Chronic Wasting Disease Undermines Efforts to Control the Spread of Brucellosis in the Greater Yellowstone Ecosystem

Supporting Information

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1 Detailed Methodology: Growth, Hunting, Disease Transmission, and Elk Movement

There are three state variables in the model: total elk population, $N_{i,t}^{(j)}$, susceptible sub-population, $S_{i,t}^{(j)}$, and infected sub-population, $I_{i,t}^{(j)}$, such that $N_{i,t}^{(j)} = S_{i,t}^{(j)} + I_{i,t}^{(j)}$. Each population is indexed by i to represent a particular location or cell, and by $t = 1, \ldots, T$ to represent time in months. There are a total of n cells. The superscript j varies from 0 to 4 to index five stages or processes that may occur within a particular month: growth/reproduction, hunting mortality, disease mortality, disease transmission, and spatial movement.[1] A state variable with index j represents the value of the state variable at the end of stage j. The index 0 is used to indicate the initial population levels at the start of a new period t, which is also the population level after the 5th stage of intra-month dynamics from period $t - 1$.

1.1 Stage 1: Elk Growth

Stage 1 is elk recruitment and natural, non-CWD mortality. This occurs at the beginning of June and only occurs in this month. Births typically occur around June. For simplicity, it is also assumed that all non-CWD natural mortality occurs in June as well. This is unrealistic, but is consistent with most models that are based on annual time steps. Reproduction only adds to the susceptible population because mother-calf transmission (vertical transmission) plays only a minor role in the spread of CWD [1]. Accordingly, it is assumed that all elk calves are born as susceptible and so

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

[1] Parentheses are used in the superscripts to distinguish intra-seasonal stages from exponents.

Reproduction and natural death are modeled by logistic growth,[2]

$$S_{i,t}^{(1)} = S_{i,t}^{(0)} + N_{i,t}^{(0)} r(1 - \frac{N_{i,t}^{(0)}}{K(F_t)}) \tag{S.2}$$

Parameter r is the intrinsic growth rate. The rate used here is the maximum estimated by [2] and close to the maximum estimated by [3] 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. The term $K(F_t)$ is the carrying capacity, which depends on the quantity of supplemental feeding at time t, F_t. Unlike in the spatial model introduced by [4], carrying capacity is specified for the entire region rather than being cell specific. This is because elk move throughout the GYE during the year but reproduce only once a year. 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. The explicit relationship between carrying capacity and feeding is

$$K(F_t) = \frac{K_0}{(1-\tau F_t)}, \text{with } \tau < \frac{1}{F^{max}}, \tag{S.3}$$

where K_0 is the natural carrying capacity of the region and τ is a parameter that measures the effectiveness of feeding in increasing carrying capacity, and F^{max} is a parameter indicating the

[2] Although elk gestation is quite long (240+ days), reproduction depends on the stage 0 population, which is the surviving population from the previous year. We also note that our model abstracts from gender and age distributions of the elk population.

maximum reasonable feeding level for the region. This specification is consistent with [5] and is of the same form used in previous bioeconomic models of wildlife disease [6].

1.2 Stage 2: Elk Hunting

Stage 2 is elk hunting, which is assumed to occur exclusively in October. The total number of harvested elk across all cells at time t, h_t, is determined by a regional planner. The number of elk harvested in an individual cell i, $h_{i,t}$, is the percentage of the total elk population inhabiting cell i multiplied by the total harvest, h_t; i.e., harvesting is distributed proportionally to population. Moreover, elk harvesting is distributed proportionally across the infected and susceptible populations because selective harvest is difficult, a common problem in wildife disease management (e.g., see [7])[3]. In October, the changes in the susceptible and infected elk populations are

$$S_{i,t}^{(2)} = S_{i,t}^{(1)} - \frac{S_{i,t}^{(1)}}{\sum_i^n N_{i,t}^{(1)}} h_t \tag{S.4}$$

$$I_{i,t}^{(2)} = I_{i,t}^{(1)} - \frac{I_{i,t}^{(1)}}{\sum_i^n N_{i,t}^{(1)}} h_t. \tag{S.5}$$

1.3 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 stage 3 changes in the susceptible and infected populations are

$$S_{i,t}^{(3)} = S_{i,t}^{(2)} \tag{S.6}$$

[3] This claim is also supported by conversations with local hunters in Laramie, WY, where CWD is endemic in the elk population.

$$I_{i,t}^{(3)} = I_{i,t}^{(2)}(1-\mu). \tag{S.7}$$

The elk mortality in (S.7) is additive in the sense that it occurs after mortality from the hunting in Stage #2. We acknowledge that in practice a portion of elk mortality might be compensatory as predation (not modeled here) or selective harvesting (also not modeled here) could act to reduce the portion of the infected elk population that experience mortality due to CWD.

1.4 Stage 4: Disease Transmission

Stage 4 is 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 [8,9,10]. This could be due to high accumulation of infectious prions in densely populated areas [8].

We adopt the standard density-dependent disease transmission function to model the number of new elk CWD infections in cell i at time t as $\beta S_{i,t} I_{i,t}$ [11,12]. This functional form is based on a contact rate that increase linearly with population density. That is, the contact rate is $\kappa N_{i,t}$, where κ is a parameter. This means total infectious contacts per susceptible individual are $\kappa N_{i,t} S_{i,t}$, with only a fraction of those contacts, $I_{i,t}/N_{i,t}$, being with infected individuals so that $\kappa N_{i,t} S_{i,t}$ represents total infectious contacts. Only a fraction of these contacts, γ, lead to infection, so that $\beta S_{i,t} I_{i,t}$ represents disease transmission, where $\beta = \gamma\kappa$ [11]. 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 [11].

