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Chronic wasting disease undermines efforts to control the spread of brucellosis in the Greater Yellowstone Ecosystem

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Abstract. Wildlife diseases pose a substantial threat to the provisioning of ecosystem services. We use a novel modeling approach to study the potential loss of these services through the imminent introduction of chronic wasting disease (CWD) to elk populations in the Greater Yellowstone Ecosystem (GYE). A specific concern is that concentrating elk at feedgrounds may exacerbate the spread of CWD, whereas eliminating feedgrounds may increase the number of elk on private ranchlands and the transmission of a second disease, brucellosis, from elk to cattle. To evaluate the consequences of management strategies given the threat of two concurrent wildlife diseases, we develop a spatiotemporal bioeconomic model. GPS data from elk and landscape attributes are used to predict migratory behavior and population densities with and without supplementary feeding. We use a 4,800 km^2 area around Pinedale, Wyoming containing four existing feedgrounds as a case study. For this area, we simulate welfare estimates under a variety of management strategies. Our results indicate that continuing to feed elk could result in substantial welfare losses for the case-study region. Therefore, to maximize the present value of economic net benefits generated by the local elk population upon CWD's arrival in the region, wildlife managers may wish to consider discontinuing elk feedgrounds while simultaneously developing new methods to mitigate the financial impact to ranchers of possible brucellosis transmission to livestock. More generally, our methods can be used to weigh the costs and benefits of human-wildlife interactions in the presence of multiple disease risks.

Key words: brucellosis; chronic wasting disease; cost–benefit analysis; elk feedgrounds; Greater Yellowstone Ecosystem; spatiotemporal models.

Introduction

The impending introduction of chronic wasting disease (CWD) to the Greater Yellowstone Ecosystem (GYE) is threatening one of our iconic ecosystems. The 100-yr-old practice of supplemental feeding of GYE elk, which has successfully limited the spread of brucellosis from elk to livestock by limiting elk movement onto ranches, may exacerbate the spread of CWD in the elk population by enhancing opportunities for CWD to spread among elk (National Academies of Sciences, Engineering, and Medicine 2017). To investigate how CWD will impact the provisioning of ecosystem services within the GYE and how the many distinct elk feedgrounds affect the risks to these services, it is critical to understand how disease transmission varies over the spatial landscape. Incorporating a spatial dimension into models of coupled ecological–economic systems allows for a richer understanding of the tradeoffs and synergies associated with ecosystem service provisioning and optimal management (Bulte et al. 2004, Qiu and Turner 2013).

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Bioeconomic models of coupled human–natural systems have been developed to study the management of wildlife disease and have been recommended as tools for managing disease in the GYE (National Academies of Sciences, Engineering, and Medicine 2017). The majority of bioeconomic models of disease management are aspatial and thus may be limited in applications where the economic and ecological impacts of management strategies may be spatially heterogeneous. To address this limitation, we develop a spatially explicit bioeconomic model of the GYE to examine the management of two infectious diseases carried contemporaneously by elk: CWD and brucellosis. A spatially explicit model is advantageous in that it can generate: (1) a more accurate assessment of economic risks (i.e., the combination of adverse ecological outcomes arising within the coupled spatial system, and the associated economic consequences arising across a heterogeneous landscape; Perrings 2005) and of how various interventions can mitigate these risks, and (2) improved species and disease management recommendations that may be spatially explicit to target areas where strategies can generate the largest net benefits.

Supplementary feeding of elk in the southern GYE during the winter and spring has been in effect since the early twentieth century to reduce winter mortality and support larger elk herds than could be sustained by natural forage alone. The larger elk herds in turn provide significant economic benefits to hunters and those who value wildlife viewing (Smith 2001, National Academies of Sciences, Engineering, and Medicine 2017). Additionally, feedgrounds help truncate the natural migratory routes of elk, thereby limiting the time elk spend on private, low-elevation ranchlands during the winter months and reducing the risk of brucellosis transmission from elk to cattle. Brucellosis risk to cattle is currently the primary GYE disease concern, and ranchers incur large regulatory costs to prevent brucellosis from spreading beyond the Designated Surveillance Area (DSA) (National Academies of Sciences, Engineering, and Medicine 2017). If a cow becomes infected, the U.S. Department of Agriculture–Animal and Plant Health Inspection Service (USDA-APHIS) requires the entire cattle herd and all contact herds to be quarantined or culled, at a significant cost to either the rancher, the states affected, the U.S. Department of Agriculture (USDA), or all three (Roberts et al. 2012).

Supplemental feeding is increasingly challenged by wildlife biologists, ecologists, and epidemiologists (Smith 2012, National Academies of Sciences, Engineering, and Medicine 2017). A major concern is the practice increases brucellosis prevalence in elk by concentrating elk populations at feedground sites (Schumaker 2010, Scurlock and Edwards 2010, Smith 2012). Feedground opponents argue that the long-term costs of increased prevalence exceed the disease protection benefits of feedgrounds. This concern has grown as CWD has spread across Wyoming and will likely soon be introduced into GYE elk populations (see Appendix S1).

The economic costs of a CWD outbreak in and around the GYE elk feedgrounds have not previously been estimated, but would negatively affect two key sectors of the region's economy: tourism and hunting. First, over four million tourists visit Yellowstone National Park every year and almost nine million visit the state of Wyoming, with many coming to view elk and other wildlife. CWD is an infectious neurodegenerative wildlife disease that causes certain death for its hosts, with infected animals being noticeably sick during latter stages of disease. Second, the public remains wary of consuming meat of infected animals, even though there is very little evidence of transmission to humans (Belay et al. 2004). Indeed, hunting activity and expenditures in Wisconsin declined following the 2002 discovery of CWD in deer populations, resulting in economic losses of between \$53 and \$79 million in 2002 and between \$45 and \$72 million in 2003 (Bishop 2004). Zimmer et al. (2012) find hunters in Alberta would be willing to spend \$20.35 per trip to prevent the incidence of CWD from increasing beyond current levels.

