MANAGEMENT OF WILDLIFE DISEASE IN A SPATIALLY EXPLICIT ECOSYSTEM: AN APPLICATION TO ELK IN WESTERN WYOMING, U.S.A.

MATTHEW MALONEY

University of Wyoming

Abstract. The imminent introduction of chronic wasting disease (CWD) to elk populations in the Greater Yellowstone Ecosystem (GYE) will alter the underlying economics of elk feeding and harvesting policies. A specific concern is that concentrating elk at feedgrounds may exacerbate the spread of CWD, making the practice of feeding elk more costly to the region. We develop a spatio-temporal bioeconomic model to determine optimal management policies in this new disease context. We use elk telemetry and landscape data to predict migratory behavior and population densities with and without supplementary feeding, eliminating the need to make assumptions about how feeding increases elk population densities and influences elk-cattle interactions, as has been necessary in non-spatial models. We use a 4,800 km^2 area around Pinedale, WY containing four existing feedgrounds as a case study, and use simulations to generate welfare estimates under a variety of management strategies. Our results suggest that wildlife managers should discontinue feeding upon the introduction of CWD to maximize the present value of economic benefits generated by the local elk population, and continuing feeding could result in welfare losses of up to $23.2 million for the case study region. We also find that the option to resume feeding if CWD prevalence is significantly lowered has value and should likely be retained.

1. Introduction

South of Yellowstone National Park, there are twenty-three sites where elk herds are provided supplementary feeding during the winter and spring months. Supplementary feeding of elk in the Greater Yellowstone Ecosystem (GYE) has been practiced since the early twentieth century, but in recent decades the practice has been challenged by wildlife biologists, ecologists, and epidemiologists. Proponents argue that the feedgrounds, which allow the GYE to support larger elk herds

Several collaborators provided helpful feedback and assistance with this work. Jerod Merkle, a post-doctoral researcher at the Wyoming Cooperative Fish and Wildlife Research Unit, played an essential role in the data collection and regression analysis necessary to calibrate elk movement. Thanks to Dave Aadland, Brant Schumaker, and Dannele Peck for providing helpful feedback throughout the research process. Thank you to Brandon Scurlock with the Wyoming Game and Fish Department and Paul Cross with the U.S. Geological Survey for providing elk telemetry data.

Draft last updated January 16, 2018.

than could be sustained by natural forage alone, provide significant economic benefits. Larger elk herds allow for a greater number of hunting permits to be issued and provide better opportunities for wildlife enjoyment by tourists. Additionally, the feedgrounds are positioned to truncate the natural migratory routes of elk so as to limit the time elk spend on private, lower elevation ranch land during the winter months. The presence of elk on private ranch land imposes two types of costs on ranchers. First, elk consume haystacks and forage intended for cattle. Second, elk can spread brucellosis to cattle. Brucellosis is nonfatal to elk, but affects their reproduction and the disease can be spread to cattle. If a cow becomes infected with brucellosis, the U.S. Department of Agriculture Animal and Plant Health Inspection Service (USDA-APHIS) requires that the entire cattle herd be quarantined or culled, at a significant cost to either the rancher, the U.S. Department of Agriculture (USDA), or both (Roberts et al., 2012). Feedground opponents argue that the long-term costs of feedgrounds exceed the benefits, in part because the practice has been shown to increase the prevalence of costly diseases by concentrating elk populations at feed sites (Scurlock and Edwards, 2010; Smith, 2012; Schumaker et al., 2010). In recent years this concern has increased as a new disease, chronic wasting disease (CWD), has spread across Wyoming and will soon be introduced into the GYE. The prevalence of CWD is higher in wild deer populations than in wild elk populations, and CWD is likely to be introduced to elk in the GYE through contact with infected deer. Wyoming's economy is highly dependent on industries that are impacted by elk populations, including hunting, tourism, and ranching, and a CWD outbreak could be extremely costly.

Chronic Wasting Disease (CWD) is an infectious, neurodegenenerative disease that affects deer, elk, moose, and reindeer. After an incubation period of 12 to 34 months, the disease results in weight loss and behavioral changes for a few weeks or months before the infected animal dies. The disease is always terminal (Smith, 2013). It is among a group of diseases known as transmissible spongiform encephalopathy (TSE) diseases, which are caused by infectious agents known as prions (Williams et al., 2002). Unlike other TSE diseases such as mad cow disease, CWD is known to be endemic in free-ranging populations (Williams, 2005; Smith, 2013). In addition to animal-to-animal contact, the disease is also believed to be spread through animals coming into contact with CWD prions in the environment (Williams et al., 2002). Cases of CWD have not yet been found in the elk herds of the GYE that receive supplementary feeding, but cases have been recently recorded in deer within 50 miles of several of the elk feedgrounds (Smith, 2013). In elk populations in southeastern Wyoming, CWD is already endemic and affects 1 to 10 percent of the population. However, in captive populations, CWD prevalence can reach greater than 50 percent, and wildlife biologists argue that the high population densities at feedgrounds may result in similarly high rates of infection (Smith, 2012). Containing such an outbreak, and managing the resulting environmental contamination by prions, would be very costly and would likely have a lasting impact on the local economy.

Research on the economic impacts of CWD in cervid populations has been, like knowledge of the disease itself, limited. Unlike other TSEs, there is no evidence that CWD can spread to humans, so threat to human health is considered to be minimal. However, the science is inconclusive regarding the possibility of transmission to humans (Belay et al., 2004), and the public remains wary of consuming meat of infected animals. Bishop (2004) found that the reduction in hunting activity and expenditures in Wisconsin following the discovery of CWD in deer populations in 2002 resulted in economic losses of between \$53 and \$79 million in 2002 and between \$45 and \$72 million in 2003. Using survey data, Zimmer et al. (2012) found that hunters would be willing to spend \$20.35 per trip to maintain CWD at current levels in Alberta and prevent further spread of the disease. In addition to hunting impacts, the introduction of CWD into the GYE could have a substantial impact on tourism. Around four million tourists visit Yellowstone National Park every year and over 10 million visit the state of Wyoming, many of whom come to view elk and other wildlife.

Bioeconomic approaches to modeling wildlife disease management have emerged in the literature over the last fifteen years, and differ from approaches found in the disease ecology literature. Fenichel et al. (2010) contrast the "conventional" approaches with bioeconomic approaches, emphasizing that bioeconomic models factor in feedback between the human and ecological systems whereas the disease ecology literature focuses on metrics exogenous to human management decisions (also see Horan et al. (2011) for a discussion of these two approaches). Prior papers using bioeconomic approaches have often found that eradication is not optimal, and much of the work has been limited to numerical rather than analytical results due to the complexity of the models. Horan et al. (2005) develop a dynamic optimization model for managing bovine tuberculosis in the Michigan deer population. The authors consider two management controls: non-selective harvesting (i.e. wildlife managers or hunters cannot tell the difference between sick and healthy deer) and supplementary feeding. The authors find that the disease is optimally maintained at low levels with intermittent feeding, but the transmission of the disease is modeled as being frequency-dependent. Fenichel and Horan (2007) improve this model by considering the same disease and controls, but with density-dependent transmission. When analyzing the model with exogenous feeding, as is the case for the model used in this paper, the authors find that eradication is not optimal for their case study, but eradication could be optimal under other parameter values. Similar to CWD, bovine tuberculosis in deer populations can spread to livestock causing economic losses. Horan et al. (2007) introduce a model in which ranchers can make investments in protecting their cattle from bovine tuberculosis, and find that the optimal prevalence levels in the host population will be higher because damages to livestock can be reduced through other means.

The model developed in this paper builds on prior bioeconomic modeling of wildlife disease management by introducing spatially explicit elk movement. Much of the uncertainty about elk management in the GYE is related to how elk move and congregate in space. The extent to which feedgrounds increase population densities during the winter and spring months, and the corresponding increase in disease transmission, depends on how elk move throughout the year with and without feedgrounds. Previous non-spatial models, such as those used in Horan and Wolf (2005) and Fenichel and Horan (2007), must make strong assumptions about the functional relationship between feeding and disease transmission. Another source of uncertainty related to how elk move in space is the extent to which feedgrounds reduce elk-cattle contacts by altering elk migration patterns. The extent to which feeding reduces such contacts is unknown, and non-spatial models must include an assumption about the relationship between feeding and elk-cattle contacts. The uncertainty surrounding how feeding influences both elk-elk and elk-cattle contacts can be resolved by using a spatially explicit model of elk movement that has a sufficiently high spatial resolution. By modeling the movement patterns of elk with and without feeding, the difference in elk population densities between feeding and no feeding scenarios can be better estimated. The model can also predict how feeding changes the number of elk that travel to lower elevation areas and come into contact with cattle. The ability to model the relationship between feeding and the location of elk is the major advantage of using a spatially explicit model; it both reduces the number of unknown parameter values and eliminates the need for assuming a simple functional form that governs the relationship between feeding and disease transmission.

Previous use of spatially explicit bioeconomic models of wildlife disease management has been limited. Horan et al. (2005) develop a model based on Sanchirico and Wilen (1999) that considers the use of a spatially explicit harvesting to manage wildlife disease. In their continuous-time dynamic model, the movement of animals between sections of the landscape is dependent on location-specific carrying capacities and a set of unchanging parameters that govern movement. Using this framework, the authors considered location-specific harvesting rates as a control to manage a disease. They derive the necessary conditions for a simple system which divides a stylized landscape into only two areas (also known as patches or cells). The migratory behavior of elk in the GYE, and how this behavior is influenced by feeding, is too complex to follow the modeling approach used in

Horan et al. (2005). Elk migration is cyclical, so the likelihood of an elk moving from one particular location to another specific location varies based on the time of year. A possible method of incorporating this would be to make the parameters that govern elk movement time-dependent, cyclical functions, as was done with fishery growth rates by Carson et al. (2008). In this paper, the method used is to model the problem in discrete time, with month-specific parameter values that govern elk movement. The month-specific parameter values are derived by fitting a resource selection function (RSF) to data on elk locations in the GYE at various times of year and landscape characteristics (e.g. elevation, abundance of vegetation, distance-to-feedground, etc.) . Simulations are used to compare welfare outcomes under alternative management strategies.

2. The Ecological Model

The total elk population, N, consists of two subpopulations: CWD-susceptible individuals, S, and CWD-infected individuals, I. There is no recovered/resistant population because CWD is chronic, and is ultimately fatal for all infected individuals. Each patch of land, or cell, will have populations of susceptible elk (no CWD), CWD-infected elk, and livestock. To capture the seasonal migratory behavior of elk and how this behavior is affected by feeding, monthly time steps are used. Within each time period, an order of events is established. The first stage within each month is elk population growth. The second stage is elk hunting. The third stage is elk mortality from CWD. The fourth stage is the disease infection dynamics, which includes CWD infection in the elk population as well as the transmission of brucellosis to livestock. The fifth stage is animal movement. The time periods are indexed by t and cells are indexed by i. There are a total of n cells. The value of state variables at the end of each stage will be denoted with a superscript in parentheses of that stage. The initial population levels prior to population dynamics, infection, contamination, and movement will be labeled with a (0) superscript.

2.1. Stage 1: Elk Growth.

Elk reproduction occurs at the beginning of June; in all other months the population does not change in stage 1. Reproduction only adds to the susceptible population because mother-calf transmission (vertical transmission) plays only a minor role in the spread of CWD (Miller and Williams, 2003), so it is assumed that all elk calves are born as susceptible. The elk population exhibits logistic growth, within an intrinsic growth rate denoted r and carrying capacity K. Unlike in the spatial model introduced by Horan et al. (2005), carrying capacity is regional rather than cell specific. This makes sense for this model because elk move throughout the GYE during the year but reproduce only once a year. Their fertility and survival is based on the characteristics of the entire region within which they move throughout the year, rather than the characteristics of any individual cell. Carrying capacity is modified by the quantity of supplemental feeding, F. The relationship between carrying capacity and feeding is consistent with Walters (2001) and is of the same form used in previous bioeconomic models of wildlife disease (Fenichel and Horan, 2007). The growth of the susceptible and infected elk populations in stage 1 is given by

$$S_{i,t}^{(1)} = S_{i,t}^{(0)} + N_{i,t}^{(0)} r \left(1 - \frac{N_{i,t}^{(0)}}{K(F_t)}\right) \tag{1}$$

$$I_{i,t}^{(1)} = I_{i,t}^{(0)} \tag{2}$$

$$\text{s.t. } N_{i,t}^{(0)} = S_{i,t}^{(0)} + I_{i,t}^{(0)} \tag{3}$$

$$K(F_t) = K_0/(1 - \tau F_t) \tag{4}$$

$$\tau \leq \frac{1}{F^{max}}, \tag{5}$$

where K_0 is the natural carrying capacity of the region, τ is a parameter that measures the effectiveness of feeding in increasing carrying capacity, and r is the intrinsic elk growth rate. The intrinsic growth rate used here is the maximum estimated by Eberhardt et al. (1996) and close to the maximum estimated by Sargeant and Oehler (2007) for non-hunted populations. This is an appropriate choice because hunting mortality is included separately. The long-term intrinsic growth rate in isolated populations may be lower, but nearly all elk in the GYE are hunted by people or killed by wolves prior to dying of natural causes.

