

# Wolf and Elk Management in a Spatial Predator-Prey Ecosystem

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July 11, 2016

**Abstract.** This paper provides insights into a complex and politically charged wildlife management problem using a spatial predator-prey model. The model is motivated by the spatiotemporal dynamics between elk, wolves, hunters and cattle ranchers in the Greater Yellowstone Ecosystem (GYE). Wildlife managers set hunting rates for elk and wolves to maximize the stream of ecosystem services derived from the GYE over time. The management component of the model considers tradeoffs between tourism, hunting, and cattle grazing currently facing wildlife managers. The predator-prey component of the model incorporates intraspecific competition and spatially explicit predation risk calibrated to the GYE. Contrary to a recent judicial ruling that has placed a moratorium on hunting wolves in Wyoming, optimal management within our model calls for more aggressive wolf hunting outside of Yellowstone National Park (YNP). The model also calls for a lower elk hunting rate, which leads to a higher steady-state population of elk, more prey for wolves, and less livestock predation. This combination of a prescribed lower elk hunting rate and higher wolf hunting rate is robust to a wide range of parameter values.

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*“The wolf’s repopulation of the northern parts of the lower forty-eight states, now well under way, will stand as one of the primary conservation achievements of the twentieth century...If we have learned anything from this ordeal, it is that the best way to ensure continued wolf survival is, ironically enough, not to protect wolves completely.”* L. David Mech<sup>1</sup>

## **1. Introduction**

This paper provides insights into a complex and politically charged wildlife management problem using a spatial predator-prey model. The model is motivated by the spatiotemporal dynamics between elk, wolves, hunters and cattle ranchers in the Greater Yellowstone Ecosystem (GYE). Our primary finding is that, unlike recent judicial decisions that have restricted wolf hunting in Wyoming<sup>2</sup>, optimal management should hunt wolves more intensively outside YNP. The intuition behind allowing higher wolf hunting rates outside YNP is straightforward. Although higher hunting rates outside YNP cause a modest decline in the overall population of GYE wolves, the population density of wolves inside YNP increases relative to the density outside YNP and elk populations are increased across the entire GYE. The spatial redistribution of wolves occurs directly due to more wolf kills outside YNP and indirectly due to wolves seeking refuge from being hunted. The managed shift in wolf densities fuels increased wolf-related tourism within YNP and favors elk-hunting and ranching outside of YNP. We also find that a more equitable distribution of ecosystem service provisioning across the U.S. states surrounding YNP can be achieved with only modest losses in welfare.

In addition to our policy prescriptions, we make three contributions to the economic literature on wildlife management. First, we advance the sizable literature on the bioeconomics of

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<sup>1</sup> L. David Mech is a renowned wolf expert and senior research scientist for the U.S. Department of the Interior’s U.S. Geological Survey. The excerpt is taken from the forward to the book “Wolf Wars”, written by Hank Fischer and published in 1995 by Falcon Press Publishing, Helena and Billings, MT.

<sup>2</sup> [www.usatoday.com/story/news/nation/2014/09/23/judge-restores-wolf-protections-wyoming/16120133/](http://www.usatoday.com/story/news/nation/2014/09/23/judge-restores-wolf-protections-wyoming/16120133/).

predator-prey systems by integrating predator interference (Hebblewhite, 2013), spatially heterogeneous predation risk (Boyce and McDonald, 1999), and an environmentally driven dispersal process (Aadland et al., 2015) into a classic Holling Type II predator-prey system. Inefficiencies can arise in ecosystem management when policies fail to account for ecosystem responses such as predation spillovers (e.g., Ragozin and Brown, 1985; Crocker and Tshirhart, 1992; Tu and Wilman, 1992; Ströbele and Wacker, 1995; Hoekstra and van den Bergh, 2005; Finnoff and Tshirhart, 2003; Fenichel et al., 2010; Horan et al., 2011; Melstrom and Horan, 2013). Predation spillovers are the net economic value of predation taking into account the impacts on prey and have generally been examined in terms of first-order and second-order population effects. Our model expands the scope of predation spillovers by incorporating higher-order population effects and predicting changes in species densities across space based on spatially explicit predation risk and intra-species interactions. Accounting for the distribution of species in this way has the potential to improve management efficiency by predicting the production of ecosystem services across space and time.

Second, we extend the literature on the joint production of species conservation and marketed commodities by exploring the effects of a protected area in a spatially explicit predator-prey system. One caveat for virtually all of the studies in this literature is that interactions between species, such as predator-prey relations, are omitted (Montgomery et al., 1999; Lichtenstein and Montgomery, 2003; Nalle et al., 2004; Polasky et al., 2005; Polasky et al., 2008). The joint production relationships for a large class of species will be influenced by: 1) dispersal responses to prey availability and predation risk (e.g., Hanski and Ovaskainen, 2000; Gardner and Gustafson, 2004) and 2) the substitutability of predator removal and protected area creation (Melstrom and Horan, 2014). Our predator-prey model is applied to elk and wolf management in the Greater Yellowstone Ecosystem (GYE). The GYE is an interesting application because

Yellowstone National Park (YNP) is a high-profile provider of ecosystem services to the U.S. The park is also positioned in the center of the GYE and does not allow hunting of elk or wolves inside its borders. YNP therefore serves as a refuge for elk and wolves, creating complex spatial and temporal dynamics. In addition, the re-introduction of wolves into the GYE has created conflict with ranchers outside YNP due to livestock depredation.

Third, we examine distributional concerns that arise between U.S. states surrounding YNP by investigating the provisioning of wildlife and marketed commodities under two different strategies for federal management of elk and wolf populations. The first is a “one-size-fits-all” strategy that sets equal harvesting rates in Montana, Idaho and Wyoming. The second is a management strategy that recognizes the geographical and habitat differences between the U.S. states. Varying hunting quotas across U.S. states recognizes differences in landscape characteristics (e.g., terrain, land cover, snowfall) and leads to unequal species populations across states. A recurring theme in the joint-production literature is that efficiency is enhanced by spatially locating species conservation and marketed commodity production according to site-specific habitat characteristics. However, if landscape-level efficiency dictates that states, counties, or municipalities should completely specialize in one type of jointly produced good, federal agencies may seek a more equitable distribution of ecosystem services. The size of the efficiency losses from such a proposal on a large geographic scale remains an open question.

## **2. Jointly produced ecosystem services on a landscape**

The model’s spatial extent covers the GYE (Figure 1) using a  $4 \times 4$  grid with the interior cells representing YNP and the perimeter cells representing mostly U.S. Forest Service (FS) and private land. Although the geographical boundaries of the GYE are not well defined and likely

reach outside our grid, the  $4 \times 4$  grid captures the management tradeoffs between YNP, FS and private lands in a tractable manner.<sup>3</sup> Each cell on the grid is approximately 540,000 acres for a total GYE grid size of 8.64 million acres. Although the GYE provides habitat to many different species, we focus on the spatiotemporal interactions between elk (*Cervus canadensis*) and gray wolves (*Canis lupus*). Elk are native to the GYE, are a primary species for hunters in the area surrounding YNP and are the primary prey of gray wolves (Smith et al., 2013). The gray wolf is also native to the GYE but was hunted to extinction during the early-to-mid 1900's. Beginning in late 1994, the gray wolf was reintroduced to GYE and has recently recovered to the point that wolves have been legally hunted in the area surrounding YNP. We also incorporate livestock as an additional source of prey for wolves. Livestock are grazed on FS and private land surrounding YNP, which is also occupied by wolves, thus creating potential conflict between ranchers and wildlife managers.

In our model, wolves and elk disperse across the grid while livestock remain on the outer cells. Elk and wolves can only be hunted outside YNP, and wolves prey on both elk and livestock. Preying on livestock outside YNP exposes wolves to hunting risks. Elk disperse across the grid in search of forage and to minimize exposure to wolves and humans based on conditions from adjacent cells. Livestock on FS and private land surrounding YNP remain constant over time as ranchers are assumed to run cow-calf or stocker operations allowing animals to graze throughout the year, gain weight, and then send the animals to market. Government officials compensate ranchers for any livestock killed by wolves, which in turn helps ranchers maintain constant livestock levels.

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<sup>3</sup> We explicitly consider wolf populations that disperse beyond our grid boundaries and refer to this movement off the grid as "leakage". This leakage is calibrated to be consistent with existing data and the model following the re-introduction of wolves into the GYE.

The model is used to explore optimal, forward-looking management strategies that account for the spatially explicit nature of the joint production relationship between three ecosystem services – tourism, hunting, and cattle grazing. With the recent removal of the gray wolf from the federal endangered species list, wolf management in the GYE has been transferred from the federal government to state wildlife management agencies. Several conservation groups have been critical of state wildlife management agencies for allowing excessive hunting of the gray wolf, calling for wolf hunting programs to be transferred back to the federal government.<sup>4</sup> To investigate these proposals, we compare state-level data on wolf hunting to optimal federal management where hunting rates are selected to maximize aggregate welfare across the GYE.