In aspatial models that include feeding, the transmission function is often modified by making the contact rate, and therefore β, a function of feeding [13,6]. An advantage of our spatial modeling approach is that such an augmentation to transmission is largely unnecessary because population densities in a cell, and hence transmission, already increase differentially in response to levels of feeding being provided in a cell. Using the density-dependent relationship defined above, the expected changes in susceptible and infected populations in stage 4 are

$$S_{i,t}^{(4)} = S_{i,t}^{(3)} - \beta S_{i,t}^{(3)} I_{i,t}^{(3)} \tag{S.8}$$

$$I_{i,t}^{(4)} = I_{i,t}^{(3)} + \beta S_{i,t}^{(3)} I_{i,t}^{(3)}. \tag{S.9}$$

To capture CWD environment-to-elk dynamics, we create an environmental contamination state variable $P_{i,t}$ that varies across space and time. The variable $P_{i,t}$ captures the prion contamination in the environment due to CWD-infected elk residency and mortality. The law of motion is

$$P_{i,t+1} = (1-\gamma)P_{i,t} + \delta_1 I_{i,t} + \delta_2 \mu I_{i,t} = (1-\gamma)P_{i,t} + \delta_P I_{i,t} \tag{S.10}$$

where $\gamma > 0$ is the decay rate and $\delta_P = \delta_1 + \delta_2 \mu$. New CWD infections from environment-to-elk transmission are then given by $\beta_P S_{i,t} P_{i,t}$, where β_P is the environment transmission parameter. Figure S.5 shows the elk-to-elk and environment-to-elk CWD transmission for the FPT

management practice. Elk-to-elk transmission falls quickly as the new (and lower) population target is realized. Both type of transmission than increase gradually over time as infections rise. The feeding scenario has fewer infections because the elk population target is much lower with supplemental feeding.

Also occurring in stage 4 is brucellosis transmission from elk to cattle. Brucellosis is a disease that, unlike CWD, is already endemic in GYE elk populations and spreads from elk to cattle. The probability of a cow being infected in cell i at time t is given by the density-dependent transmission function $\beta_B \theta_{B,t} N_{i,t}$, where β_B is the brucellosis transmission parameter and $\theta_{B,t}$ is the brucellosis prevalence in the elk population (so that $\theta_{B,t} N_{i,t} = I_{i,t}$ for brucellosis).

For simplicity, the disease dynamics of brucellosis in the elk population are not modeled by a compartmental SI framework. Rather, 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 [14] estimate a prevalence of 3.7% in unfed populations and 21.9% in fed populations. Schumaker et al. [15] report rates of less than 5% in unfed populations and a slightly higher estimate of 26% in fed populations. Recent data in unfed elk herds in the GYE show evidence of increasing brucellosis prevalence in unfed elk populations [16]. Using this data, the relationship between the steady-state brucellosis prevalence, $\hat{\theta}_B$, and feeding is assumed to take the following linear form:

$$\hat{\theta}_B(F_t) = \underline{\theta}_B + (\bar{\theta}_B - \underline{\theta}_B)\frac{F_t}{F^{max}}, \tag{S.11}$$

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

$$\theta_{B,t} = \theta_{B,t-1} + \delta(\hat{\theta}_B(F_t) - \theta_{B,t-1}), \tag{S.12}$$

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 $N_{i,t}L_{i,t}$ in the transmission function, where $L_{i,t}$ is the number of cattle (livestock) in cell i in period t. 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 transmission to cattle occurs between January and June. The expected number of newly-infected cattle in cell i in period t is

$$\beta_B \theta_B(F_t) N_{i,t}^{(3)} L_{i,t}^{(3)}. \tag{S.13}$$

If a cow becomes infected with brucellosis, the U.S. Department of Agriculture Animal and Plant Health Inspection Service (USDA-APHIS) requires the entire cattle herd be quarantined or culled, at a significant cost to the rancher, the states, the U.S. Department of Agriculture (USDA), or all three entities [17]. Note that brucellosis infections in cattle are so rare that equation

(S.13) 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 section 2.2 below.

1.5 Spatial Structure & Stage 5: Elk Movement

The final stage in each period is elk movement. We assume all elk (infected and susceptible) move in a two-dimensional rectangular grid consisting of n 25 km^2 cells. The cell index 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 S.1.

The likelihood of an elk moving from any cell i to any cell j in stage 5 is governed by the $n \times n$ 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

$$\mathbf{S}_{\mathbf{t+1}}^{(\mathbf{0})} = \mathbf{J}\mathbf{S}_{\mathbf{t}}^{(\mathbf{4})} \tag{S.14}$$

$$\mathbf{I}_{\mathbf{t+1}}^{(\mathbf{0})} = \mathbf{J}\mathbf{I}_{\mathbf{t}}^{(\mathbf{4})}, \tag{S.15}$$

where S and I are $n \times 1$ column vectors of the susceptible and infected populations. J is calculated by taking the Hadamard product (element by element multiplication) of two $n \times n$ matrices, M and Z, and then normalizing the columns to sum to 1.

The first matrix (M) is a movement matrix. Each element of M, $m_{i,j}$, gives the rate 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[4]. M is generated by first calculating a symmetric $n \times n$ matrix, which we call Q, that contains the shortest rook movement distances from the center of any cell i to the center of any other cell j. Letting $q_{i,j}$ be an element of Q, M is generated by performing the following operation on each element of Q:

$$M = G(q_{i,j} + 2.5) - G(max\{q_{i,j} - 2.5,0\}). \tag{S.16}$$

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

The construction of the movement matrix, M, is best illustrated through an example. Consider the 3×3 landscape in Figure S.2, in which numbers denote the cell index and the cell size is 25 km^2. Consider the element of M that corresponds to moving from cell 1 to cell 5. First, the shortest paths from the center of cell 1 (point A) to the center of cell 5 (point B) are determined if elk are constrained to rook movement. The line in Figure S.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 (i.e., cells 3, 5, and 7).