2.2. **Stage 2: Elk Hunting.** In stage 2, elk are hunted. In each period, the regional planner determines the total number of elk to be harvested, h_t. For simplicity, the total quantity of elk are harvested in October; in all other months the elk population is unchanged by hunting. Elk hunting is distributed proportionally across the infected and susceptible populations, because selective harvest is not possible – CWD-positive elk can not be distinguished from healthy elk until the very late stages of the disease. Additionally, the number of elk hunted in each cell is proportional to the cell population. In October, the changes in the susceptible and infected elk populations are

$$S_{i,t}^{(2)} = S_{i,t}^{(1)} - \frac{S_{i,t}^{(1)}}{N_{i,t}^{(1)}} h_t \tag{6}$$

$$I_{i,t}^{(2)} = I_{i,t}^{(1)} - \frac{I_{i,t}^{(1)}}{N_{i,t}^{(1)}} h_t. \tag{7}$$

2.3. **Stage 3: Mortality from CWD.** In stage 3, the elk population is reduced from CWD mortality, where μ is the monthly CWD mortality rate. The changes in the infected and susceptible populations in stage 3 are

$$S_{i,t}^{(3)} = S_{i,t}^{(2)} \tag{8}$$

$$I_{i,t}^{(3)} = I_{i,t}^{(2)}(1-\mu). \tag{9}$$

2.4. **Stage 4: Disease Transmission.** In the epidemiology literature, it is typical to model disease transmission as either frequency-dependent or density-dependent. For density-dependent transmission, the probability that a susceptible individual comes into contact with an infected individual increases as population density increases. Studies have shown that CWD outbreaks in captive elk populations result in much higher prevalence rates than in wild populations, suggesting that in unnaturally high concentrations of elk, CWD transmission must depend on population densities (Williams et al., 2014; Argue et al., 2007; Smith, 2012). This could be due to high accumulation of infectious prions in densely populated areas (Williams et al., 2014). In this paper, we choose to model CWD transmission as density-dependent and consider the effects of concentrating elk populations at feedgrounds.

Following a standard approach in the epidemiology literature for density-dependent disease transmission, we model the number of new elk CWD infections in cell i at time t as $\beta S_{i,t} I_{i,t}$ (Begon et al., 2002; McCallum et al., 2001). This is the CWD transmission function, and the simple functional form depends on the assumption that contacts increase linearly with population density. β is the infection coefficient, which is the product of two constants: the probability of infection conditional on contact, and a coefficient that measures how contacts increase linearly with population density (Begon et al., 2002). In a spatial model, β must scale inversely with the area in which S and I are being counted. For example, a spatial model with 5 km^2 cells will require a β that is 5 times larger than a model with 25 km^2 to result in the same infection rate. This adjustment is not necessary if S and I are interpreted as population densities rather than population counts, as is common in much of the epidemiology literature (Begon et al., 2002).

In our model, the infection rate is unique to each cell and influenced by the number of susceptible and infected individuals in each cell. Unlike non-spatial models in the literature, the transmission function does not need to be modified based on feeding decisions. In non-spatial models that include feeding, the transmission function is often modified by multiplying a baseline transmission function by an expression that is increasing in feeding (Horan and Wolf, 2005; Fenichel and Horan, 2007).

An advantage of our modeling approach is that an additional assumption about the functional relationship between feeding and disease transmission does not need to be made. As population densities increase in a cell, the product SI in the transmission function increases and the infection rate increases. Using this relationship, the expected changes in susceptible and infected populations in stage 4 due to susceptible individuals becoming infected with CWD are

$$S_{i,t}^{(4)} = S_{i,t}^{(3)} - \beta S_{i,t}^{(3)} I_{i,t}^{(3)} \tag{10}$$

$$I_{i,t}^{(4)} = I_{i,t}^{(3)} + \beta S_{i,t}^{(3)} I_{i,t}^{(3)}. \tag{11}$$

Also occurring in stage 4 is brucellosis transmission from elk to cattle. Brucellosis is a disease that, unlike CWD, is already endemic in elk populations in the GYE and spreads from elk to cattle. Transmission of brucellosis from elk to cattle is also modeled as density dependent, and the number of new cattle infections in cell i at time t is given by the transmission function $\beta_B \theta_{B,t} N_{i,t} L_{i,t}$. N is the total number of elk in a specific cell and L is the number of cattle (livestock) in a specific cell. $\theta_{B,t}$ is the brucellosis prevalence in the elk population. Although the disease dynamics of brucellosis in the elk population are not fully modeled, it is assumed that there are different steady-state prevalence levels in fed and unfed populations and it takes time to transition from one steady state to another. Unlike CWD, brucellosis has been observed in elk populations in the GYE and the prevalence of the disease is much lower in unfed populations. Scurlock and Edwards (2010) estimate a prevalence of 3.7% in unfed populations and 21.9% in fed populations. Schumaker et al. (2010) report rates of less than 5% in unfed populations and a slightly higher estimate of 26% in fed populations. Using this data, the relationship between the steady-state brucellosis prevalence, $\hat{\theta}_B$, and feeding is assumed to take the following linear form:

$$\hat{\theta}_B(F_t) = \underline{\theta}_B + (\bar{\theta}_B - \underline{\theta}_B)\frac{F_t}{F^{max}}, \tag{12}$$

where $\underline{\theta}_B$ is the steady-state brucellosis prevalence observed in unfed populations and $\bar{\theta}_B$ is the prevalence observed in fed populations. It is assumed that it takes time for the brucellosis prevalence to transition from one steady-state to another if the feeding status is changed, and therefore $\theta_{B,t}$ requires a time subscript. The brucellosis prevalence in the elk population is governed by the equation

1	3	5
2	4	6

FIGURE 1. Example of Cell Indexing

$$\theta_{B,t} = \theta_{B,t-1} + \delta\Big(\hat{\theta}_B(F_t) - \theta_{B,t-1}\Big), \tag{13}$$

where δ is a parameter that determines how quickly convergence occurs, and is bounded between zero and one.

In this model, feeding affects brucellosis transmission by altering the number of elk that travel into lower elevations and inhabit the same space as cattle, changing the product NL in the transmission function. Because the primary mechanism of elk-cattle brucellosis transmission is cattle coming into contact with aborted elk fetuses (abortions are the result of brucellosis infections), we assume that transmission to cattle can only occur between January and June. For January through June, the expected number of cattle infected with brucellosis by elk in cell i in period t is

$$\beta_B \theta_B(F_t) N_{i,t}^{(3)} L_{i,t}^{(3)}. \tag{14}$$

If a cow becomes infected with brucellosis, the U.S. Department of Agriculture Animal and Plant Health Inspection Service (USDA-APHIS) will require that the entire cattle herd be quarantined or culled, at a significant cost to either the rancher, the U.S. Department of Agriculture (USDA), or both (Roberts et al., 2012). Note that brucellosis infections in cattle are so rare that equation (14) will likely be less than 1 for reasonable parameter values. The economic costs of brucellosis infection and the behavior of ranchers in response to the brucellosis threat are discussed in the next section of the paper.

2.5. **Spatial Structure & Stage 5: Elk Movement.** The final stage in each period is elk movement. It is assumed that there is no difference in the movement of infected and susceptible elk. Elk move in a two-dimensional rectangular grid consisting of a total of n 25 km^2 cells. Cells are indexed by i such that i corresponds to a position in two-dimensional space by counting down columns first and then across rows, beginning at the northwest corner of the landscape. For example, for a 2 x 3 grid, $i = 5$ refers to the cell in the first row and third column as shown in Figure 1.

The likelihood of an elk moving from any cell i to any cell j in stage 5 is governed by the n x n transition matrix J. Noting that each column of J sums to 1 so that every elk has to either stay in place or travel to another cell, the movement of elk in stage 5 is given by

$$\boldsymbol{S}_{\boldsymbol{t+1}}^{\boldsymbol{(0)}} = \boldsymbol{J}\boldsymbol{S}_{\boldsymbol{t}}^{\boldsymbol{(4)}} \tag{15}$$

$$\boldsymbol{I}_{\boldsymbol{t+1}}^{\boldsymbol{(0)}} = \boldsymbol{J}\boldsymbol{I}_{\boldsymbol{t}}^{\boldsymbol{(4)}}, \tag{16}$$

where S and I are n x 1 column vectors of the susceptible and infected populations. J is calculated by taking the Hadamard product (element by element multiplication) of two n x n matrices and then normalizing the columns to sum to 1. The first matrix is a movement matrix, M. Each element of M gives the probability of an elk moving the distance required to reach a point in cell j from the center of cell i in a month, if following "rook" movement[1]. The elements of the second matrix, $Z_{m,F}$, are probabilities of an elk inhabiting a particular cell divided by the probability of an elk inhabiting some other location within its home range (an odds ratio), conditional on the landscape characteristics of the cell. These values are generated by fitting a resource selection function (RSF) using data on elk movement and habitat characteristics in the GYE. There are 24 different Z matrices, one for each month for each type of elk population (fed and unfed). The subscript m denotes the month (1 to 12) and F denotes the feeding status (1 or 0). The subsequent paragraphs discuss these matrices in more detail.

The construction of the movement matrix, M, is best illustrated through an example. Consider the 3 x 3 landscape in Figure 2, in which numbers denote the cell index and the cell size is 25 km^2. To calculate the element of M that corresponds to moving from cell 1 to cell 5: First, the distance of the shortest path from the center of cell 1 (point A) and to the center of cell 5 (point B) is determined if elk are constrained to rook movement. The line in Figure 2 shows one of the two shortest possible paths from point A to point B, and the distance from A to B on this path is 10 km. The probability of traveling exactly 10 km is zero, so instead we consider the probability of traveling the range of distances that would put the elk in cell 5 if following the path drawn. To do this, we take the difference between the CDF of the exponential distribution evaluated at the distance between points D and A (12.5 km) and evaluated at the distance between points C and A (7.5 km). This gives the probability of the elk traveling the range of distances required for it to be inhabiting cell 5 after one month of travel. This probability will be the same for traveling to all equidistant cells (cells 3, 5, and 7).

[1]Rook movement restricts elk to moving due north, south, east, or west. They cannot travel diagonally across cells.

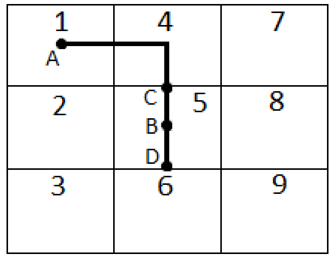

FIGURE 2. Example of Elk Movement in a 3x3 Landscape

In summary, M is generated by first calculating a symmetric n x n matrix, which I will call A, that contains the shortest rook movement distances from the center of any cell i to the center of any other cell j. Letting $a_{i,j}$ be an element of A, M is generated by performing the following operation on each element of A:

$$M = G(a_{i,j} + 2.5) - G(max\{a_{i,j} - 2.5, 0\}). \tag{17}$$

where G is the CDF of the exponential distribution with parameter $\hat{\lambda}$.

A resource selection function (RSF) is a common tool in ecology to predict the location and movement of organisms based on habitat characteristics. In this application, the RSF value for cell i is $w(X_i)$, where X_i is a vector of landscape characteristics for cell i. We use a standard RSF with the log-linear form:

$$w(\boldsymbol{X_i}) = exp\big(\boldsymbol{X_i'\zeta}\big). \tag{18}$$

where ζ is a vector of coefficients that need to be estimated. Descriptions of all the landscape characteristics included in X are given in Appendix A. The value of $w(X_i)$ can be interpreted as the probability of an elk inhabiting a particular cell divided by the probability of an elk inhabiting some other location within its home range (an odds ratio). If a specific set of cells is designated as a home range for an elk, as we do in this research, w is proportional to the probability of an elk inhabiting a particular cell. In other words, ratios of RSF values accurately estimate the relative probability of a animal populations inhabiting one area compared with other areas (Johnson et al., 2006). Parameter estimates for the vector ζ were obtained using a mixed-effects logistic regression (see Appendix A for a detailed description of the procedure used to estimate the parameter values). In order to capture elk migratory behavior, separate parameter values were estimated for every month. This allows the RSF to capture migratory behavior because the effect of landscape characteristics on the likelihood of elk being present varies throughout the year. For example, during the summer months, the parameter estimate for elevation is expected to be positive because elk prefer higher elevation areas during the summer. During the winter, elk prefer lower elevation areas so the parameter is expected to be negative. The RSF can also be used to capture the effects of feeding on elk movement. The data set used to estimate RSF parameters includes observations in regions where elk are fed and in regions where elk are not fed. By estimating separate parameter values for fed and unfed populations, the effect of feeding on elk movement is reflected in the parameter values. Predictably, for the months before, during, and after feeding, the parameter values for the distance-to-feedground variable are much larger in magnitude than the other parameter values (see Tables A.1 and A.2 for parameter estimates). A total of 24 sets of RSF parameters were estimated: one for each month for each of the two population types (fed and unfed). The matrix Z for month m and population F is an n x n matrix consisting of n duplicated columns generated by taking the product of an n x 1 vector of the estimated RSF functions for each cell and a 1 x n ones vector:

$$Z_{(m,F)} = \begin{bmatrix} exp\big(\boldsymbol{X_1'}\hat{\boldsymbol{\zeta}}_{\boldsymbol{(m,F)}}\big) \\ exp\big(\boldsymbol{X_2'}\hat{\boldsymbol{\zeta}}_{\boldsymbol{(m,F)}}\big) \\ \vdots \\ exp\big(\boldsymbol{X_n'}\hat{\boldsymbol{\zeta}}_{\boldsymbol{(m,F)}}\big) \end{bmatrix} \begin{bmatrix} 1 & 1 & \dots & 1 \end{bmatrix}. \tag{19}$$

X_i is the vector of RSF covariates for cell i, and m and F subscripts are used to denote month and feeding status. Taking the Hadamard (element-by-element) product of M and Z, and then dividing each column by the sum of the column elements gives the transition matrix J. The intuition is as follows: An element of Z gives a value proportional to the probability of an elk inhabiting a particular cell, as a function of land characteristics only. These values are then adjusted based on the probability of an elk travelling the distance required to inhabit a cell by multiplying them by the elements of matrix M, creating a modified matrix of RSF values. An element of M is the probability that an elk travels the distance required to inhabit cell j from some other cell i. The elements of M and Z are nonzero. The Hadamard product of these two matrices is then normalized so that the columns add up to 1, imposing that every elk either stays in place or moves to another cell.

Referring back to the 3 x 3 grid in Figure 2 can help illustrate the logic of this approach. Suppose that an elk beginning in cell 1 is migrating to a feedground located in cell 9, but this trip takes more than 1 month. The elk could take the path shown, and then continue through cell 6 to reach its destination. The probability of the elk traveling the distance required to be in cell 5 after one month is given by an element of M. Alternatively, the elk could choose an equidistant path to

9 through cells 7 and 8. Why might the elk choose one path over the other? The vegetation, elevation, and other landscape characteristics might be more favorable along the path through 5 and 6, implying higher RSF values for 5 and 6 than for 7 and 8. By multiplying the elements of M and Z both distance and landscape attractiveness influences the likelihood of an elk inhabiting a cell.