## **2.1 Welfare and optimal management**

In the GYE, resource managers are concerned with balancing tourism, hunting, and cattle grazing while maintaining sustainable populations of elk and wolves above some safe minimum level as proposed by Bishop (1978). These lower thresholds or critical levels are the population level of the species at which irreversible and potentially large opportunity costs are imposed on the ecosystem or ecosystem collapse occurs. The three ecosystem services capture the joint production of consumptive (wolf hunting) and non-consumptive (tourism) use values<sup>5</sup> generated by wolves, as well as detrimental impacts of wolves (elk hunting, cattle grazing). To provide clear comparisons between policies that affect the provisioning of the ecosystem services, each

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<sup>4</sup> For example, see [www.sierraclub.org/lay-of-the-land/2014/09/federal-protections-restored-wyoming-wolves](http://www.sierraclub.org/lay-of-the-land/2014/09/federal-protections-restored-wyoming-wolves) and [www.defenders.org/press-release/victory-wolves-wyoming](http://www.defenders.org/press-release/victory-wolves-wyoming).

<sup>5</sup> Gray wolves may also generate significant non-use values such as option value, bequest value, and existence value (Loomis and White, 1996; Chambers and Whitehead, 2003; Richardson and Loomis, 2009). For example, society may benefit from knowing that gray wolves exist in the wild even if they do not plan to travel to the GYE to view wolves. We consider the effect of these additional non-use values on optimal management in the sensitivity analysis in Table 3. While the inclusion of these values increases the total ecosystem benefits that gray wolves provide, it does not significantly alter the optimal spatial-dynamic management strategy. For exposition, we note this outcome and proceed with three ecosystem services.

service is enumerated in monetary terms. By monetizing the flows of ecosystem services, we can consistently compare various services across time and space.

Let aggregate welfare be given by the discounted sum of the three ecosystem services over time and space:

$$Welfare = \sum_{t=0}^T e^{-\rho t} (\pi_{\text{hunting}}(h_{E,t}, h_{W,t}) + \pi_{\text{tourism}}(W_t^{GYE}) + \pi_{\text{livestock}}(W_t^{GYE}, L_t)) \quad (1)$$

where  $\rho$  is society's discount rate. The first term within parentheses in equation (1) captures the ecosystem services from hunting, where  $h_{E,t}$  and  $h_{W,t}$  are the sums of harvested elk and wolves over all cells outside YNP. The second term within parentheses,  $\pi_{\text{tourism}}(W_t^{GYE})$ , captures the ecosystem services realized from wolf-driven tourism in the GYE, where  $W_t^{GYE}$  is the aggregate number of wolves in the GYE. The third term,  $\pi_{\text{livestock}}(W_t^{GYE}, L_t)$ , captures livestock ecosystem services measured as producer profits less predation losses.<sup>6</sup> An optimal federal hunting policy will maximize (1) by choosing elk and wolf hunting rates ( $h_E$  and  $h_W$ ) subject to the constraint that total elk and wolf populations do not fall below minimum viable levels,  $\bar{E}$  and  $\bar{W}$ .<sup>7</sup>

## 2.2 Pre-dispersal laws of motion

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<sup>6</sup> We do not include indemnity payments or compensation that ranchers receive for wolf predation in the social welfare function as the compensation to ranchers lowers government spending elsewhere and is taken to be a wash.

<sup>7</sup> The ecosystem services in (1) capture three of the most important GYE services, but there are likely to be additional ecosystem services (and potential costs) associated with wolves and elk. For example, wolves are often considered a keystone species that may lead to trophic cascades throughout the ecosystem and healthy elk populations may contribute to tourism benefits. On the negative side, higher elk populations may compete for forage, spread disease, and eat rancher's haystacks. To incorporate these additional benefits and costs, we vary the welfare parameters associated with wolves and elk in a sensitivity analysis to see if our policy recommendations are robust to these changes.

Each cell on the grid is represented by a row  $i = 1, \dots, 4$  and a column  $j = 1, \dots, 4$  index. Time is discrete with  $t$  representing annual intervals.<sup>8</sup> The state variables in the system are wolf, elk, and livestock densities. Each state variable is defined by a density in period  $t$  on cell  $(i, j)$  and are given respectively by  $W_t^{(i,j)}$ ,  $E_t^{(i,j)}$  and  $L_t^{(i,j)}$ . The management (control) variables in the system are elk and wolf harvest rates,  $h_E^{(i,j)}$  and  $h_W^{(i,j)}$ , where  $0 \leq h_E^{(i,j)}, h_W^{(i,j)} \leq 1$ . Based on hunting data from each state that shows annual wolf harvests are roughly a constant proportion of the respective populations, we specify proportional harvesting such that total harvests are given by  $h_{E,t}^{(i,j)} = h_E^{(i,j)} \times E_t^{(i,j)}$  and  $h_{W,t}^{(i,j)} = h_W^{(i,j)} \times W_t^{(i,j)}$ . Hunting is not allowed in YNP so  $h_{E,t}^{(i,j)} = h_{W,t}^{(i,j)} = 0$  for  $(i, j) = (2,2), (2,3), (3,2)$  and  $(3,3)$ .

Since this is a discrete-time model, it is important to specify the timing of actions within each year  $t$ . We assume that growth, predation, natural death and hunting occur prior to dispersal. Therefore, the laws of motion for the pre-dispersal state variables (indicated by the subscript “pre”) are

$$E_{t,pre}^{(i,j)} = \left(1 + g_{E,t}^{(i,j)}\right)E_t^{(i,j)} - F_{E,t}^{(i,j)}W_t^{(i,j)} - h_{E,t}^{(i,j)} \quad (2)$$

and

$$W_{t,pre}^{(i,j)} = \left(1 + g_{W,t}^{(i,j)} - d_W\right)W_t^{(i,j)} - h_{W,t}^{(i,j)} \quad (3)$$

where  $g_{E,t}^{(i,j)}$  and  $g_{W,t}^{(i,j)}$  are the elk and wolf growth rates,  $F_{E,t}^{(i,j)}$  is the functional response (Hastings, 1997) that governs the number of elk killed per wolf,  $d_W$  is the natural mortality rate

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<sup>8</sup> One drawback of annual intervals is that we are unable to model seasonal variations, such as YNP elk migrating south during the winter in search of forage. In future research, we intend to explore shorter time intervals that allow us to model seasonal effects such as migration, snowpack levels, and tourism.



of wolves, and the state variables without the “pre” subscript indicate densities after dispersal.<sup>9</sup>

Elk population growth is assumed to vary by cell and follows a logistic function with intrinsic growth rate  $r_E$  and a cell-specific carrying capacity  $K^{(i,j)}$  (Hastings, 1997) following<sup>10</sup>

$$g_{E,t}^{(i,j)} = r_E \left( 1 - \frac{E_t^{(i,j)}}{K^{(i,j)}} \right). \quad (4)$$

Wolf population dynamics are determined by predation success. Following Hastings (1997), we assume the wolf population growth depends on the number of elk consumed ( $F_{E,t}^{(i,j)} W_t^{(i,j)}$ ) and on the number of livestock consumed ( $F_{L,t}^{(i,j)} W_t^{(i,j)}$ ),

$$g_{W,t}^{(i,j)} = \gamma \left( F_{E,t}^{(i,j)} + F_{L,t}^{(i,j)} \right), \quad (5)$$

where  $\gamma > 0$  is a scale parameter that translates caloric intake from prey into wolf growth and

$F_{L,t}^{(i,j)}$  is the functional response that governs the number of livestock killed per wolf.

Because the livestock population on each cell is fixed due to re-stocking, the livestock functional response is a cell-specific constant,  $F_{L,t}^{(i,j)} = F_L^{(i,j)}$ .

Predation is often treated as Type II functional response (Holling, 1959),

$$F_{E,t}^{(i,j)} = \frac{a E_t^{(i,j)}}{1 + ah E_t^{(i,j)}}, \quad (6)$$

where  $a$  is the attack rate and  $h$  is the handling rate. Notice that equation (6) implies predation is proportional to predator density, which is consistent with the idea that predators only compete

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<sup>9</sup> The functional response recognizes that as the number of elk increases the rate of elk capture per wolf cannot increase indefinitely. The relationship between the functional response and the predation rate is  $p_{E,t}^{(i,j)} = F_{E,t}^{(i,j)} W_t^{(i,j)} / E_t^{(i,j)}$ . Unlike functional responses that are measured in units of prey per predator, predation rates are unitless measures that give the proportion of the prey population that are killed.

<sup>10</sup> Since cattle and elk both compete for grass, the carrying capacity of elk outside YNP is likely to be a function of cattle populations. However, we assume the number of cattle are fixed on each cell according to the number of issued grazing permits.

through the depletion of prey. However, predator interference is common among territorial species where time devoted to capturing prey must be reallocated to direct contests with other individuals (Ruxton et al., 1992). To capture this behavior in wolves, Hebblewhite (2013) recently advocated the use of functional responses that depends on both elk and wolves,

$$F_{E,t}^{(i,j)} = \frac{aE_t^{(i,j)}}{(W_t^{(i,j)})^m + ahE_t^{(i,j)}}, \quad (7)$$

where  $m \geq 0$  is the degree of predator interference (Skalaski and Gilliam, 2001). The predator interference term captures inter-pack competition effects that lead to lower predation success. For instance, a larger number of wolf packs within a cell limits predation rates through increasing competition for space and prey. If the degree of predator competition is zero ( $m = 0$ ), the functional response collapses to the traditional Holling Type II response in equation (6). Here, we explore the properties of functional responses that are dependent on both predators and prey within a spatially explicit model of optimal management.

