value multiplied by the amount of forage in the entire pasture. Updates each tick if grazed, and each day through addition or subtraction of forage from the entire pasture through forage growth or senescence. Forage growth or senescence each day is estimated as a function of smoothed seasonal growth curves derived from USDA-NRCS ecological site descriptions.
	Selection	Selection value of each pixel is determined by the hypothesis being tested as a function of biomass quantity, slope, or a combination of biomass and slope (Unitless, varying between 0 and 100).
	DOM	Digestible organic matter present in each pixel (g m^{-2}). Determined through an equation estimating DOM from biomass (Figure 3).
	IDOM	Indigestible organic matter present in each pixel (g m^{-2}). Determined by subtracting the DOM from the Biomass of each pixel.
	Times-Grazed	The number of times a pixel has been grazed by a steer.
Steers	Role	Role assigned to each steer; leader, follower, or independent.
	Weight	Weight of steer (kg)
	Water	Tracker of need for water. Set to 60 when water is visited and decreased by 1 each five-minute tick, indicating thirst twice each 10-hr day.
	Rest	Tracker of rest behavior. When set to 1, steers rest. When set to 0, steers execute model procedures.
	Daily-TSG / Total-TSG	Trackers of time-spent-grazing. Increased by 1 each tick if not resting. Total-TSG is updated throughout the entire grazing season. Daily-TSG is reset to 0 at the beginning of each day.

	Daily-BioM / Total-BioM	Trackers of biomass consumed by each steer (g). Total-BioM is updated throughout the entire grazing season. Daily-BioM is reset to 0 at the beginning of each day.
	Daily DOM / Total-DOM	Trackers of digestible organic matter consumed by each steer (g). Total-DOM is updated throughout the entire grazing season. Daily DOM is reset to 0 at the beginning of each day.
	Daily IDOM / Total-IDOM	Trackers of indigestible organic matter consumed by each steer (g). Total-IDOM is updated throughout the entire grazing season. Daily IDOM is reset to 0 at the beginning of each day.
	Discovered-Sites	A list of discovered sites kept by each lead steer. Discovered sites are patches remembered by the lead steer, which the herd will return to in the Travel to New Site procedure if reference memory is enabled (Hypotheses 7, 9, 10).
	Current-Site-Condition	Rating of current patch condition; Good, Bad, or Neutral. This is determined by the lead steer comparing the current patch in a radius of 20 m with knowledge of patches at the feeding-site scale. The patch rating is then shared with the rest of the herd.
Globals	Day	Tracker of day number in the model. Days are either 120 5-m ticks or 156 ticks (Hypothesis 10). The model stops after 140 days have passed.
	Water-Locations	Set of pixels with water status. Spatially explicit based on locations of real stock tanks at CPER.
Inputs	Number-Steers	Number of steers in the pasture. Set to 24 for this exercise.
	Kgs-Per-Hectare	The amount of forage (kg) in the pasture at the start of the model. This is input through the forage-growth submodel.
	Herd-Cohesion-Factor	Determines distance between herdmates. Set to 8 for this exercise (Jablonski et al., 2018).
	Selection-Curve	The peak biomass-concentration of pixels preferred by steers. Can be set from 80-140 g m^{-2} in increments of 10. Pixels receive increasing selection values up to this peak and decreasing selection values beyond this peak. Can also be set to “Max-Biomass” where selection values increase at a constant rate with biomass-concentration of pixels.
	Slope-Modifier	Factor that reduces the role slope plays in determining the selection value of pixels. Used in Hypotheses 5-10. Ranges from 0.1 to 1.0 in 0.1 increments.
	Good-Site-Memory	Length (days) of reference memory of steers. Set to 20 days for this exercise (Bailey et al., 1996).

	Bad-Site-Tolerance	Episodic memory threshold of steers. Increases by 1 if steers visit a good site, decreases by 1 if steers visit a bad site. If the score falls below this threshold, steers move to a new site when testing hypotheses where episodic memory is enabled (8-10). Initialized to -5 for this exercise.
	DOM-Threshold	Amount of digestible organic matter that can be consumed by a steer before resting for the remainder of the day, in terms of percent body weight. Set to 2.7% for this exercise (National Resource Council, 1996).
	IDOM-Threshold	Amount of indigestible organic matter that can be consumed by a steer before resting for the remainder of the day, in terms of percent body weight. Set to 0.9% for this exercise (National Resource Council, 1996).

The model operates at a discrete time scale (ticks) of 5 minutes each, chosen to match the interval between GPS fixes received by the collars deployed at CPER. Days are tracked, with the length of a day differing depending on the hypothesis being tested. A day is either 120 ticks (10 hours, approximate average time GPS-collared steers were observed to graze each day) or 156 ticks (13 hours, approximate maximum time GPS-collared steers were observed to graze each day). A full 24-hour day was not necessary, as grazing distribution was the primary focus, and time spent by cattle when not grazing (resting, traveling, drinking) was not simulated. Each model simulation runs for 140 days, representing the time period from mid-May to early October, which corresponds to the grazing season at CPER.

Steers in the model make grazing decisions at different spatial scales, corresponding to the spatial scales defined by Bailey (1996). Every model tick, each steer consumes forages from ~5 pixels chosen from a cone of varying dimensions. The individual pixels represent a feeding station, or the forage available to a steer without moving its front legs. The cone represents the movement rate through the patch spatial scale, described as the animal's reorientation to a new location. The cone's dimensions change depending on the quality of the patch (Figure 1) and reflect the turn angles and velocities of GPS-collared steers at CPER when grazing. The quality of the patch is determined by the leader steer comparing the pixels in a 20-pixel radius with the pixels within the largest spatial scale, the feeding site. Cone dimensions of the patches are illustrated in Figure 1. The feeding site is a collection of patches in a contiguous spatial area that animals graze during a foraging bout. Due to the relatively small size of the replicate pastures, the feeding site is assumed to be the entire pasture, as steers at CPER have been observed to traverse across their entire pasture in one foraging bout. Depending on the hypothesis being tested, steers make grazing decisions at the feeding site scale with either knowledge of the entire pasture, or with knowledge of a collection of remembered patches within the pasture.

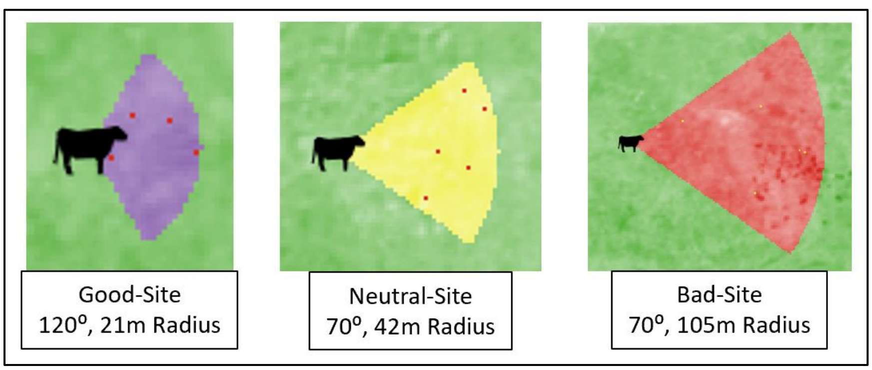

Figure 1: Cone sizes of forage available to steers at the patch level spatial scale depending on the quality of the patch assessed by the lead steer.

2.3.3 Process Overview and Scheduling

Figure 2 describes the model process for each tick as executed by steers, depending on their role and the hypothesis being tested. The procedures executed by the steers are described in the form of pseudo-code in Table 4.

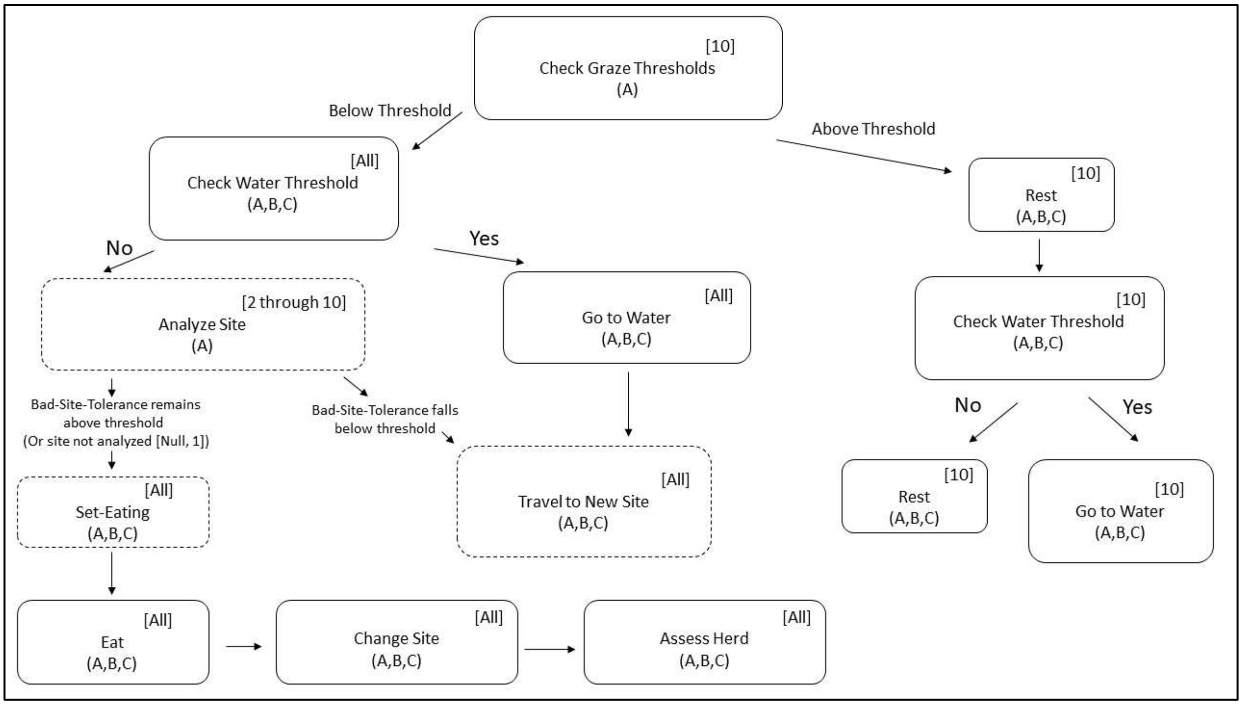

Figure 2. Flow chart describing the model process for each tick in a simulation, executed by steers. Brackets in the upper-right of each box represent the hypotheses in which the procedure is executed. Letters underneath each procedure represent the roles of steers executing the command (A = Leaders, B = Followers, C = Independents). Procedures in solid boxes are executed the same way regardless of the hypothesis being tested. Procedures in dashed boxes vary in their execution depending on the hypothesis being tested.

Table 4: Procedures present in the ABM.

Procedure	Description
Check Graze Thresholds	This procedure is only present when testing Hypothesis 10. The lead steer compares the amount of indigestible and digestible organic matter it has consumed against the indigestible organic matter threshold and digestible organic matter threshold, respectively, set to 0.9% and 2.7% of the steers weight, respectively. If it is below those thresholds, it grazes.
Check Water Thresholds	Present in all hypotheses. Each steer checks its' hydration level, which reaches 0 every 60 ticks. This results in two visits to water each day, which is consistent with the average number of water visits observed from the GPS-equipped steers.
Go to Water	Present in all hypotheses. The lead steer chooses the closest water location (stock tank) in the pasture and all steers in the herd move there. All steers graze from two pixels every 126 m on the way to water, which simulates light grazing while traveling. Steers travel in a straight line from their current

	location to the water location. Steers then travel to a new site as chosen by the lead steer.
Analyze Site	Present in hypotheses 2 through 10. The lead steer compares the average selection value of the pixels in a 20 m radius with the average selection value of the pixels in the feeding site (pasture, or collection of patches within the pasture, depending on hypothesis). The patch is considered good or bad if its' average selection value is one standard-deviation above or below, respectively, the average selection value of the feeding site. Otherwise the patch is considered neutral. All herdmates set their site condition to that of the lead steer. For hypotheses with reference memory enabled (7,9,10), the cutoff for a good site is reduced to 0.5 standard deviations above the average selection value of the feeding site after 20 days, as the feeding site average selection value increases rapidly as steers only remember the best patches they have visited. For hypotheses with episodic memory enabled (8,9,10), the lead steer adds or subtracts 1 to its' site tolerance score if at a good or bad site, respectively. If this site-tolerance score falls below a threshold set by the user, all steers travel to a new site.
Set-Eating	Present in all hypotheses. Herdmates set their heading to the heading of the leader. All steers view pixels in a cone centered on their medial line with dimensions dependent on patch quality (Figure 1). Steers choose 5 pixels within the cone to eat from. Selection of pixels is dependent on the hypothesis being tested. If there are not 5 pixels to choose from in the cone because the steer is close to a fence, the steer eats from fewer than 5 pixels.
Eat	Present in all hypotheses. All steers remove 20% of the forage from each pixel chosen in the set-eating procedure. This amount was chosen as it approximates the amount of forage a steer would consume if eating from one pixel min^{-1} from pixels with an average amount of forage for 10 hours in order to reach its' estimated daily forage intake (National Resource Council, 1996). Steers update their state variables for forage consumed, and pixels update state variables for forage remaining, selection value, and times-grazed.
Change Site	Present in all hypotheses. The lead steer moves to the pixel that is the furthest distance from its starting point within the cone of patch selection that is has eaten from. Herdmates move to a random pixel within a given radius around the leader. Radius is set by the user in the form of the herd-cohesion factor, which for this exercise was held constant at 8. This results in followers choosing a pixel within 80 m of the leader, and independents choosing a pixel within 120 m of the leader. Steers can only move to a pixel that is within the pasture boundary.
Assess-Herd	Present in all hypotheses. This procedure was taken directly from Jablonski et al. (2018) and maintains the herd-level arrangement of steers. Follower and independent steers move to a pixel unoccupied by other steers that fulfills the

	distance requirements set by the herd-cohesion-factor. This procedure also pushes independent steers to the periphery of the herd. The lead steer remains in the center of the herd.
Travel to New Site	Present in all hypotheses. Steers either move to a random patch in the pasture (Hypotheses Null, 1,2,3,4, 5, 6, 8), or to a remembered patch in the pasture (Hypotheses 7, 9, 10). If there are no remembered patches, the steers move to a random patch. The lead steer chooses a pixel to move to and moves to this pixel in a straight line. Followers and independents choose a pixel in a given radius around the lead steer's chosen pixel (80 m or 120 m here, respectively) and move to this pixel in a straight line. All steers graze from two pixels every 126 m while traveling to the new site, simulating light grazing.
Rest	Present in Hypothesis 10 only. All steers remain on the pixel they currently occupy and do nothing.