We assume feeding policy is binary (i.e. feed at current levels or do not feed at all). Other levels of feeding are not considered because it is unclear how these scenarios would influence elk movement. A reduced feeding level, for example, could entail either reducing the quantity of feed or reducing the duration of feeding. It is not clear how to adjust the RSF parameter values to accommodate these scenarios, and this could be the subject of future research.

3. The Bioeconomic Model

A bioeconomic model is used to maximize the regional welfare generated by elk populations. In the GYE, three industries are primarily affected by elk management: hunting (which includes businesses that provide services to hunters and the sale of licenses), tourism, and ranching.

3.1. **Hunting.** CWD has two negative consequences for welfare generated from hunting activities. First, mortality from the disease reduces the available stock from which to harvest. Second, the presence of CWD in a region causes a shift in demand as hunters may choose to hunt elsewhere in order to reduce their risk of harvesting an infected animal[2]. Bishop (2004) found that the reduction in hunting activity and expenditures in Wisconsin following the discovery of CWD in deer populations in 2002 resulted in economic losses of between \$53 and \$79 million in 2002 and between \$45 and \$72 million in 2003. Zimmer et al. (2012) also found evidence of hunter aversion to CWD, estimating that hunters would be willing to spend \$20.35 per trip to maintain CWD at current levels in Alberta and prevent further spread of the disease. To capture this demand effect, expenditure by individual hunters is modeled as a decreasing function of CWD prevalence. For simplicity, we assume that the market for elk hunting is sufficiently large that the region acts as a price-taker with respect to quantity of licenses issued, but the region will experience reduced demand in response to CWD in the elk population. In response to a CWD-induced shift in the demand curve, elk license costs, as well as the prices charged by outfitters and hunter accommodations, must adjust downward to maintain any particular harvest level. We assume that the price is zero if all elk are infected with CWD (hunters will choose to hunt elsewhere) and that

[2]The Center for Disease Control recommends that hunters not consume infected meat (Belay et al., 2004).

prices are inversely proportional to the CWD prevalence. Formally, let Y be the price of an index of goods and services purchased by hunters per elk harvested (including licenses, accommodations, and travel expenditures). Omitting time subscripts, we let $Y(h;\theta)$ be the regional inverse demand curve, where h is the quantity of elk harvested and θ is the regional CWD prevalence. The market for elk hunting is large enough such that regional harvest level does not influence price. However, hunters will express a preference for other elk hunting areas if CWD increases. The relationship between CWD prevalence and total hunter expenditures in time t is given by the equation

$$Y_t = (1 - \theta_t)\bar{Y}. \tag{20}$$

Total regional hunting expenditures in period t are $h_t Y_t$.

3.2. **Tourism Industry & Existence Value.** In addition to the benefits from hunting elk, the presence of elk in the GYE provides value to the local economy by drawing wildlife viewers. Elk populations may also have an inherent existence value. For model tractability, these values are combined and assumed to be linear in the population so that each elk produces existence and tourism benefits of value v. The total existence and tourism benefits are calculated using the total elk population at the beginning of each period, and are given by

$$v \sum_{i=1}^{n} N_{i,t}^{(0)}. \tag{21}$$

A constant marginal tourism benefit of elk is a strong assumption that may be relaxed for future analysis, as it is likely that the per-elk benefits are decreasing in the overall elk population. That tourism benefits are not spatially explicit is also a strong assumption that could be relaxed in future analysis.

3.3. **Ranching Industry Damages and Rancher Self-Protection.** As discussed earlier, elk populations impose costs on ranchers through the spread of brucellosis to cattle. If brucellosis is detected in a cattle herd, the USDA-APHIS will determine if the cattle herd must be culled or quarantined. If the herd is culled, the USDA partially compensates the ranchers. If quarantined, the rancher must pay the cost of feeding the animals over the period of quarantine (rather than allowing them to graze) (Roberts et al., 2012). It is assumed that ranchers are running cow-calf operations, and herds are quarantined if an infection is detected, which has become more common with USDA budget limitations (Roberts et al., 2012). We denote the per-cow cost of a quarantine

q. For simplicity, we assume that the cows in any individual cell at time t constitute a herd. Recall that equation (14) gives the expected number of cows located in cell i becoming infected in time t. The herd has to be quarantined if one or more cows contract the disease from elk, and the disease may then spread through the herd. Therefore, damages are not increasing in the number of cattle infections – the herd is quarantined if one infection is detected and there are no additional costs if a second cow contracts the disease from elk in the same period. The probability of an individual cow becoming infected in cell i at time t is $\beta_B \theta_{B,t} N_{i,t}$. Recognizing that the expected number of infections in each cell follows a binomial distribution, the probability of at least one cow becoming infected is

$$1 - (1 - \beta_B \theta_{B,t} N_{i,t}^{(3)})^{L_{i,t}}. \tag{22}$$

This can be interpreted as the probability of a quarantine in cell i at time t. In the absence of any measures to reduce the risk of cattle contracting the disease, the expected economic damages from brucellosis at time t are

$$D_t = q \sum_{i=1}^{n} L_{i,t} \left(1 - (1 - \beta_B \theta_{B,t} N_{i,t}^{(3)})^{L_{i,t}} \right). \tag{23}$$

Ranchers can invest in self-protection measures to prevent cattle from being infected with brucellosis during the winter. These measures have varying levels of cost, and range from low-cost options such as fencing haystacks to high-cost options such as delayed grazing (Roberts et al., 2012). We assume ranchers can invest in self-protection that is 100% effective in preventing the transmission of brucellosis at a per-cow, per-period cost of c. For the herd located in cell i at time t, with $L_{i,t}$ animals, a risk-neutral rancher will invest in self-protection if and only if the expected damages exceed the cost of self-protection, i.e.

$$q L_{i,t} \left(1 - (1 - \beta_B \theta_{B,t} N_{i,t}^{(3)})^{L_{i,t}} \right) > c L_{i,t}. \tag{24}$$

An indicator variable, $SP_{i,t}$ takes on a value of 1 if ranchers invest in self-protection for cell i at time t, and 0 if they do not. The expected economic damages from brucellosis in period t become

$$D_t = q \sum_{i=1}^{n} L_{i,t} (1 - SP_{i,t}) \left(1 - (1 - \beta_B \theta_{B,t} N_{i,t}^{(3)})^{L_{i,t}} \right). \tag{25}$$

The total self-protection costs include those incurred by both ranchers and the government. With the costs incurred by ranchers denoted c and those incurred by government denoted c_g, total costs are

$$(c + c_g) \sum_{i=1}^{n} SP_{i,t} L_{i,t}. \tag{26}$$

3.4. **Welfare Function.** A regional planner seeks to maximize the discounted sum of expected welfare by choosing a sequence of harvest levels, h_t, and by making the binary feeding decision, F_t. The objective function is

$$W = \sum_{t=0}^{T} \frac{1}{(1+\rho)^t} \left(h_t Y_t + v \sum_{i=1}^{n} N_{i,t}^{(0)} - D_t - (c + c_g) \sum_{i=1}^{n} SP_{i,t} L_{i,t} - z \sum_{i=1}^{n} N_{i,t}^{(0)} F_t \right) \tag{27}$$

where z is the cost of feeding per elk. Harvesting policies at different levels of feeding will be evaluated using simulations.

4. Case Study Area in the Southern GYE

We employ a 4,800 km ^{2} study area near Pinedale, WY. This area is one of the southernmost portions of the GYE at the southwestern slope of the Wind River Mountain Range, within Sublette County. The area contains four feed sites near the town of Pinedale, Wyoming, and elk in this area are likely to be some of the first in the GYE to encounter CWD. The area is also chosen because wolves are not present in large numbers. In areas farther north, wolves play an important role in elk population dynamics, and it is also hypothesized that predation may play a role in regulating disease in prey populations (Wild et al., 2011). Wildlife viewing/tourism benefits can be reasonably excluded from the model as tourists interested in viewing wildlife typically will travel farther north to the National Elk Refuge or Yellowstone National Park. The study area is a 12x16 grid of 25 km^2 cells near Pinedale, WY as shown in Figure 3[3]. The green dots represent four elk feeding sites. Red lines represent typical elk migration patterns. The different colors of the map indicate land ownership: light green is U.S. Forest Service (USFS), light yellow is U.S. Bureau of Land Management (BLM), state-owned land is blue, and private land is white. The U.S. Consumer Price Index is used to adjust all parameter estimates denominated in dollars to 2015 dollars.

[3] Although the initial case study area is a 12x16 grid in the Pinedale area, this is extremely flexible. Data for the entire region are available, and the code is currently written so that any grid within the GYE can be selected. The entire area for which the data are available is shown in Figure B.1 in Appendix B.

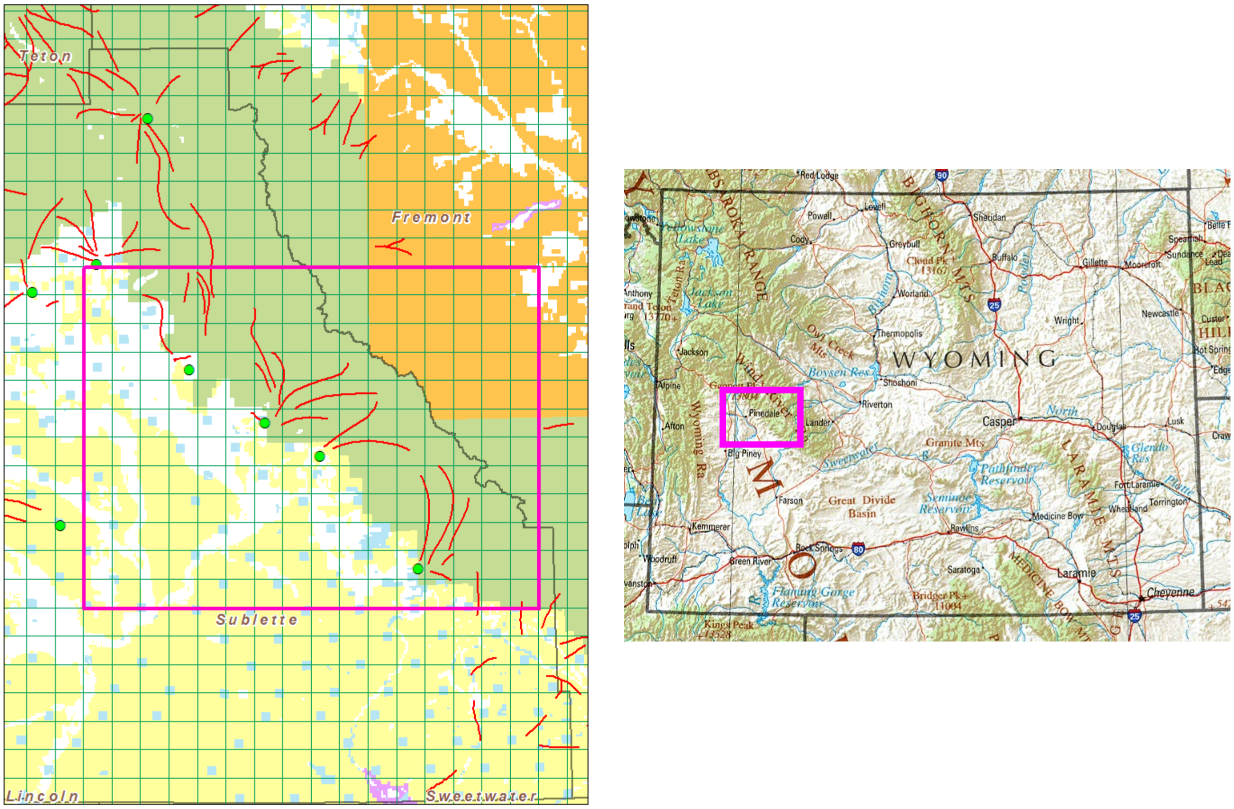

FIGURE 3. Case Study Area: Pinedale, WY Region

4.1. **Carrying Capacity & Feeding Costs.** We assume that feedgrounds alter population dynamics by altering the carrying capacity in the logistic growth function, $K(F)$. In practice, carrying capacities are difficult to estimate. Lubow and Smith (2004) estimate that the carrying capacity for the larger Jackson Elk Herd (JEH) is 59,000 under existing feeding policies. No such estimate is available for the Pinedale Elk Herd. This JEH carrying capacity estimate will be used in conjunction with the Wyoming Department of Game and Fish population counts at the four feedgrounds located in our study area to estimate the carrying capacity for our simulations. The population counts for the four feedgrounds as of 2015 are: Soda Lake (1017), Scab Creek (668), Muddy Creek (571), and Fall Creek (648)[4]. The population target for the JEH is 11,000 individuals (Wyoming Game and Fish Department, 2016a), which is 18.6% of the carrying capacity estimated by Lubow and Smith (2004). This ratio can be applied to the total feedground population count of 2,904 to arrive at a carrying capacity estimate of approximately 15,613 under existing feeding practices (Wyoming Game and Fish Department, 2016b).

[4]Wyoming Game & Fish Unpublished Data

According to the Wyoming Game and Fish Department, the FY 2015 budget for feedgrounds was \$2,814,068 and 14,800 elk were estimated to have utilized feedgrounds (Wyoming Game and Fish Department, 2015). This implies an annual per-elk cost of feeding of \$190.14, or \$15.85 per-month if the cost is spread out over the year. The monthly cost is denoted z in the model. The parameter values used in this case study are shown in Table 1.

4.2. **Ranching Values.** Cells with greater than 50% private land are classified as private. For each private cell, unpublished agricultural data[5] are used to derive a herd size estimate of 197.8 head of adult cows per private cell (denoted L_p in Table 1) . From July to October, cattle only graze on USFS land and the total cattle population is evenly distributed across USFS cells. From April to June, cattle graze on BLM land and the total cattle population is evenly distributed across BLM cells. For the remainder of the year, cattle occupy private land (197.8 head per cell).