Wolf-elk predation risk will vary over space due to landscape characteristics (e.g., the type of vegetation, slope of the land, distance to roads, and snowpack levels) not captured in equation (7). Hebblewhite et al. (2005) and Kauffman et al. (2007) have recommended the use of resource selection functions (RSFs) to estimate *relative* predation risk, where predation risk at a particular location is estimated relative to the predation risk at a reference location. In keeping with this strand of research, we create a spatially explicit functional response

$$\tilde{F}_{E,t}^{(i,j)} = F_{E,t}^{(i,j)} \times RSF(\mathbf{x}^{(i,j)}) \quad (8)$$

where

$$RSF(\mathbf{x}^{(i,j)}) = \text{Exp}(\boldsymbol{\beta}'\mathbf{x}^{(i,j)}), \quad (9)$$

and  $\mathbf{x}^{(i,j)}$  is a vector of landscape covariates. Kauffman et al. (2007) estimate the vector of  $\boldsymbol{\beta}$  parameters using data from the Northern Range of YNP and a logistic functional form. Figure 2 shows the similarity of our estimates of predation risk to those published in Kauffman et al. (2007) on Yellowstone's Northern Range, while Figure 3 shows these estimates over the entire  $4 \times 4$  GYE grid. Since we are using a spatially explicit model of predator-prey dynamics in the GYE, we combine the RSF estimated in Kauffman et al. (2007) with the traditional functional responses in (6) and (7).

In Figure 4, we show the prey-dependent Type II spatial functional response for three different cell-specific levels of RSF. Cells #1, #2 and #3 have landscape characteristics that cause the probability of a successful wolf-elk kill to progressively increase, pivoting the functional response up about the origin. For the special case of  $\boldsymbol{\beta}' = 0$ , the functional response reverts to the traditional Holling Type II response that does not depend on landscape heterogeneity.

Combining the spatial functional response in equation (9) with equations (3) and (5), we can write the pre-dispersal law of motion for wolves as

$$W_{t,pre}^{(i,j)} - W_t^{(i,j)} = \gamma \left( \frac{aE_t^{(i,j)} RSF(\mathbf{x}^{(i,j)})}{(W_t^{(i,j)})^m + ahE_t^{(i,j)}} + F_L^{(i,j)} \right) W_t^{(i,j)} - d_W W_t^{(i,j)} - h_{W,t}^{(i,j)}. \quad (10)$$

Equation (10) shows the different mechanisms that influence local wolf populations before they begin the dispersal process, which we discuss next.

### 2.3 Dispersal laws of motion

We assume the dispersal process that governs elk and wolf movement across the grid is given by first-order queen contiguity so that elk and wolves are only allowed to move to neighboring and diagonally adjacent cells over a single time period. This is a reasonable assumption given the large scale of each cell – over 500,000 acres – and we calibrate accordingly so there is little movement between cells in equilibrium. Dispersal is modeled as a two-stage process whereby animals first consider local conditions and decide whether to move from the local cell (Aadland et al., 2015). In the second stage, dispersal is then assumed to depend on the relative attractiveness of neighboring cells. Livestock are assumed to remain on their local cells.

Beginning-of-period elk and wolf populations in each cell are

$$E_{t+1}^{(i,j)} = \theta_{E,t}^{(i,j) \rightarrow (i,j)} E_{t,pre}^{(i,j)} + \sum_{n \in N} \theta_{E,t}^{(i,j)_n \rightarrow (i,j)} E_{t,pre}^{(i,j)_n} \quad (11)$$

and

$$W_{t+1}^{(i,j)} = \theta_{W,t}^{(i,j) \rightarrow (i,j)} W_{t,pre}^{(i,j)} + \sum_{n \in N} \theta_{W,t}^{(i,j)_n \rightarrow (i,j)} W_{t,pre}^{(i,j)_n} \quad (12)$$

where dispersal rates are given by the  $0 \leq \theta \leq 1$  variables and the notation  $(i,j)_n$  refers to the neighbors of cell  $(i,j)$ . The first terms in (11) and (12) specify the number of elk and wolves that remain on cell  $(i,j)$ , where  $\theta_{E,t}^{(i,j) \rightarrow (i,j)}$  and  $\theta_{W,t}^{(i,j) \rightarrow (i,j)}$  are the residence rates on cell  $(i,j)$  in period  $t$ . Therefore, the fraction of elk and wolves that disperse to neighboring cells in period  $t$  is given by  $1 - \theta_{E,t}^{(i,j) \rightarrow (i,j)}$  and  $1 - \theta_{W,t}^{(i,j) \rightarrow (i,j)}$ , respectively. Elk and wolves disperse to neighboring cells if conditions in those cells are preferred to the current cell. The dispersal parameters are assumed to have the following functional form:

$$\theta_{species,t}^{(i,j) \rightarrow (i,j)} = 1 - \text{Exp} \left( -\Lambda_{species,t}^{(i,j)} \right), \quad (13)$$

where  $\Lambda_{species,t}^{(i,j)}$  is an index of environmental factors that cause species either to remain in the current cell or disperse to neighboring cells. Recent research suggests that environmental features such as distance to roads, steepness of terrain, presence of wolves, etc. influence dispersal patterns of elk (Fortin et al., 2005; Forester et al., 2007). Similarly, wolf movement has been shown to depend on the levels of intraspecific strife, proximity to human activity, the density of prey, likelihood of successful predation, etc. (Thurber et al., 1994; Bergman et al., 2006; Hebblewhite and Merrill, 2008).

We assume the variable dispersal term for elk is given by

$$\Lambda_{E,t}^{(i,j)} = \left( \delta_E^{(i,j)} - \widehat{E}_{t,pre}^{(i,j)} - \widetilde{F}_{E,t}^{(i,j)} \widehat{W}_t^{(i,j)} - \widehat{h}_{E,t}^{(i,j)} \right), \quad (14)$$

where  $\delta_E^{(i,j)}$  is a cell-specific intercept and a hat (^) over a variable indicates that it is measured as a proportion of the grid-wide steady-state average. By measuring the variables as a proportion of the grid-wide steady-state averages, each term in equation (14) is scaled to have a similar impact on dispersal near steady state. A negative sign in front of a variable in  $\Lambda_{E,t}^{(i,j)}$  specifies that elk will disperse away from cell  $(i,j)$  when the variable in cell  $(i,j)$  is higher than the average value across the grid. The first term,  $-\widehat{E}_{t,pre}^{(i,j)}$ , represents the idea that, all else equal, higher elk density in the local cell reduces the amount of forage and causes elk to disperse to neighboring cells. The second term,  $-\widetilde{F}_{E,t}^{(i,j)} \widehat{W}_t^{(i,j)}$ , represents dispersal to neighboring cells due to predation risk. Predation risk in cell  $(i,j)$  might increase because of higher wolf density or because the landscape is favorable to wolf-elk predation (Hebblewhite and Merrill, 2008b). The final term,  $-\widehat{h}_{E,t}^{(i,j)}$ , represents increased elk hunting pressure, which is generally associated with increased human activity and access to roads.

The variable dispersal term for wolves is assumed to follow

$$\Lambda_{W,t}^{(i,j)} = \left( \delta_W^{(i,j)} - \widehat{W}_{t,pre}^{(i,j)} + \widehat{F}_{E,t}^{(i,j)} \widehat{W}_t^{(i,j)} - \widehat{h}_{W,t}^{(i,j)} + \widehat{L}_t^{(i,j)} \right). \quad (15)$$

Equation (15) is similar to equation (14) but is adjusted to reflect the fact that wolves are a predator. The term  $-\widehat{W}_{t,pre}^{(i,j)}$  captures inter-pack wolf competition rather than the abundance of forage (Lewis et al., 1997). As wolves prey on elk and livestock,  $\widehat{F}_{E,t}^{(i,j)} \widehat{W}_t^{(i,j)}$  and  $\widehat{L}_t^{(i,j)}$  have positive signs because wolves are drawn to cells with higher than average predation success.<sup>11</sup>

Equation (13) implicitly specifies the rates at which species exit current cells. However, it does not specify which neighboring cells are chosen. Dispersal rates into neighboring cells are determined by the attractiveness of a neighboring cell relative to all other neighboring cells. This structure is convenient and reflects that species make decisions based on local, not global, information characteristic of group-living species (Danchin and Wagner, 1997). The dispersal rates are

$$\theta_{species,t}^{(i,j) \rightarrow (i,j)_n} = \left( 1 - \theta_{species,t}^{(i,j) \rightarrow (i,j)} \right) \left( \frac{\Lambda_{species,t}^{(i,j)_n}}{\sum_{n \in N} \Lambda_{species,t}^{(i,j)_n}} \right). \quad (16)$$

The first term in parentheses represents the fraction of animals that disperse to neighboring cells, while the second term represents the attractiveness of conditions in the  $n^{th}$  cell relative to the set of  $N$  neighboring cells. The product of the two terms equals the overall fraction of animals that disperse in period  $t$  from cell  $(i,j)$  to the  $n^{th}$  neighboring cell.<sup>12</sup>

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<sup>11</sup> In practice, wolf packs are territorial while offspring routinely disperse to identify new territory and form breeding pairs (Gese and Mech, 1991). These more complex dynamics are crudely captured by our dispersal process, where the fixed component represents the territorial nature of wolves and the variable component represents new pack creation and dispersing pups.

<sup>12</sup> Our use of a combination of residence rates and dispersal rates can be thought of as a discrete-space approximation of a dispersal kernel. Thus parameterization of equation (13) and (16) is akin to selecting a functional form for a dispersal kernel.