At the start of each day in the model, steers add 0.91 kg to their weight, approximating the average daily weight gain of steers at CPER. Steers also reset their state variables representing daily forage intakes. When testing hypotheses that include steers' ability for using reference memory, steers with the role of leader remove patches from their memory that were discovered by the steer longer ago than their reference memory length, determined by the analyst and set to 20 days for this exercise (Bailey et al., 1996).

Pixels add forage at the start of each day in the model. Patches are assigned an amount of forage added based on the pixels' NDVI and the amount of overall forage added to the pasture as a whole, calculated from a corresponding model of forage production (D. Augustine, unpublished measures of forage production, 2013 – 2018). The forage production model uses the Ecological Site Descriptions ([ESDs]; USDA 2007a; USDA 2007b) and the ratio of areas represented by the ecological sites present in each pasture replicate (Loamy Plains and Sandy Plains) to estimate the amount of forage present in each pasture replicate each day of an average precipitation year. The amount of forage added to or removed from the pasture is input as g m^{-2} and allocated to each pixel by multiplying this input with each pixels' NDVI value divided by the average NDVI value of all pixels. This method distributes the forage so that pixels with higher relative NDVI values grow more forage throughout the grazing season than pixels with low NDVI values.

2.3.4 Design Concepts

Basic Principles – This model was developed with the principle of parsimony, in that the patterns of cattle grazing distribution may be the result of the simplest explanation. Guided by this principle, the model is first run with the null hypothesis that cattle grazing distributions are the result of steers grazing in a fenced pasture, having the need to visit water twice a day, form a herd, and otherwise select pixels for grazing at random. Additional hypotheses then add complexity to this null hypothesis. These hypotheses can then be assessed on whether the added complexity results in a better fit of simulated grazing distributions to observed grazing distributions. For hypotheses in which multiple values for a variable were tested, the value of the variable that resulted in the best model fit was carried forward to the next hypothesis; while it is often appropriate to test all possible combinations of variables, this approach was adopted due to time limitations for running simulations.

Emergence – As this model assigns basic behavioral rules to steers, the resulting patterns are considered emergent. These patterns include the grazing distribution, the amount of forage consumed, the distances steers travel, and the times spent grazing.

Adaptation, Objectives, Learning, and Predictions – Adaptation is present in several of the hypotheses tested here. Steers have the objective of eating from the best pixels available to them. The determination of which pixels are best is dependent on the hypothesis being tested, but this assessment is adaptive in that it changes depending on their location in the pasture, the growth and senescence of forage, and the foraging of herdmates. In hypotheses with memory included, steers adapt to their environment by returning to a good patch after visiting water or after leaving a bad patch due to their intolerance for grazing in bad areas. Steers have the objectives of grazing from the best pixels, and maintaining their water, rest, and herding requirements. Steers exhibit learning in hypotheses in which memory is enabled. The learning comes in the form of remembering the best patches they have visited and using this learning to evaluate new patches they encounter. Steers use prediction in hypotheses with episodic memory enabled, in that they predict that moving to a new patch will result in better pixels to forage from than are available to them currently.

Sensing and Interaction – Steers are able to sense the pixels in their cone of vision and the other steers in their herd. Lead steers are able to sense the pasture at the feeding site level. Steers interact with each other in that they only occupy pixels without other steers on them, and that fulfill the requirements of being an appropriate distance from the lead steer and other herdmates to form a herd. Steers can sense the water location that is closest to them.

Stochasticity – The stochastic elements of this model are present in the null hypothesis, where steers choose from random pixels within their patch-level cone when grazing. There is also stochasticity in several hypotheses where steers return to a random patch after visiting water, or after leaving a bad site. In models with more than one lead steer, not presented here, the herd each steer belongs to is a function of the random location of steers at the start of the model.

Observation – Each tick in the model the lead steer(s) add their coordinates within the pasture to an export file. At the end of each day in the model, the lead steer(s) write to a file their daily time spent grazing, daily indigestible organic matter consumed, daily digestible organic matter consumed, daily biomass consumed, and the mean daily biomass consumed by the herd. At the end of the model run (140 days) a raster of the number of times each pixel was grazed is exported. This raster serves as a measure of the grazing distribution.

2.3.5 Initialization

At the start of the model, pixels within the pasture boundary are assigned an NDVI value from the underlying 1 m^2 NDVI raster. Pixels are assigned a slope value from the 1 m^2 slope raster. Pixels are assigned water status from the raster of water locations. The initial amount of forage in the pasture is set to the value provided from the corresponding model of forage production (Augustine, unpublished measures of forage production, 2013 – 2018) and converted to g m^{-2}. The forage is distributed to the pixels using Equation 1.

$$ForageConcentration\left(\frac{g}{m^2}\right) * \left(\frac{Pixel\ NDVI\ Value}{Average\ NDVI\ Value}\right) \qquad \text{(Eq 1)}$$

Two equations (2 and 3) were tested using the amount of biomass in each pixel to determine the amount of digestible organic matter in each pixel, using Equation 2a or 3a for days 1 - 50 in the model, and Equation 2b or 3b for days 50 - 140. The amount of indigestible organic matter in each pixel is assigned by taking the total biomass and subtracting the digestible organic matter. Equation 2 is displayed graphically in Figure 3. Equation 3 is displayed graphically in Figure 4.

$$DOM = (0.75 * Biomass) - (0.001818 * Biomass^2) \quad \text{(Eq 2a)}$$

$$DOM = (75 * Biomass) - \frac{(Day*7*Biomass)}{50} - (0.1818 * Biomass^2) \quad \text{(Eq 2b)}$$

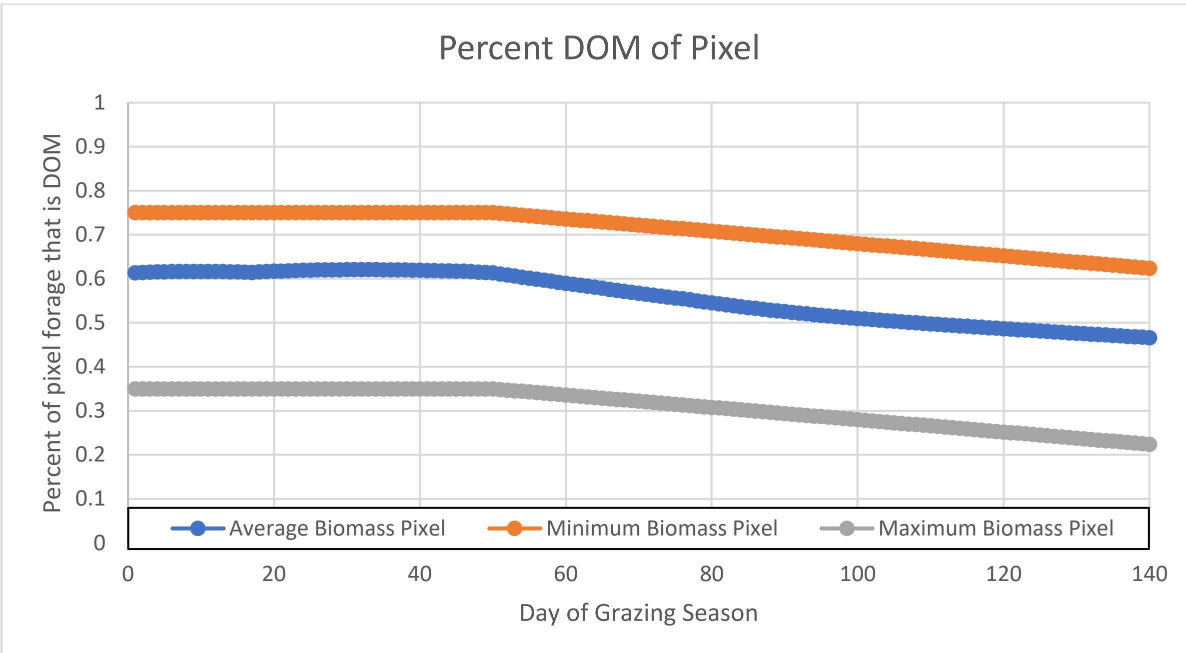

Figure 3: Graphical representation of Equation 2, used to determine the percent of biomass in each pixel considered digestible organic matter.

$$DOM = (0.8 * Biomass) - (0.001818 * Biomass^2) \quad \text{(Eq 3a)}$$

$$DOM = (80 * Biomass) - \frac{(Day*7*Biomass)}{50} - (0.1818 * Biomass^2) \quad \text{(Eq 3b)}$$

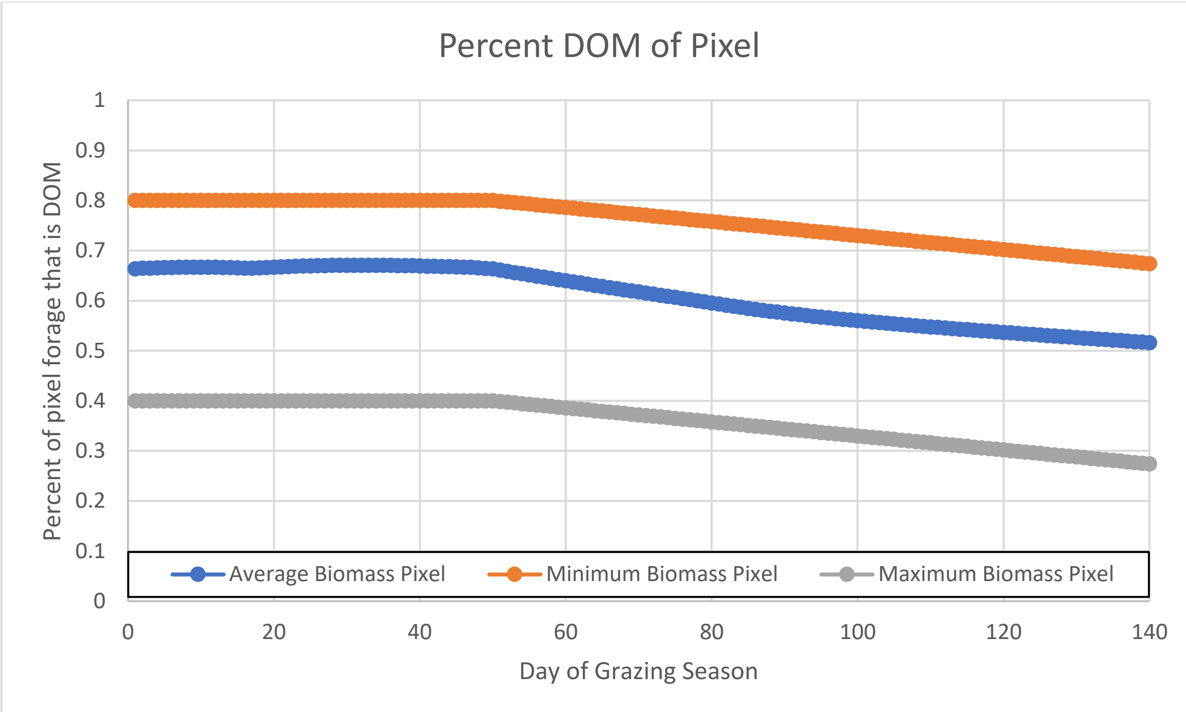

Figure 4: Graphical representation of Equation 3, used to determine the percent of biomass in each pixel considered digestible organic matter.