Using information from Wilson (2011), Roberts et al. (2012) provide estimates of the costs of culling or quarantining a herd of cattle if directed to do so by the USDA due to brucellosis infection. The herd considered in Roberts et al. (2012) consists of 400 adult cows. Ranchers incur an annual loss of \$40,181 if the animals are culled and they are partially compensated, or an annual loss of \$134,818 if the animals are quarantined, both in 2010 dollars (Roberts et al., 2012; Wilson, 2011). We assume that herds are quarantined if an infection is detected, which has become more common with USDA budget limitations (Roberts et al., 2012). Assuming a herd size of 400 adult cows, the annual cost of a brucellosis quarantine per adult cow is \$337.05 in 2010. Dividing this by 12 gives the monthly quarantine cost per cow. Because brucellosis transmission from elk to cattle occurs primarily through cattle contact with aborted elk fetuses, it is assumed that brucellosis can only be spread to cattle from January to June. Because transmission can only occur one half of the year, annual costs are converted to bi-monthly costs. Adjusting to 2015 dollars, we assume $q = (\$366.25/6) = \$61.04$.

Two of the least expensive self-protection measures to prevent brucellosis transmission are fencing haystacks and an adult vaccine booster. The annualized cost of fencing haystacks for a cow-calf operation of 400 adult cows is \$103 in 2010. The annualized cost of an adult vaccine booster for a ranching operation of the same size is \$797 in 2010 dollars (Roberts et al., 2012; Wilson, 2011). Combined, the annual cost of these two protection measures is \$977.97, or \$2.44 per adult cow in 2015 dollars. Self-protection measures are much longer lasting than a single month (e.g. fencing). However, we simplify our analysis by converting annual costs into monthly costs and

[5] Data provided by Dannele Peck, U.S. Department of Agriculture Agricultural Research Service (USDA ARS)

assuming ranchers make decisions monthly. This allows us to abstract from the timing of investment decisions and the depreciation of self-protection assets (e.g. fencing). However, because it is only possible for cows to be infected during six of the twelve months of the year, using monthly costs would underestimate rancher expenditures. We address this by doubling the monthly costs, so that investing in self-protection in all six months where transmission is possible is equal to the annual estimated costs derived from Roberts et al. (2012). Dividing the annual cost of self-protection by 6 gives the bi-monthly per-cow self-protection cost, c, of \$0.41 used in this analysis. It is estimated that the vaccine booster protects 65 to 75% of cattle (Roberts et al., 2012), so it is reasonable to assume that effective fencing combined with vaccination might approach the 100% protection assumed in our model. Vaccination is subsidized by the Wyoming Livestock Board (WLSB), so in addition to the cost of vaccination incurred by the ranchers themselves, the government incurs a annualized cost of \$814.98 or \$2.04 per adult cow. This corresponds to \$0.34 per adult cow on a bi-monthly basis, which is used for c_g in the model. Ranchers alone make the decision to purchase self-protection, but some of their self-protection costs are subsidized by the government.

4.3. **Hunting Value.** According to the U.S. Fish & Wildlife Service's 2011 Survey of Fishing, Hunting, and Wildlife-Associated Recreation, the average expenditure per hunter on hunting is \$1,457, excluding licences (U.S. Department of the Interior, U.S. Fish and Wildlife Service, and U.S. Department of Commerce, U.S. Census Bureau, 2011). In 2015 dollars, this is \$1,583. According to the Wyoming Game and Fish Department, the average cost of an elk license in Wyoming in 2015 was \$140.87, and there were 71,890 licenses sold to a total of 58,266 hunters (Wyoming Game and Fish Department, 2015). So each hunter bought an average of 1.234 licenses at a cost of \$140.87 each, plus \$1,583 in other expenditures, for a total of \$1,756.81. The elk hunting success rate was 44.5%, so the average expenditure per elk harvested is estimated to be \$3,948. This value will be used for $\bar{Y}$.

4.4. **Disease Parameters.** The CWD transmission coefficient, β, is unknown. Recall that the prevalence of CWD in wild populations has been observed at 1 to 10% (Smith, 2012), but is 50% or greater for captive populations with very high densities. Based on this evidence, we assume the following criteria for plausible values of β: first, at low population densities without feeding CWD prevalence after 20 years will remain below 5%. Second, at very high population densities with supplemental feeding, CWD prevalence after 5 years will exceed 30%. To analyze the former criterion, a 20-year simulation is run where unfed elk are harvested to maintain a target population of 1,950, which is approximately two-thirds of the current population. We run this simulation

Table 1. Pinedale, WY Region Parameter Values

	Description	Value	Source
L_p	cows per private cell	197.8	unpublished data
μ	CWD mortality rate	0.128 (annualized)	derived from Williams et al. (2014)
r	elk intrinsic growth rate	0.28	Eberhardt et al. (1996); Sargeant and Oehler (2007)
$K(0)$	carrying capacity	7,806.5	Lubow and Smith (2004), Wyoming Game & Fish
$\bar{Y}$	CWD-free harvest value	\$3,948	U.S. Fish and Wildlife Service, Wyoming Game & Fish
z	feeding cost per elk	\$190.14 (annualized)	Wyoming Game & Fish
β	CWD transmission rate	0.00045	calibrated
τ	feeding capacity param.	0.5	assumption
ρ	discount rate	0.03 (annualized)	assumption
$\underline{\theta}_b$	min bruc. prev	0.05	Schumaker et al. (2010)
$\bar{\theta}_b$	max bruc. prev	0.26	Schumaker et al. (2010)
β_B	elk-cattle bruc. trans	.000044	Horan et al. (2007)
q	avg. quarantine cost	\$61.04	Roberts et al. (2012)
c	private self-protect cost	\$0.41	Roberts et al. (2012)
c_g	gov't self-protect cost	0.34	Roberts et al. (2012)
δ	bruc. dissipation rate	0.1 (annualized)	assumption

with gradually increasing values of β to find an upper bound on β; values of β larger than this upper bound lead to CWD prevalence levels of greater than 5% after 20 years. To analyze the latter criterion, a 20-year simulation is run where elk are fed but not hunted so that the population increases rapidly. We run this simulation with gradually decreasing values of β to find a lower bound on β; values of β below this lower bound lead to CWD prevalence levels of less than 30% after 20 years. This calibration exercise yielded a lower bound of 0.00006 and an upper bound of .00084. We set β to 0.00045, which is the midpoint of these two values.

The transmission coefficient of brucellosis transmission from elk to cattle, β_B, is also uncertain. Cases of herd infection are very rare, so β_B should be chosen such that infections are very improbable if feeding is continued. Calibration is difficult because, as the risk of brucellosis transmission from elk to cattle rises, more ranchers invest in self-protection, and infection risk remains low. In order to calibrate β_B, one would need data on rancher investments in self-protection as well as the frequency of cattle infections. Information in the literature is scarce. Dobson and Meagher (1996) use a simple model to estimate a value of between .0005 and .001 for the brucellosis transmission rate among elk and bison in the GYE, but these estimates lead to unrealistically high levels of infection. Horan et al. (2007) analyze the transmission of bovine tuberculosis between deer and cattle using a similar model. They calibrate their model to observed rates of infection to reach an estimated transmission rate of .000044. We chose to use this value in our analysis because it yields plausible results: at a value of .000044, our model predicts a 15.6% chance of at least one brucellosis infection in our study area if current management practices continue. This implies that an infection is expected to occur on average every 6.4 years, which is roughly consistent with observed infection rates.

The parameter δ governs how quickly brucellosis prevalence declines from the high prevalence observed in fed populations ($\bar{\theta}_B$) to the low prevalence observed in fed populations ($\underline{\theta}_B$) when feeding is discontinued. We assume that the difference between these two values decreases by 10% each year. Future work will be aimed toward reducing the uncertainty around this parameter.

4.5. **Elk Movement.** Elk move in space according to the methodology outlined in Section 2.5 using the parameter values outlined in Appendix A. Figures 4 and 5 show heat maps of elk population densities in March simulated by our movement model, assuming the current population level of 2,900. In the feeding case (Figure 4), elk are all concentrated around the feedground sites. In the non-feeding case (Figure 5), elk are less concentrated but more are located on low elevation, private land. The same two heat maps for the month of August, when elk are at higher elevations, are shown in Appendix B.

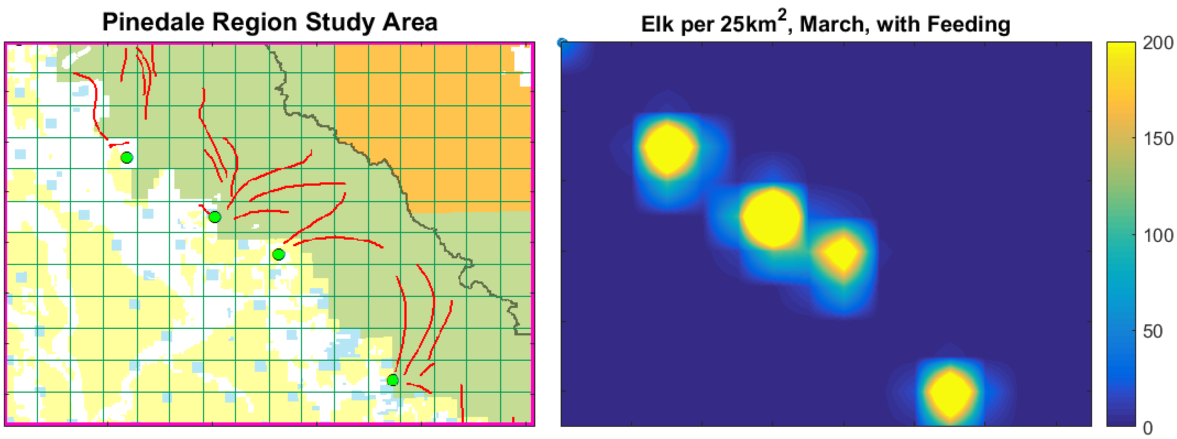

FIGURE 4. Elk Location in March, Feeding

The left image is a map of the study area, with base colors indicating land ownership. White is private land, green is U.S. Forest Service land, yellow is Bureau of Land Management land, and blue is state-owned land. Green dots are feedground locations, and red lines indicate typical elk migration patterns. The right image shows our model's prediction of elk population density in March, assuming feeding and current population levels.

5. Management Strategies

5.1. **Fixed Population Target.** The first management strategy is to harvest such that the population stays at a fixed level. The code cycles through fixed population targets from 0 to 6,000 (approximately double the current population serviced by the four feedgrounds considered in this case study), at intervals of 50, to find the population target that maximizes welfare. This procedure

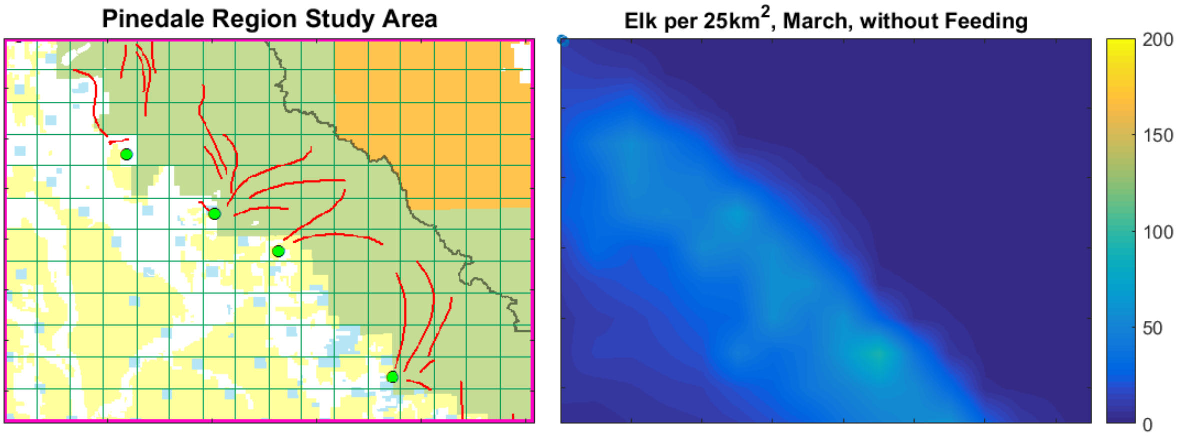

FIGURE 5. Elk Location in March, No Feeding

The left image is a map of the study area, with base colors indicating land ownership. White is private land, green is U.S. Forest Service land, yellow is Bureau of Land Management land, and blue is state-owned land. Green dots are feedground locations, and red lines indicate typical elk migration patterns. The right image shows our model's prediction of elk population density in March, assuming feeding is discontinued but current population levels are maintained.

is repeated with and without supplementary feeding to determine which feeding policy results in higher welfare.

5.2. **Fixed Harvest Rate.** The second management strategy explored using our model is to harvest a specific percentage of the elk population (a fixed harvest rate) every year. We then cycle through feasible harvest rates, at one percentage point intervals, to find the fixed harvest rate that maximizes welfare. This procedure is repeated with and without supplementary feeding to determine which feeding policy results in higher welfare.

5.3. **Population Target Switching.** For many models in the wildlife disease literature, including the one presented in this paper, complete eradication of the disease in not possible in finite time without also eradicating the host population (Horan et al., 2011). Horan et al. (2011) discusses an alternative framework in which an arbitrarily small prevalence level is chosen at which the disease is considered to be eliminated, and then a new phase begins in which the disease is considered to be absent from the system. The third management strategy used in this study, population target switching, is inspired by this alternative framework. Initially, the elk population is reduced to some target, $\underline{N}$, so that the population density is low enough for the CWD prevalence to decline. When the disease prevalence reaches the eradication threshold, ϵ, the disease is considered to be eradicated and the population is allowed to increase to a higher population target, $\bar{N}$. Two things could occur at this higher population target: (1) it is maintained indefinitely and the disease prevalence approaches zero as long as there are no additional exogenous introductions of the disease through, for example, deer populations, or (2) $\bar{N}$ is high enough that the disease prevalence begins to grow again and increases above ϵ, at which point the population is reduced to $\underline{N}$ again. Whether the behavior becomes cyclical or θ approaches zero over time depends on whether $\bar{N}$ exceeds the host-density threshold. The host-density threshold is the population level at which the disease prevalence remains constant, conditional on the current disease prevalence. This can be explicitly solved for in many non-spatial models. In this analysis, ϵ is set to 0.005. The optimal combination of $\underline{N}$ and $\bar{N}$ is determined numerically. Candidate values for $\underline{N}$ range from 0 to 4,000 and intervals of 50 are used. Candidate values for $\bar{N}$ range from 1,000 to 6,000 and intervals of 50 are used. The code finds the combination of $\underline{N}$ and $\bar{N}$ that results in the highest welfare value. This procedure is repeated with and without supplementary feeding to determine which feeding policy results in higher welfare.