An important emerging consideration for GYE elk management, particularly in the face of disease transmission, is how elk move and congregate in space (Merkle et al. 2018). Brucellosis transmission (and likely future CWD transmission) among elk, and also to local cattle, depends on how spatially explicit management, such as feedgrounds, affect population densities and elk movement throughout the year. Previous bioeconomic models of wildlife disease management involving supplemental feeding (Horan and Wolf 2005, Fenichel and Horan 2007b) have been aspatial. Aspatial models must make strong assumptions about how changes in feeding affect animal densities and resultant disease transmission, both within the elk population and to cattle, which may greatly oversimplify calculations of transmission likelihoods and ensuing economic impacts. As indicated above, the spatial impacts of feedgrounds on elk migration patterns affecting cattle risks are considered especially important (Jones et al. 2014).

Spatial models have been critical for understanding and designing strategies for addressing a variety of environmental issues such as climate change, pollution dynamics, wildlife migration, and land use (Veldkamp and Lambin 2001, Pearson and Dawson 2003, Guisan and Thuiller 2005, Jerrett et al. 2005). For example, spatial pollution models are more accurate for assessing health and ecosystem impacts, and for designing spatially explicit policies that can mitigate these impacts more cost effectively. Spatially explicit modeling of elk movement helps advance our understanding of how alterations in supplemental feeding can be used to influence elk densities across space and wildlife disease transmission. A spatial model is also important because CWD can be passed to elk through environmental contamination, so it is important to keep track of where elk currently reside and where they have been in the past. Aspatial models are often used to assess economically efficient management because of the difficulty of integrating human behavior with biological systems. We address this difficulty by coupling realistic and practical elk management strategies with a spatial bioeconomic model to assess the welfare (discounted flow of ecosystem net benefits) associated with current supplemental feeding policies and counterfactual policies where supplemental feeding is either eliminated or reduced in a spatially strategic manner. Our hypothesis is that the introduction of CWD will alter the costs and benefits of supplemental elk feeding and require new elk management strategies that will redistribute the costs and benefits to stakeholders in the region.

Results indicate that with the introduction of CWD into these elk populations, the additional risk feedgrounds generate outweighs the benefits they provide. With the introduction of CWD and our proposed adapted management practices, the distribution of ecosystem services changes and leads to a situation where certain stakeholders may require compensation for their diminished level of ecosystem services.

Models and Methods

Our study area is a 4,800-km^2 area around Pinedale, Wyoming, USA, which contains four existing feedgrounds. This area is at the southwestern slope of the Wind River Mountain Range within Sublette County and one of the southernmost portions of the GYE. We chose this area for two reasons: (1) elk in this area are likely to be some of the first in the GYE to encounter CWD and (2) 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). The study area is broken down into a 12 $\times$ 16 grid of 25-km^2 cells (Fig. 1). Simulations are used to generate welfare estimates under a variety of harvesting and feeding management strategies.

The model contains one wildlife species (elk), two diseases (CWD and brucellosis), and one livestock species (cattle). We treat brucellosis as endemic in the elk population whereas CWD is modeled as being newly introduced to the study area. The total elk population, which consists of subpopulations defined by health status (e.g., susceptible, infected), is denoted $N_{i,t}$, where $i \in \{1, \ldots n\}$ indexes distinct patches of land or cells and $t \in \{1, \ldots, T\}$ indexes time. Monthly time steps are used to capture the seasonal migratory behavior of elk and how this behavior is affected by feeding. To model elk population changes, we establish an order of the population-related events or stages that may (but do not necessarily) occur within a month. The first stage is elk population growth. The second stage is elk hunting. The third stage is elk mortality from CWD, assuming that CWD is always terminal (Williams et al. 2002). The fourth stage is disease infection dynamics, which includes elk-to-elk, elk-to-environment, and environment-to-elk disease transmission as well as the transmission of brucellosis to livestock. The fifth stage is animal movement.

Stages 1–3: Elk growth, hunting, and CWD mortality

Elk growth, recruitment less natural mortality, is assumed to occur only at the beginning of June; stage 1 does not occur in any other month. For each cell, the elk population exhibits logistic growth, with an intrinsic growth rate denoted r and carrying capacity, K. Carrying capacity, $K(F)$, is modified to be an increasing function of the quantity of supplemental feeding, F (Walters 2001). Unlike the spatial model in Horan et al. (2005), carrying capacity applies to the entire region rather than each cell because the case study area is relatively small.

The regional planner (e.g., Wyoming Game and Fish Department) determines the total number of elk to be harvested in each October, h_t; no harvests occur in other months. For simplicity and because the Pinedale region is a comparatively small region in the GYE, elk harvests are specified for the entire region, with harvests on both public and private lands being distributed proportionately to the total Pinedale elk population (this latter assumption is relaxed in our sensitivity analysis in Appendix S1). Moreover, elk hunting is distributed proportionally across the infected and susceptible populations because selective harvesting is difficult, except in the later stages of the disease. In each period, the CWD-infected elk population is reduced from CWD mortality according to a fixed CWD mortality rate, μ.

Stage 4: Disease transmission

CWD transmission.—Chronic wasting disease elk-to-elk dynamics are modeled using an SI compartmental model where $S_{i,t}$ and $I_{i,t}$ are the number of susceptible (CWD-free) and CWD-infected elk in cell i at time t, with $N_{i,t} = S_{i,t} + I_{i,t}$ (recall that CWD is always fatal). For future reference, we also denote $\theta_{\text{CWD},i,t} = I_{i,t}/N_{i,t}$ as the prevalence of CWD in elk. The number of new CWD infections in cell i at time t is modeled according to the standard density-dependent transmission function $\beta_{\text{CWD}} S_{i,t} I_{i,t}$ (McCallum et al. 2001, Begon et al. 2002), where β_{CWD} is the infection coefficient. Transmission may vary considerably across cells due to differences in cell-specific population densities. There is considerable uncertainty regarding CWD transmission rates. Given this uncertainty, we carefully explain our calibration procedure and we also perform a sensitivity analysis in Appendix S1. Note that the calibration is scale-dependent so that if we had increased the resolution of the model (i.e., smaller cells), the CWD transmission parameter would adjust so as to have little impact on equilibrium disease prevalence and transmission rates. We also note that other transmission functions are possible