The selection value of the pixel, dependent on the hypothesis being tested, is determined from either the biomass, slope, or both biomass and slope together. All other pixel variables are set to 0.

The number of steers, chosen by the model user, are created and placed on random pixels within the pasture. The steers are randomly assigned roles in the ratio of 85% followers, 10% independents, and 5% leaders. Followers and independents are assigned the lead steer closest to them as their leader and form a herd with this leader throughout the model. All steers with the same leader are set with each other as herdmates. Steers are set an initial weight of 281 kg, the average starting weight of yearling steers in the beginning of the grazing season at CPER. All other steer variables are set to 0. An image of each of the pasture replicates initial conditions is in Figure 5.

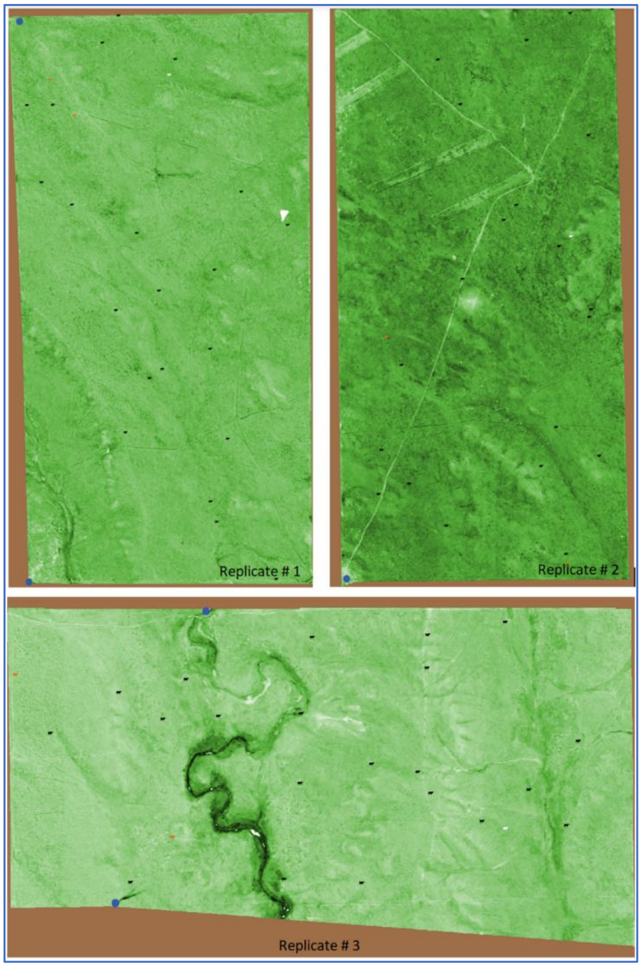

Figure 5: Pasture replicates at the initial state of model. Pixels are shaded green based on their NDVI value. Brown areas are outside the pasture. Water locations are shown in blue. Lead steers are white, independents are orange, and followers are black.

2.3.6 Input Data

Mean daily forage biomass production was estimated in each simulated pasture using the monthly growth curves from the Ecological Site Descriptions for the Loamy Plains, Sandy Plains, and Salt Flat Ecological Sites in eastern Colorado (USDA 2007a,b,c). These were to generate smoothed daily growth curves for each ecological site, assuming total annual production of 84 g m^{-2} on Loamy Plains and 123 g m^{-2} on Sandy Plains and Salt Flats (USDA 2007a,b,c). For each simulated pasture, the total annual production as a weighted mean of the percent of the pasture in each of the three ecological sites was calculated. Simulations start on May 15th of a given year, at which point it was assumed that 21% of total current-year forage production had already occurred. Daily forage production was calculated according to Figure 6, where production increased at an exponentially saturating rate from day 1 to 42, declined linearly from day 42 to 80, and then declined exponentially from day 80 to day 140. This function was selected to follow the phenological patterns in the Ecological Site Descriptions while providing smoothed values on a daily instead of a monthly basis.

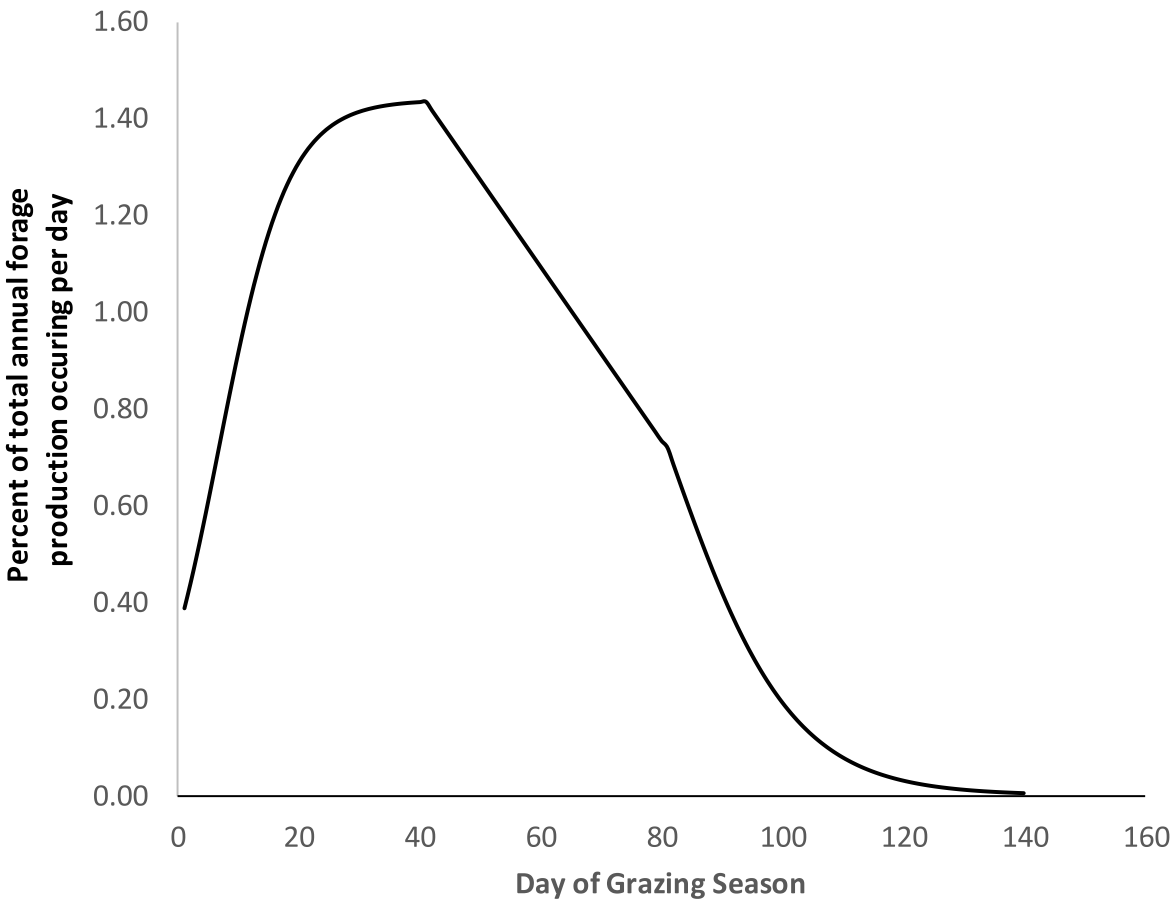

Figure 6: Assumed percent of total annual forage produced on a daily basis for a 140-day grazing season beginning on May 15th.

The amount of standing dead forage biomass carried over from the previous year on a daily basis was also calculated. Starting on May 15th, 42 g m^{-2} of standing dead residual biomass on Loamy Plains, and 51 g m^{-2} of standing dead on Sandy Plains and Salt Flats was assumed (USDA 2007a,b,c). In the absence of grazing, it is assumed that this residual biomass is transferred to the litter layer (and becomes unavailable as forage) according to Figure 7, which adopts a slow loss rate in May, a more rapid loss rate in June with warming temperatures, and then a slower rate again in July as the more recalcitrant portion of the biomass is finally transferred to litter. It is assumed that residual biomass from the previous year declines to zero on August 1st.

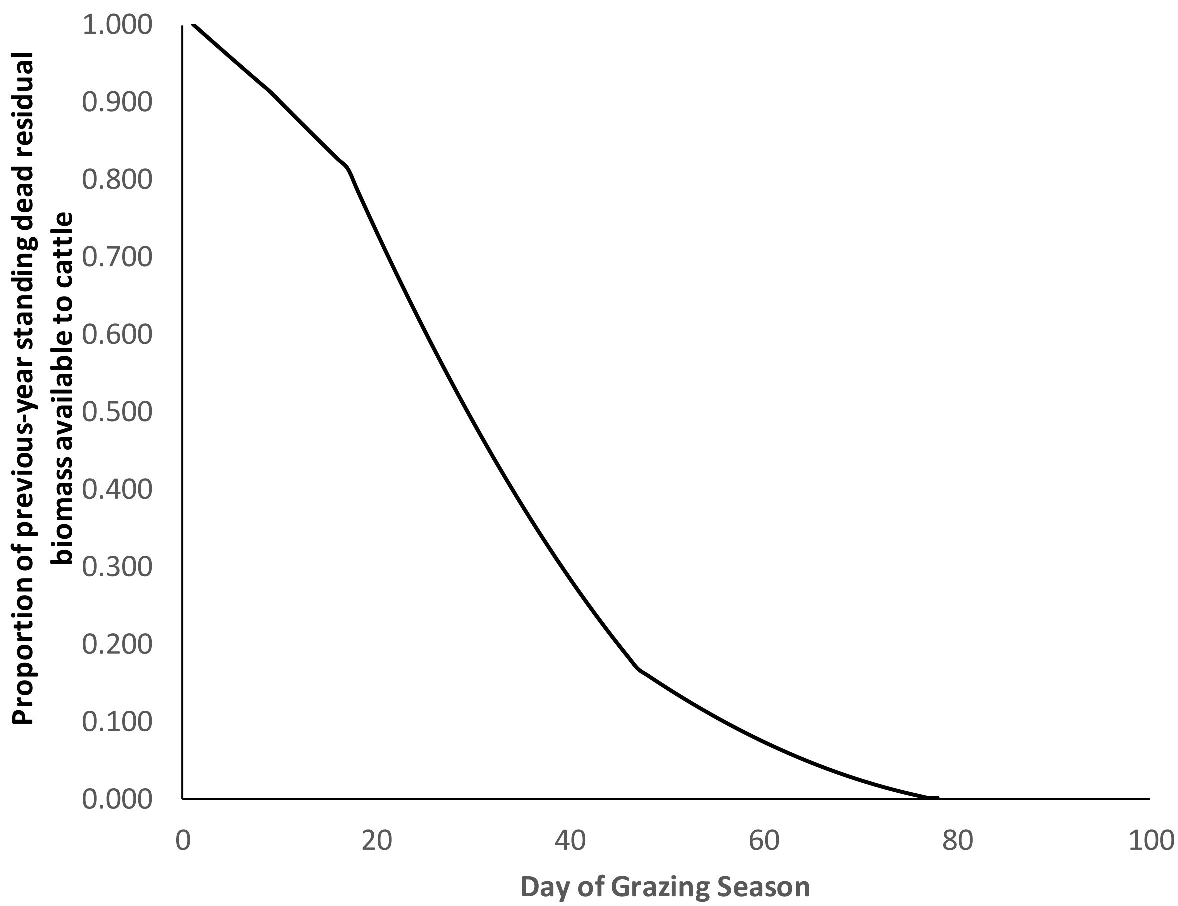

Figure 7: Assumed proportion of previous-year standing dead residual biomass available to cattle over the grazing season beginning on May 15th.

Total mean forage biomass on a daily basis (in g m^{-2}) is then calculated as the sum of current-year production and previous-years residual biomass. This calculated amount is then distributed to each pixel in the simulated pasture, based on the pixel's NDVI value, using Equation 1.

2.4 Hypothesis Testing

I adjusted model processes to fit each hypothesis, as described below. In situations of uncertainty for a given variable, I conducted simulations over a range of values, and the best fitting model was then carried forward through the rest of the hypothesis testing. For each hypothesis, I assumed that cattle graze in a herd, visit water twice per day, eat from one pixel per minute, and consume 20% of the biomass in each pixel from which they eat. For all hypotheses except Hypothesis 10, I assumed cattle graze for ten hours per day. For each hypothesis, I ran ten simulations to account for stochasticity in the model. For hypotheses where I tested ranges of variables, I ran ten simulations for each value.

Null Hypothesis – Cattle select pixels to graze at random at the feeding station level.