### 3. A hypothetical simulation under current management

To illustrate the spatiotemporal dynamics of the model presented in Section 2 (see the attached Appendix for details on the calibration procedure), we introduce a one-time disturbance in the (2,2) cell of the grid that reduces elk populations by 50%. The (2,2) cell corresponds to the northwest corner of YNP.<sup>13</sup> Figure 5A shows the equilibrium and temporal dynamics of elk populations across the entire  $4 \times 4$  GYE grid over a 50-year period. The long-run equilibrium levels are given by the intersection with the vertical axis in period  $t = 1$ .<sup>14</sup> The model predicts high elk densities in the central four cells that make up YNP, primarily because hunting is not allowed in YNP. In period  $t = 2$ , elk populations in cell (2,2) fall suddenly by 50% from approximately 4,000 to 2,000 elk. With fewer elk in cell (2,2), the amount of available forage increases in the following period and draws in elk from neighboring cells. The growth rate for the elk population in cell (2,2) also increases through logistic growth being well below carrying capacity. As elk from neighboring cells disperse to cell (2,2), the elk population in neighboring cells begins to fall. This causes a ripple effect across the grid as elk populations in the fourth row and fourth column also begin to decline. However, with fewer elk in each cell, the cells become relatively more desirable for migration and there are higher rates of in-cell reproduction. Over time, dispersal and growth push the system back to equilibrium levels.

The dispersal patterns of elk are difficult to see in Figure 5A. In Figure 5B, we graph net dispersal, which gives the number of elk dispersing into a given cell minus the number of elk dispersing out of the cell. Equilibrium net dispersal is shown as the intersection with the vertical

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<sup>13</sup> The disturbance is hypothetical but could represent an extremely cold winter or a disease outbreak that significantly reduces the size of elk herds.

<sup>14</sup> Attaining an analytical solution for the steady state (equilibrium) of the spatial predator-prey system is not feasible given the complexity of the system. There is the possibility of multiple equilibria in the system. However, we have used a wide range of starting values in the numerical search algorithm for the steady state and have consistently found a unique steady state. Despite this evidence, the existence of multiple equilibria cannot be ruled out with certainty.

axis at period  $t = 1$ .<sup>15</sup> Recall that there is a small amount of dispersal (1%) in equilibrium with the net dispersal positive for most of the outer cells and negative for YNP. Figure 5B shows that net dispersal immediately increases in cell (2,2) and falls in neighboring cells after the disturbance. This reflects the fact that elk find cell (2,2) more attractive after the drop in elk population and subsequent increase in forage.

Figure 6A shows how wolf densities change over time in response to the decline in elk in cell (2,2). The majority of the wolves reside in YNP because it is a refuge from hunting and has habitat favorable for successful predation. In terms of spatiotemporal dynamics, wolf density in cell (2,2) falls after the disturbance because the amount of prey is cut in half and wolves disperse out from the cell. The general trend after the disturbance is for wolf populations to decline across the grid because elk populations decline in cell (2,2) and the surrounding area, which causes a significant prey shortage. Fewer elk, through the numeric response given in equation (4), imply that the wolf reproduction rates will not keep pace with natural death and hunting on outer cells. Gradually, as elk populations return to equilibrium, wolf populations will also return to equilibrium and highlight the model's stability.

#### **4. Optimal wolf and elk management**

Variations over time and space in wolf and elk management influence ecosystem service provisioning in the GYE. We focus on quantifying the ecosystem service impacts of spatial variations in wolf and elk hunting rates, while constraining elk and wolf populations to remain above minimum viable levels.

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<sup>15</sup> We note that although the total number of elk and wolves are fixed in equilibrium, they are allowed to vary across cells and the totals can vary over time in response to disturbances or changes in management. We also note that even in equilibrium, the model is fluid so that a very small number of elk and wolves are continually dispersing to neighboring cells.



The full optimal control problem maximizes equation (1) by choosing time-varying wolf and elk hunting rates subject to the minimum-viable population restrictions. The Euler equations include first-, second-, and higher-order population effects. First-order effects involve direct impacts on wolf populations from wolf harvesting. Second-order effects involve indirect, once-removed impacts on wolf populations through reproduction, predation, and dispersion. Higher-order effects also impact wolf populations through reproduction, predation, and dispersion, but they operate through multiple channels before feeding back to wolf populations.

Take for example the Euler equation for wolf hunting at time  $t$ :

$$\begin{aligned}
& \underbrace{\frac{\partial(\pi_{\text{hunt}}(h_{E,t}, h_{W,t}) + \pi_{\text{tourism}}(W_{t,\text{pre}}^{\text{GYE}}) + \pi_{\text{livestock}}(W_{t,\text{pre}}^{\text{GYE}}, L_t))}{\partial h_{W,t}}}_{\text{first-order effects}} \\
& + e^{-\rho} \underbrace{\frac{\partial(\pi_{\text{hunt}}(h_{E,t+1}, h_{W,t+1}) + \pi_{\text{tourism}}(W_{t+1,\text{pre}}^{\text{GYE}}) + \pi_{\text{livestock}}(W_{t+1,\text{pre}}^{\text{GYE}}, L_{t+1}))}{\partial h_{W,t}}}_{\text{second-order effects}} \\
& + \sum_{j=2}^{T-t} e^{-j\rho} \underbrace{\frac{\partial(\pi_{\text{hunt}}(h_{E,t+j}, h_{W,t+j}) + \pi_{\text{tourism}}(W_{t+j,\text{pre}}^{\text{GYE}}) + \pi_{\text{livestock}}(W_{t+j,\text{pre}}^{\text{GYE}}, L_{t+j}))}{\partial h_{W,t}}}_{\text{higher-order effects}} = 0 \quad (17)
\end{aligned}$$

Solving (17) along with the elk Euler equation, all the laws of motion, dispersal equations, etc., across all time periods is a daunting task. Aadland et al. (2015) describe a linearization procedure that would allow, in principle, for the full solution. However, given the level of ecological detail and dispersal processes for elk and wolves, that procedure is likely intractable for the current model. To allow an optimal solution, we make the common assumption (add citations) and assume proportional harvesting at a fixed rate unless the so the populations fall below minimum viable levels, at which time harvesting rates are set to zero. This allows harvesting quotas to vary over time, but at a fixed proportion of the relevant species population.

Optimization is performed using a grid search over various fixed elk and wolf hunting rates to maximize the sum of discounted ecosystem services over a  $T = 50$  year management horizon. The initial value ( $t = 1$ ) in equation (1) is given by the steady state of the GYE model using actual elk and wolf hunting rates ( $h_{E,Actual} = 0.22$  &  $h_{W,Actual} = 0.21$ ) over the outer grid cells. Starting in period  $t = 2$ , the elk and wolf harvesting rates are then set at new levels for the remainder of the time horizon. The grid search then selects a new combination of hunting rates over the range  $(h_{E,Actual}, h_{W,Actual}) \pm 0.2$  at increments of 0.01. The optimization is performed subject to the constraint that  $\bar{E} \geq 0.75E_{SS}$  and  $\bar{W} \geq 0.75W_{SS}$ , where  $E_{SS}$  and  $W_{SS}$  are the equilibrium aggregate populations of elk and wolves in the GYE, respectively. If either constraint binds over the planning horizon, we rule out the harvesting strategy. This is similar to what happens when a species is ‘listed’ under the U.S. Endangered Species Act (ESA). The biological requirements for removing the wolves from the ESA list included at least 300 wolves across three recovery areas, which is close to our  $\bar{W} \geq 0.75W_{SS}$  constraint if you allow for leakage off our grid.<sup>16</sup>

#### 4.1 “One-size-fits-all” harvest levels

Figure 7 shows the ecosystem net benefit surface (from equation (1)) across various elk and wolf harvesting rates when the rates are uniformly applied across all cells in the grid. The optimal hunting rates are  $h_E^* = 0.16$  and  $h_W^* = 0.33$ , resulting in a sum of discounted net benefits equal to \$5.15 billion. Ignoring discounting, this amounts to a positive net flow of benefits from ecosystem services (i.e., hunting, tourism and cattle ranching less livestock predation) equal to approximately \$103 million per year. In contrast, the sum of discounted net

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<sup>16</sup> <https://www.nps.gov/yell/learn/nature/wolfrestorationinfo.htm>.

benefits from the current hunting rates is \$5.03 billion over the  $T = 50$  period. This amounts to a present-value loss of \$120 million in ecosystem benefits over the 50 year period from the current suboptimal policy. By increasing wolf hunting and decreasing elk hunting rates, fewer wolves and more elk will inhabit the outer cells of GYE. This results in less livestock depredation and more elk harvests, while maintaining a viable population of wolves and elk throughout the GYE.<sup>17</sup>

The shape of the welfare surface in Figure 7 reveals several interesting features of optimal management. First, welfare is relatively more sensitive to wolf hunting rates than elk hunting rates. This sensitivity is due to wolves being a predator and high-profile species. As such, the hunting of wolves impacts livestock predation and tourism directly, while elk hunting only has indirect effects on these two outcomes. Also, because success rates for wolf hunting are so low, raising the harvest rate means significant increases in the number of hunter recreation days in the field. Second, the welfare surface exhibits thresholds where certain combinations of elk and wolf hunting rates cause the minimum-viable population restrictions to bind and a moratorium to be placed on hunting. The gray shaded area in Figure 7 is considered a suboptimal region because the hunting rate combination causes one or both of the species to fall below minimum-viable levels and trigger a federal harvesting moratorium. That the threshold and optimum are so close indicates the need for careful management – a minor perturbation in hunting rates can flip the system into a moratorium. Although it is not modeled here, risk-averse wildlife managers may wish to choose an optimum slightly off the welfare ridge with lower harvesting rates to lower the risk of a federally imposed moratorium, in the event that the ecosystem experiences an unanticipated disturbance. Third, the direction of the ridge in the welfare surface reveals a

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<sup>17</sup> Even though the optimal harvest rate for elk,  $h_E^* = 0.13$ , is lower than the current rate of  $h_E = 0.22$ , the corresponding increase in wolf harvesting causes the long-run number of elk harvested to increase from approximately 2650 to 3550 elk. However, there will be an intermediate period where the number of elk harvested declines.

tradeoff between wolf hunting rates and elk hunting rates. In order to avoid a federally imposed hunting moratorium, hunting rates for wolves must decrease when elk hunting rates increase (and vice versa). The take-home message is that either elk or wolf hunting rates must be lowered to maintain minimum viable population levels, since elk are a primary prey for wolves. Under uniform management, the highest ecosystem net benefits involve aggressive wolf hunting and lower elk hunting rates.