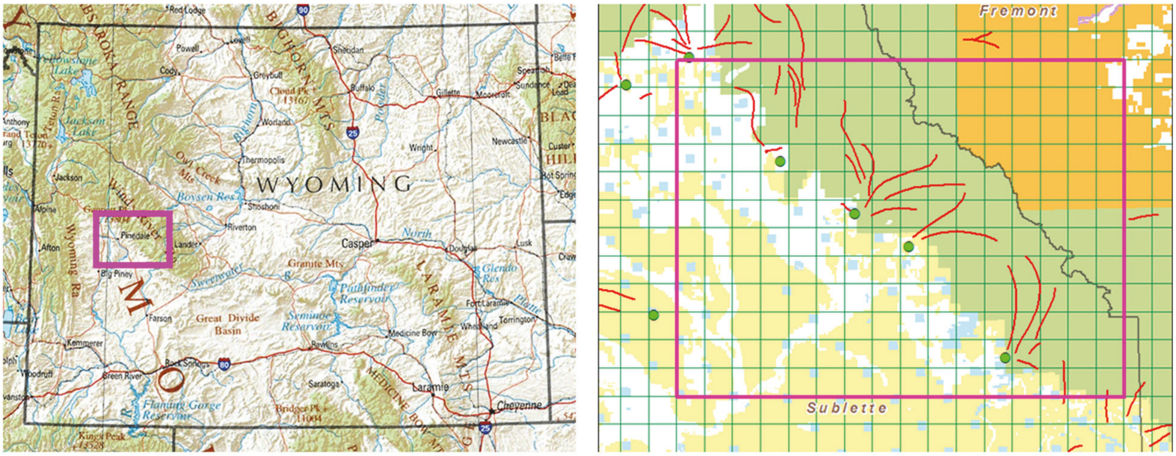

Fig. 1. Case study area with four elk feedgrounds near Pinedale, Wyoming, USA. The green dots on the right graph indicate the location of the four elk feedgrounds. The red lines indicate approximate elk migration routes provided by the Wyoming Game and Fish Department. Green indicates U.S. Forest Service land, yellow indicates U.S. Bureau of Land Management land, and white indicates private land.

(McCallum et al. 2001) and are investigated in Appendix S1.

New CWD infections from environment-to-elk transmission are given by $\beta_{PRION}S_{i,t}P_{i,t}$, where β_{PRION} is the environment transmission parameter and $P_{i,t}$ is an environmental contamination state variable that varies across space and time. Variable $P_{i,t}$ indicates the level of prion contamination in the environment due to CWD-infected elk residency and mortality. The law of motion for this state variable is

$$P_{i,t+1} = (1 - \gamma_{PRION})P_{i,t} + \delta_{PRION}I_{i,t} \quad (1)$$

where $\gamma_{PRION} > 0$ is the slow decay rate (Saunders et al. 2008) and δ_{PRION} is the elk-to-environment transmission parameter.

Transmission may vary considerably across cells due to cell-specific population densities and environmental conditions. Aspatial models that include feeding generally model β as a function that is increasing in feeding (Horan and Wolf 2005, Fenichel et al. 2010). An advantage of our spatial modeling approach is that the transmission function does not need to be modified based on feeding decisions. This is because population densities, and hence transmission, in a cell respond to relative feeding opportunities in that cell.

Brucellosis.—Unlike CWD, brucellosis is already endemic in GYE elk populations and spreads occasionally from elk to cattle. Transmission of brucellosis from elk to cattle is modeled as density dependent, with the probability of a cow being newly infected with brucellosis in cell i at time t given by $\beta_{BRUC}\theta_{BRUC,t}N_{i,t}$, where β_{BRUC} is the brucellosis transmission parameter. Here, $\theta_{BRUC,t}$ is the prevalence of brucellosis in elk and $N_{i,t}$ is the total number of elk in the cell, so that the number of infected elk in cell i at time t is $\theta_{BRUC,t}N_{i,t}$. An SIR model is not used for elk brucellosis dynamics. Rather, we assume $\theta_{BRUC,t}$ transitions to one of two steady-state prevalence levels depending on whether the elk population is fed or unfed. Scurlock and Edwards (2010) estimate a prevalence of 3.7% in unfed populations and 21.9% in fed populations. Schumaker (2010) reports rates of less than 5% in unfed populations and 26% in fed populations. Recent data in unfed elk herds in the GYE show evidence of increasing brucellosis prevalence in unfed elk populations (see Appendix S1 for further details). Based on this evidence, we initially assume that brucellosis is 26% in both unfed and fed elk populations. In the *Sensitivity Analysis* section of Appendix S1, we allow prevalence levels to be different and transition between the two prevalence levels. A convergence parameter, δ_{BRUC}, governs the rate of this transition.

Feeding affects brucellosis transmission to cattle in two ways. First, the larger prevalence level due to feeding means elk that come into contact with cattle are more likely to be infected, increasing risks to cattle. Second, feeding reduces the number of elk that travel into lower elevations and inhabit the same space as cattle. 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 only occurs between January and June.

Stage 5: Elk movement

We assume there is no difference in the movement of infected and susceptible elk. The likelihood of an elk moving from any cell i to any cell j in stage 5 is governed by an $n \times n$ transition matrix J. J is calculated by taking the Hadamard product (element by element multiplication) of two $n \times n$ 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 (i.e., elk move due north, south, east, or west. See Appendix S1: Figs. S1, S2 and Section S1.5). 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) to data on elk movement and GYE habitat characteristics, such as elevation and available green plant biomass. There are 24 different **Z** matrices, one for each month for each type of elk population (fed and unfed). These methods are based on many of the principles of the Master Equation approach to calculating animal space use outlined in Merkle et al. (2017). A detailed description of the movement methodology, along with the RSF estimation procedure and parameter estimates, can be found in Appendix S1: Sections S1.5, S2.5. 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

$$S_{t+1} = JS_t \quad (2)$$

$$I_{t+1} = JI_t \quad (3)$$

where S and I are $n \times 1$ column vectors of the susceptible and infected populations.

Fig. 2 shows heat maps of predicted elk population densities in March simulated by our movement model under two cases. In the case where all feedgrounds are open, elk are all concentrated around the feedground sites. In the case where all feedgrounds are closed, elk are less concentrated but more are located on low elevation, private land. In August, however, the two heat maps look similar (see Appendix S1: Figs. S3, S4).