Description - Pixels within each pasture replicate were assigned selection values at random. Cattle did not select at the patch level, and therefore ate from pixels within a cone with neutral site dimensions throughout the model (Figure 1).

Hypothesis 1 – Cattle select pixels to graze with the most biomass at the feeding station level.

Description - Cattle select for pixels with the most biomass in a cone with neutral site dimensions throughout the model (Figure 1).

Hypothesis 2 – Cattle select pixels at random at the feeding station level and select at the patch level for most biomass.

Description - Cattle select for pixels within a cone at random, but the cone's dimensions vary based on the patch quality, simulating movement rate through the patch. Patch quality is determined with the assumption that the lead steers have complete knowledge of the entire pasture. The lead steer compares the selection value of pixels in a patch radius of 20 m with the average selection value of the entire pasture. Patches with values 1 standard deviation higher or lower than the pasture are considered good, or bad, respectively. Selection value of pixels is a linear function of maximum biomass.

Hypothesis 3 – Cattle select pixels for maximal biomass at both the feeding station and patch level.

Description - Cattle select at the patch level for maximum biomass as they do in Hypothesis 2. Cattle also choose pixels with most biomass at the feeding station level.

Hypothesis 4 – Cattle select pixels based on a combination of forage quantity and quality at both the feeding station and patch levels, where the optimum combination occurs at an intermediate biomass.

Description – Because forage quality often varies inversely with forage biomass in both space and time, ruminant herbivores often select swards with lower biomass than those where they could maximize their short-term intake rate in terms of forage quantity (Laca 1992; Bergman

2000; Wilmshurst et al., 2000). Here, I hypothesize that cattle prefer to graze pixels at both the feeding station and patch level which have an optimal, intermediate biomass based on the quality/quantity tradeoff. For yearling cattle with a body size of 280 – 400 kg, this optimal biomass is estimated to be 100 g m^{-2}based on Figure 2 of Wilsmhurst et al. (2000). I assigned pixels a selection value ranging from 0-100 based on their biomass, and conducted four different sets of simulations assuming the optimal biomass value was 80, 100, 120, or 140 g m^{-2}. Pixel selection values were assigned using a broken stick model, where pixels with no biomass and the pixel with the most biomass in the pasture were given a selection value of zero, pixels with the optimal forage concentration were given a selection value of 100, and linear functions were fit between these points (Figure 8).

Figure 8: Broken stick models determining pixel selection value based on biomass concentration for each of the replicate pastures.

Hypothesis 5 - Cattle select for pixel quality at the feeding station and patch level, determined by the slope of the pixels.

Description - Cattle select from pixels with the least amount of slope at both the feeding station and patch level. Pixels were assigned a selection value from 0 to 100, where pixels with a slope of zero were assigned a selection value of 100, and the pixel with the highest slope was assigned a selection value of zero. Linear equations were fit to these points for each pasture replicate and used to assign selection values to the remaining pixels in each pasture.

Hypothesis 6 - Cattle select for pixel quality at the feeding station and patch level, determined by a combination of biomass concentration and slope.

Description – Cattle select for pixels with the highest selection value at both the feeding station and patch level. Selection for each pixel was determined by combining the best fitting selection function for biomass concentration from Hypotheses 3 and 4 with the slope of the pixel through a weighting function using Equation 4:

$$Selection\ Value = \frac{Biomass\ Selection * (Slope\ Selection * Slope\ Modifier)}{100} \quad \text{(Eq 4)}$$

Where the biomass selection is taken from the best model of Hypotheses 3 and 4, and slope selection was taken from Hypothesis 5. The slope modifier was included to decrease the magnitude of slope in the selection equation, as cattle should be primarily focused on consuming forage. This prevented cattle from continually selecting the same pixel with little slope several times over, even if it had little to no biomass remaining. Slope modifier values of 0.1, 0.3, and 0.5 were tested in this hypothesis.

Hypothesis 7 – Cattle select for pixel quality at the feeding station and patch level, determined by a combination of biomass concentration and slope. Cattle use reference memory to return to good quality patches after visiting water.

Description – Cattle select pixels at the feeding station level as described in Hypothesis 6. Cattle select at the patch level for the same qualities in Hypothesis 7, but the feeding site level that they base patch quality on is different. In this hypothesis, the lead steer begins the model run with ten patches, evenly spaced across the pasture, as remembered sites. The lead steer then compares the quality of each patch it visits with its set of remembered sites. Patches with average selection values one standard deviation above the average selection value of the remembered sites are considered good, and these patches are added to the list of remembered sites. Individual remembered sites are "forgotten" every 20 days in the model (Laca, 1995; Bailey et al., 1996). After 20 days, the list of remembered sites has consistently high measures of selection. When these sites are compared against new patches, the new patches are rarely a standard deviation better than the list of remembered sites. To account for this, after 20 days, the threshold for considering a new patch a "good quality" patch is reduced to 0.5 standard deviations above the average of remembered sites. Steers adjust their patch level cone dimensions in respect to the quality of the patch they are visiting.

Hypothesis 8 - Cattle select for pixel quality at the feeding station and patch level, determined by a combination of biomass concentration and slope. Cattle use episodic memory to leave bad quality patches.

Description – Cattle select at the feeding station and patch level as described in Hypothesis 6 using the best fitting slope modifier. Cattle use the entire pasture as the feeding site level to compare patch quality. The lead steer is assigned a “Bad-Site-Threshold”, which is a threshold that if fallen below, cattle will leave the patch they are at and move to a random patch in the pasture. The lead steer keeps track of the quality of patches it visits. Starting with a counter at zero, if the steer visits a bad quality patch, it reduces this counter by 1, and if it visits a good quality patch, increases this counter by 1. Neutral sites do not impact this counter. If the count falls below the Bad-Site-Threshold, set to -5, the steers will stop grazing leave the patch they are at and relocate to a random patch in the pasture. This hypothesis attempts to mimic the steers’ ability for episodic, or working memory, which lasts approximately eight hours (Bailey et al., 1996).

Hypothesis 9 - Cattle select for pixel quality at the feeding station and patch level, determined by a combination of biomass concentration and slope. Cattle use episodic memory to leave bad quality patches. Cattle use reference memory to return to good quality patches after leaving water, and when leaving a bad patch.

Description – This hypothesis combines the memory abilities demonstrated in Hypotheses 7 and 8. Cattle begin with a subset of remembered patches at the feeding site level, as in Hypothesis 7. Cattle keep track of the quality of patches they visit, as in Hypothesis 8. When the Bad-Site-Threshold is met, cattle return to a good quality patch from the list of remembered patches. Cattle also return to a patch from the list of remembered patches when leaving water, as in Hypothesis 7.

Hypothesis 10 - Cattle select for pixel quality at the feeding station and patch level, determined by a combination of biomass concentration and slope. Cattle use episodic memory to leave bad *quality patches. Cattle use reference memory to return to good quality patches after leaving water, and when leaving a bad patch. Cattle are limited in time-spent-grazing by reaching thresholds of either digestible or indigestible organic matter consumed.*

Description – Cattle select at the feeding station and patch level as in Hypothesis 9. Cattle are limited in their time-spent-grazing by either reaching thresholds of digestible or indigestible organic matter consumed. The digestible organic matter consumed threshold is set to 2.7% of the steers body weight (National Resource Council, 1996). The indigestible organic matter consumed threshold was assessed with two thresholds, 1% and 0.9% of steers body weight (National Resource Council, 1996). The two digestible organic matter equations (Equations 2 and 3), discussed earlier, assigning the ratio of digestible and indigestible organic matter per pixel, were assessed in this hypothesis. This resulted in four combinations of indigestible organic matter thresholds and digestible organic matter equations, described in Table 5. If cattle do not reach either threshold, they will graze for 13 hours, which is the approximate maximum time spent grazing observed from GPS-collar equipped steers.

Table 5: Descriptions of model scenarios assessed for Hypothesis 10.

Model Run	**Description**
Scenario 1	Digestible Organic Matter Equation: Equation 1 Indigestible Organic Matter Consumed Threshold: 0.9% of Body Weight
Scenario 2	Digestible Organic Matter Equation: Equation 2 Indigestible Organic Matter Consumed Threshold: 0.9% of Body Weight
Scenario 3	Digestible Organic Matter Equation: Equation 1 Indigestible Organic Matter Consumed Threshold: 1% of Body Weight
Scenario 4	Digestible Organic Matter Equation: Equation 2 Indigestible Organic Matter Consumed Threshold: 1% of Body Weight

2.5 Model Validation

At the end of the simulated grazing season, a raster is exported from the model which represents the number of times each 1 m^2 cell was grazed. The output of each model is aggregated to a 30 m^2 spatial scale, using a sum of total times grazed. This scale was chosen because managers are more concerned with the general intensity of grazing occurring in the pasture rather than at a fine spatial scale of 1 m^2. Data processing was performed in R using the package raster (Hijmans et al., 2015). Cells occurring within 50 m of a pasture corner, or within 75 m of a water source were clipped from the data, as these areas are heavily used by steers, and are generally void of palatable vegetation due to trampling, so grazing here is improbable (Augustine and Derner, 2014). Data were t normalized and broken into decile categories using Equation 5.

$$\frac{(Raster.Value - Raster.Minimum)}{(Raster.Maximum - Raster.Minimum)} * 10 \tag{Eq 5}$$

For each pasture replicate, I used the GPS-collar data from two steers grazing over a time period of two grazing seasons to calculate the total number of grazing fixes occurring in each 30 m^2 grid cell. Data were normalized into decile categories using Equation 5. In each pasture, the number of pixels falling into each decile category was heavily skewed, as shown in Figure 9.

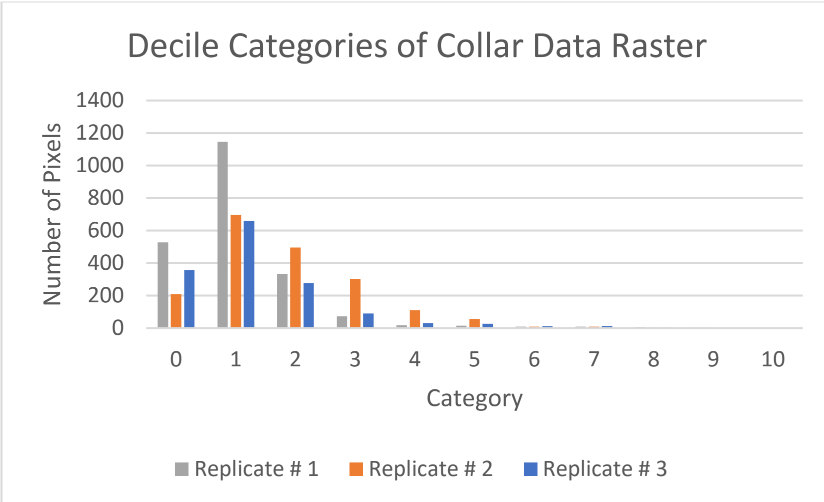

Figure 9: Decile categories of pixels from 30 m^2 raster of GPS collar grazing fixes.

This skew is due to a few pixels receiving a high number of grazing fixes, and the majority of the pasture receiving 0 – 2 grazing fixes. To account for this skew, both the model output data and the collar data was reclassified so that categories 0, 1, and 2 remained the same, and classes 3 through 10 were summed into one class, renamed class 3. The resulting distribution of grazing fixes in each pasture is shown in Figure 10.

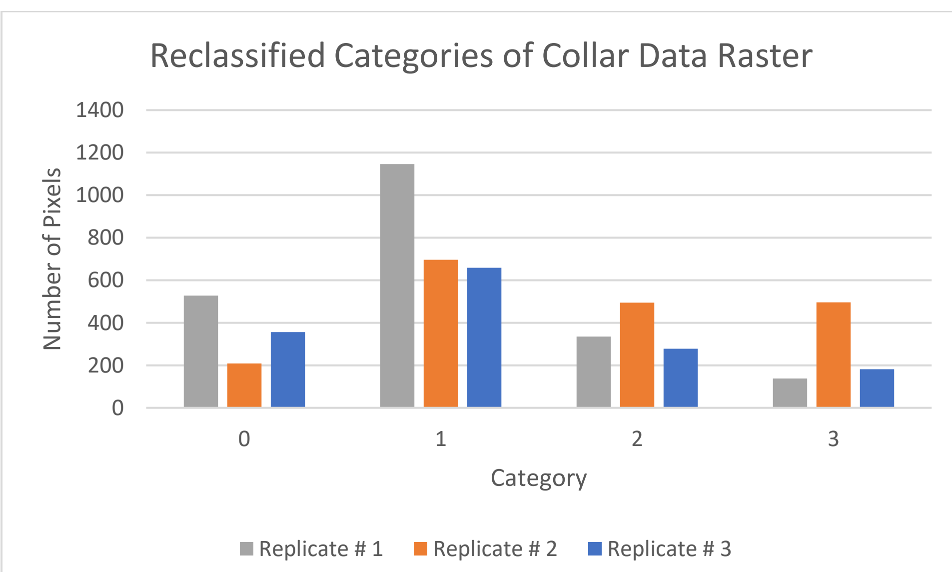

Figure 10: Reclassified categories of pixels from 30 m^2 raster of GPS-collar grazing fixes.