Figures 8A and 8B show the spatial and temporal patterns of elk and wolves in response to the new optimal hunting rates. Higher levels of wolf hunting and lower levels of elk hunting lead to a steady increase in elk populations outside YNP. Initially, elk populations remain relatively constant in YNP, but over time the YNP elk populations increase as elk disperse into YNP. As the elk population outside YNP increases due to less hunting, the elk find it optimal to move into YNP where the forage is relatively more abundant. Figure 8B shows that the increases in wolf hunting from  $h_W = 0.21$  to  $h_W^* = 0.33$  cause wolf populations outside YNP to decline. Wolves are more heavily hunted outside YNP, and in response, seek refuge in YNP. Over time, movement into YNP and the greater abundance of prey leads to a higher concentration of wolves inside YNP. In sum, the impact of optimal management is to increase elk populations across the entire GYE (see Figure 9A) and cause wolves to take refuge in YNP. Aggregate wolf populations in the GYE fall sharply at first (see Figure 9B) but recover over time as the amount of prey increases. The new optimal hunting rates also cause the distribution of wolves to change so there are relatively fewer wolves outside YNP. This has the added benefit of less livestock predation and conflict with ranchers while only marginally decreasing the level of wolf-driven tourism.

#### **4.2 State-specific harvest levels**

Table 1 compares wolf harvest rates for two different federal management regimes. The first regime is discussed in Section 4.1 and sets a uniform “one-size-fits-all” wolf harvest rate across the three U.S. states (Idaho, Montana and Wyoming) that border YNP. The optimal wolf harvest rate under this regime is  $h_W^* = 0.33$ ; higher than the current rate of  $h_W^* = 0.22$ , but not too high to trigger a federal harvesting moratorium. The second regime also considers federal management of the wolf population but allows for different rates to be set across the three states. In this case, the optimal strategy calls for stark differences in the optimal wolf harvesting rates across the states and an increase in total ecosystem service benefits in the GYE. This highlights the heterogeneity within the GYE and a primary contribution of our spatially explicit model. The optimal strategy, allowing for spatially heterogeneous elk predation risk, is for aggressive wolf harvesting in Idaho ( $h_{W,ID}^* = 0.91$ ) and more moderate hunting in Montana ( $h_{W,MT}^* = 0.33$ ) and Wyoming ( $h_{W,WY}^* = 0.28$ ) in order to avoid the harvesting moratorium.<sup>18</sup> The prescribed aggressive wolf harvesting in Idaho does not trigger a harvesting moratorium because the “listing” of wolves in our model is based on ecosystem-wide, not state-specific, populations. Varying the harvest rates across states results in a total increase in ecosystem service benefits of approximately \$11 million (in current dollars) over the “one-size-fits-all” policy. The \$11 million increase hides the fact that there are multiple impacts on GYE services as policymakers move to a state-specific harvesting strategy for wolves. By greatly increasing wolf hunting rates (or equivalently increasing harvest quotas) in Idaho, the flow of ecosystem services associated with wolf tourism and wolf hunting decline. However, these losses are more than compensated by the increased flow of ecosystem services from livestock grazing and elk hunting, in addition to the one-year increase in benefits from wolf hunting in Idaho. The largest contributor to

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<sup>18</sup> See Figure 1 to identify the grid cells located in Idaho, Montana and Wyoming. Cells (3,1) and (4,1) are located in Idaho. The top row of cells and cell (2,1) are located in Montana. All other cells are located in Wyoming. To see the steady-state populations of elk and wolves under current and “one-size-fits-all” optimal harvesting, see the intercepts in Figures 5A, 6A, and 8.

ecosystem services from increasing the Idaho wolf hunting rate is the reduction in livestock predation caused by the lower wolf population. We also investigate how sensitive the state-specific management strategy is to the modeling of spatially heterogeneous elk predation risk via the resource selection functions. The results from the last row of Table 2 show that, while optimal harvesting rates do depend on spatially heterogeneous predation risk, it is not the primary driver of the prescribed high wolf hunting rates in Idaho.

Finally, we note that with spatially variable management there are winners and losers that may require an equitable system of transferring the benefits across states because of the extreme differences in the hunting rates. However, the modest welfare gains from state-specific harvest rates suggest that transaction costs may undermine such a system. Specifically, if the cost of negotiating, administering, and enforcing transfer payments exceeds \$11 million, such a system would actually decrease total welfare. In this case, equity concerns may be addressed with a smaller loss in welfare by adopting the one-size-fits-all policy described in section 4.1.

## 5. Sensitivity analysis

In this section, we investigate whether our policy recommendations are robust to changes in key parameter values or assumptions regarding functional forms. Table 2 summarizes the changes we make to the model, the new optimal harvesting rate for wolves, and the associated change in ecosystem services.

We consider sixteen variations of the model to ensure the results are not driven by particular parameter value or specification. The results of Table 2 are sorted by the optimal wolf harvesting rate, in ascending order. Fifteen of the sixteen simulations prescribe a higher wolf harvesting rate than the current rate of  $h_W = 0.22$ . The exception is the case where welfare is

linear in the aggregate GYE wolf population. In this case, societal welfare does not exhibit diminishing returns to increases in the GYE wolf population. This implies that lowering wolf hunting rates, and thus raising GYE wolf populations, continues to increase tourism revenues at a constant rate. Overall, while there is a moderate degree of variation in the optimal rates across the specifications, the sensitivity analysis shows that our primary management prescription of more aggressive wolf hunting and a lower elk hunting rate outside YNP is robust and not overly dependent on particular values of the parameters.

In addition, the direction of the changes in optimal hunting rates makes sense. Although we do not discuss all sixteen cases, we highlight a few of the more interesting results. To begin, note that the optimal elk harvesting rate is consistently in the range of  $h_E^* = 0.10$  to  $h_E^* = 0.19$ , which is lower than the current estimated rate of  $h_E = 0.21$ . As discussed earlier, lowering the elk harvesting rate does not necessarily imply fewer successful *total* elk harvests if the reduction in the elk harvesting *rate* is accompanied by an increase in the wolf harvesting rate. We now discuss the two other cases that result in lower optimal wolf harvesting rates than in the baseline specification. First, consider the case of a higher average wolf-livestock predation rate,  $\bar{p}_L = 0.05$ . When the wolf-livestock predation rate is higher, significantly more wolves reside in the cells outside YNP. As a result, the optimal wolf hunting rate must decline so too many wolves are not killed, which would in turn trigger a harvesting moratorium on wolves. Second, consider the case where the threshold for the harvesting moratorium on either elk or wolves is raised from 75% to 90% of their respective steady-state populations. This effectively tightens the federal restriction on ‘listing’ elk or wolf populations under the endangered species act. The change requires a reduction in wolf hunting or otherwise aggregate GYE wolf populations will fall below 90% of the original steady state and trigger a wolf harvesting moratorium. This is an

intuitive result and implies that more stringent population restrictions by federal agencies will require simultaneous reductions in hunting rates.

## **6. Discussion of the results**

Three key patterns emerge from our investigation into the optimal management of a wolf-elk-livestock ecosystem. First, ecosystem responses are species, spatial, and temporally specific. Aggregations across any of these dimensions may lead to sub-optimal management prescriptions and unaccounted for ecosystem service flows. Second, if management aggregates across space and time, the best option is to harvest the predator heavily and the prey lightly. Third, if management is spatially disaggregated across zones, the intensity of predator harvests varies significantly across space, requiring an ecosystem service net benefit sharing rule to avoid inequities between management zones.

Our results also complement the literature on marine protected areas (MPA). Ecologists have argued that MPAs provide a win-win outcome by protecting fish species and increasing fish stock for commercial fisheries outside the MPA. Sanchirico and Wilen (2001) show that the benefits of MPAs depend critically on fishery management outside the MPA. Our results yield similar conclusions for a predator-prey system in a terrestrial protected area. While YNP provides tourism benefits inside the park, the optimal level of protection provided by YNP depends on the nature of hunting and livestock management outside the park, as well as the spatiotemporal ecosystem responses to management.

There is increasing recognition of the importance of spatial heterogeneity in economic models of renewable resources (Sanchirico and Wilen, 1999; Smith et al., 2009; Epanchin-Niell and Wilen, 2013). This spatial heterogeneity creates an inherent challenge for wildlife



management and often yields optimal harvest rates that vary considerably across space. Our use of resource selection functions in a spatially explicit natural resource model is a preliminary attempt to address this challenge and integrate advances in ecological modeling into economic models of optimal wildlife management.