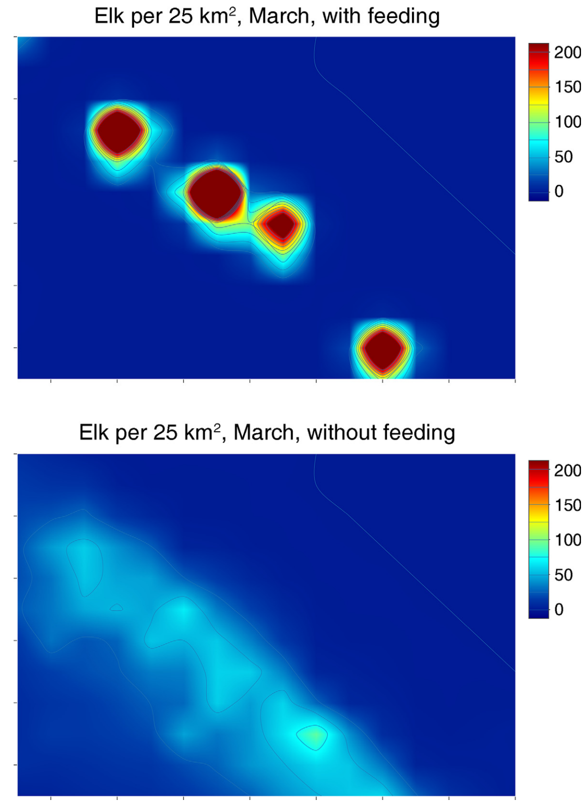

Fig. 2. Elk population densities with and without feedgrounds for the case study area. The top graph shows the prediction of our movement model for the status quo scenario in which elk are fed during the winter. All elk are concentrated around feedground locations with a few on private land. The bottom graph shows the prediction of our movement model for the counterfactual scenario in which elk feedgrounds are closed. Elk are less concentrated but are more prevalent on private land. An interpolation method is used to smooth the population densities.

The bioeconomic model

A bioeconomic model is used to track the economic and ecological incentives for optimal management. Regional welfare consists of net hunting benefits less brucellosis and biosecurity costs incurred by ranchers. We assume CWD only affects hunters' welfare with two negative economic consequences. First, mortality from the disease reduces the elk population size from which to harvest, increasing harvest costs and therefore reducing hunter demand (Kauffman et al. 2012). Second, the presence of CWD in a region causes a shift in demand as hunters may choose to hunt elsewhere to reduce their risk of harvesting an infected animal (Bishop 2004, Zimmer et al. 2012). To capture this demand shift, we model net marginal willingness to pay (net of hunting expenditures) as a decreasing function of CWD prevalence. For simplicity and because the Pinedale region contributes only a small portion of regional elk harvests, we assume the marginal value of CWD-free elk harvests in this region is fixed and that the region acts as a price-taker with respect to quantity of licenses issued.

Let $\underline{Y}$ be the constant net marginal value of hunting CWD-free elk in the Pinedale region. Following Schumaker (2010), the net marginal value of harvesting CWD-infected elk is zero. This means the aggregate net marginal value of hunting in the Pinedale region in time t is

$$Y_t = \left(1 - \theta_{\mathrm{CWD},t}\right)\underline{Y} \quad (4)$$

where $\theta_{\mathrm{CWD},t}$ is regional CWD prevalence. Total regional hunting welfare in period t is $h_t Y_t$. The sensitivity analysis in Appendix S1 includes scenarios with lower hunter demand response to CWD.

A potential limitation is that the prescribed reductions in elk populations may not be feasible in the short term through hunting only, particularly if hunters do not have access to private lands. If elk depopulation to achieve a population target also required efforts from the Wyoming Game & Fish Department (WGFD), then these additional harvests would create an agency cost rather than a hunting benefit. This was confirmed through personal communication with WGFD officials. To account for this possibility, we assume there is a maximum number of elk that can be successfully hunted within the year and that the WGFD organizes any additional harvests at a fixed cost per elk. Harvest welfare is therefore the difference between hunting benefits and (if necessary) agency depopulation costs. See Appendix S1 for further details regarding agency depopulation costs.

It is assumed that ranchers are running cow–calf operations, which are the primary type of operation in the GYE and the type primarily at risk from brucellosis. These herds are quarantined if a brucellosis infection is detected, a regulatory response that has become more common than whole-herd depopulation given USDA and state budget limitations, in addition to rule changes (Roberts et al. 2012). We denote the per-cow cost of a quarantine q. For simplicity, assume that the $L_{i,t}$ cows in any individual cell at time t constitute a herd. The herd has to be quarantined for at least one year if one or more cows contract the disease from elk. Quarantine costs (damages to ranchers) in a cell are independent of the number of cattle brucellosis infections; after the first infected cow is detected and the herd is quarantined, there are no additional costs if more cows in the herd become infected in the same period. Recognizing that the expected number of brucellosis infections in each cell follows a binomial distribution, the probability of at least one cow becoming infected is

$$1 - (1 - \beta_{\mathrm{BRUC}}\theta_{\mathrm{BRUC},t}N_{i,t})^{L_{i,t}}. \quad (5)$$

Assuming perfect disease monitoring, Eq. 5 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 that ranchers in the Pinedale region incur from brucellosis at time t, absent any self-protection measures (described below), are

$$D_t = q\sum_{i=1}^{n} L_{i,t}\left(1 - \left(1 - \beta_{\mathrm{BRUC}}\theta_{\mathrm{BRUC},t}N_{i,t}\right)^{L_{i,t}}\right). \quad (6)$$

In addition to damages from brucellosis, we also include elk-dependent costs such as destruction of fences, damages to crops, and general forage depredation from elk on private land. These depredation costs are assumed to be proportional to the number of elk such that the total costs on private land are given by $c_N \times N_{i,t}$, where c_N is the monthly cost per elk. Each cell is either denoted as private or public land, but only cells denoted as private land are subject to depredation costs.

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 delaying grazing (Roberts et al. 2012). For simplicity, we assume ranchers can choose a level of self-protection against brucellosis infection 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 total 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 $100 \times c_{\mathrm{GOVT}}$ percent through government subsidies.