5.4. **Population Target and Feed Switching.** This scenario is identical to population target switching, except supplemental feeding is determined by the disease prevalence. If the CWD prevalence is above ϵ, elk are not fed. If the prevalence is below ϵ, feeding is resumed.

6. Case Study Results & Discussion

6.1. **Simulation Conditions.** Simulations start at the beginning of March ($t = 0$). At this time of year, almost all elk are located around feedgrounds. Accordingly, the position of all elk at $t = 0$ is shown in Figure 4, with all elk convened at the feedgrounds. The number of elk started at each feedground corresponds to the latest available population count. The population counts for the four feedgrounds as of 2015 are: Soda Lake (1,017), Scab Creek (668), Muddy Creek (571), and Fall Creek (648)[6]. CWD is introduced exogenously to the southermost feedground (Scab Creek), which could occur by infected deer herds coming into contact with the elk population. It is assumed that 87 elk are infected at $t = 0$, which corresponds to an initial prevalence level of 3% for the entire initial population of 2,904. Simulations are run for 100 years. A long enough time horizon was chosen such that the lack of a terminal value on the elk population would not significantly affect the analysis. At the chosen discount rate of 0.03, a dollar at year 100 has lost 95% of its value in present-value terms. Welfare generated from the elk population beyond 100 years in the future will not substantially alter welfare estimates.

[6]Wyoming Game & Fish Unpublished Data

6.2. **Fixed Population Target Results.** The first management strategy considered is to harvest such that the population stays at a fixed level. If feeding is discontinued, the welfare-maximizing population target is 2,950, and the total expected welfare generated from the elk population is $61.67 million. This result suggests that a population larger than the current population of approximately 2,900 can be maintained without feeding, which is inconsistent with the claim that current population levels cannot be supported without feeding. This could be an indication that our estimate of carrying capacity is too high. The welfare-maximizing population target if feeding is continued is 1,350, and the total expected welfare generated from the elk population is $38.50 million. The introduction of CWD increases the marginal cost of having an additional elk in the population, so intuitively it is optimal to decrease the population level. If a population target management strategy is pursued, our model predicts that it is optimal to discontinue feeding, and doing so could lead to welfare gains of $23.17 million and a higher elk population. Furthermore, the population reduction required to maximize welfare if feeding is continued is substantial, and unlikely to be politically feasible. Figures 6 and 7 show the progression of variables over time for the fixed harvest rate strategy simulations. Because brucellosis transmission, elk reproduction, and hunting only occur during parts of the year, the data series shown in these figures are smoothed using either trailing 12-month sums (TTMS) or trailing 12-month averages (TTMA). The first chart in each figure shows the elk population, the second shows CWD prevalence, the third shows brucellosis costs, and the fourth shows the number of elk harvested during the most recent hunting season.

One difference between the feeding and non-feeding scenarios that can be observed in Figures 6 and 7 is brucellosis costs. In the non-feeding scenario, brucellosis self-protection costs paid by ranchers (the red line) initially increase to over $15,000 per year as ranchers invest in self-protection in response to more elk coming onto private land during the winter. These costs decline over time as the brucellosis prevalence in the elk population declines because they are no longer concentrating at feedgrounds and because the overall population is reduced. Over time, more ranchers choose to forego investments in self-protection and instead assume the risk of brucellosis infection, as is indicated by the increasing blue line. More ranchers would choose to assume this risk if self-protection investments were not subsidized by the government, whose costs are given by the light blue line. The government subsidies, in the form of payments for vaccinations, are nearly as high as the private ranchers' total self-protection expenditures (which include the private portion of vaccination costs as well as fencing costs). Even though total brucellosis costs decline over time in the no feeding scenario, they remain higher than in the feeding scenario for every period.

This suggests that, if only considering private costs, opposition to stopping feeding is a rational policy position for ranchers. Another interesting result is that harvesting to maintain the welfare-maximizing population target of 1,350 in the feeding case results in a constant trailing 12-month average of CWD prevalence. The CWD prevalence is cyclical within the course of a year, but the 12-month average stays at 3.94%.

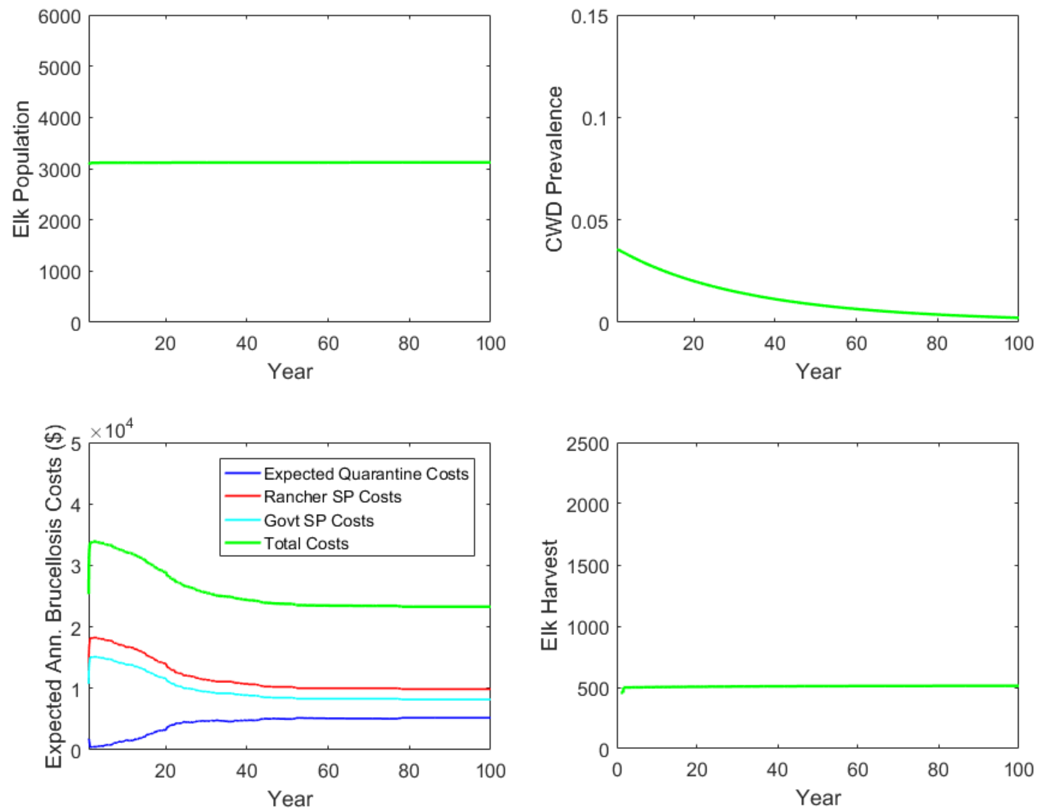

FIGURE 6. Fixed Population Target Results, No Feeding

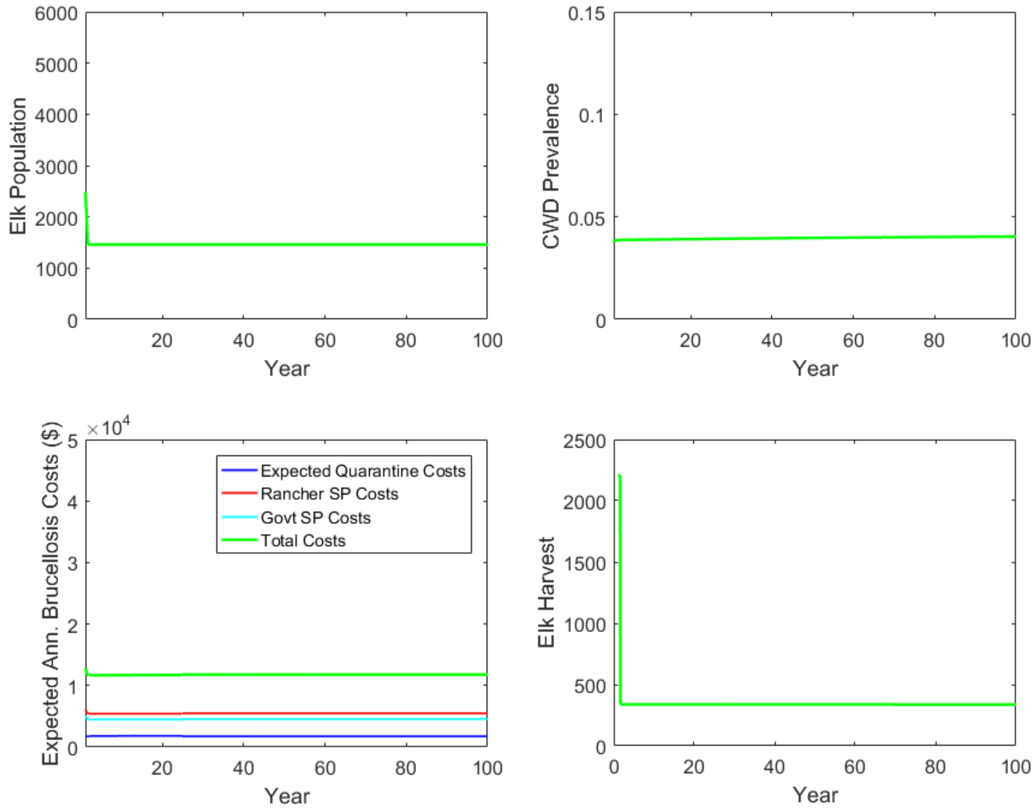

FIGURE 7. Fixed Population Target Results, Feeding

Figures 8 and 9 illustrate some of the effects of CWD on the biology and economic productivity of the elk population at 20 years ($t = 240$). Figure 8 illustrates the effect of CWD on annual population growth at varying population targets. The figure contains two charts: one if feeding is continued and one if feeding is stopped. The blue curve is the logistic growth curve in the absence of any CWD in the population, and shows how many elk can be harvested each year in the absence of CWD at each population target. The orange curve shows the growth function net of CWD mortality, and shows how many elk can be harvested in year 20 at each population target. The red curve is the CWD prevalence at year 20 as a function of the population target chosen, with prevalence shown on the secondary y-axis. These charts are illustrative in pointing out the impact that CWD has on the growth, or biological productivity, of the elk herd and is independent of any economic assumptions made about the relationship between CWD prevalence and hunter demand. Note that in the absence of CWD, growth in the feeding scenario is much, much higher than in the no feeding scenario across population targets. However, the gap between the non-CWD growth function (blue) and the growth function net of CWD mortality (orange) is much larger in the feeding scenario. In the absence of feeding, CWD prevalence remains very low at population targets below 3,000, and then increases rapidly as the population target increases above 3,000. If feeding continues, CWD prevalence begins to increase rapidly at a population target of around only 1,000.

Figure 9 illustrates the effect of CWD on the economic productivity of the elk herd after 20 years ($t = 240$). The figure contains two charts: one if feeding is continued and one if feeding is stopped. Each chart contains three monetary values as a function of the population target. The blue curve is the value of the annual elk harvest in the absence of CWD. The orange curve shows the total value with CWD. The gap between the blue and orange curves can be broken down into two components. The first component is the decrease in value from being able to hunt fewer elk due to the loss in biological productivity shown in the previous figure (8). The second component is the decrease in value of the elk that are harvested due to a decrease in hunter demand (hunter expenditures per harvested elk are $\bar{Y}(1-\theta)$ rather than $\bar{Y}$). The difference between these two lines shows the cost imposed by CWD at each population target. This difference is relatively small in the non-feeding scenario, but large in the feeding scenario, illustrating how CWD offsets the potential economic benefits of feeding. The third data series shows the sum of all brucellosis and feeding costs as a function of the population target. In the non-feeding scenario, there are no feeding costs, and the first chart illustrates how small brucellosis costs are compared with the reduction in harvesting benefits from CWD. However, the relatively large increase in harvest value from discontinuing feeding is a benefit that is spread across many individuals, whereas the increased brucellosis costs are borne by a small group of ranchers. The first chart in the feeding scenario also illustrates how costly feeding is – these costs are substantially higher than brucellosis costs, but are also shared more broadly rather than borne by a small number of ranchers. Figures B.4 and B.5 in Appendix B show these same charts at five years ($t = 60$).