## References

- Aadland, D., Sims, C., & Finnoff, D. (2015). Spatial dynamics of optimal management in bioeconomic systems. *Computational Economics*, 45(4), 545-577.
- Bergman, E.J., Garrott, R.A., Creel, S., Borkowski, J.J., Jaffe, R., & Watson, F.G.R. (2006). Assessment of prey vulnerability through analysis of wolf movements and kill sites. *Ecological Applications*, 16(1), 273-284.
- Boyce, M.S. (1995). Anticipating consequences of wolves in Yellowstone: model validation. *Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, Edmonton, Alberta, Canada*, 199-209.
- Boyce, M.S., & McDonald, L.L. (1999). Relating populations to habitats using resource selection functions. *Trends in Ecology & Evolution*, 14(7), 268-272.
- Caplin, A., & Leahy, J. (2004). The social discount rate. *Journal of Political Economy*, 112(6), 1257-1268.
- Chambers, C.M. & Whitehead, J.C. (2003). A contingent valuation estimate of the benefits of wolves in Minnesota. *Environmental and Resource Economics*, 26(2), 249-267.
- Crocker, T.D. & Tschirhart, J. (1992). Ecosystems, externalities, and economies. *Environmental and Resource Economics*, 2, 551-567.
- Danchin, E., & Wagner, R.H. (1997). The evolution of coloniality: the emergence of new perspectives. *Trends in Ecology & Evolution*, 12(9), 342-347.
- Duffield, J.W., Neher, C.J., & Patterson, D.A. (2008) "Wolf recovery in Yellowstone Park: Visitor attitudes, expenditures, and economic impacts." *Yellowstone Science*, 16(1), 20-25.
- Epanchin-Niell, R.S., & Wilen J.E. (2015) Individual and cooperative management of invasive species in human-mediated landscapes. *American Journal of Agricultural Economics*, 97(1), 180-198.
- Epanchin-Niell, R.S., & Wilen, J.E. (2012). Optimal spatial control of biological invasions. *Journal of Environmental Economics and Management*, 63(2), 260-270.
- Fenichel, E.P., Horan, R.D., & Bence, J.R. (2010). Indirect management of invasive species through bio-controls: a bioeconomic model of salmon and alewife in Lake Michigan. *Resource and Energy Economics*, 32(4), 500-518.
- Finnoff, D., & Tschirhart, J. (2003). Harvesting in an eight-species ecosystem. *Journal of Environmental Economics and Management*, 45(3), 589-611.

- Forester, J.D., Ives, A.R., Turner, M.G., Anderson, D.P., Fortin, D., Beyer, H.L., Smith, D.W., & Boyce, M.S. (2007). State-space models link elk movement patterns to landscape characteristics in Yellowstone National Park. *Ecological Monographs*, 77(2), 285-299.
- Fortin, D., Beyer, H.L., Boyce, M.S., Smith, D.W., Duchesne, T., & Mao, J.S. (2005). Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology*, 86(5), 1320-1330.
- Gardner, R.H., & Gustafson, E.J. (2004). Simulating dispersal of reintroduced species within heterogeneous landscapes. *Ecological Modelling*, 171(4), 339-358.
- Garrott, R.A., Bruggeman, J.E., Becker, M.S., Kalinowski, S.T., & White, P.J. (2007). Evaluating prey switching in wolf-ungulate systems. *Ecological Applications*, 17(6), 1588-1597.
- Gese, E.M., & Mech, L.D. (1991). Dispersal of wolves (*Canis lupus*) in northeastern Minnesota, 1969-1989. *Canadian Journal of Zoology*, 69(12), 2946-2955.
- Hanski, I., & Ovaskainen, O. (2000). The metapopulation capacity of a fragmented landscape. *Nature*, 404(6779), 755-758.
- Hastings, A. (Ed.). (1997). *Population biology: concepts and models*. Springer.
- Hebblewhite, M. (2013). Consequences of ratio-dependent predation by wolves for elk population dynamics. *Population Ecology*, 55(4), 511-522.
- Hebblewhite, M., & Merrill, E. (2008). Modelling wildlife–human relationships for social species with mixed-effects resource selection models. *Journal of Applied Ecology*, 45(3), 834-844.
- Hebblewhite, M. & Merrill, E. (2008b). Multiscale wolf predation risk for elk: does migration reduce risk? *Oecologia*, 152, 377-387.
- Hebblewhite, M., Merrill, E.H., & McDonald, T.L. (2005). Spatial decomposition of predation risk using resource selection functions: an example in a wolf–elk predator–prey system. *Oikos*, 111(1), 101-111.
- Hoekstra, J., & van den Bergh, J.C. (2005). Harvesting and conservation in a predator–prey system. *Journal of Economic Dynamics and Control*, 29(6), 1097-1120.
- Holling, C.S. (1959). The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. *The Canadian Entomologist*, 91(05), 293-320.
- Horan, R.D., Fenichel, E.P., Drury, K., & Lodge, D.M., (2011). Managing ecological thresholds in coupled environmental–human systems. *Proceedings of the National Academy of Sciences* 108, 7333–7338.
- Hussain, A.M.T., & Tschirhart, J. (2013) Economic/ecological tradeoffs among ecosystem services and biodiversity conservation. *Ecological Economics*, 93, 116-127.

- Jin, S., Yang, L., Danielson, P., Homer, C., Fry, J., & Xian, G. (2013). A comprehensive change detection method for updating the National Land Cover Database to circa 2011. *Remote Sensing of Environment*, 132, 159-175.
- Kauffman, M.J., Varley, N., Smith, D.W., Stahler, D.R., MacNulty, D.R., & Boyce, M.S. (2007). Landscape heterogeneity shapes predation in a newly restored predator–prey system. *Ecology Letters*, 10(8), 690-700.
- Kydland, F.E., & Prescott, E.C. (1982) Time to build and aggregate fluctuations. *Econometrica*, 1345-1370.
- Lewis, M.A., White, K.A.J., & Murray, J.D. (1997). Analysis of a model for wolf territories. *Journal of Mathematical Biology*, 35(7), 749-774.
- Lichtenstein, M.E., & Montgomery, C.A. (2003). Biodiversity and timber in the Coast Range of Oregon: inside the production possibility frontier. *Land Economics*, 79(1), 56-73.
- Loomis, J.B. and White, D.S. (1996). Economic benefits of rare and endangered species: summary and meta-analysis. *Ecological Economics*, 18(3), 197-206.
- Melstrom, R.T., & Horan, R.D. (2013). Managing excessive predation in a predator-endangered prey setting. *Ecological Economics*, 90, 85-93.
- Melstrom, R.T., & Horan, R.D. (2014). Interspecies management and land use strategies to protect endangered species. *Environmental and Resource Economics*, 58(2), 199-218.
- Messier, F. (1994). Ungulate population models with predation: a case study with the North American moose. *Ecology*, 75(2), 478-488.
- Montgomery, C.A., Pollak, R.A., Freemark, K., & White, D. (1999). Pricing biodiversity. *Journal of Environmental Economics and Management*, 38(1), 1-19.
- Moore, M.A., Boardman, A.E., Vining, A.R., Weimer, D.L., & Greenberg, D.H. (2004). Just give me a number! Practical values for the social discount rate. *Journal of Policy Analysis and Management*, 23(4), 789-812.
- Nalle, D.J., Montgomery, C.A., Arthur, J.L., Polasky, S., & Schumaker, N.H. (2004). Modeling joint production of wildlife and timber. *Journal of Environmental Economics and Management*, 48(3), 997-1017.
- Park, T., Loomis, J.B., & Creel, M. (1991). Confidence intervals for evaluating benefits estimates from dichotomous choice contingent valuation studies. *Land Economics*, 64-73.
- Polasky, S., Nelson, E., Lonsdorf, E., Fackler, P., & Starfield, A. (2005). Conserving species in a working landscape: land use with biological and economic objectives. *Ecological Applications*, 15(4), 1387-1401.

- Polasky, S., Nelson, E., Camm, J., Csuti, B., Fackler, P., Lonsdorf, E., ... & Haight, R. (2008). Where to put things? Spatial land management to sustain biodiversity and economic returns. *Biological Conservation*, 141(6), 1505-1524.
- Ragozin, D.L., Brown Jr., G., (1985). Harvest policies and nonmarket valuation in a predator-prey system. *Journal of Environmental Economics and Management*, 12, 155-168.
- Ramler, J.P., Hebblewhite, M., Kellenberg, D., & Sime, C. (2014). Crying wolf? A spatial analysis of wolf location and depredations on calf weight. *American Journal of Agricultural Economics*.
- Richardson, L. and Loomis, J. (2009). The total economic value of threatened, endangered and rare species: An updated meta-analysis. *Ecological Economics*, 68(5), 1535-1548.
- Ruxton, G.D., Gurney, W.S.C., & De Roos, A.M. (1992). Interference and generation cycles. *Theoretical Population Biology*, 42(3), 235-253.
- Sanchirico, J.N., & Wilen, J.E. (1999). Bioeconomics of spatial exploitation in a patchy environment. *Journal of Environmental Economics and Management*, 37(2), 129-150.
- Sanchirico, J.N. & Wilen, J.E. (2001). A bioeconomic model of marine reserve creation. *Journal of Environmental Economics and Management*, 42, 257-276.
- Skalski, G.T., & Gilliam, J.F. (2001). Functional responses with predator interference: viable alternatives to the Holling type II model. *Ecology*, 82(11), 3083-3092.
- Smith, D.W., Peterson, R.O., & Houston, D.B. (2003). Yellowstone after wolves. *BioScience*, 53(4), 330-340.
- Smith, M.D., Sanchirico, J.N., & Wilen, J.E. (2009). The economics of spatial-dynamic processes: applications to renewable resources. *Journal of Environmental Economics and Management*, 57(1), 104-121
- Solomon, M.E. (1949). The natural control of animal populations. *The Journal of Animal Ecology*, 1-35.
- Steele, J.R., Rashford, B.S., Foulke, T.K., Tanaka, J.A., & Taylor, D.T. (2013). Wolf (*Canis lupus*) predation impacts on livestock production: direct effects, indirect effects, and implications for compensation ratios. *Rangeland Ecology and Management*, 66(5), 539-544.
- Ströbele, W.J., & Wacker, H. (1995). The economics of harvesting predator-prey systems. *Journal of Economics*, 61(1), 65-81.
- Thurber, J.M., Peterson, R.O., Drummer, T.D., & Thomasma, S.A. (1994). Gray wolf response to refuge boundaries and roads in Alaska. *Wildlife Society Bulletin*, 61-68.