The second matrix, Z, has elements z_i that are probabilities of an elk inhabiting a

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

particular cell divided by the probability of an elk inhabiting any other location within its home range, 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 $Z_{\mu,F}$ matrices, one for each month for each type of elk population (fed and unfed). The subscript μ denotes the month (1 to 12) and the subscript F denotes the feeding status.

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:

$$w(\mathbf{X_i}) = exp(\mathbf{X_i}'\boldsymbol{\zeta}). \tag{S.17}$$

where ζ is a vector of coefficients that need to be estimated. Descriptions of all the landscape characteristics included in X are given in section 2.5. 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 any other location within its home range. 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 estimate the relative probability of animal populations inhabiting one area compared with other areas [18]. Parameter estimates for the vector ζ were obtained using a mixed-effects logistic regression (see section 2.5 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 S.2 and S.3 for parameter estimates). The influence of elk density on movement is not included in the model. 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 μ and population F is an $n \times n$ matrix consisting of n duplicated columns generated by taking the product of an $n \times 1$ vector of the estimated RSF functions for each cell and a $1 \times n$ vector of ones:

$$Z_{\mu,F} = \begin{bmatrix} exp(\mathbf{X_1}'\hat{\boldsymbol{\zeta}}_{\boldsymbol{\mu},\mathbf{F}}) \\ exp(\mathbf{X_2}'\hat{\boldsymbol{\zeta}}_{\boldsymbol{\mu},\mathbf{F}}) \\ \vdots \\ exp(\mathbf{X_n}'\hat{\boldsymbol{\zeta}}_{\boldsymbol{\mu},\mathbf{F}}) \end{bmatrix} [1 \quad 1 \quad 1]. \tag{S.18}$$

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 traveling 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 3×3 grid in Figure S.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.

2 Model Calibration and Parameter Values

2.1 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 [19] 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)[5]. The population target for the JEH is 11,000 individuals [20], which is 18.6% of the carrying capacity estimated by [19]. This ratio can be applied to the total elk population that visits the four feedgrounds in our case study (2,904) to arrive at a carrying capacity estimate of approximately 15,613 under existing feeding practices [21].

To simplify the analysis, we treat supplemental elk feeding as a binary choice and apply the normalization $\tau = 0.5$. Therefore, if $F = 1$, supplemental feeding is set at current levels and the carrying capacity is $K(F = 1) = 15{,}613 = \frac{K_0}{(1-\tau F_t)} = \frac{K_0}{(1-0.5\times 1)}$, such that $K_0 = 7{,}806.5$. If the elk feedgrounds are closed, then $F = 0$ and the carrying capacity is $K(F = 0) = K_0$ is at its natural level. We also consider spatial variation in feeding, such that some feedgrounds remain open and others are closed down. In future research, we intend to consider a continuous feeding variable such that F can be selected from the range of $(0, F^{max})$.

According to the Wyoming Game and Fish (WGF) Department, the FY 2015 budget for feedgrounds was $2,814,068 and 14,800 elk were estimated to have used feedgrounds [22]. This implies an annual per-elk cost of feeding of $190.14, or $15.85 per month if the cost is spread out evenly over the year. The monthly cost is denoted c_z in the model. The parameter values used in this case study are shown in Table S.1.

2.2 Ranching Values

[5] WGF unpublished data

Cells with greater than 50% private land are classified as private. For each private cell, unpublished agricultural data[6] are used to derive a herd size estimate of 197.8 head of adult cows per private cell (see Table S.1). From July to October, cattle are assumed to 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 [23], Roberts et al. [17] 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 [17] 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 [17,23]. We assume that herds are quarantined for a year if an infection is detected, which has become more common with USDA budget limitations [17]. 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 $q = (\$366.25/6) = \$61.04$.

Ranchers can invest in self-protection measures to reduce the risk of brucellosis infection during the winter. These measures have varying levels of cost, ranging from low-cost options such as vaccination to high-cost options such as building elk-proof fence and delayed grazing [3]. For simplicity, we assume ranchers can choose a level of self-protection against brucellosis infection

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

as represented by the indicator variable: $\Phi_{i,t} \in [0,1]$, where $\Phi_{i,t} = 0$ indicates no protection and $\Phi_{i,t} = 1$ indicates full protection. The effectiveness of the self-protection is given by the function $\varphi_{i,t} = \varphi_0 \Phi_{i,t}^{\varphi_1}$ such that the probability of at least one cow in a cell becoming infected in expression (5) is reduced by $100 \times \varphi_{i,t}$ percent. The per-cow bi-monthly cost of self-protection is given by the function $c_{i,t} = c_0 \Phi_{i,t}^{c_1}$, which is reduced for the rancher by $100 \times c_g$ percent through government subsidies.

We now turn to the calibration of the self-protection effectiveness and cost functions. To begin, we assume that the self-protection effectiveness function is linear and full intensity is 100% effective. These two assumptions imply that $\varphi_0 = \varphi_1 = 1$. To calibrate the self-protection cost function, we specify three points along the curve as shown in Figure S.6. First is the origin with $\Phi = 0$, which is associated with zero self-protection costs (and zero effectiveness). Second is the endpoint with $\Phi = 1$, which is associated with full effectiveness against brucellosis infection at a bi-monthly cost of $25,966 for a rancher with 200 head ($c_0 = \$25{,}966/200$ per cow). To ensure 100% effective self-protection, it will require an action such as building an elk-proof fence around the perimeter of the winter pasture and continuing to feed the animals during the "shoulder" season when elk are calving and there is risk of brucellosis transmission. The annualized cost of building a 15-year lifespan elk-proof fence around the entire 20 km perimeter of a cell assuming a 3% discount rate is $126,226 per year [24]. The cost of feeding a herd of 200 cows from April 15 to July 20 is estimated to be an additional $22,527 per year [23]. The total annual cost of these two protective measures is therefore $155,793 per year or $25,966 on a bi-monthly basis.