I compared rasters of predicted versus observed distributions of grazing fixes using the Fuzzy Kappa statistic (Kfuzzy). While other spatially-explicit ABMs have been validated using root mean square error (Kang and Aldstadt, 2018; Frescino et al., 2001), this method is subject to misinterpretation (Willmott and Matsuura, 2005). Root mean square error has been used for point-based ABMs, but is less appropriate for a continuous spatial arena, such as the raster format used in this exercise. Kfuzzy is similar to the traditional Kappa statistic (Cohen, 1960), often used for assessing the similarities between observed and predicted raster results (Visser and Nijs, 2006). Traditional Kappa compares two maps to determine their percentage agreement, while accounting for the proportion of agreement explained through pure chance (Visser and Nijs, 2006). A disadvantage of the traditional Kappa statistic is that it is very sensitive to location and category of compared raster cells (illustrated in Figure 11). Most observers of the rasters in Figure 11 would agree that the Predicted 1 Matrix is more similar to the Observed Matrix than the Predicted 2 Matrix is. When comparing these rasters with either the traditional Kappa statistic or the Percent Agreement statistic, both predicted matrices receive the same measure of similarity. However, using Kfuzzy, Predicted 1 is considered more similar to the observed matrix than Predicted 2 is, because Kfuzzy allows for vagueness of location through the use of a neighborhood and distance decay function, so that the observer's tolerance for spatial error is considered. A Kfuzzy value of 0 indicate that the rasters are as similar as chance alone, and a value of 1 indicates the rasters are identical.

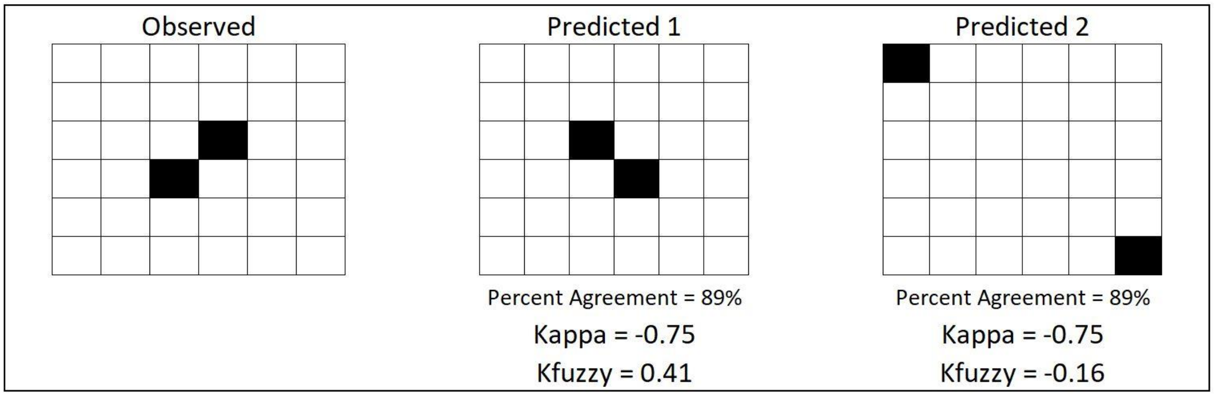

Figure 11: A demonstration of the comparison between Percent Agreement, Kappa, and Kfuzzy in measuring similarity to observed data. By allowing for fuzziness of location, Kfuzzy considers Predicted 1 to be more similar to the Observed Matrix than Predicted 2. Adapted from Figure 6 in Visser and Nijs, 2006.

Validating a spatially explicit model can help to understand the uncertainty embedded in model assumptions, and to explore linkages between model parameters and spatial patterns (Kang and Aldstadt, 2018). kFuzzy provides a single metric of model similarity to observed data that can be used to compare across models and test hypotheses of variables and rules embedded within the models. kFuzzy was restricted to using a crisp matrix of category comparison (Visser and Nijs, 2006).

Using the software Map Comparison Kit (v3.2; Visser and Nijs, 2006), I calculated the Kfuzzy statistic for each pair of predicted versus observed rasters. The software allows for varying the settings for fuzziness of location and fuzziness of category under which Kfuzzy is calculated. I used a linear distance decay function with a radius of four pixels for the fuzziness of location in all analyses. No fuzziness of category was used due to the small number of reclassified categories.

In Hypothesis 10, the amount of time each steer grazes per day is allowed to vary depending on the quantity and quality of forage consumed over the day. Output from simulations of this hypothesis was validated by comparing the daily time-spent-grazing from the model with the range of daily time-spent-grazing observed from GPS collared steers in 2014 and 2016.

3. RESULTS

I first examined a null model, and then examined models parameterized according to hypotheses 1 through 10 sequentially. For each hypothesis, ten simulations were run, and the average Kfuzzy was calculated. In instances where multiple parameter estimates were tested for a given hypothesis, ten simulations were run for each parameter value, and the result that maximized the average Kfuzzy statistic across all replicates was carried onto the next hypothesis (Figure 12).

The null model was the best performing model in replicate 1 and performed better than chance alone (Kfuzzy greater than 0) in replicates 2 and 3 (Figure 12). Hypothesis 1, where steers selected for maximum biomass at the feeding station level, performed worse than the null model in replicates 1 and 2, but was better than the null model, and was the second-best model overall in replicate 3 (Figure 12). Hypothesis 2, in which steers select for maximum biomass at the patch level and graze randomly at the feeding station level, showed an improvement from Hypothesis 1 in replicates 1 and 2, but a sharp decrease in model fit in replicate 3 (Figure 12).

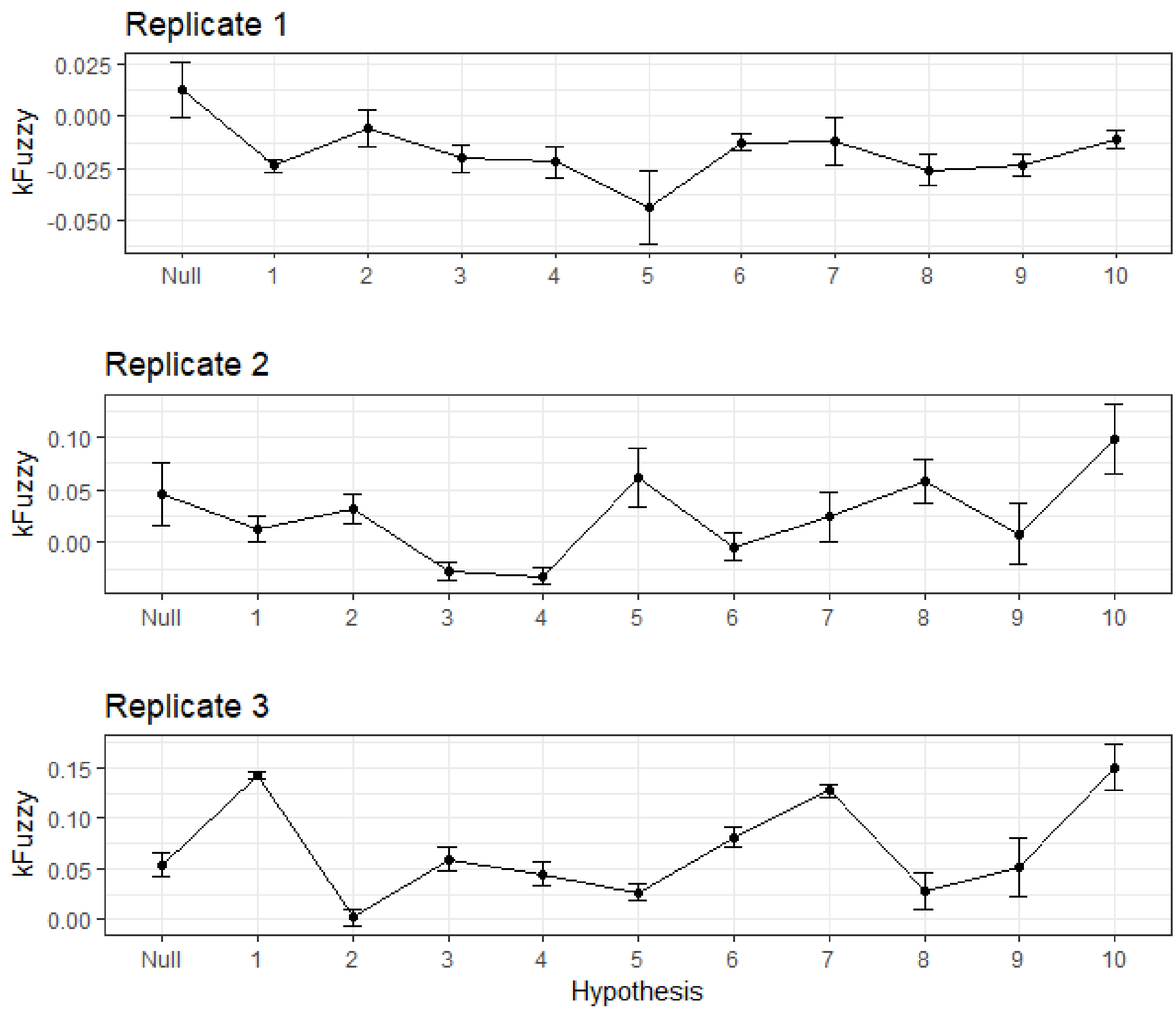

Figure 12: Model validation results from all hypotheses analyzed. The best fitting model results are shown for hypotheses with multiple variable values tested (Hypotheses 4, 6, and 10). Points represent mean kFuzzy values for each hypothesis. Error bars represent 95% confidence intervals from ten model runs.

Hypothesis 3, in which steers selected for maximum biomass at both the feeding station and patch levels, was compared directly with Hypothesis 4, in which steers select at both levels for pixels with an optimal biomass concentration defined by the broken stick models in Figure 8. In all replicates, Hypothesis 3 outperformed all optimal biomass concentration values tested in Hypothesis 4 (Figure 13). Based on these results, steers select for maximum biomass in all subsequent hypotheses involving selection based on biomass (Hypotheses 6 through 10).

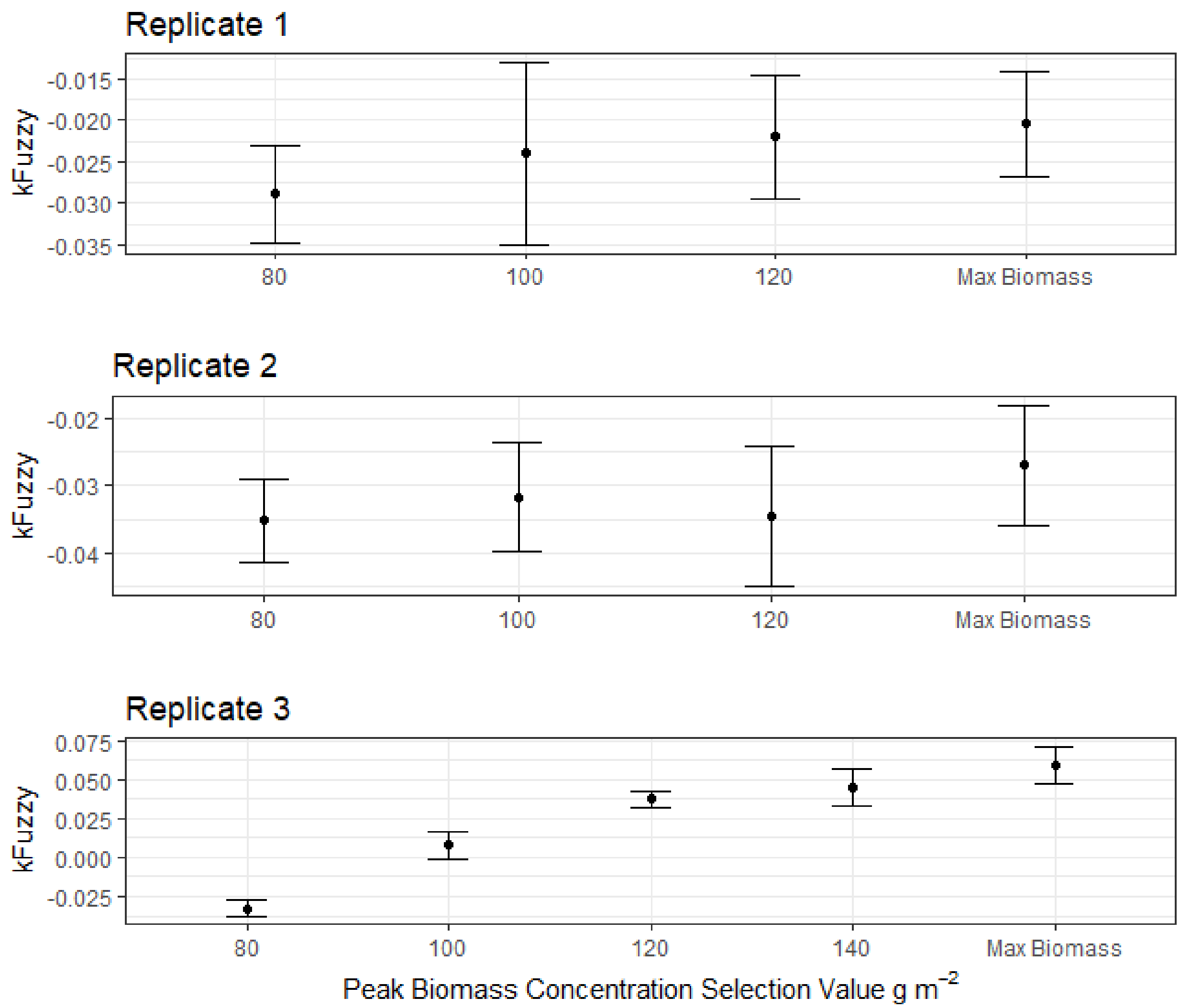

Figure 13: Model validation results from Hypotheses 3 and 4 from each pasture replicate. Points represent mean kFuzzy value for each biomass concentration value simulated steers select for. Error bars represent 95% confidence intervals from ten model runs.