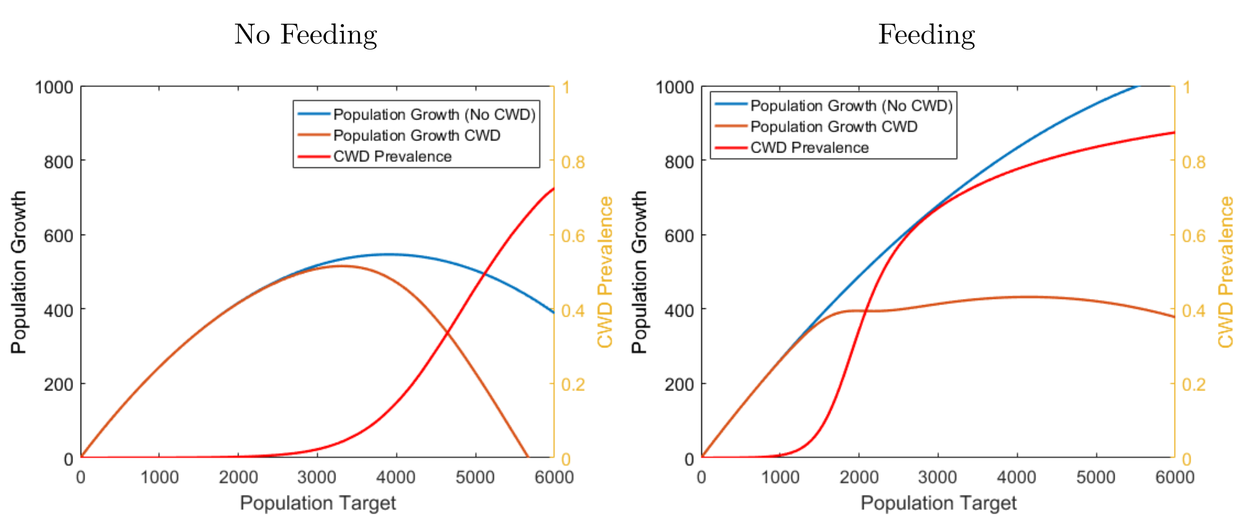

FIGURE 8. Biological Productivity & CWD Prevalence at 20 Years

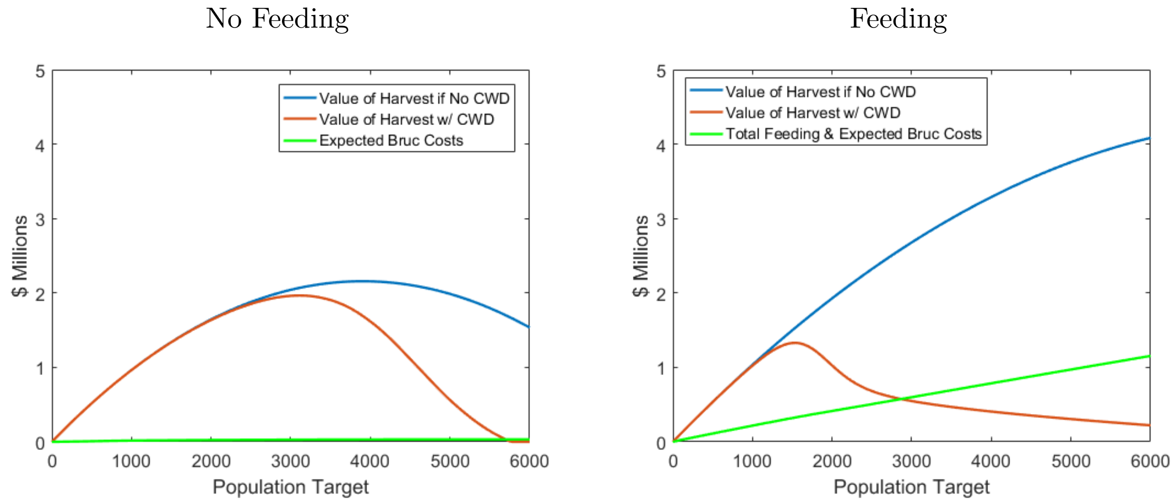

FIGURE 9. Harvest Value & Costs at 20 Years

6.3. **Fixed Harvest Rate Results.** The second management strategy considered is harvesting a fixed percentage of the elk population each year. The welfare-maximizing harvest rate if feeding is discontinued is 0.15, and the total expected welfare generated from the elk population is $61.51 million. This is slighly less than the $61.67 million generated from the optimal population target strategy, suggesting that the population target is a better management strategy. The welfare-maximizing harvest rate if feeding is continued is 0.20, and the total expected welfare generated from the elk population is $31.73 million. The higher harvest rate under the feeding scenario is intuitive: the shadow value of an elk (the value of leaving in situ) decreases as feeding increases because feeding increases the cost of an additional elk due to greater disease risk. If a fixed harvest rate management strategy is pursued, our model predicts that it is optimal to discontinue feeding, and doing so could lead to welfare gains of $29.78 million. Figures 10 and 11 show the patterns over time for the fixed harvest rate strategy simulations. If feeding is continued (Figure 11), the CWD prevalence initially increases to nearly 40% and only begins to fall after the population declines.

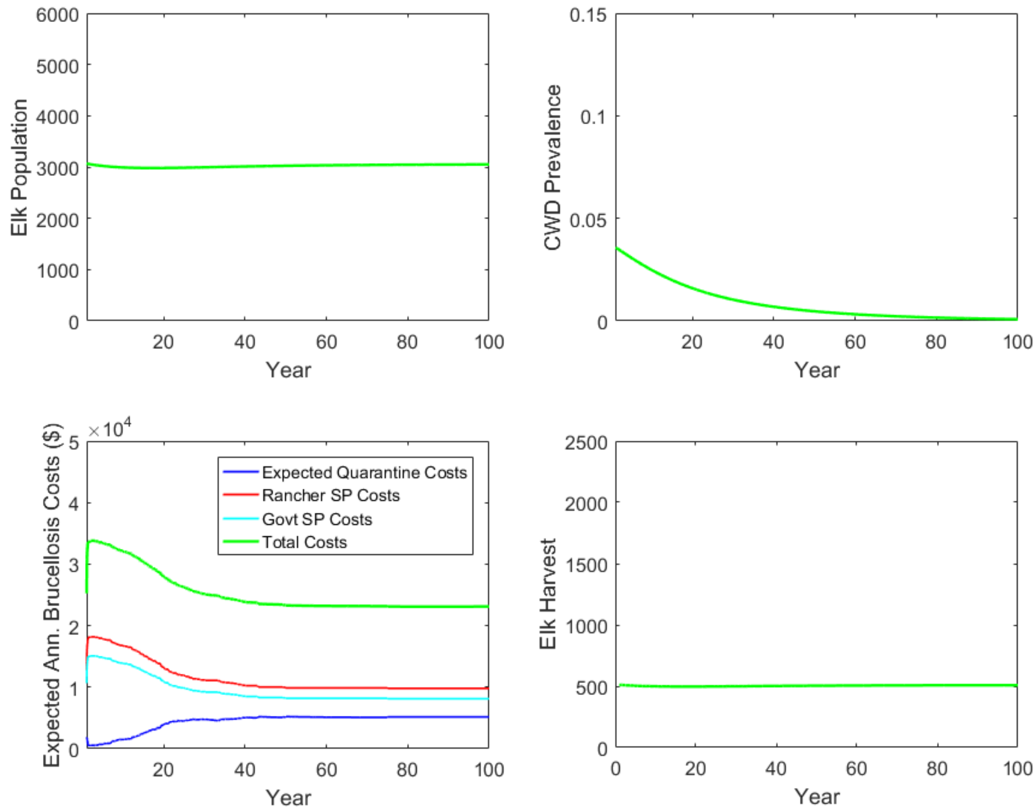

FIGURE 10. Fixed Harvest Rate Results, No Feeding

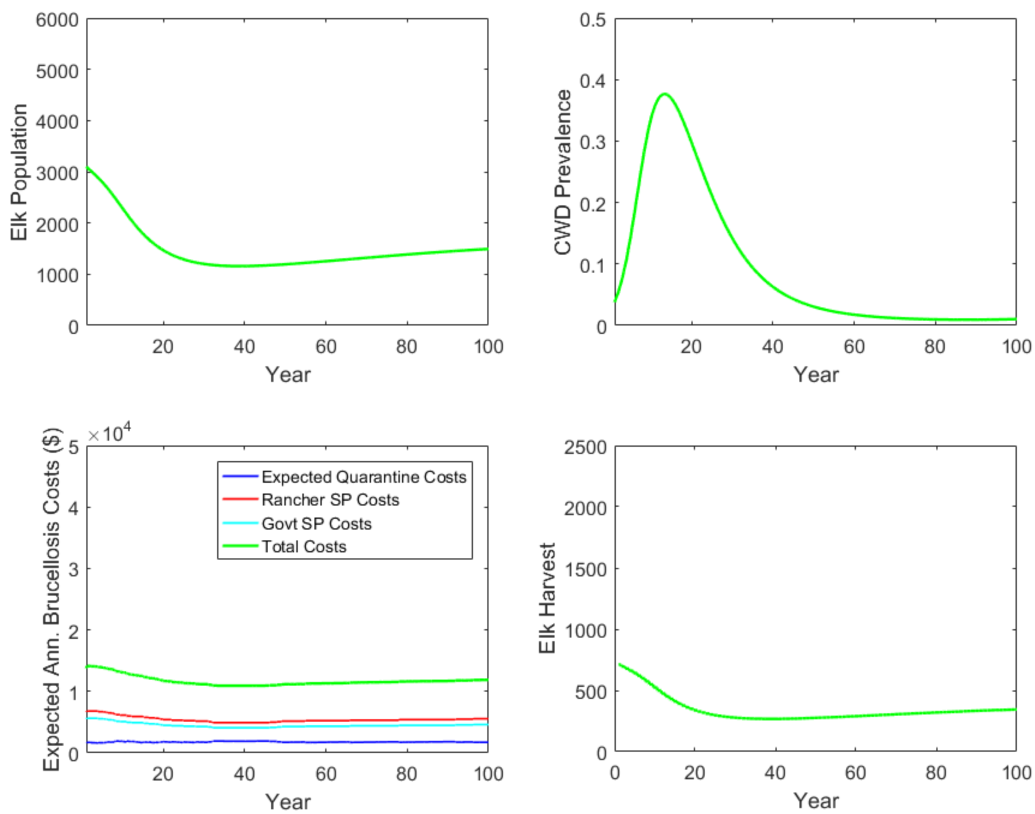

FIGURE 11. Fixed Harvest Rate Results, Feeding

6.4. **Population Target Switching Results.** The population target switching management strategy (PTS) gave surprising results. Our initial intuition was that allowing the population target to increase following the near elimination of the disease would result in increases in welfare. However, adding this additional management flexibility did not result in any gains in welfare over having a single population target. Recall that $\underline{N}$ is the population target if CWD prevalence exceeds ϵ and $\bar{N}$ is the population target if CWD prevalence is below ϵ. If animals are not fed, the welfare maximizing $\underline{N}$ and $\bar{N}$ were both 2,950, and the welfare generated from the elk population is \$61.67 million – identical to the strategy of managing to a single population target. If feeding is continued, the welfare-maximizing $\underline{N}$ is 1,350. In this scenario, the disease never falls below ϵ and $\bar{N}$ is never used at a population target. The population is managed to a single target of 1,350 and the results are identical to the single population target strategy (welfare of \$38.50 million). The results for feeding and no feeding are identical to the population target results previously shown in Figures 7 and 6.

6.5. **Population Target and Feed Switching Results.** This strategy generated the highest welfare estimate. Under this strategy, the welfare-maximizing $\underline{N}$ and $\bar{N}$ are 2,400 and 3,800. Estimated welfare is \$63.63 million, which is 3.2% greater than the welfare generated by the next best strategy tested in our analysis (\$61.67 million). Figure 12 shows the time series results for this strategy. CWD prevalence decreases until it falls below 0.5% at around year 22, at which point feeding resumes and the population target increases to 3,800. This results in a brief boom in the population, and a CWD prevalence rebounds to over ϵ. Next, there is a large harvest of elk to bring the population back down to 2,400 and feeding is discontinued. This cycle continues for the remaining years of the simulation.

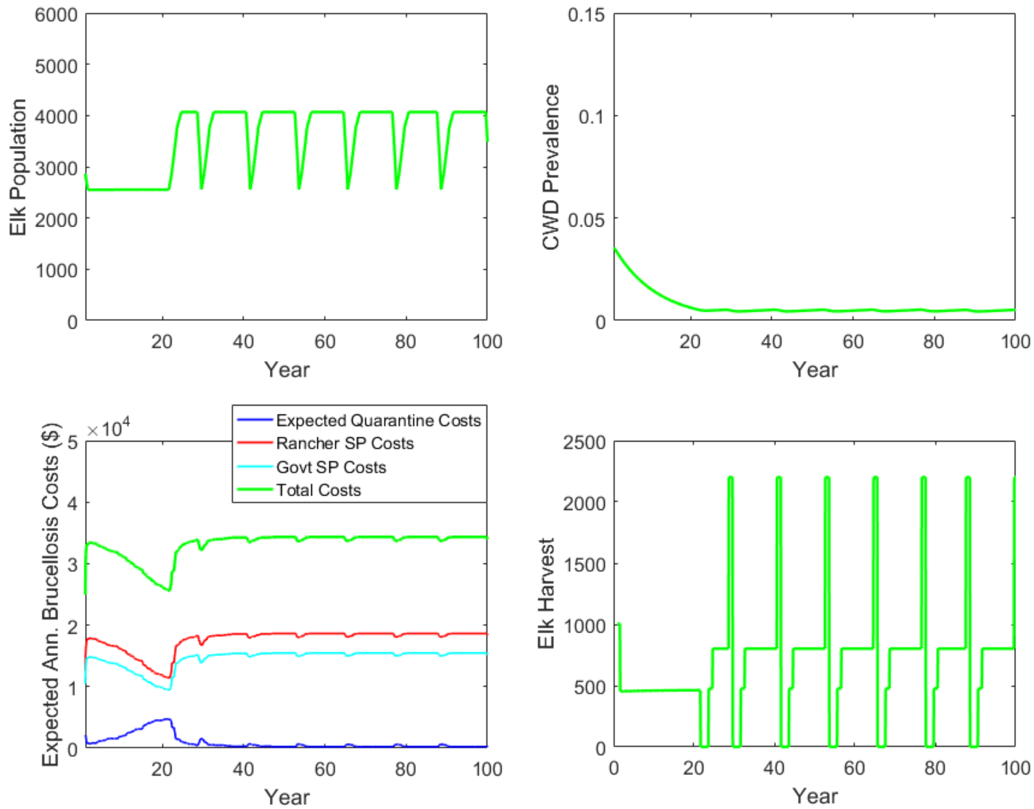

FIGURE 12. Population Target and Feed Switching Results

While this strategy results in the highest expected welfare, it is unclear if a such a policy would be feasible. As illustrated in the fourth chart in Figure 12, increasing the population target from 2,400 to 3,800 requires that there be no harvesting for two years, which could be disruptive to the local economy in a way that is not captured in the model. For example, the Wyoming Game & Fish Department relies on hunting license fees for funding, and might fire employees in response to the hiatus in hunting and hire new employees after the hiatus. This strategy also results in the highest brucellosis costs. After an initial decline, brucellosis costs remain over $30 thousand after the first feeding cycle is initiated. The intermittent feeding results in brucellosis being spread at feedgrounds and remaining more prevalent in the elk population. Nearly all ranchers choose to invest in self-protection after the first feeding cycle, resulting in high self-protection costs and low expected quarantine costs.