For the herd located in cell i at time t, with $L_{i,t}$ cows, a risk-neutral rancher will invest in self-protection up to the point where the expected marginal reduction in damages equals the marginal cost of self-protection, i.e.

$$\varphi'_{i,t}qL_{i,t}\left(1 - \left(1 - \beta_{\mathrm{BRUC}}\theta_{\mathrm{BRUC},t}N_{i,t}\right)^{L_{i,t}}\right) = c'_{i,t}L_{i,t}(1 - c_{\mathrm{GOVT}}) \quad (7)$$

where $\varphi'_{i,t}$ and $c'_{i,t}$ are the derivatives of the effectiveness and cost functions with respect to $\Phi_{i,t}$, respectively. If the expected marginal reduction in damages are always greater (less) than the marginal private cost of self-protection, then the optimal level of self-protection is $\Phi^*_{i,t} = 1$ ($\Phi^*_{i,t} = 0$). With self-protection, the expected economic damages from brucellosis in period t become

$$D_t = q\sum_{i=1}^{n} L_{i,t}\left(1 - \varphi^*_{i,t}\right)\left(1 - \left(1 - \beta_{\mathrm{BRUC}}\theta_{\mathrm{BRUC},t}N_{i,t}\right)^{L_{i,t}}\right) \quad (8)$$

where $\varphi^*_{i,t}$ is the effectiveness of optimal self-protection $\Phi^*_{i,t}$. The total self-protection costs include those incurred by both ranchers and the government. With $c^*_{i,t}$ denoting the self-protection costs that are optimal to ranchers, total costs are

$$\sum_{i=1}^{n} c^*_{i,t}L_{i,t}. \quad (9)$$

Welfare function

A regional planner concerned with societal economic efficiency seeks to maximize the discounted sum of expected economic welfare, W, by choosing the elk harvest levels, h_t, and by deciding whether or not to provide supplemental feed to elk, subject to rancher self-protection choices in response to brucellosis risks. For simplicity, we specify $F_{i,t}$ as a binary variable such that $F_{i,t} = 1$ indicates feeding at current levels and $F_{i,t} = 0$ indicates no feeding. Some simulations will involve cell-specific feeding while others will involve a single feeding choice for the region. Discounted expected welfare is

$$W = \sum_{t=0}^{T} \frac{1}{(1+\rho)^t} \begin{pmatrix} h_t Y_t - D_t - \sum_{i=1}^{n} c_N N_{i,t} \\ - \sum_{i=1}^{n} c^*_{i,t} L_{i,t} - z \sum_{i=1}^{n} N_{i,t} F_{i,t} \end{pmatrix} \quad (10)$$

where z is the cost of feed per elk and ρ is the discount rate. Discounting over time is standard in the economics literature and implies that earlier time periods will receive a larger weight in the welfare function. This is because individuals generally prefer receiving benefits now rather than later (Arrow et al 1996). As a reminder, the components of welfare in Eq. 10 from left to right are (1) hunting benefits, (2) expected brucellosis damages, (3) elk depredation costs on private land, (4) optimal brucellosis self-protection costs, and (5) supplemental feeding costs.

Elk management practices

We focus on three elk management practices that are relatively transparent and straightforward to implement: fixed population target (FPT), fixed harvesting rate (FHR), and population target switching (PTS). The two "fixed" alternatives involve fixing either the target population size or the hunting rate as a percentage of the elk population and restricting them to be the same in every period. The "switching" alternative is analogous except it allows the flexibility to alter the population target if the prevalence of CWD is sufficiently low. Each of these scenarios model brucellosis and CWD risks, with one exception: the FPT and current management practices are also modeled for the case where there are only brucellosis risks (no CWD). These no-CWD scenarios are considered the baseline scenarios, as most existing discussions of disease management ignore the effects of CWD (Bienen and Tabor 2006) and focus on the management of brucellosis transmission risks to livestock. Each strategy is selected given the self-protection measures chosen by ranchers.

We also evaluate two types of feeding strategies. First, each alternative indicated above is evaluated under two feeding options that are not spatially differentiated: feed at the (constant) status quo levels or to discontinue feeding at all feedgrounds. Second, we consider spatial management strategies under the FPT practice with CWD where all possible subsets of feedgrounds are closed. There are four feedgrounds and 16 possible configurations where anywhere from zero to four feedgrounds are closed. Since we already consider the cases where no feedgrounds are closed and all feedgrounds are closed, there are an additional 14 spatial configurations to evaluate.

A search algorithm is used to identify the population target (and mix of open and closed feedgrounds in the spatial feedground case) that produces the most economically efficient outcome, i.e., that maximizes the present value of net economic benefits as given by Eq. 10, given the available management tools examined here. For the FPT practice, the number of elk hunted each year is determined by taking the difference between the current population and a population target that remains constant over time. With an FHR practice, a fixed percentage of elk are hunted each year. The PTS practice determines a number of elk hunted each year by taking the difference between the current population and one of two population targets: one target is used if the CWD prevalence is below a population management threshold, ε, and another is used if the CWD prevalence is above this threshold. The threshold is exogenous and meant to represent the level when CWD prevalence is sufficiently low in the relevant elk population. There is not a similar threshold for brucellosis since brucellosis dynamics are not modeled apart from prevalence transitioning in response to changes in the feeding regime.

Simulations start at the beginning of March. At this time of year, almost all elk are located around feedgrounds. The number of elk started at each feedground corresponds to the latest available population counts. The names and latest publicly available population estimates for the four feedgrounds are Soda Lake (1,017), Scab Creek (668), Muddy Creek (571), and Fall Creek (648) (see Appendix S1 for further details). Brucellosis prevalence is initially assumed at the steady state value for a feeding regime, 26%, consistent with the current practice of feeding elk. CWD is introduced exogenously to the Scab Creek Feedground; this introduction is likely to occur by infected deer herds coming into contact with the elk population. It is assumed that 87 elk are initially infected with CWD, which corresponds to an initial prevalence level of approximately 3% for the entire initial study area population of 2,904. Simulations are run for 100 yrs, but discounting causes the first couple of decades to have a significantly higher weight in determining the strategy that maximizes social welfare.

Simulation Results

The simulation results for the various scenarios are presented in Table 1, with ecological and economic tradeoffs depicted in Fig. 3. We reiterate that a spatially explicit model is a key component in developing an efficient management strategy. CWD transmission depends on where elk are currently located, and environmental transmission depends on where elk have resided in the past. Brucellosis transmission from elk to cattle, although a fairly rare occurrence, also depends on the location of elk. A spatially explicit model is required to accurately measure these dual disease risks.