In Hypothesis 5, steers select for pixels with the least amount of slope at the feeding station and patch levels. This resulted in a better model fit than selecting based on biomass (Hypothesis 3) in replicate 2, but a worse model fit in replicates 1 and 3 (Figure 12). An underlying issue with this hypothesis is that steers repeatedly grazed from the same pixels, despite there being little to no biomass remaining in these pixels after being grazed the first few times. This is due to biomass concentrations having no influence on selection and slope remaining constant for each pixel throughout the simulations. While Hypothesis 5 resulted in a better model fit than selecting for biomass in replicate 2, the fine scale grazing distribution was considered unrealistic.

To account for the unrealistic fine-scale selection occurring in Hypothesis 5, Hypothesis 6 uses a combination of slope and biomass to determine pixel selection and uses a slope modifier to limit the influence of slope relative to biomass (Equation 4). Slope modifiers of 0.1, 0.3, and 0.5 were tested. While no slope modifier resulted in significant model improvement over the others, 0.5 was the best slope modifier in replicates 2 and 3, and 0.1 was best in replicate 1 (Figure 14). Based on these results, a slope-modifier of 0.4 was used in Hypotheses 7 through 10. In every replicate, pixel selection based on a combination of slope and biomass (Hypothesis 6) performed better than selection based on biomass alone (Hypothesis 3) (Figure 12).

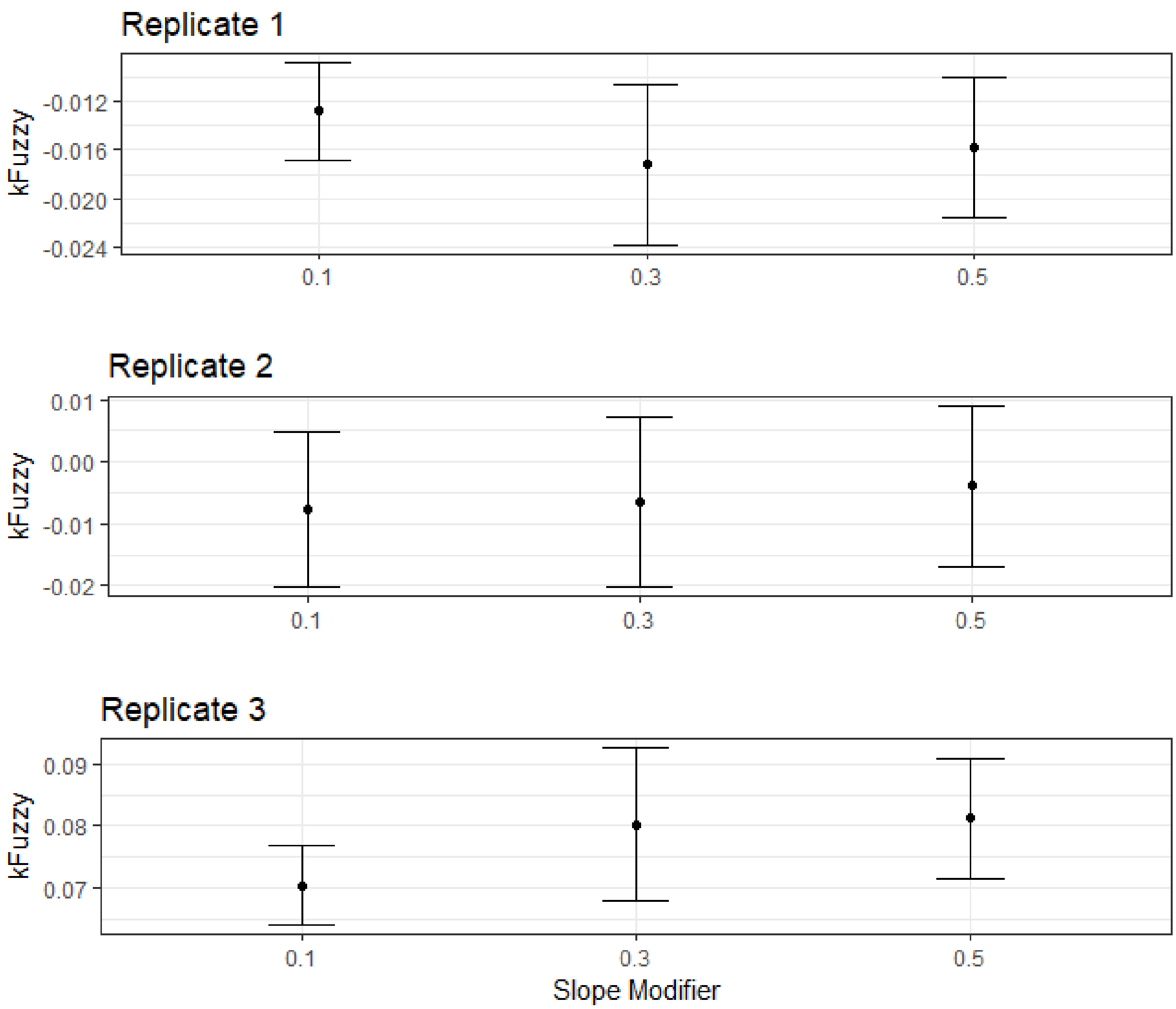

Figure 14: Model validation results from Hypothesis 6 for each pasture replicate. Points represent mean kFuzzy value for each slope modifier value that influences the selection value of pixels (Equation 4). Error bars represent 95% confidence intervals from ten model runs.

In Hypothesis 7, steers select for pixels in the same way as Hypothesis 6, but also use reference memory to return to good-quality patches. In all replicates, Hypothesis 7 improved the model fit over Hypothesis 6. In Hypothesis 8, steers select for pixels in the same way as Hypothesis 6 and use episodic memory to leave bad-quality patches. Hypothesis 8 performed worse than Hypotheses 6 and 7 in replicates 1 and 3, but better in replicate 2 (Figure 12).

Hypothesis 9 uses both reference and episodic memory, as steers use episodic memory to leave bad-quality patches, and reference memory to return to good-quality patches after visiting water or when leaving a bad-quality patch. Hypothesis 9 performed better than episodic memory alone, and worse than reference memory alone in replicates 1 and 3 (Figure 12). In replicate 2, Hypothesis 9 performed worse than either reference memory or episodic memory alone (Figure 12).

In Hypothesis 10, steers select for pixels and use memory in the same way as Hypothesis 9, but grazing time is varied based on forage intake limits instead of being held constant at 10 hours per day. Hypothesis 10 resulted in the best model fit for replicates 2 and 3 and was only outperformed by the null model in replicate 1 (Figure 12).

Scenarios for Hypothesis 10 were assessed to determine if the time spent grazing by simulated steers aligned with the time spent grazing by real steers, as estimated from GPS collar data. Two collared steers in each pasture, in 2014 and 2016, were used in the analysis. For the pasture with lowest total biomass production and low heterogeneity (replicate 1), model simulations aligned with observed grazing times. However, for the two replicates with greater mean forage biomass and greater heterogeneity (replicates 2 and 3), simulated grazing time was approximately two to three hours less than observed grazing time (Figure 15).

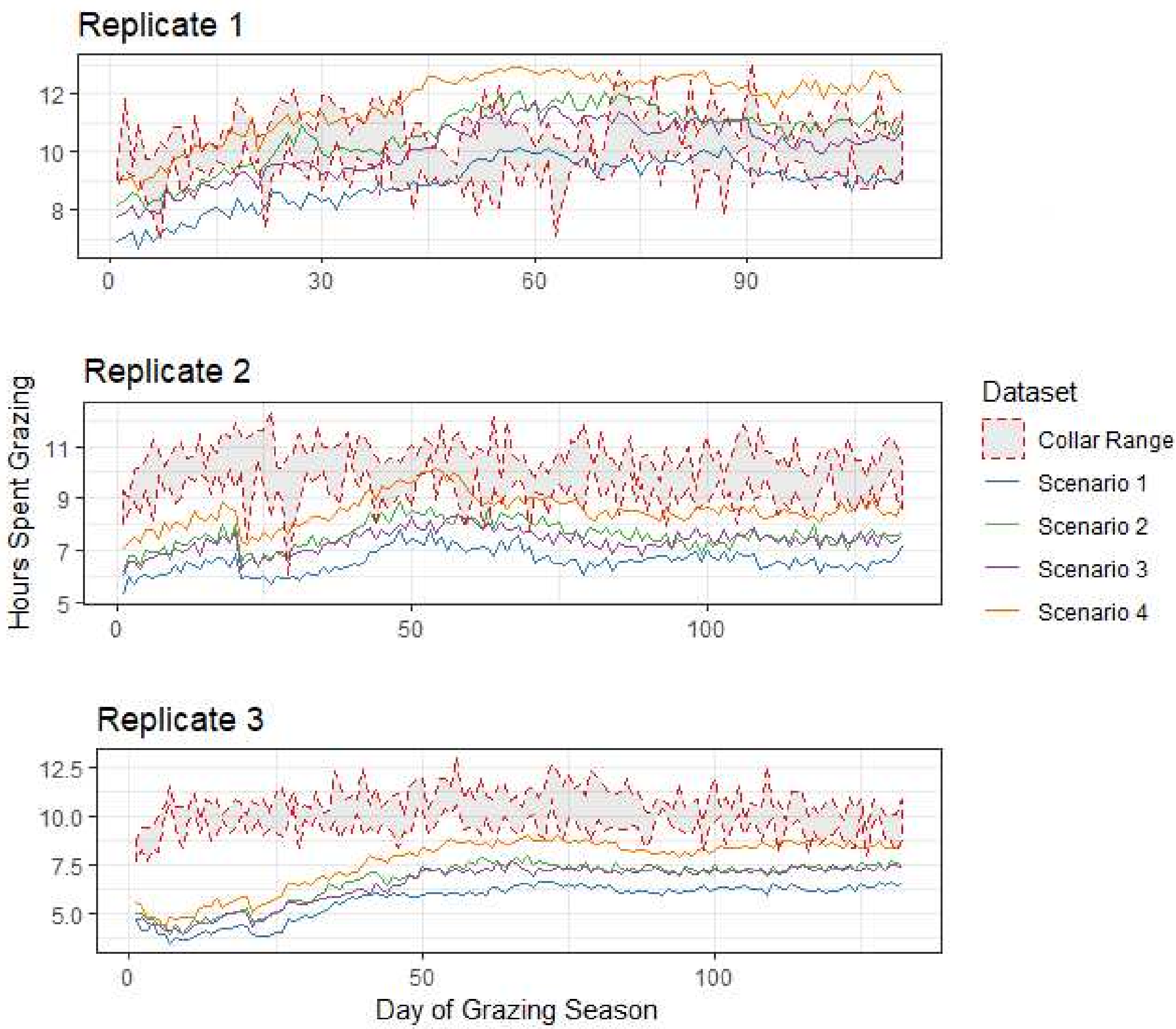

Figure 15: Time spent grazing by GPS-collared steers and simulated steers for three replicate pastures in the shortgrass steppe of eastern Colorado, over the course of the grazing season. GPS-collar data comes from two steers in each replicate pasture in 2014 and in 2016, and grazing time was inferred using the velocity method (Gersie et al., 2019). The range displayed is the least and most time spent grazing by a steer for each day of grazing. For replicate 1, GPS collar data were only available through day 113. Simulated steers' grazing time is based on the scenario tested in Hypothesis 10 (Table 5).