7. Conclusion & Future Work

Our results suggest that the concerns of biologists, ecologists, and epidemiologists about the consequences of the impending introduction of CWD are warranted, and that the continuation of feeding could result in welfare losses of over $20 million. Our results also show the potential value of resuming feeding if CWD is nearly eliminated. The management strategy that results in the highest welfare estimate is to discontinue feeding until the disease dissipates, and then to reintroduce feeding at this later date. This strategy gives a welfare estimate that is approximately $2 million larger than estimates generated by any management strategies that eliminated feeding completely.

Our results also suggest that discontinuing feeding will, at least initially, increase brucellosis-related costs for ranchers. However, our model predicts that these costs are far outweighed by the economic benefits associated with reducing the risk of a CWD outbreak. The benefits of avoiding a CWD outbreak are diffuse, accruing to hunters, guides, outfitters, and other regional businesses that cater to hunters. In contrast, the increased brucellosis-related costs fall on a relatively small number of ranchers. A policy could be devised to compensate the losers of discontinuing feeding with the gains of the winners. One potential policy recommendation is to increase self-protection subsidies to ranchers as feeding is discontinued. This subsidy could be phased out as the brucellosis prevalence in the elk population falls over time in the absence of feeding.

There are several extensions to the ecological model that could improve the accuracy of our welfare predictions, at the cost of more complexity. First, wolves should be introduced to the model to factor in their impact on elk population and disease dynamics. Wild et al. (2011) proposes that wolves may act as a natural disease control mechanism in prey by eliminating infected, weak individuals from the population. Disease control may be an unrecognized ecosystem service benefit generated by wolf populations. Second, recent research has shown that some members of the elk population show greater susceptibility to CWD than others due to genetic variation (Williams et al., 2014). Over the time horizon considered in our simulations, a significant shift in the genetic makeup of the population would be expected to occur as elk with the more favorable genotype survive and reproduce more effectively. The third extension that could improve the model would be including the infectious CWD prions that accumulate in the environment as an additional state variable and source of infections. Managing the disease may become extremely difficult if the environment becomes too saturated with prions, and feedgrounds could become reservoirs of these infectious agents.

Extending this model to the rest of the GYE can easily be done with our existing data and code. The area around Pinedale, WY was a suitable case study because of the lack of wolves and wildlife viewing tourists relative to the rest of the GYE. However, if the model is applied to elk populations farther north, we recommend that the wildlife viewing value of elk and the impact of wolf populations on elk mortality and disease dynamics be included in the model.

References

Argue, C. K., Ribble, C., Lees, V. W., McLane, J., and Balachandran, A. (2007). Epidemiology of an outbreak of chronic wasting disease on elk farms in saskatchewan. *Can. Vet. J.*, 48(12):1241–1248.

Begon, M., Bennett, M., Bowers, R. G., French, N. P., Hazel, S. M., and Turner, J. (2002). A clarification of transmission terms in host-microparasite models: numbers, densities and areas. *Epidemiol. Infect.*, 129(1):147–153.

Belay, E. D., Maddox, R. A., Williams, E. S., Miller, M. W., Gambetti, P., and Schonberger, L. B. (2004). Chronic wasting disease and potential transmission to humans. *Emerg. Infect. Dis.*, 10(6):977–984.

Bishop, R. C. (2004). The economic impacts of chronic wasting disease (CWD) in wisconsin. *Hum. Dimensions Wildl.*

Boyce, M. S., Vernier, P. R., Nielsen, S. E., and Schmiegelow, F. K. A. (2002). Evaluating resource selection functions. *Ecol. Modell.*, 157(2–3):281–300.

Carson, R. T., Granger, C., Jackson, J., and Schlenker, W. (2008). Fisheries management under cyclical population dynamics. *Environ. Resour. Econ.*, 42(3):379–410.

Dobson, A. and Meagher, M. (1996). The population dynamics of brucellosis in the yellowstone national park. *Ecology*, 77(4):1026–1036.

Eberhardt, L. E., Eberhardt, L. L., Tiller, B. L., and Cadwell, L. L. (1996). Growth of an isolated elk population. *J. Wildl. Manage.*, 60(2):369–373.

Fenichel, E. P. and Horan, R. D. (2007). Jointly-determined ecological thresholds and economic trade-offs in wildlife disease management. *Nat. Resour. Model.*, 20(4):511–547.

Fenichel, E. P., Horan, R. D., and Hickling, G. J. (2010). Management of infectious wildlife diseases: bridging conventional and bioeconomic approaches. *Ecol. Appl.*, 20(4):903–914.

Horan, R., Wolf, C. A., Fenichel, E. P., and Mathews, K. H. (2005). Spatial management of wildlife disease. *Applied Economic Perspectives and Policy*, 27(3):483–490.

Horan, R. D., Fenichel, E. P., and Melstrom, R. T. (2011). Wildlife disease bioeconomics. *International Review of Environmental and Resource Economics*, 5(1):23–61.

Horan, R. D. and Wolf, C. A. (2005). The economics of managing infectious wildlife disease. *Am. J. Agric. Econ.*, 87(3):537–551.

Horan, R. D., Wolf, C. A., Fenichel, E. P., and Mathews, K. H. (2007). Joint management of wildlife and livestock disease. *Environ. Resour. Econ.*, 41(1):47–70.

Johnson, C. J., Nielsen, S. E., Merrill, E. H., Mcdonald, T. L., and Boyce, M. S. (2006). Resource selection functions based on Use–Availability data: Theoretical motivation and evaluation methods. *J. Wildl. Manage.*, 70(2):347–357.

Lubow, B. C. and Smith, B. L. (2004). Population dynamics of the jackson elk herd. *J. Wildl. Manage.*, 68(4):810–829.

Manly, B., McDonald, L., Thomas, D., McDonald, T., and Boyce, M. (2002). *Where elk roam: conservation and biopolitics of our national elk herd.* Kluwer Academic Publishers, Dordrecht, the Netherlands.

Mao, J. S., Boyce, M. S., Smith, D. W., Singer, F. J., Vales, D. J., Vore, J. M., Merrill, E. H., and Hudson (2005). HABITAT SELECTION BY ELK BEFORE AND AFTER WOLF REINTRODUCTION IN YELLOWSTONE NATIONAL PARK. *J. Wildl. Manage.*, 69(4):1691–1707.

McCallum, H., Barlow, N., and Hone, J. (2001). How should pathogen transmission be modelled? *Trends Ecol. Evol.*

Miller, M. W. and Williams, E. S. (2003). Prion disease: horizontal prion transmission in mule deer. *Nature*, 425(6953):35–36.

Nakagawa, S. and Schielzeth, H. (2013). A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods Ecol. Evol.*, 4(2):133–142.

Proffitt, K. M., Gude, J. A., Hamlin, K. L., Garrott, R. A., Cunningham, J. A., and Grigg, J. L. (2011). Elk distribution and spatial overlap with livestock during the brucellosis transmission risk period. *J. Appl. Ecol.*, 48(2):471–478.

Roberts, T. W., Peck, D. E., and Ritten, J. P. (2012). Cattle producers economic incentives for preventing bovine brucellosis under uncertainty. *Prev. Vet. Med.*, 107(3–4):187–203.

Sanchirico, J. N. and Wilen, J. E. (1999). Bioeconomics of spatial exploitation in a patchy environment. *J. Environ. Econ. Manage.*, 37(2):129–150.

Sargeant, G. A. and Oehler, M. W. (2007). Dynamics of newly established elk populations. *J. Wildl. Manage.*, 71(4):1141–1148.

Schumaker, B. A., Mazet, J., Treanor, J., Wallen, R., and others (2010). A risk analysis of brucella abortus transmission among bison, elk, and cattle in the northern greater yellowstone area. *Technical Report for the National Park Service.*

Scurlock, B. M. and Edwards, W. H. (2010). Status of brucellosis in free-ranging elk and bison in wyoming. *J. Wildl. Dis.*, 46(2):442–449.

Smith, B. (2012). *Where elk roam: conservation and biopolitics of our national elk herd.* Globe Pequot, Guilford, Connecticut.

Smith, B. L. (2013). Elk winter feeding= disease facilitation. *The Wildlife Professional*, (Winter 2013).

Thomas, J., Black Jr., H., Scherzinger, R., and Pedersen, R. (1979). Deer and elk. wildlife habitats in managed forests: the blue mountains of oregon and washington. *USDA Forest Service Agricultural Handbook*, 553.

U.S. Department of the Interior, U.S. Fish and Wildlife Service, and U.S. Department of Commerce, U.S. Census Bureau (2011). 2011 national survey of fishing, hunting, and wildlife-associated recreation. Technical report.

Walters, S. (2001). Landscape pattern and productivity effects on source–sink dynamics of deer populations. *Ecol. Modell.*, 143(1–2):17–32.

Wild, M. A., Hobbs, N. T., Graham, M. S., and Miller, M. W. (2011). The role of predation in disease control: a comparison of selective and nonselective removal on prion disease dynamics in deer. *J. Wildl. Dis.*, 47(1):78–93.

Williams, A. L., Kreeger, T. J., and Schumaker, B. A. (2014). Chronic wasting disease model of genetic selection favoring prolonged survival in rocky mountain elk (cervus elaphus). *Ecosphere*, 5(5):1–10.

Williams, E. S. (2005). Chronic wasting disease. *Vet. Pathol.*, 42(5):530–549.

Williams, E. S., Miller, M. W., Kreeger, T. J., Kahn, R. H., and Thorne, E. T. (2002). Chronic wasting disease of deer and elk: A review with recommendations for management. *J. Wildl. Manage.*, 66(3):551–563.

Wilson, B. (2011). *Economic impacts of brucellosis outbreaks in Wyoming cattle herds under alternative federal policies (Unpublished Thesis).* University of Wyoming, Laramie, WY.

Worton, B. J. (1989). Kernel methods for estimating the utilization distribution in home-range studies. *Ecology*, 70(1):164–168.

Wyoming Game and Fish Department (2015). Wyoming game and fish department 2015 annual report. Technical report.

Wyoming Game and Fish Department (2016a). Jackson elk herd unit (e102)brucellosis management action plan update. Technical report.

Wyoming Game and Fish Department (2016b). Pinedale elk herd unit (e108)brucellosis management action plan update. Technical report.

Zimmer, N. M. P., Boxall, P. C., and Adamowicz, W. L. (2012). The impacts of chronic wasting disease and its management on recreational hunters. *Canadian Journal of Agricultural Economics/Revue canadienne d'agroeconomie*, 60(1):71–92.

Appendix A. Resource Selection Function Methodology

To predict elk space use, we parameterized a separate Resource Selection Function (RSF) for each month of the year and for elk that were exposed to supplemental feedgrounds and those that were not (totaling 24 RSFs) (Manly et al., 2002). A resource selection function relates covariate values of used points with available points drawn from a given availability distribution (Johnson et al., 2006). We developed our RSFs at the home range or third order scale where we sampled available points from a polygon representing the area used by each animal over the course of a year.

To reduce autocorrelation in our data, we subsampled the observed GPS collar data to a single randomly selected point per day. We only used data for an individual within a month if we had acquired at least 25 days of GPS data in that month. For each individual in each year, we calculated an annual home range based on the 99% contour of the utilization distribution, calculated using a bivariate normal kernel of the subsampled GPS points and the reference method to select smoothing parameters (Worton, 1989). For the used points collected for each individual in each year in each month, we randomly sampled a paired number of locations within the individuals annual home range to represent availability.

For each used and available point we extracted a number of landscape variables expected to influence elk resource selection in the area (Mao et al., 2005; Proffitt et al., 2011; Thomas et al., 1979);. These variables included:

- elevation (30m, U.S. Geological Survey National Elevation Dataset)
- overall productivity or biomass of a habitat patch each year calculated as the annual integrated Normalized Difference Vegetation Index (NDVI, 250m resolution, MODIS data (Pettorelli et al. 2005))
- maximum snow depth a given pixel received in a given year (1 km, SNODAS)
- The density of roads (including highways and jeep trails; U.S. Department of Commerce, Bureau of the Census) within a buffer of 2.5 km of the location.

Table A.1. Resource Selection Function Parameter Estimates – Fed Elk

Variable	January	February	March	April	May	June	July	August	September	October	November	December
(Intercept)	**2.12698**	**6.86411**	**4.93429**	**3.02894**	**-1.4405**	**-1.582**	**-3.30648**	**-3.97746**	**-4.24344**	**-1.40013**	**-0.6293**	**2.13824**
csumNDVImax	**3.12765**	-0.43052	**-0.74397**	0.16473	**2.98265**	**1.23605**	-0.23068	0.264	**1.47375**	**0.98502**	**1.69571**	**1.66964**
dist2fg	**-56.0351**	**-207.174**	**-91.5381**	**-34.1306**	**-9.40695**	**2.61032**	**14.55429**	**13.91468**	**11.9445**	**1.27136**	**-11.2662**	**-28.8587**
elevation	-0.28399	-0.06304	0.10841	0.10242	**0.22855**	0.07258	**0.4436**	**0.17662**	0.02341	0.04312	0.07762	-0.04264
kmRoads	**-3.07656**	-2.36325	**-1.41314**	-0.16719	**-1.12881**	**-0.83484**	**-5.35431**	**-3.75847**	**-1.88077**	**-1.63026**	**-0.86245**	**-0.71405**
max_swe	**-2.10827**	-0.70841	**-2.61467**	**-3.31465**	**-1.20089**	**0.49536**	**2.20901**	**2.21308**	**1.93022**	**0.58119**	**-0.39728**	**-3.67315**
perc_forest	**-3.26298**	**-2.10616**	**-2.21904**	**-1.82222**	**-0.6527**	**0.25365**	0.22044	**1.99141**	**2.06511**	**0.66538**	**0.2342**	**-1.71651**
perc_herb	**3.38512**	-3.27595	**3.02469**	**2.04928**	**1.31673**	-0.23084	**-0.7705**	0.3761	**0.77459**	**0.55864**	**2.17832**	**2.62358**

Bold estimates are significant at the 5% level.