First consider the current management practice scenario (without CWD). Here we see that social welfare is driven by harvest welfare, with comparatively small agricultural and feeding costs (92% and 68% smaller than harvest welfare, respectively). This result, which is in contrast to traditional GYE concerns about disease impacts to agriculture, arises here because cattle quarantines, while costly, are rare events. The relatively significant role of harvest welfare also drives the optimal strategies in the alternative scenarios we consider. We now turn to these other scenarios.

Fixed population target

First consider the FPT strategy with no CWD. When feeding occurs, the population target is increased 55% and social welfare is increased by 11% relative to the current strategy. Agricultural costs increase by 44% and feeding costs increase by 51% in this scenario. However, because these costs were comparatively small to begin with, the impacts on social welfare are determined primarily by the 26% ($15.75 million) increase in the present value of harvest net benefits. Now consider the case where feeding is discontinued. We have calibrated the model such that social welfare is unchanged in this particular scenario (see Appendix S1 for more details about this calibration, and the sensitivity analysis where parameters and the assumptions about hunter access to private lands and CWD transmission functions are varied). In this regard, our analysis is neutral on the question of whether supplemental feeding is economically optimal under the FPT strategy prior to the introduction of CWD. Still, this scenario provides insight into how discontinuing feeding alters the optimal population target and the consequent allocation of costs and benefits to hunters and farmers. The population target is reduced 31% when feeding is discontinued, primarily because harvest opportunities are diminished by reduced ecological productivity (Fig. 3). Note that agricultural costs increase very little without supplemental feeding due to the smaller population target and ability to self-protect against brucellosis infection risk.

Now consider the FPT strategy with CWD. Relative to the case of no CWD, the population target is reduced 79% and social welfare is reduced 68% when CWD risks are present and feeding occurs. This is largely because CWD significantly reduces elk productivity even at moderate population target levels (Fig. 3), resulting in significant adverse welfare impacts to hunters. Some of these adverse impacts are offset by choosing a much smaller target in the presence of CWD risks. Herein lies an important trade-off: all else being equal, the smaller target means increased harvest costs and less ecological productivity to support harvesting activities, but a larger target would fuel CWD transmission to produce a larger decline in ecological productivity so that even fewer harvests would be sustainable. As in the current strategy scenario, the welfare reduction in the case of CWD risks are primarily due to reduced harvest welfare (72%), stemming from a much smaller elk population. Agricultural costs (i.e., expected brucellosis quarantining, brucellosis self-protection and depredation) decline by 74%, but these costs are relatively small in comparison to the other economic impacts and therefore have less of an impact on social welfare.

Chronic wasting disease has a smaller impact on population targets (31% reduction relative to FPT with no feeding or CWD) and welfare (20% reduction) when

Table 1. Summary of simulation results under various management practices and feeding scenarios in the case study area.

Management practice	Feed	Elk population target or rate	CWD prevalence (%)	Social welfare and components (millions of US$)†			
				Social welfare	Harvest welfare	Feeding costs	Agricultural costs
Current (no CWD)	yes	2,904	0.0	35.52	59.46	19.08	4.85
FPT (no CWD)	yes	4,500	0.0	39.32	75.21	28.90	6.99
FPT (no CWD)	no	3,100	0.0	39.32	46.43	0	7.11
FPT	yes	950	4.1	12.46	20.78	6.51	1.81
FPT	no	2,150	2.7	31.46	36.49	0	5.03
FHR	yes	26%	13.8	13.73	20.04	4.96	1.35
FHR	no	17%	4.4	31.92	36.92	0	5.00
PTS	yes	900; 1600	5.6	13.97	22.80	6.58	2.25
PTS	no	1,850; 2,400	4.1	32.19	37.13	0	4.94
Spatial FPT‡	yes	250	26.0	4.08	4.85	0.49	0.28

Notes: FPT, fixed population targeting; FHR, fixed harvest rate; PTS, population target switching. Chronic wasting disease (CWD) prevalence is a trailing 12-month average at year 20.

†Social welfare is calculated as in Eq. 10, harvest welfare is the discounted value of hunting benefits less any necessary Wyoming Game & Fish depopulation costs, and other costs are expressed as discounted values. Agricultural costs include expected brucellosis quarantine costs, self-protection costs, government vaccination subsidies, and depredation costs.

‡The spatial FPT case shown in Table 1 is only one of the possible spatial configurations; all feedgrounds are closed except for Fall Creek, as shown in Fig. 4.

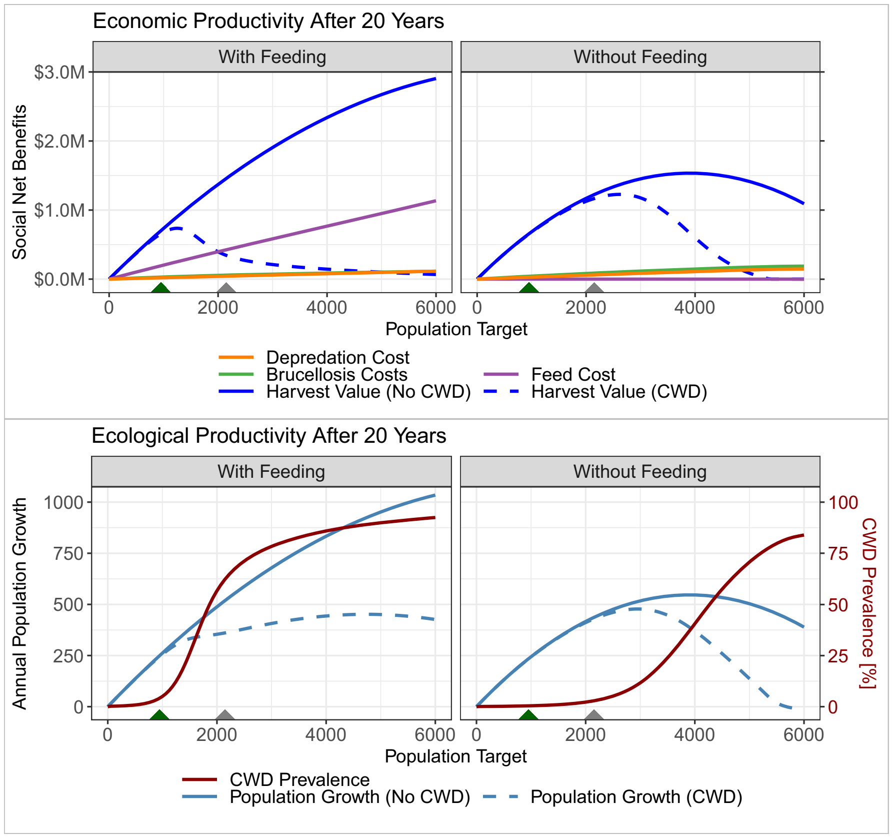

Fig. 3. Ecological and economic productivity at year 20 for various elk population targets under the fixed population target (FPT) management practice. Population growth, chronic wasting disease (CWD) prevalence, and annual economic values at year 20 ($t = 20$) are plotted as functions of the population target. Values are shown for two scenarios: one in which feedgrounds remain open and one in which feedgrounds are closed starting at time $t = 0$. The top plots show the economic data series. The bottom plots show the ecological data series. The dark green and gray triangles along the horizontal axes depict the optimal population targets with and without feeding.