Tu, P.N., & Wilman, E.A. (1992). A generalized predator-prey model: Uncertainty and management. *Journal of Environmental Economics and Management*, 23(2), 123-138.

U.S.D.A. (2013). Wyoming Agricultural Statistics.

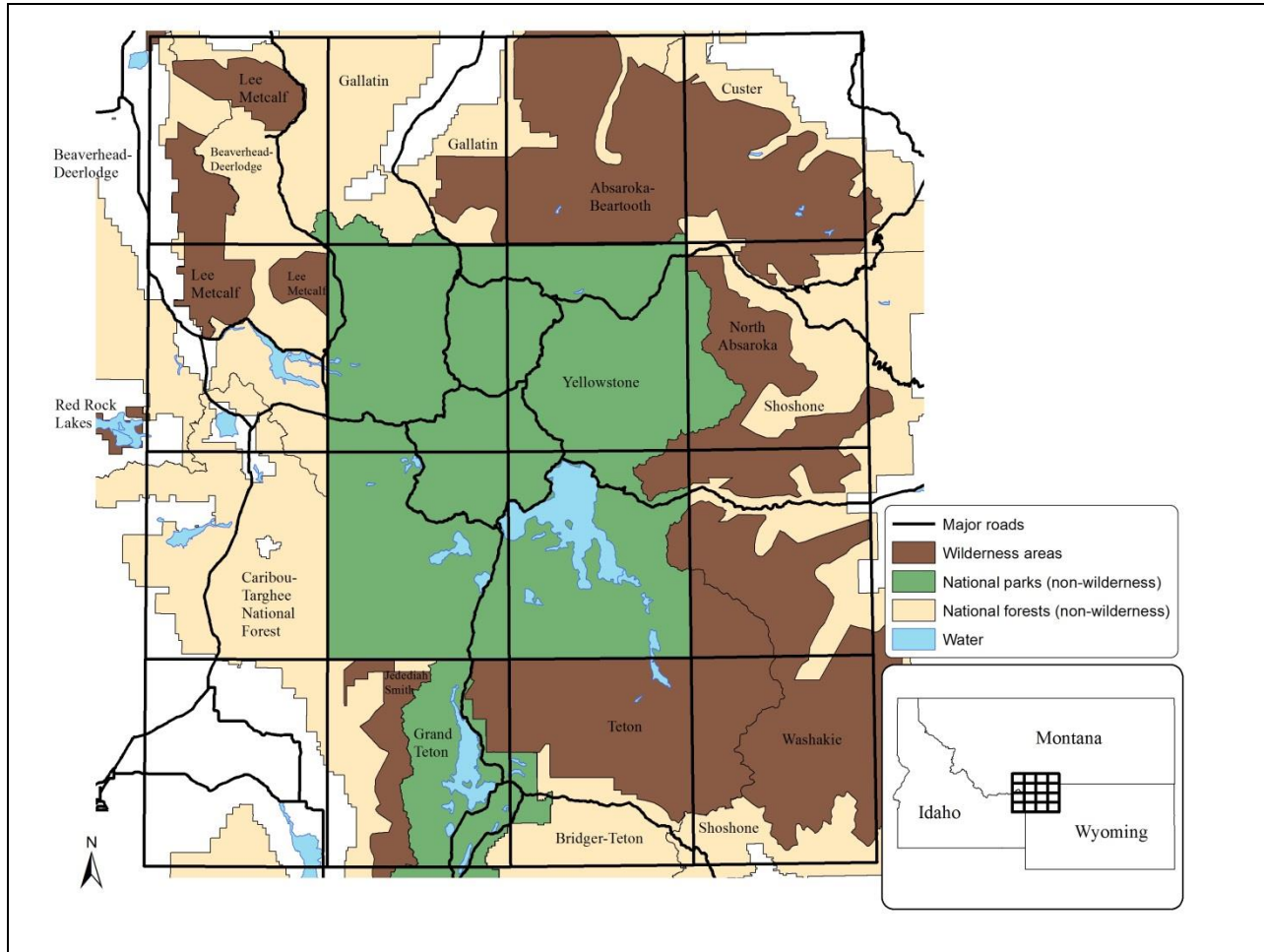
Walsh, R.G., Johnson, D.M., & McKean, J.R. (1992). Benefit transfer of outdoor recreation demand studies, 1968–1988. *Water Resources Research*, 28(3), 707-713.

Wilenski, J.E. (2007) Economics of spatial-dynamic processes. *American Journal of Agricultural Economics*, 89(5), 1134-1144.

Wright, G.J., Peterson, R.O., Smith, D.W., & Lemke, T.O. (2006). Selection of northern Yellowstone elk by gray wolves and hunters. *Journal of Wildlife Management*, 70(4), 1070-1078.

Wyoming Game and Fish Department. 2013. Wyoming Game and Fish Department 2013 Annual Report of Big and Trophy Game Harvest pp. 429-437. Wyoming Game and Fish Department, 5400 Bishop Blvd. Cheyenne, WY 82006.

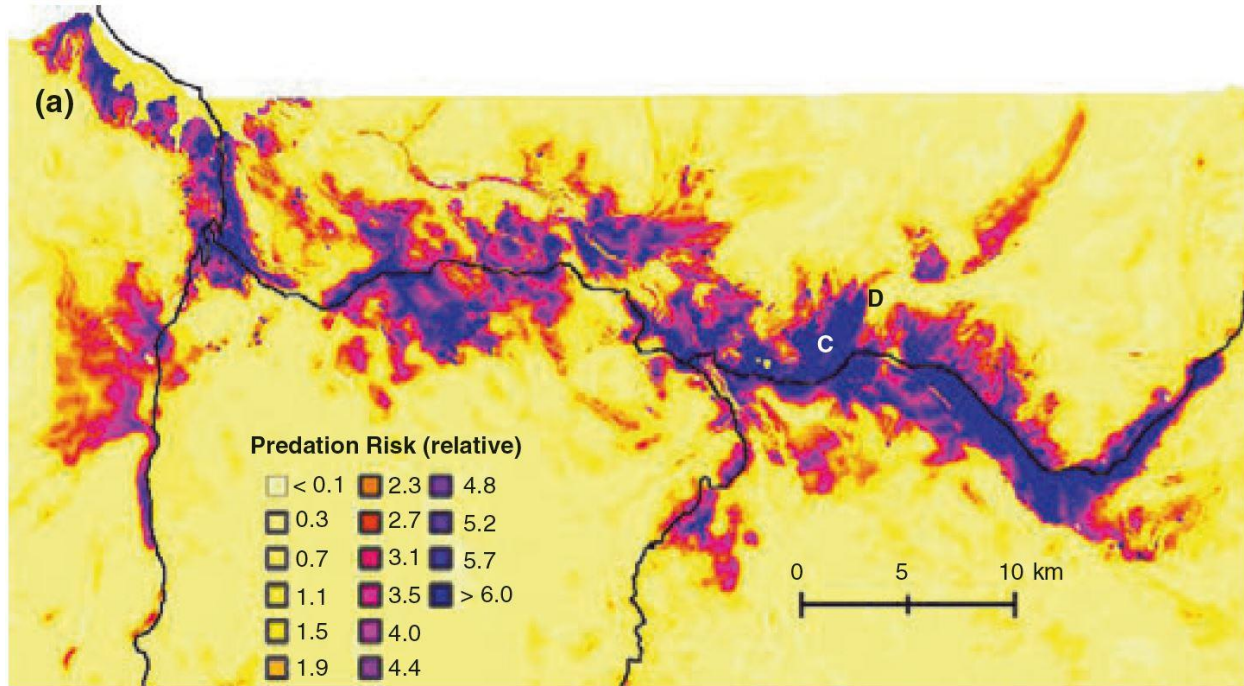
Figure 1. Greater Yellowstone Ecosystem 4 × 4 Grid