- The percent of pixels within a buffer of 2.5 km of the location that were native herbaceous, including grassland and sedge herbaceous land cover types classified by the 2011 National Land Cover Database (30m)
- The percent of pixels within a buffer of 2.5 km of the location that were forested, including deciduous, evergreen, and mixed forest land cover types classified by the 2011 National Land Cover Database (30m)
- Distance to the nearest feedground location

We parameterized the 24 RSFs using mixed-effects logistic regression. We accounted for pseudoreplication (individual-year random effects) in our GPS data by specifying a random intercept for each individual in each year. We assessed correlation among variables and found Pearson correlations coefficients to always be < 0.5, and variance inflation factors were always < 3. We validated the robustness of RSFs using 5-folds cross-validation following the methods of Boyce et al. (2002). We also report conditional R2 as a measure of the relative amount of variance explained in the data by each RSF model (Nakagawa and Schielzeth, 2013).

The mixed logit function is

$$ln\left(\frac{p_{ki}}{1-p_{ki}}\right) = \boldsymbol{X_i'\zeta} + u_k \tag{28}$$

where X_i is the set of landscape characteristics for cell i and u_k is a normally distributed random variable with mean 0 and variance σ^2. u_k is the individual-year random effect attributable to elk k in year i elk telemetry data sample. The parameters in ζ are estimated using maximum likelihood using the R function *glmer*. A predicted probability, $\hat{p}_{ik}$, as a function of coefficient values is

$$\hat{p}_{ki} = \int_{-\infty}^{\infty} \frac{exp(\boldsymbol{X_i'\zeta} + u_k)}{1 + exp(\boldsymbol{X_i'\zeta} + u_k)} f(u)du, \tag{29}$$

where $f(u)$ is the normal probability density function (pdf). The *glmer* function estimates this integral to construct a likelihood function, and then estimates the parameters using maximum likelihood estimation. Coefficient estimates are shown in tables A.1 and A.2.

Table A.2. Resource Selection Function Parameter Estimates – Unfed Elk

Row Labels	January	February	March	April	May	June	July	August	September	October	November	December
(Intercept)	**2.72662**	**1.41943**	**1.47861**	**2.16724**	**-0.93242**	**-1.58929**	-0.16532	**-1.2771**	**-1.20171**	**-2.75601**	**-0.58483**	**1.84758**
csumNDVImax	0.27644	**0.77723**	**1.32563**	**1.63985**	**4.22616**	**2.10688**	**-1.31606**	**0.40149**	**0.59716**	**1.22952**	**1.49611**	**1.20654**
dist2fg	**-3.25891**	**-1.35942**	**-1.66438**	**-4.47263**	**-3.48294**	**-1.7313**	**-2.56639**	**-1.02247**	**-1.76561**	**-0.93808**	**-1.83983**	**-2.01354**
elevation	-0.07363	0.0051	-0.0294	0.05128	0.05098	**0.17262**	**0.24167**	-0.09797	-0.06296	0.18138	0.0451	-0.21111
kmRoads	-0.0975	0.33748	0.00462	**-2.11781**	**-1.48789**	**-3.10393**	**-8.75573**	**-9.7379**	**-8.11956**	**-4.14936**	**-1.94794**	**-2.54546**
max_swe	**-5.24647**	**-4.77689**	**-4.35522**	**-4.06948**	**-1.94536**	**1.13522**	**3.18697**	**2.5372**	**1.39898**	0.15515	**-2.31122**	**-2.70291**
perc_forest	**-1.20466**	**-1.38017**	**-2.87483**	**-3.37132**	**-1.06508**	**0.74996**	**0.65645**	**2.59417**	**2.99117**	**3.80605**	**1.95245**	**-1.35096**
perc_herb	**-1.38734**	**-1.89499**	**-1.53297**	**-1.20542**	**-1.51252**	**-2.21077**	**2.13206**	0.65695	**0.99499**	**2.62605**	**0.77614**	**-1.33331**

Bold estimates are significant at the 5% level.

Appendix B. Additional Figures

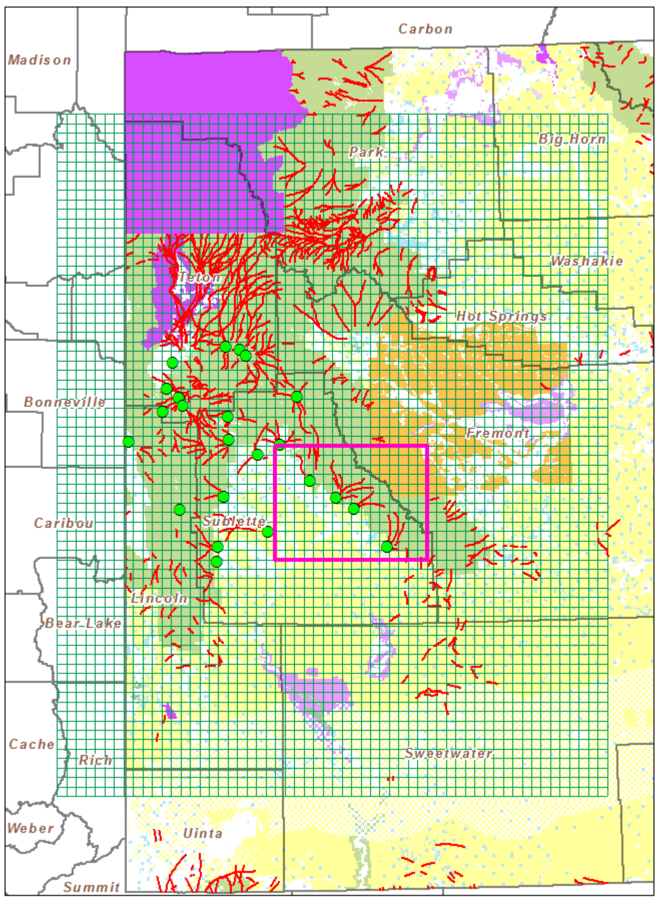

Figure B.1. Grid Illustrating Feasible Study Area using Our Data
White is private land, green is U.S. Forest Service land, yellow is Bureau of Land Management land, and blue is state-owned land. Green dots are feedground locations, and red lines indicate typical elk migration patterns.

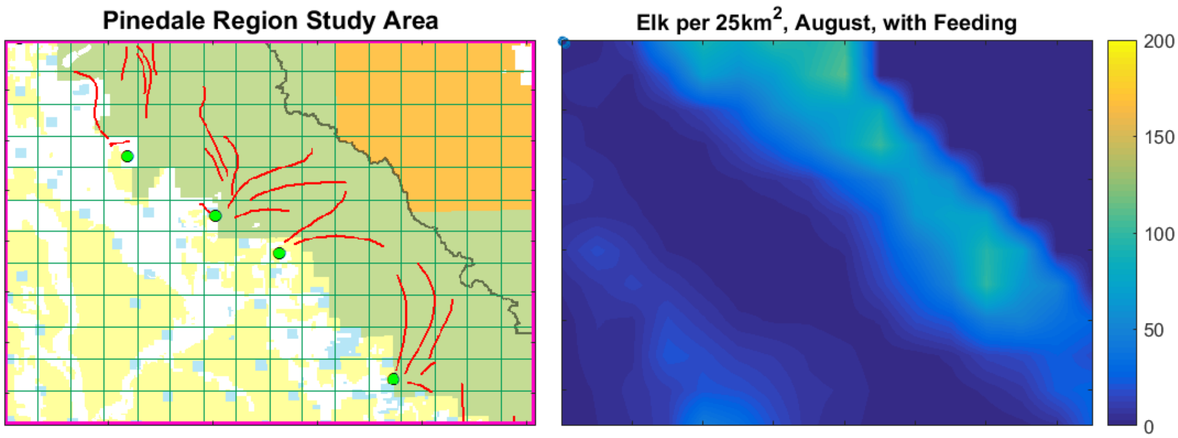

FIGURE B.2

The left image is a map of the study area, with base colors indicating land ownership. White is private land, green is U.S. Forest Service land, yellow is Bureau of Land Management land, and blue is state-owned land. Green dots are feedground locations, and red lines indicate typical elk migration patterns. The right image shows our model's prediction of elk population density in August, assuming feeding is discontinued but current population levels are maintained.

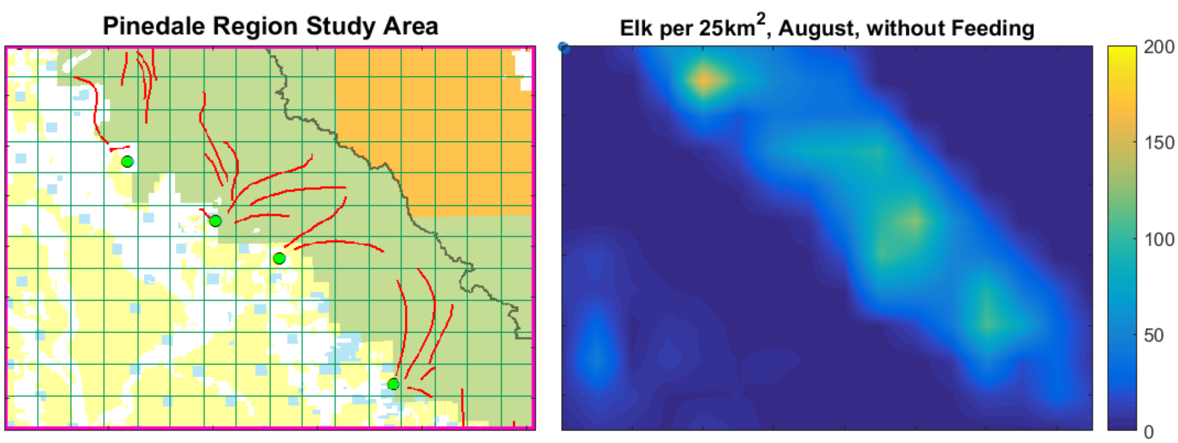

FIGURE B.3

The left image is a map of the study area, with base colors indicating land ownership. White is private land, green is U.S. Forest Service land, yellow is Bureau of Land Management land, and blue is state-owned land. Green dots are feedground locations, and red lines indicate typical elk migration patterns. The right image shows our model's prediction of elk population density in August, assuming feeding is discontinued but current population levels are maintained.

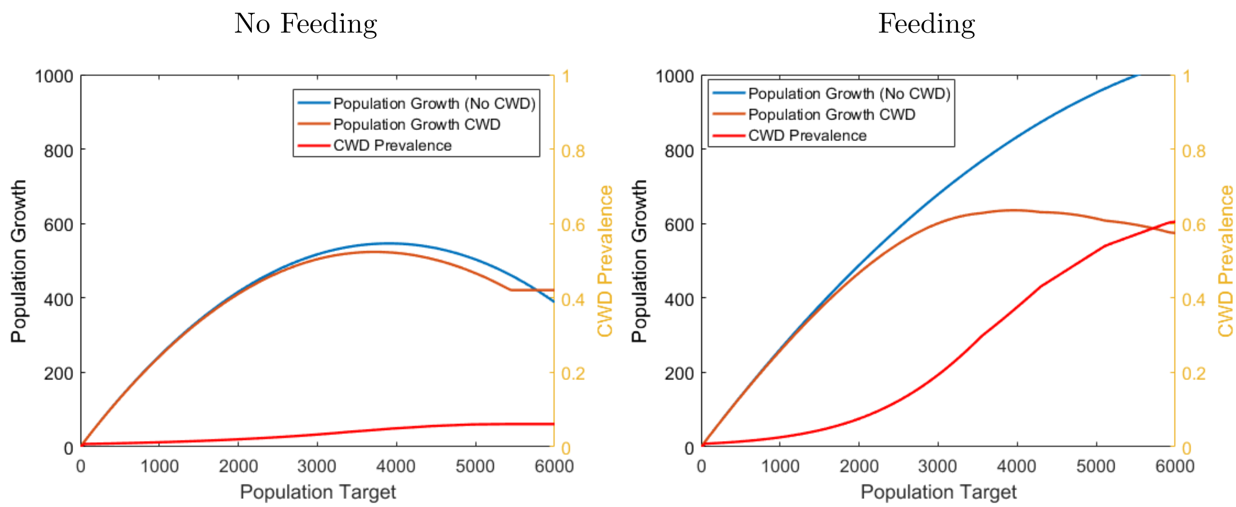

FIGURE B.4. Biological Productivity & CWD Prevalence at 5 Years

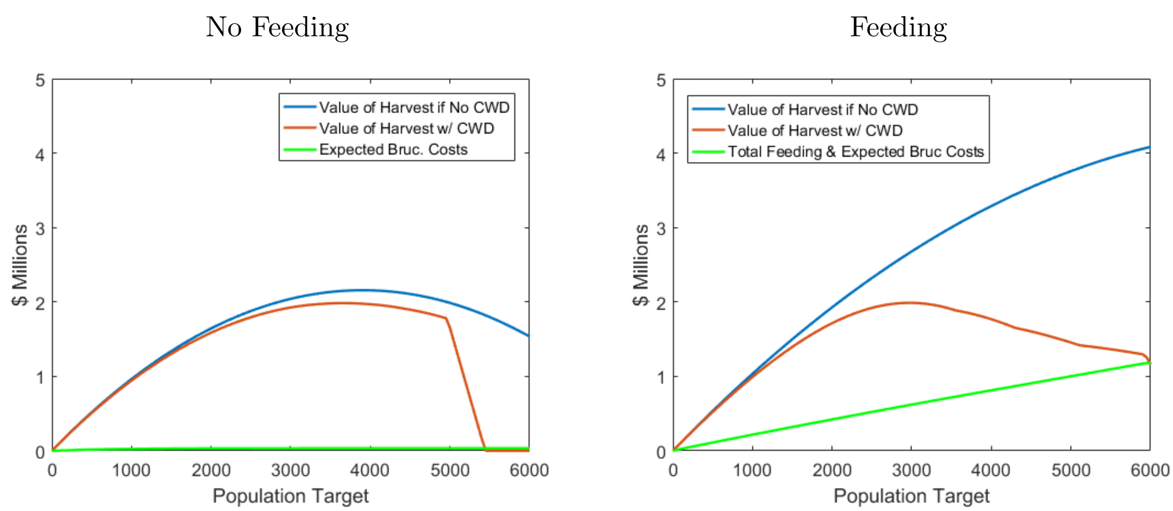

FIGURE B.5. Harvest Value & Costs at 5 Years