feeding is discontinued. This is because the productivity impacts of CWD are smaller when there is no feeding (Fig. 3), and so, there are fewer economic benefits to adjusting the population target in this case. The reduction of agricultural costs (29%) is also modest given the relatively small costs arising in the CWD-free case.

An important difference between the CWD-free and CWD scenarios is that the elk population target is much larger with feeding in the CWD-free case, whereas the target is smaller with feeding in the presence of CWD. In the CWD-free case, feeding provides significant hunting benefits with a comparatively small increase in brucellosis costs. In contrast, when CWD is present, feeding imposes a significant cost to hunters because the congregation of elk at feedgrounds increases CWD prevalence. As a result, managers may wish to consider discontinuing feeding in the presence of CWD, although ranchers experience greater costs in this case. The larger brucellosis and depredation costs arise because in the short term, feedground closures spur elk movement to private lands. While the long-term costs of brucellosis eventually diminish, the short-term costs are weighed more heavily due to discounting. These results indicate that, under the FPT scenario, hunters switch their preferences about feeding in response to CWD risks and associated elk population targets: hunters prefer feeding without CWD risks, as might be expected, but the opposite is true when there are CWD risks.

Fixed harvest rate

The second strategy considered is harvesting a fixed percentage of the elk population each year. This strategy allows depopulation to occur more gradually than under the FPT strategy. First consider the case where feeding is continued. The welfare-maximizing fixed harvest rate is 26%, and social welfare is 10% higher than the FPT strategy with feeding. In contrast, we found (not reported in Table 1) the FPT strategy to be preferred when there are no limits on elk hunting and thus no agency costs. This result indicates that, with limits on the number of elk that can be hunted within a year, it is better to achieve elk population reductions gradually via the FHR strategy because discounted agency depopulation costs are reduced when they are spread over a slightly longer time horizon.

The optimal fixed harvest rate declines to 17% if feeding is discontinued, with social welfare only slightly higher than that arising under the optimal FPT strategy. The small welfare difference indicates that the costs of gradual depopulation in terms of increased disease transmission and reduced ecological productivity are approximately offset by the benefits of avoiding agency depopulation costs. The primary difference between the FPT and FHR practices is that CWD prevalence initially spikes to 21% in the FHR feeding case because the elk population cannot be reduced as quickly in this case, but hunting alone is able to achieve the desired elk population over time.

Population target switching

The population target switching management strategy (PTS) with $\varepsilon = 4.0\%$ yields surprising results. We expected the flexibility of allowing the population target to increase following the reduced prevalence of the disease would lead to an improvement in welfare. However, adding this additional management flexibility did not produce substantial welfare gains relative to having a single population target. PTS does not improve welfare estimates much because the added management flexibility is limited (e.g., relative to a time-varying population target) and populations that are above 950 elk with feeding (which is the corresponding target in the FTP case) or 2,150 elk without feeding quickly lead to higher CWD prevalence levels. Such an increase in CWD prevalence triggers a decrease in the population target under the PTS strategy. The benefit associated with a brief increase in the population target (and elk productivity) is almost entirely offset by the cost of a CWD outbreak, so such an increase leads to only small economic gains.

Spatially strategic management

One advantage of the spatial bioeconomic model is the ability to investigate management strategies that vary over space. Here we consider 14 combinations of hypothetical closures of different subsets of feedgrounds to see if strategically located supplemental feeding under FPT management with CWD can generate a level of social welfare similar to that under full termination of the supplemental feeding program. In the simulations, we use the same RSF coefficients and variables for the full feeding scenario, but adjust feeding levels and scale steady-state brucellosis prevalence (θ_{BRUC}) down according to the percent of feedgrounds that are closed. The main finding from these simulations is that strategically closing a subset of existing feedgrounds results in an economic loss. The reason that closing certain feedgrounds (e.g., ones farther from an elk migration route or closer to private land) does not improve welfare is that elk will simply congregate more densely at the feedgrounds that remain open (see Fig. 4 for elk population densities for one of the possible combinations: one feedground is left open and three are closed). Because elk density will increase as elk disperse to the remaining open feedground(s), CWD will spread even more rapidly through the population and cause a sharp welfare loss to hunters. Since elk population management is determined jointly with CWD transmission and elk dispersal, the optimal management response is to greatly reduce the elk population target to limit the density-dependent spread of CWD. This is similar to the dispersal spillovers caused by the creation of protected areas (Sanchirico and Wilen 2001) and closing areas to harvests, although the spillovers in our case are negative due to higher species density and more rapid disease transmission.

Discussion

A number of biologists, ecologists, and epidemiologists have expressed concerns about the consequences of continuing supplementary feeding of elk in the GYE, especially given the impending introduction of CWD. Using a spatially explicit bioeconomic model, our results suggest the continuation of feeding and current elk population management could result in present-value welfare losses of US$19 million if CWD is introduced for our case-study area. The welfare losses are likely to be larger for the entire GYE region. In contrast, for the hypothetical case where there is no risk of CWD being introduced into the study area, supplemental feeding along with adapted harvest management would provide the highest social welfare, including to the benefit of both ranchers and the hunting industry. The results differ because of the economically optimal elk management response to CWD risks. Specifically, elk management responses to CWD risks result in much lower elk population targets to reduce density-dependent and environmental transmission of CWD. As feeding fuels CWD risks, the targets would have to be even lower, with significantly lower benefits to hunters, when feeding occurs. As feeding is also an expensive practice in its own right (Dean 1980, Boroff 2013, Boroff et al. 2016), it is better from an economic perspective to eliminate feeding and increase population targets relative to the targets with feedgrounds.