Scenarios in Hypothesis 10, which limited time spent grazing by steers, were compared with Hypothesis 9, which assumed that steers graze for ten hours a day, to compare the amount of forage consumed by simulated steers (Figure 16). Daily forage intake rates range from 1 to 3% of body weight (Holechek and Vavra, 1982; Cordova and Pieper, 1978; National

Resource Council, 1996). Without thresholds limiting the time spent grazing by steers (Hypothesis 10), steers exceeded this range in pasture replicates 2 and 3 but remained within this range in pasture replicate 1 (Figure 15). Enabling rules that limit time spent grazing based on indigestible or digestible organic matter consumed (Hypothesis 10) decreased the amount of forage consumed by steers in replicates 2 and 3 but raised the amount of forage consumed in pasture replicate 1 (Figure 16). These rules also resulted in a similar pattern of time spent grazing by steers (Figure 15). In pasture replicate 1, steers needed to graze more than ten hours a day at some point in the grazing season to achieve intake thresholds in all four scenarios tested under Hypothesis 10 (Table 5; Figure 15). Steers grazed less than 10 hours per day under all Hypothesis 10 scenarios in replicates 2 and 3 (Figure 15). These simulated grazing times were generally within the range of observed grazing times inferred from GPS-collared steers in pasture replicate 1, but below the observed range in replicates 2 and 3.

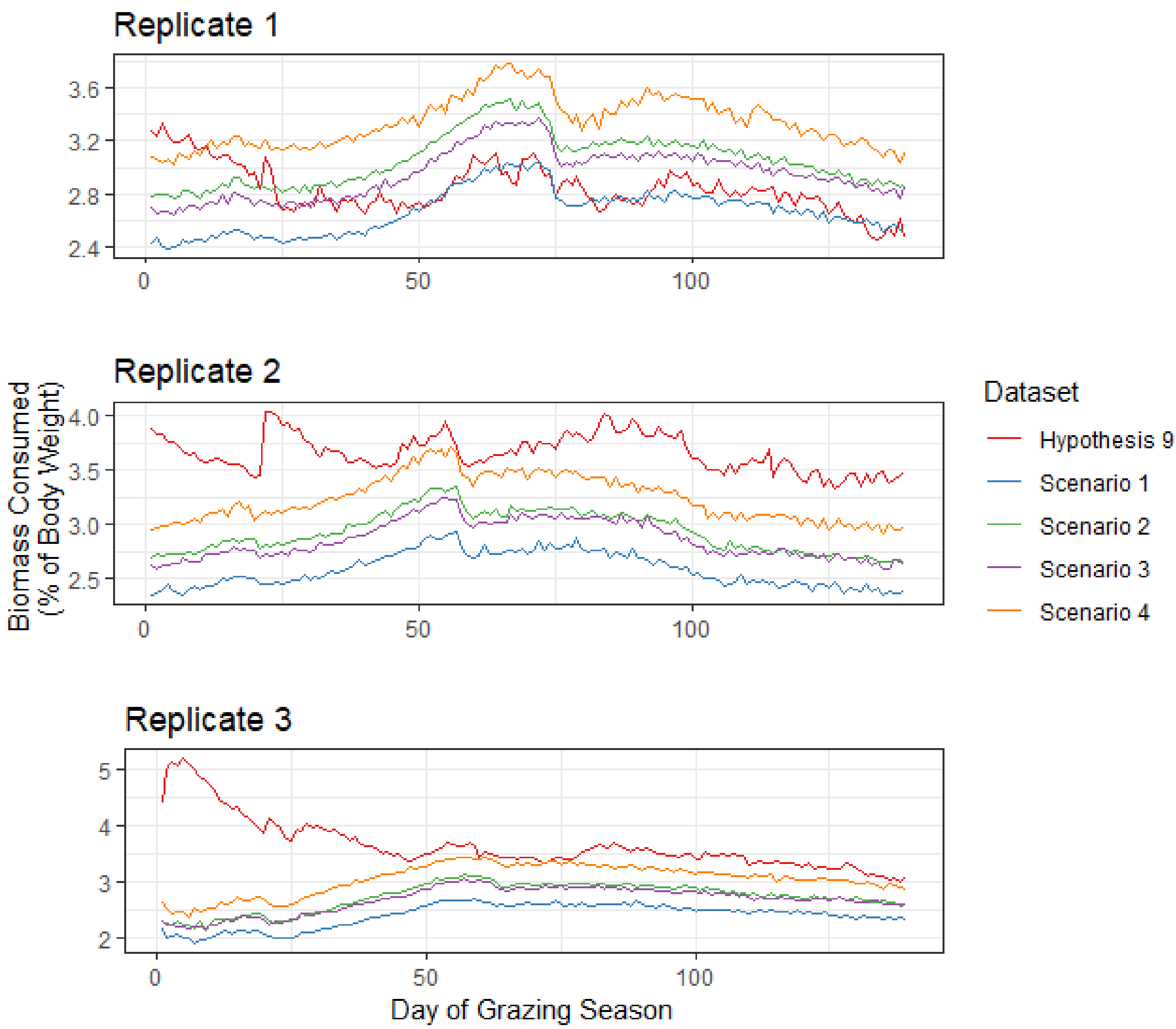

Figure 16: Forage consumed by simulated steers in Hypotheses 9 and 10 for each pasture replicate, displayed as percent of body weight of steers. Hypothesis 9 placed no limit on forage intake and assumed that steers grazed for 10 hours each day. In contrast, under Hypothesis 10 data, daily forage intake of steers could be limited either by maximum daily indigestible or digestible organic matter intake thresholds. Scenarios 1 – 4 vary in the specific parameterization of these thresholds, as described in Table 5.

4. DISCUSSION

Modeling herbivore foraging behavior within an ABM has enabled researchers to reveal the underlying mechanisms guiding foraging decisions by individuals (Dumont and Hill, 2003). Here, I present the first known spatially-explicit ABM of cattle grazing in the short grass steppe ecosystem designed for this purpose. Formulation of a generalized model of cattle grazing in the short grass steppe depends upon a wide range of assumptions regarding the spatial and temporal scales at which cattle make decisions, and these assumptions often influence one another. While applying a generalized model to cattle grazing behavior has proven difficult, this exercise has revealed insights into the foraging behavior of yearling steers and can serve as a framework for the development of a more complex ecosystem model of grazing systems in the short grass steppe.

4.1 Forage Selection

Hypotheses 3 and 4 analyzed the foraging decisions made by steers at the feeding station and patch level based on forage quality and quantity. Wilmshurst et al. (2000) discussed this selection as an interaction between the nutritional quality of the grass and the rate at which the grass can be processed in the ruminant's gut. As grass swards grow biomass, the quality of the grass decreases due to the accumulation of structural carbohydrates, which take longer to digest (Waite, 1963; Illius and Gordon, 1992). The size of the herbivore also plays a role, as ruminants with larger guts can hold more forage. Based on the model presented by Wilmshurst et al. (2000), a 280 kg steer is predicted to select for grass patches with an optimal biomass of 100 g m^{-2}. However, my ABM-based analysis of this optimal forage concentration revealed that steers in the short grass steppe may be selecting for patches with the highest forage concentration instead of selecting for patches that optimized the balance between forage quality and quantity (Figures 12 and 13). However, selecting for pixels with the most biomass often resulted in selecting for pixels with a biomass concentration close to the estimated optimal concentration of 100 g m^{-2}, as the highest initial biomass concentrations in pasture replicates 1 and 2 was approximately 127 g m^{-2} and 124 g m^{-2}, respectively (Table 2). Pasture replicate 3, which had a maximum biomass concentration of approximately 211 g m^{-2}, revealed a stronger selection for maximum biomass concentrations, although this model fit was not significantly stronger than when selecting for biomass concentrations of 140 g m^{-2}.

The short grass steppe ecosystem is a relatively low biomass ecosystem, where primary production generally ranges from 50 to 155 g m^{-2} (Milchunas and Lauenroth, 1989), and supports forage of relatively high quality. The tallgrass prairie, by contrast, contains forage concentrations that range from approximately 300 g m^{-2} to 600 g m^{-2} (Abrams et al., 1986). In the short grass steppe, swards with the highest forage concentrations are not far off from the optimal concentration suggested by Wilmshurst et al. (2000), when viewed within the context of grassland varying to nearly 6-fold more than the optimal patch biomass for yearling steers. As a result, steers in the shortgrass steppe may be driven to select for patches with maximum biomass and forego selection for optimal quality, as patches with maximum biomass concentrations may still be of sufficient quality. A caveat of these results is that biomass concentrations were not measured directly and were instead estimated using NDVI (Gaffney et al., 2018) and production estimates from ecological site descriptions (USDA 2007a,b,c). These estimates are based on NDVI-based predictions of ANPP over the entire grazing season, rather than for a specific day within the growing season. As a result, it remains unclear how well spatial variation in NDVI from imagery collected at a single point in time early in the growing season adequately correlates with total ANPP for the entire year. Unless the assumption used to assign forage concentrations to pixels using NDVI (Equation 1) is validated, selection behaviors regarding specific biomass concentrations cannot be confirmed.

4.2 Slope Selection

Slope plays a role in foraging decisions made by cattle, as cattle prefer relatively level ground and limit their use of hillsides (Ganskopp and Vavra, 1987). Hypothesis 5 tested the influence of slope on grazing distributions in the absence of any influence of forage concentration. For pasture replicates 1 and 3, this hypothesis resulted in the lowest model fit compared to all others (Figure 12). However, for pasture replicate 2, this resulted in relatively high model fit (Figure 12). Simulations of replicates 1 and 3 revealed clearly unrealistic fine-scale grazing distributions, as steers grazed from the pixels with the least slope repeatedly, despite there being little to no biomass there. To account for this, Hypothesis 6 combined selection rules regarding slope and forage concentrations and allowed the influence of slope to be less than the influence of forage concentration according to Equation 4. Hypothesis 6 resulted in a better fit than Hypothesis 5 for pasture replicates 1 and 3, but not replicate 2, indicating that slope has a stronger influence over grazing distributions than forage concentration in replicate 2. However, this may simply be due to the spatial arrangement of slopes within a pasture. Pasture replicate 2 has a large hill on the eastern side of the pasture, away from any water sources (Gersie et al., 2019). Pasture replicates 1 and 3 have sloped features throughout the pasture, and near water sources. This allows steers in replicate 2 to avoid slopes, while steers in replicates 1 and 3 must traverse slopes when visiting water.

Modifying the degree of influence of slope in selection rules in Hypothesis 6 did not result in significant differences (Figure 14). This suggests that in the short grass steppe, slope does not strongly influence grazing distribution. This may be due to the relatively gentle terrain of the region, as the average slope in each pasture was less than 4 degrees (Table 2). Cattle limit their use of slopes in rugged terrain, but this behavior was not exhibited in some habitats with gentle terrain (Ganskopp and Vavra, 1987). Season-specific models in the short grass steppe have shown that cattle grazing distribution is influenced by topography in periods of vegetation senescence (Gersie et al., 2019).

4.3 Memory Ability

Cattle exhibit both episodic and reference memory in experiments (Bailey, 1989; Laca, 1995). Hypotheses 7, 8, and 9 analyzed the influence of memory on grazing distributions. In replicates 1 and 3, reference memory alone performed better than either episodic memory, or both episodic and reference memory together (Figure 12). In replicate 2, episodic memory alone performed better than either reference memory or both reference memory and episodic memory together. This result may have arose in part because of the way memory was coded into the model. Reference memory involved returning to good quality sites, while episodic memory involved leaving bad quality sites. In pasture replicate 2, episodic memory would have guided steers to leave the hill in the pasture, as it was of poor quality due to its slope and low forage biomass. Having steers repeatedly leave this poor site would result in a better fit than the reference memory alternative of returning to good quality sites, as the rest of the pasture was likely of homogenous quality and was grazed relatively evenly in real world observation. In contrast, pasture replicates 1 and 3 did not have any obvious poor-quality patches, so including episodic memory and guiding simulated steers to leave perceived poor-quality patches led them to leave areas that were likely of adequate quality in real world observation, or at least of quality that did not necessitate leaving the patch without grazing. Reference memory alone performed particularly well in pasture replicate 3, which was the most heterogeneous and contained swales with high biomass. As simulated steers selected for high biomass concentrations, having them return to the swales using reference memory was also a behavior likely occurring in real-world steers.

Bailey et al. (1996) noted that reference memory is limited at smaller spatial scales by the large number of sites to be remembered. Having steers remember individual patches, as coded in this model, is likely unrealistic, as there are too many 20 m radius patches within a pasture of this size to be remembered. It is more likely that reference memory is exhibited by cattle at the feeding site level. As pasture replicate 2 was relatively homogenous, there is little difference at a feeding site level, and therefore reference memory did not result in significant model improvement. Pasture replicate 3, however, is more heterogeneous, and consists of different vegetation communities that could be considered unique feeding sites. Using reference memory to delineate the differences between these feeding sites would likely improve cattle grazing efficiency in real life, and therefore encoding this behavior into the ABM resulted in improved model fit for this pasture replicate.