The third is the interior point. We assume a self-protection intensity index of $\Phi = 0.5$ will lead to $3,124 in bi-monthly costs (and reduce the probability of a quarantine by 50%). The protection level of $\Phi = 0.5$ assumes three imperfect self-protection measures: fencing haystacks,

vaccination and hazing elk. The annualized cost of fencing haystacks for a cow-calf operation of 400 adult cows is $103 in 2010, and the annualized cost of an adult vaccine booster for a ranching operation of the same size is $797 in 2010 dollars [17,23]. Combined, the annual cost of these two protection measures for an operation of 200 adult cows (the approximate stocking density for our 5×5 km cell) is $489. Hazing costs are assumed to $100 per day over a six month period for an annual total of $18,255. The total annual self-protection costs are $18,744, or $3,124 on a bi-monthly basis.

Using these three points and the functional forms described above, the calibrated values of the free curvature parameter is $c_1 = 3.055$. The fitted function and the three calibration points (red dots) are shown in Figure S.6. Later in this document, we implement a full sensitivity analysis, which includes variation in the self-protection parameters.

In addition to damages from brucellosis, we also include the costs related to destruction of fences, damages to crops, and general depredation from elk on private land. These costs are assumed to be proportional to the number of elk on private land such that the total costs are given by $c_N \times N_{i,t}$, where c_N is the monthly cost per elk. The depredation cost c_N is set to $10 per elk per month.[7]

2.3 Harvesting Values

The net value of elk harvests within the GYA is the economic surplus acrruing to hunters and to local suppliers of hunting products and services. Assuming hunters already possess most of their gear, the primary cost of a hunting trip involves services. This means hunter expenditures, which are simply a transfer payment to service providers, do not affect aggregate surplus in this

[7] Unpublished Wyoming Game & Fish data

sector. Aggregate surplus in this sector is then the total willingness to pay by hunters less the opportunity cost of service provision.

Published estimates of these values are scarce. Focusing on elk hunting in Oregon, Fried et al. [25] report mean hunter expenditures of $297/trip. Assuming these revenues accrue to local businesses and that these businesses receive a 30 percent markup, then the costs of service provision are $207.90. Dividing this value by the success rate of 41 percent yields the unit cost of a harvested elk to be $507.07, which we adopt. Fried et al. [25] also estimated the mean willingness to pay for a harvested elk (or the marginal willingness to pay for a harvested elk, MWTP) to be approximately $2250 when adjusted to 2015 dollars. This number is based on estimates of hunting trip benefits as well as assumptions about the probability of obtaining a shot at an elk and the ensuing success rate. Uncertainty about these values means there is wide variabiltiy in the MWTP value. We choose a willingness to pay per trip value of $307, the probability of obtaining a shot at an elk of 0.6748, and an ensuing success rate of 0.41. The trip value is only slightly above the reported mean value to ensure the value exceeds the cost per trip. The success rate is the same as Fried et al.'s value, and the probability of attaining a shot is 0.31 of a standard deviation from their estimate. These values result in a MWTP of $1553.74, and a net MWTP of Y = $2208 in 2015 dollars. We choose this value both because it is reasonable and because, absent CWD, it yields identical social welfare with and without supplemental feeding. By calibrating the harvest value in this way, our analysis remains neutral on whether supplemental feeding is economically optimal prior to the introduction of CWD into the case study area. Later in this document, we perform a sensitivity analysis where the elk harvest benefit is varied over a wide range of values and our main results do not change.

If the prescribed reductions in elk populations are not feasible in the short term through

hunting only, the Wyoming Game & Fish Department may be required to coordinate elk depopulation activities via a catch-and-slaughter approach to achieve a population target. This depopulation would impose a cost on the agency rather than provide a benefit to hunters. We assume that for our case study area, a maximum of 1,000 elk can succesfully be hunted within a year and the remainder of the necessary harvests are achieved by the agency at a fixed cost of $406.20 per elk. The maximum of 1,000 elk is derived from 2018 Wyoming Game & Fish elk harvest surveys (https://wgfd.wyo.gov/) and the depopulation cost (in 2015 dollars) is calculated using Table A.3.1. in Boroff et al. [24] assuming no equipment or brucellosis testing costs.

2.4 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% [10], but is 30% or greater for high-density captive populations. 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 may exceed 30%. To analyze the former criterion, a 20-year simulation is run where unfed elk are harvested to maintain a target population of 2,000, which is approximately two-thirds of the current population of the case study area around Pinedale, WY. We run this simulation 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 0.00084. We set $\beta = 0.00045$, which is the midpoint of these two values and experiment with other values in the sensitivity analysis.

There are three parameters to calibrate in the environmental contamination equations. The environmental prion decay is set at a very low annualized rate $\gamma = 0.01$ [26]. Given the available data, it is not possible to calibrate the environmental contamination parameter, δ_P, and the environment-to-elk transmission parameter, β_P. Therefore, we normalize so that $\delta_P = 1$ and select β_P such that the year-20 average CWD prevalence is 10% in an unfed population held fixed at the current population of 2,904. The resulting value is $\beta_P = 0.000003473$.

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 confidently calibrate β_B, we 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 [27] use a simple model to estimate a value of between 0.0005 and 0.001 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. [28] 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 0.000044. We chose to use this value in our analysis because it yields plausible results: at a value of $\beta_B = 0.000044$, 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.

2.5 Elk Movement

Elk move in space according to the methodology outlined in Section 1.5. To predict elk movement, we parameterize separate Resource Selection Functions (RSFs) for each month of the year and for elk that were exposed to supplemental feedgrounds and those that were not (totaling 24 RSFs) [29]. An RSF relates covariate values of used points with available points drawn from a given availability distribution [18]. 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 [30]. For the used points collected for each individual in each year in each month, we randomly sampled a paired number of locations within the individual's annual home range to represent availability.