The benefits and costs of elk management in response to CWD risks accrue differently to hunters and ranchers. Discontinuing feeding will, especially in the first year, increase brucellosis and depredation costs for ranchers associated with elk using private lands. However, our model predicts that these costs are outweighed by the economic benefits to hunters, guides, outfitters, and other regional businesses that provide goods and services to hunters. These benefits accrue to a relatively large and diffuse number of people, whereas the increased brucellosis-related costs fall on a relatively small number of local ranchers. Economic theory suggests that a system could be devised wherein those who gain from

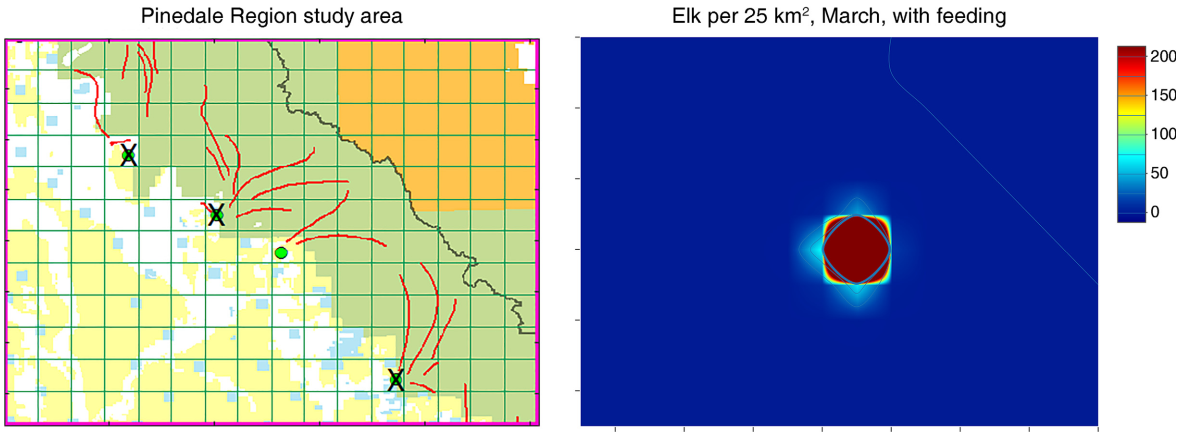

Fig. 4. Elk population density heat map when Fall Creek feedground remains open. The left graph is copied from Fig. 1 with an "X" through feedgrounds that are closed in the model simulations. The remaining open feedground is Fall Creek. The graph on the right shows a heat map of elk density around the Fall Creek feedground during March.

discontinuing feeding in response to CWD could compensate those who lose. Compensation could, for example, help ranchers increase self-protection and mitigate depredation as feeding is discontinued. Eventually, the need for increased self-protection against brucellosis, and a potential role for compensation, should dissipate as the prevalence in the elk population falls over time in the absence of feeding. Note that, since aggregate economic welfare is maximized in our neutral cost–benefit analysis, post-compensation outcomes can leave all stakeholders better off than when policies are driven by analyses that weight stakeholder groups unevenly (e.g., based on political power considerations).

One possible limitation to our analysis is that brucellosis costs to ranchers are uncertain, particularly if feedgrounds are closed. Potential additional costs may include larger brucellosis infection risks to cattle (i.e., greater probability or cost of infection), or behavioral responses to mitigate this risk such as having to transport cattle outside of the area during the transmission risk period to keep elk from comingling with cattle. To assess the worst-case scenario for ranchers, we force all ranchers to invest in elk-proof fence around their winter pasture and delay grazing on public land until the risk of brucellosis transmission is negligible. It is equivalent to setting the self-protection intensity to $\Phi_{i,t} = 1$ for all ranchers. Under this FPT scenario, the welfare gap between supplemental feeding (−US$179.8 million) and no supplemental feeding (−US$158.8 million) is US$21.0 million, which is similar to the case where ranchers choose the level of brucellosis self-protection. Full protection is very expensive for ranchers (hence the negative net welfare values) and not the preferred option, yet the analysis still indicates that discontinuing feeding is economically optimal. This, along with the consistent findings from the sensitivity analysis in Appendix S1, suggests that our main result, the costs of continuing to feed elk after the introduction of CWD outweigh the benefits, is robust.

We close by discussing some possible extensions to the analysis. First, it might be interesting to examine whether attempts to manage elk age and sex distributions could improve the efficiency and effectiveness of disease management (Fenichel and Horan 2007a). Second, if wolves enter the study area, they could be incorporated into the model to factor in their current and future impact on the elk population, livestock, and disease dynamics under alternative strategies for managing CWD and brucellosis. Wild et al. (2011) proposes that wolves may act as a natural disease control mechanism in deer by eliminating infected, weak individuals from the population. Assuming a similar mechanism occurs with elk, disease control may be an unrecognized ecosystem service benefit generated by wolf populations. Third, 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 might occur as elk with the more favorable genotype survive and reproduce more effectively (O'Rourke et al. 1999, Monello et al. 2017). A fourth extension would be to use better data, if and when it becomes available, to more accurately calibrate the environmental contamination and transmission processes for CWD. Lastly, the presence of elk in the GYE is known to provide value to the local economy by drawing wildlife viewers. However, for our case study, we assume wildlife viewing and tourism benefits can be reasonably excluded from the model because tourists interested in viewing wildlife typically travel farther north to the National Elk Refuge or Yellowstone National Park. That said, our model does not account for welfare losses arising from local residents or visitors having to watch elk suffer from either the effects of CWD or inadequate feed resources in the absence of feedgrounds, particularly during severe winters. Such costs and benefits will need to be added in the future if this model is applied to other areas in the GYE where wildlife viewing tourism is more significant.

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Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.2129/full

Data Availability

The input data sets required to run the simulations shown in this paper, including the RSF regression coefficients but excluding the elk telemetry data used to estimate the coefficients, are openly available in Figshare at https://doi.org/10.6084/m9.figshare.11862810. The elk telemetry data set used to estimate the RSF coefficients is available from ScienceBase at https://doi.org/10.5066/f7474803.