4.4 Overall Results

In pasture replicates 2 and 3, the best performing model was the most complex model, analyzed in Hypothesis 10. This model was not significantly better than the Null Hypothesis model in pasture replicate 2, and not significantly better than a model selecting solely for most biomass (Hypothesis 1) in replicate 3. In pasture replicate 1, the best performing model was the Null Hypothesis model, which was the only model for this pasture with an average kFuzzy value above zero.

These results suggest that in relatively homogenous pastures, at timescales covering entire, or multiple, grazing seasons, steers do not exhibit, through grazing distribution, the selective behaviors described in this model. Instead, steers graze relatively evenly in these pastures, and a random model that accounts for steers' need of water fits this distribution better than a more complex model with selective foraging rules. In pastures with more heterogeneity, such as replicate 3, cattle have more opportunity to exhibit selective behaviors, and the more complex model performed better than a random model, and better than chance alone (Figure 12).

4.5 Forage Consumption and Time Spent Grazing

Cattle in the Western United States usually consume quantities of forage dry matter in the range of 1 to 3% of body weight each day (Cordova and Pieper, 1978), with other estimations around 2.5% (National Resource Council, 1996). These results suggest that in pastures with lower amounts of forage, such as replicate 1 (Table 2), this model is representing the rate of forage consumption by steers reasonably well, but that in pastures with higher biomass levels, such as pasture replicates 2 and 3, steers are consuming forage at a faster short-term rate in the model than is observed in reality. In the model it was assumed that cattle consume 20% of the biomass from each pixel from which they graze. Reducing or scaling this by the amount of available forage could extend the grazing time of simulated steers to more closely resemble observed data.

For models where forage digestibility could limit daily grazing time, parameter estimates that limited indigestible fill to 0.9% of body weight generally resulted in the best model fit in terms of simulated steers consuming approximately 2.5% of their body weight in forage (Figure 16), and in terms of grazing distribution (Figure 12). However, simulated steers grazed less time per day than observed steers under this scenario (Figure 15), and in every replicate pasture steers stopped grazing because their indigestible organic matter threshold was met. This suggests that steers may be grazing selectively at the bite level, which was not included in this model, as it was assumed that steers consumed 20% of each of the indigestible and digestible organic matter present in each pixel. Future efforts may require adjusting these percentages to simulate selective behavior at the bite level, as cattle may consume a larger percentage of digestible organic matter and smaller percentage of indigestible organic matter from each feeding station they visit by selecting at the bite level (Bailey et al., 1996). This would increase the time simulated steers grazed each day, as they could consume more forage without reaching the estimated 0.9% of body weight indigestible organic matter intake limit.

4.6 Model Limitations

A limitation of this model is that it lacks the inter-annual spatial variability of forage quality and quantity throughout the grazing season. Using NDVI measured at a 1 m^2 spatial scale near the beginning of the grazing season enabled me to quantify fine-scale spatial variation in forage quantity, but sacrificed the temporal patterns of forage quantity and quality that likely ultimately guide livestock grazing distributions. While the NDVI data used here was of fine spatial scale (1 m^2), it is only a snapshot of the temporal spatial patterns of forage quality that changes throughout the grazing season. At the time this data was collected, vegetation is in a phase of rapid growth, and nearly all the pasture is of adequate forage quality and quantity. Carrying this pattern of forage distribution throughout the model may be an inaccurate representation of forage growth and senescence patterns observed throughout the grazing season. My model assumed that pixels with high relative NDVI values grow more vegetation throughout the grazing season (Equation 1). However, this same method subtracted more vegetation from relatively high NDVI pixels in times of forage senescence (Figure 6), resulting in the same relative distribution of forage in the beginning of the grazing season be carried out throughout the simulation, with the only variation attributed to forage removal by simulated steers. These high-NDVI pixels often represent swales and lowlands within the pasture, which not only have higher amounts of biomass, but also retain biomass longer throughout periods of receding vegetation, due to their higher levels of nutrients and soil moisture (Milchunas and Lauenroth, 1989). Gersie et al. (2019) found that grazing distributions at CPER were relatively even in the first half of the grazing season under vegetation growth conditions, but that the distributions became more concentrated in swales and flat plains, and correspondingly reduced in uplands, during the second half of the grazing season when vegetation was senescing. Simulated steers, programmed to forage selectively, may be exhibiting these behaviors in response to a snapshot of vegetation uniformity throughout the pastures, instead of responding to more pronounced patterns of differences in vegetation quantity and quality that are present later in the grazing season. A solution to this problem may come from incorporating multiple sets of NDVI data throughout the simulation, in the form of Landsat-MODIS fusion rasters (Walker et al., 2012). These data sets use temporally fine-scaled, but spatially coarse scaled, NDVI data from MODIS (Maccherone and Frazier, 2020), in combination with temporally coarse-scaled, but spatially fine-scaled data from Landsat (Jenner and Dunbar, 2019) to interpolate NDVI data at a daily time scale at 30 m resolution. Initializing the model with NDVI data taken from NEON, and then updating the vegetation patterns with MODIS-Landsat data at fixed intervals throughout the simulation may obtain a more realistic pattern of vegetation distribution throughout the simulation. This approach could better account for the need to construct models of livestock foraging patterns that adapt to seasonal differences (Senft et al., 1983; 1985; Gersie et al., 2019).

Another related issue with this ABM is not within the model itself, but in its validation. Over the course of an entire grazing season, grazing distributions observed at CPER are relatively even. The grazing system guiding the traditional management portion of the CARM study was developed under a paradigm of rangeland management that promotes homogeneity of grazing (Fuhlendorf and Engle, 2001). This system, with relatively small pastures and evenly spaced water sources, was devised to increase livestock production by reducing the inherent landscape heterogeneity caused by topo-edaphic features and herbivore behavior (Fuhlendorf and Engle, 2001). Testing hypotheses regarding steer foraging behavior may not be ideal within a system that is inherently designed to suppress selective foraging by livestock. The heterogeneity of grazing distributions evident at shorter time scales may be masked by the homogenous pattern of grazing distributions demonstrated at larger temporal scales. To better assess the ABM designed here, it may be appropriate to validate the model at shorter timeframes, particularly during periods when upland vegetation is beginning to senesce, instead of analyzing the model relative to grazing distribution averaged over the entire grazing season or multiple grazing seasons.

In this modeling effort, the goal was to produce a general model that could be applied broadly within semi-arid rangelands. However, due to inconsistencies of model fit between pasture replicates (Figure 12), such a model may not be possible. Cattle in this system are only able to make grazing decisions on the range of environmental variables contained within their pastures, and not over the wider range of variables present across the ecosystem. For example, in pasture replicate 3, having cattle select for an optimal biomass concentration seemed appropriate because there is a wide range of biomass concentrations present in pixels across the simulated pasture (Table 2). Applying a similar broken stick model (Figure 8) to pasture replicates 1 and 2 is less appropriate, as nearly all the pixels in those pastures are close to the optimal biomass concentration suggested by Wilmhurst et al. (2000). Additionally, having steers make grazing decisions based on slope may be appropriate within pastures containing significant slopes (replicate 2), but less appropriate in pastures containing only small variations of slope. Having steers use reference memory to navigate pastures containing distinct feeding sites may be appropriate, but less so in homogenous pastures containing one large feeding site. Striking a balance between inter- and intra-pasture variations across environmental variables should be a focus of future modeling efforts.

4.7 GPS Collar Limitations

While the GPS collars deployed at CPER achieve an accurate measure of both time and steer location, there are gaps in their ability to quantify steer behavior. While Augustine and Derner (2014) were able to develop an algorithm that inferred cattle behavior from GPS collars equipped with activity sensors, many of these activity sensors malfunctioned during periods studied here. This resulted in the need to use steer velocity to infer behavior. This method is more subject to error, as some periods of rest or travel may be incorrectly classified as grazing, or vice-versa. This may have caused issues in validating the model spatially, as a disproportional amount of traveling fixes near water may have been classified as grazing. The method used may have caused issues in validating the model temporally as well, with grazing time by collared steers being inaccurate. Another shortcoming is that only two steers in each pasture wore collars, so analyses of herd-level social behaviors were not possible. Observations of steers under traditional management at CPER indicate that all steers in the pasture form and maintain one cohesive herd much of the time, but this may not always be true. This would become more of an issue in simulations of larger pastures with more cattle, as herd dynamics likely become more complex as the number of cattle in a pasture increases.

4.8 Future Modeling Efforts

A future use of this model will be analyzing model performance under the adaptive management scenario within the ongoing CARM experiment at CPER. In this style of management, a group of stakeholders manage a herd of ca. 240 steers in an adaptive manner that addresses goals to reach desired outcomes for vegetation, wildlife, and livestock. During 2014 - 2019, the stakeholder group chose to use one large herd of yearling steers to rotate among 8 pastures each year, with 2 of the 10 pastures reserved each year for rest (i.e., no grazing), or as emergency forage in severe drought. Preliminary analyses of GPS-collar data at CPER has suggested that cattle in the adaptive treatment exhibit grazing behaviors that differ from steers in traditional management. Measures of cattle weight gain have shown that steers in the adaptive herd are also gaining less weight on average. Hypotheses as for why rotational grazing is not beneficial include: a) animals in large herds are expending more energy to locate sufficient forage than those in smaller herds, b) differences in diet quality at different stocking densities are sufficient to explain these results, independent of energy expenditure, c) movement rates among animals in the two groups are sufficiently different to lead to changes in weight gain, and d) grazing facilitation (increased production of re-growing plants in grazed patches) is present in continuous grazed pastures, but not in rotational pastures, leading to a sufficient difference in diet quality. Applying this ABM to the adaptive management treatment and using it to track steer movement rates, intake rates, grazing times, and grazing distributions could help to address these hypotheses.

While cattle behavior and distribution are the focus of this project, many rangeland managers are interested in how these phenomena impact ecosystem processes like vegetation response to grazing. An existing ecosystem model, APEX (Agricultural Policy/Environmental eXtender; http://epicapex.tamu.edu/apex/) has been developed by the Texas A&M AgriLife Research Program, the Blackland Research and Extension Center, and partners (e.g., Gassman et al., 2010; Zilverberg et al., 2017). This model is spatially explicit and has a daily time-step. APEX is used by many Natural Resource Conservation Service professionals to predict outcomes of land management. APEX uses inputs regarding hydrology, soil type, past climate, weather, land use, and conservation practices to predict future ecosystem conditions. The model represents landscape dynamics, including climate variability, plant growth and competition, and livestock grazing. APEX uses a more general representation of livestock grazing, where whole pastures are considered to have equal grazing pressure.

An overarching goal of this project is to link an agent-based model of cattle grazing with an ecosystem process model such as APEX to more accurately represent the spatial patterns of grazing distribution in an ecosystem process model. The linking of these models is more complex than the scope of this project and may use a different platform than NetLogo. However, this agent-based model developed in NetLogo can serve as a testbed to parameterize a model of cattle grazing behavior that can be linked with an ecosystem process model like APEX. The resulting linked model can then serve as a tool to predict the outcomes of management strategies and environmental variability on ecosystem processes. Linking this ABM to a model like APEX would also address some of the limitations of the model discussed earlier. By having a more accurate representation of vegetation growth patterns, simulated steers can make foraging decisions on a more realistic spatial and temporal distribution of environmental conditions.

5. CONCLUSION

In developing an ABM of cattle foraging behavior, I found that selective foraging decisions encoded in the model were more appropriate in heterogeneous pastures than homogenous pastures. In homogenous pastures, steers graze relatively evenly over the course of an entire grazing season, and do not have the opportunity for selective behavior. Heterogeneous pastures allow for more selection to occur, and the ABM presented here performed best in the most heterogeneous pasture.

For each model tested, model performance varied for each simulated pasture. As each pasture has its own suite of environmental conditions, it was difficult to obtain consistent parameter values to guide selective behaviors. For example, in a pasture with a large hill, having cattle select for pixels with no slope resulted in a better model fit than when these same rules were applied in a pasture that was relatively flat.

Outperforming a null model of random grazing, with respect to trips to water and pasture boundaries, required the most complex model. This means that a combination of selective behaviors results in a better model fit than when these behavioral rules are applied in isolation. Enabling memory rules in the model improved the model fit, although reference memory was found to be more appropriate than episodic memory. Applying rules that prevented simulated steers from grazing after meeting digestive restraints resulted in a more accurate model of cattle grazing distribution, and better reflected forage consumption and time spent grazing by actual steers.

There is seasonal variation in cattle grazing distribution patterns that result from changes in forage quality and quantity over time. Using NDVI data captured at the beginning of the grazing season was not a sufficient representation of this temporal pattern. Future modeling efforts may need to incorporate fine scale NDVI data to better simulate changes in vegetation over time. This may be achieved by using coarser scaled Landsat-MODIS fusion NDVI data, or by linking this ABM with a more complex ecosystem model, such as APEX.

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