For each used and available point we extract a number of landscape variables expected to influence elk resource selection in the area [31,32,33]. These variables include:

- 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 (csumNDVI, 250m resolution, MODIS data [34])
- Maximum snow depth a given pixel received in a given year (max_swe, 1 km, SNODAS)
- 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 (km_roads)
- 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 (perc_herb, 30m)
- 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 (perc_forest, 30m)
- Distance to the nearest feedground location (dist2fg)

We parameterize the 24 RSFs using mixed-effects logistic regression. We account for pseudoreplication (individual-year random effects) in our GPS data by specifying a random intercept for each individual in each year. We assess correlation among variables and found Pearson correlations coefficients to always be < 0.5, and variance inflation factors were always < 3. We validate the robustness of RSFs using 5-folds cross-validation following the methods of Boyce et al. [35]. We also report conditional R^2 as a measure of the relative amount of variance explained in the data by each RSF model [36]. Coefficient estimates are shown in Tables S.2 and S.3.

2.6 Sensitivity Analysis

To assess the robustness of the results, we perform a sensitivity analysis by running the fixed population targeting (FPT) algorithm after the introduction of CWD under an array of alternative parameter values. Recall, CWD has spread across Wyoming and will likely soon be introduced into GYE elk populations [37]. The various parameter values were created by multiplying each of the default parameter value by factors of 0.01, 0.1, 0.5, 0.75, 1.25, 1.5, 10, and 100. Only one parameter value was changed at a time; the remaining parameters were held at their default values. The optimal population target, welfare, and feeding choice were recorded for all alternative parameter values. The present-value welfare loss (in millions of dollars) from continuing the supplemental feeding program is shown in Table S.4 for an array of alternative parameter values. Positive values indicate a welfare loss from continuing to feed, while negative values indicate that continuing to feed is economically optimal. Cells with "n/a" either have parameter values that fall outside logical bounds or the simulations[8] failed. The "†" symbol indicates that the optimal elk population target is zero either with feeding, without feeding, or both. Eliminating the entire elk population from the case study region is likely to be politically infeasible or suboptimal so these cases are marked accordingly. There are no parameter values with positive elk population targets where it is economically optimal to continue feeding, which suggests our main result is robust.

The welfare estimates are most sensitive to changes in the CWD transmission rate, the carrying capacity, the cost of feed, the intrinsic elk growth rate, the value of a harvested elk, and

[8] The 100-year time horizon for the simulations eliminates the need to make an assumption about the terminal values at the end of a shorter time horizon. If we were to use a terminal value at time T_* instead of running the simulation for another $T - T_*$ years, it is likely that discounting the benefits to time T_* would probably be the best way to estimate that terminal value. This argues for choosing a long time horizon and discounting the benefits accordingly.

the discount rate. Discontinuing feeding is a robust management strategy, as there were no cases of alternative parameters where feeding is economically optimal and the elk population target is positive. A possible criticism of our analysis is that the default carrying capacity of 7,806.5 may be too high. With a carrying capacity of half that size (3,903.25), the welfare loss is 57% lower, but it is still optimal to discontinue feeding.

Finally, to investigate the relationship of CWD to hunter demand, we modified the demand relationship to include an additional coefficient, V:

$$Y_t = (1 - V\theta_t)\bar{Y}. \tag{S.19}$$

In our default analysis, V is equal to one. To test the possibility of CWD having a smaller influence on demand, we re-ran the FPT analysis under an array of smaller values for V: 0.01, 0.1, 0.5, and 0.75. The results are shown in the last row of Table S.4. Results are insensitive to changes in V because it remains optimal to manage elk so that the CWD prevalence remains low (so θ_t is small), and it is still optimal to discontinue feeding.

Table S.1. Case Study (Pinedale, WY, USA) Parameter Values

	Description	Value	Source
L_p	cows per private cell	197.8	unpublished data
μ	CWD mortality rate	0.128 (annualized)	derived from [8]
r	elk intrinsic growth rate	0.28	[2, 3]
$K(0)$	carrying capacity	7,806.5	[19], WGF
$\bar{Y}$	CWD-free harvest value	$2,808	U.S. FWS, WGF
z	feeding cost per elk	$190.14 (annualized)	WGF
β	elk-elk CWD transmission rate	0.00045	calibrated
β_P	environ-elk CWD transmission rate	0.000003473	calibrated
γ	environmental prion decay rate	0.01 (annualized)	assumption
δ_P	environmental contamination	1.0	assumption
τ	feeding capacity parameter	0.5	assumption
ρ	discount rate	0.03 (annualized)	assumption
$\underline{\theta}_b$	min brucellosis prevalence*	0.26	[15]
$\bar{\theta}_b$	max brucellosis prevalence*	0.26	[15]
β_B	elk-cattle brucellosis transmission	0.000044	[28]
q	average quarantine cost	$61.04	[17]
φ_0	quarantine risk scale parameter	1.00	assumption
φ_1	quarantine risk curvature parameter	1.00	assumption
c_0	self-protect cost scale parameter	129.83	calibrated
c_1	self-protect cost curvature parameter	3.06	calibrated
c_N	monthly cost per elk on private land	$10	WGF
c_g	government subsidy fraction	0.5	assumption
δ	brucellosis dissipation rate	0.1 (annualized)	assumption

Notes. WGF = Wyoming Game & Fish; FWS = Fish and Wildlife Service *See [38,39] for recent elk populations at the four feedgrounds in our case study area, and evidence of higher brucellosis prevalence in unfed elk herds.

Table S.2. Resource Selection Function Parameter Estimates – Fed Elk

Variable	Jan.	Feb.	March	April	May	June	July	August	Sept.	Oct.	Nov.	Dec.
(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**
csumNDVI	**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
km_roads	**-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**

Note. Bold estimates are significant at the 5% level.

Table S.3. Resource Selection Function Parameter Estimates – Unfed Elk

Variable	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
(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**
csumNDVI	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
km_roads	-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**

Note. Bold estimates are significant at the 5% level.

Table S.4. Sensitivity Analysis: Welfare Loss in Millions of Continuing to Feed Elk after CWD (Parameters Scaled Up and Down)

Parameter	Multiplier								
	0.01	0.1	0.5	0.75	1	1.25	1.5	10	100
L_p	\$20.95	\$20.93	\$20.45	\$19.84	\$19.00	\$17.96	\$16.71	**-\$0.86**†	**-\$54.77**†
μ	\$16.90	\$17.09	\$17.97	\$18.51	\$19.00	\$19.44	\$19.82	\$5.77	\$0.03
r	\$0.32†	\$0.32†	\$9.19	\$14.30	\$19.00	\$23.18	\$26.79	n/a	n/a
$K(0)$	n/a	\$93.20†	\$9.28	\$14.86	\$19.00	\$22.13	\$24.55	\$38.00	\$40.87
$\bar{Y}$	\$0.41†	\$0.56†	\$11.10	\$15.15	\$19.00	\$22.79	\$26.51	\$150.32	\$1,456.06
z	\$12.10	\$12.77	\$15.66	\$17.37	\$19.00	\$20.59	\$22.12	\$33.33†	\$65.79†
β	\$9.32	\$11.68	\$18.23	\$19.31	\$19.00	\$18.33	\$17.52	\$5.46	n/a
β_P	\$19.04	\$19.58	\$20.20	n/a	\$19.00	\$18.38	\$17.79	\$8.90	n/a
γ	\$18.64	\$18.67	\$18.82	\$18.91	\$19.00	\$19.09	\$19.18	\$20.49	\$19.38
τ	\$20.39	\$20.28	\$19.73	\$19.39	\$19.00	\$18.61	\$18.19	n/a	n/a
ρ	\$55.18	\$48.69	\$30.04	\$23.48	\$19.00	\$15.85	\$13.55	\$1.60	\$0.23
$\underline{\theta}_b$	\$21.28	\$21.06	\$20.12	\$19.56	\$19.00	\$18.46	\$17.94	n/a	n/a
$\bar{\theta}_b$	\$18.19	\$18.27	\$18.61	\$18.81	\$19.00	\$19.19	\$19.37	n/a	n/a
β_B	\$20.93	\$20.75	\$19.95	\$19.48	\$19.00	\$18.54	\$18.10	\$6.35	n/a
q	\$20.93	\$20.75	\$19.96	\$19.48	\$19.00	\$18.54	\$18.09	\$5.10	**-\$0.22**†
φ_1	\$20.88	\$20.42	\$19.41	\$19.14	\$19.00	\$18.95	\$18.93	\$0.23†	\$0.23†
c_0	\$19.90	\$19.14	\$19.03	\$19.02	\$19.00	\$19.00	\$18.99	\$18.96	\$18.94
c_1	\$0.23†	\$0.23†	\$18.94	\$18.94	\$19.00	\$19.10	\$19.21	\$20.42	\$20.88
c_N	\$20.29	\$20.17	\$19.65	\$19.33	\$19.00	\$18.68	\$18.37	\$8.47	**-\$0.87**†
c_g	\$19.03	\$19.03	\$19.03	\$19.02	\$19.00	\$18.96	\$18.85	n/a	n/a
V	\$18.34	\$18.69	\$19.14	\$19.11	\$19.00	n/a	n/a	n/a	n/a

The number in each cell is the difference in the present-value welfare without supplemental feeding less with supplemental feeding. The management practice is FPT after the introduction of CWD. †At least one of the two population targets for elk is zero. "n/a" cells refer to cases where the parameters exceed logical bounds or the simulations failed. Cells where the welfare difference is negative are in bold.

Figure S.1. Example of Cell Indexing in a 2 × 3 Landscape

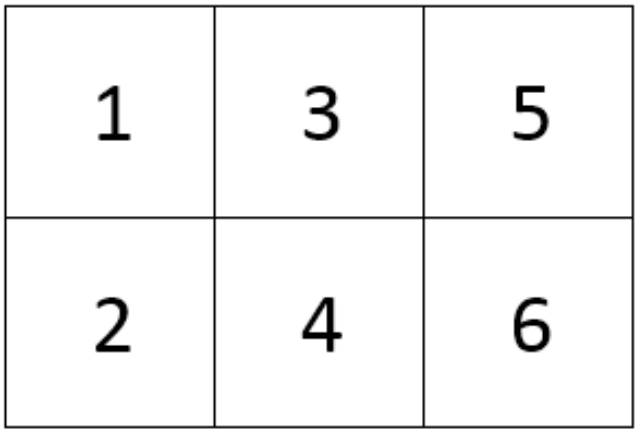


Figure S.2. Example of Elk Movement in a 3 × 3 Landscape

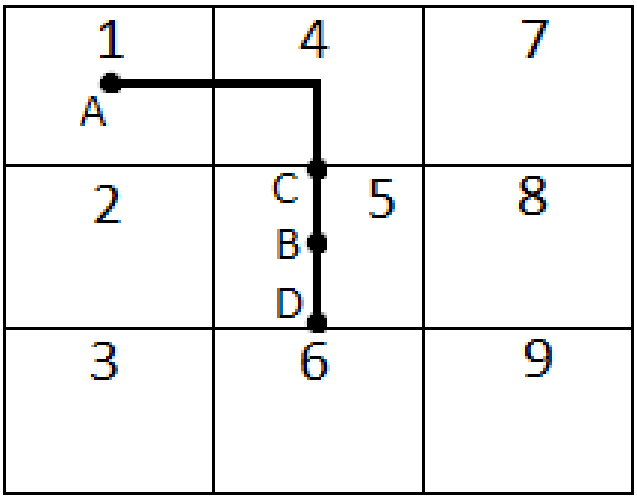


Figure S.3. Elk Population Density with Feeding (August)

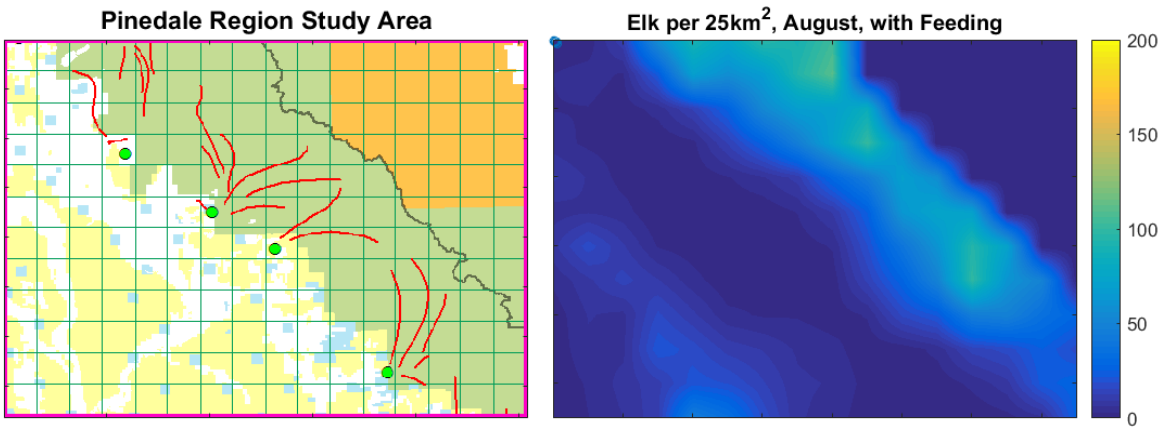


Figure S.4. Elk Population Density without Feeding (August)

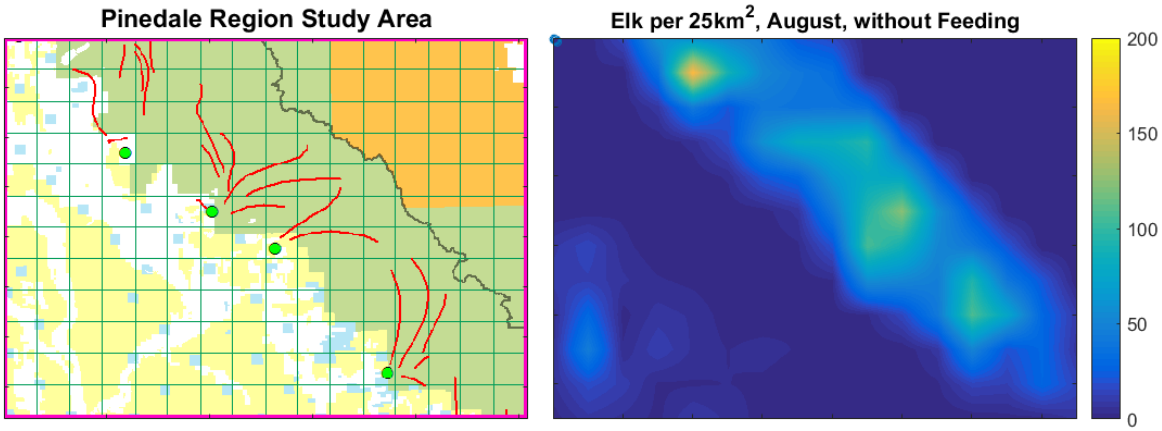
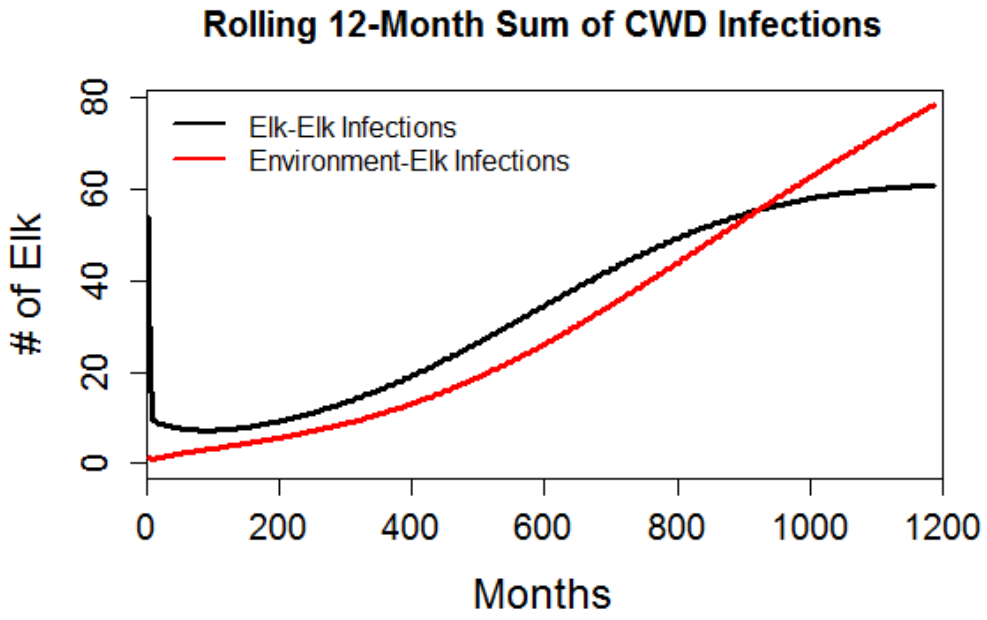


Figure S.5. Elk CWD Infections over Time using the Optimal FPT Strategy

Feeding Scenario



Non-Feeding Scenario

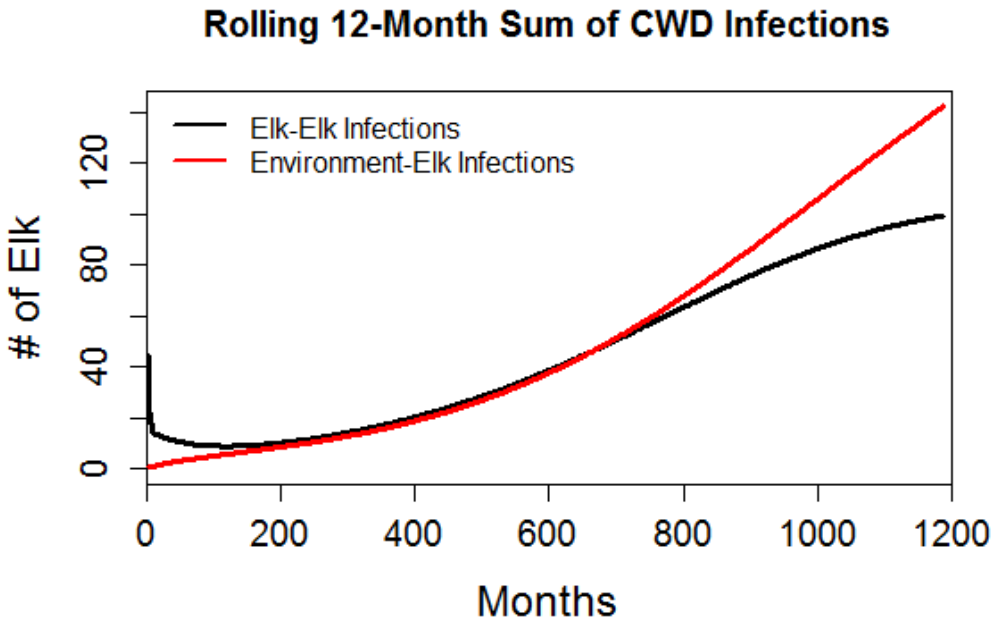
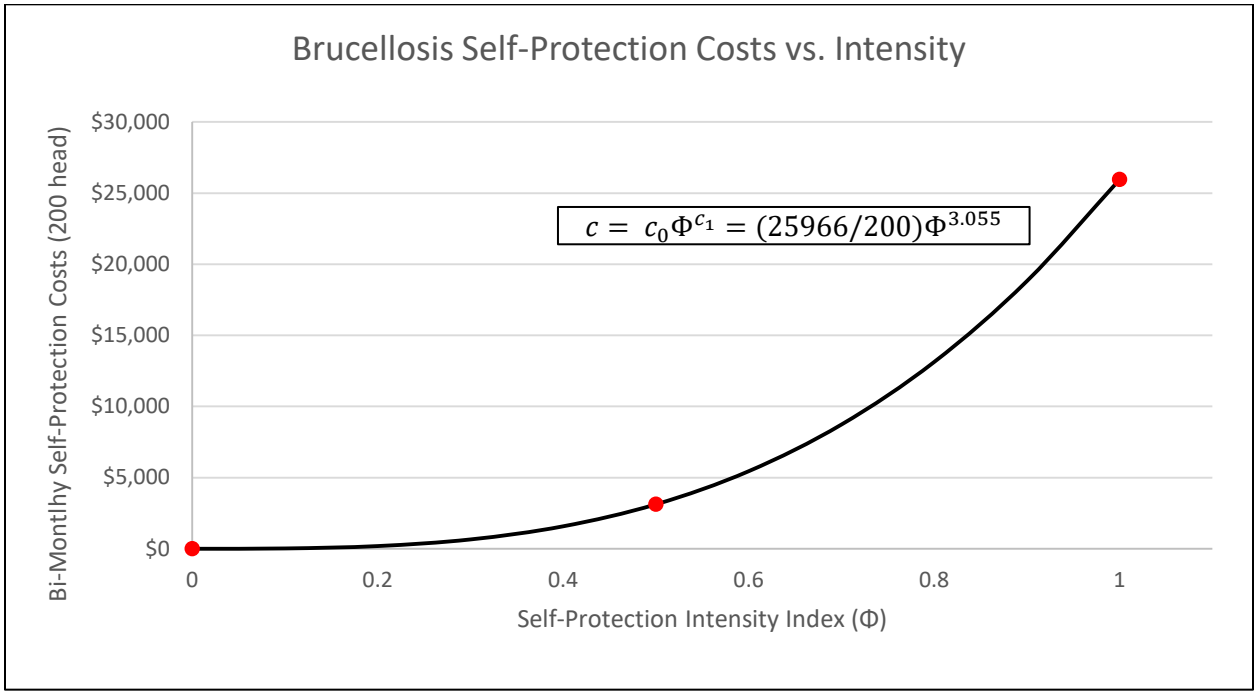


Figure S.6. Calibration of Brucellosis Self-Protection Cost Function



Notes. Three points (●) are used to calibrate the function above. The first is the origin: $\Phi = 0$. Zero self-protection has zero effectiveness and zero costs. The second is the endpoint: $\Phi = 1$. This is full self-protection with 100% effectiveness against brucellosis is estimated to have a bi-monthly cost c_0 = \$25,966/200 = \$129.83 per cow for a herd of 200 cows. The third is the interior point. As described in the text, we assume a self-protection intesity index of $\Phi = 0.5$ will have a bi-monthly cost of \$3,124/200 = \$15.62 per cow and reduce the probability of a quarantine by 50%.

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