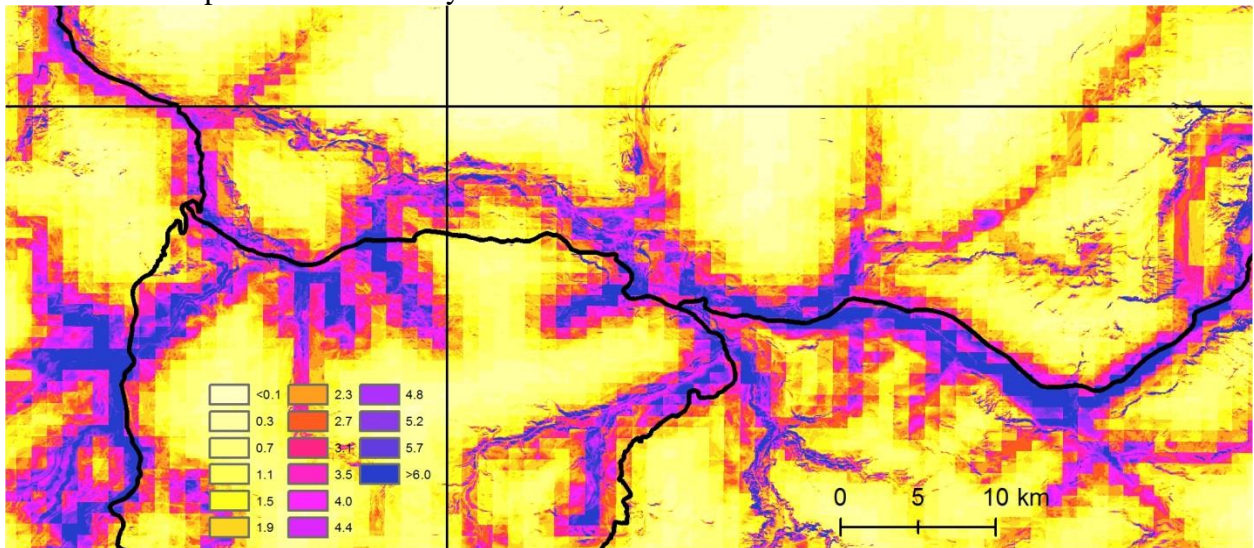
Notes. The 4 by 4 grid was constructed manually in GIS with same-sized cells of approximately 844 square miles. Water was identified using the NLCD2011 dataset. Roads and state boundaries are from 2013 TIGER/Line Shapefiles. National Forest System boundaries are from the USDA's Administrative Forest Boundaries dataset. National Park Service boundaries are from the University of New Mexico's Earth Data Analysis Center. White areas within the grid are private or state-owned land.

Figure 2. Comparison of Wolf-Elk Predation Risk on Yellowstone’s Northern Range

Panel A. Kauffman et al. (2007)



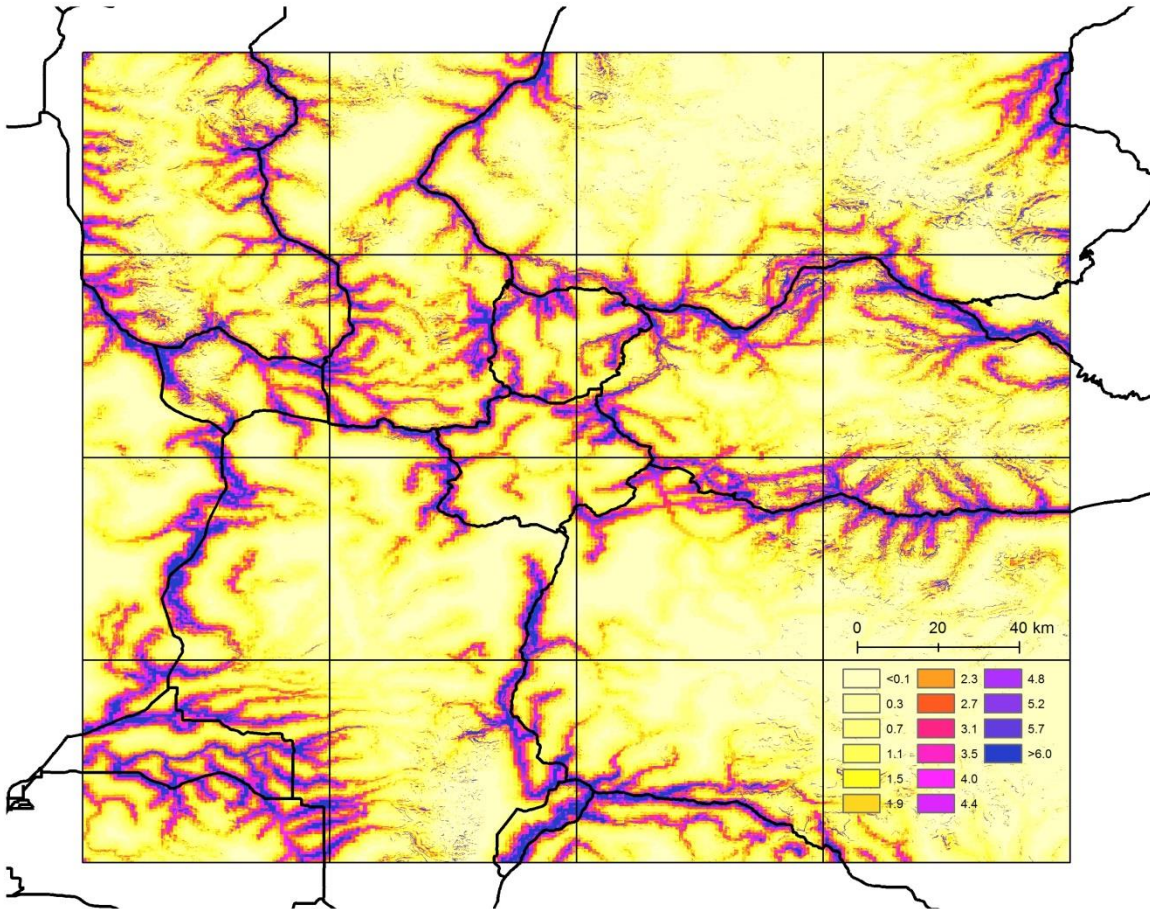
Panel B. Our Spatial Predator-Prey Model



Notes. Snow water equivalent (SWE) uses average annual snowfall (inches) from Snow Course (SC) contour arc data between 1958 and 1972. These data were interpolated across space and converted from inches to SWE by dividing by 10. Openness is calculated using a 500m x 500m “moving window” and summing those cells that are grasslands or open conifer (deciduous forest, mixed forest and shrub scrub). Slope units are in decimal degrees and Euclidean distances were used for river and road distance calculations (measured in meters). Elk and wolf density effects on relative predation risk are omitted (set to zero). Our predation risk was then scaled linearly by a factor of 5 to match our predator-prey model visually to Kauffman et al. (2007) using consistent legend breaks.

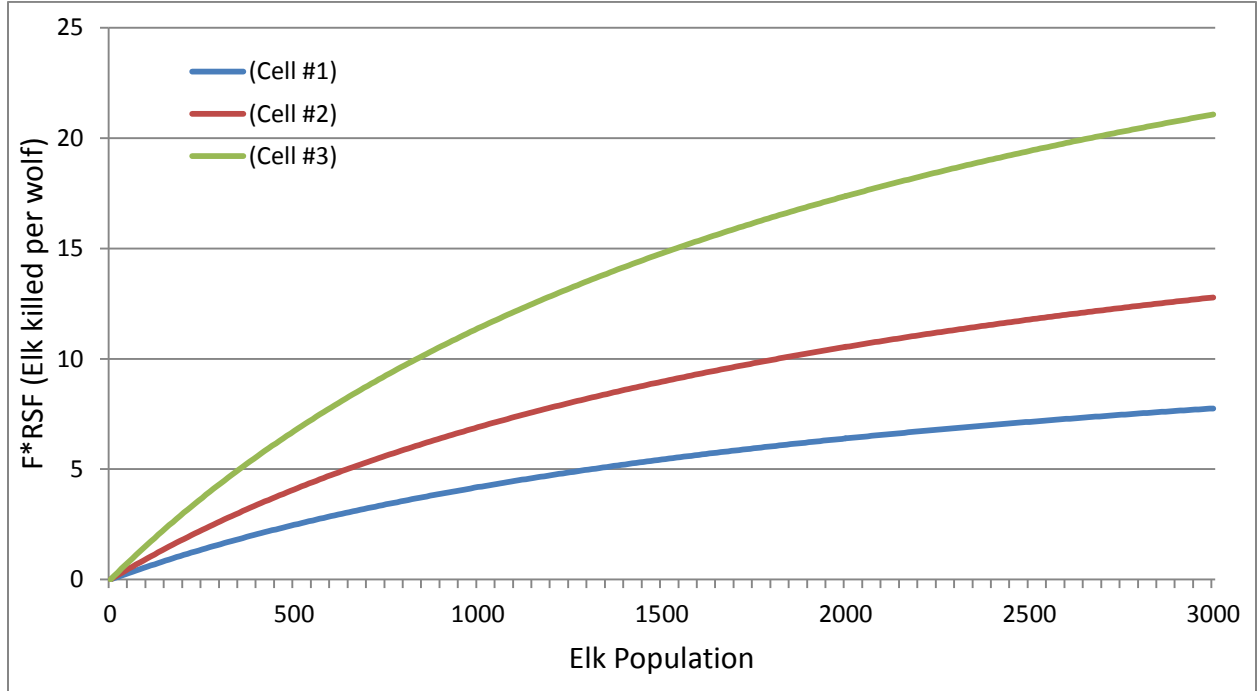


Figure 3. Spatial Variation in Wolf-Elk Predation Risk for the Entire 4 × 4 GYE Grid



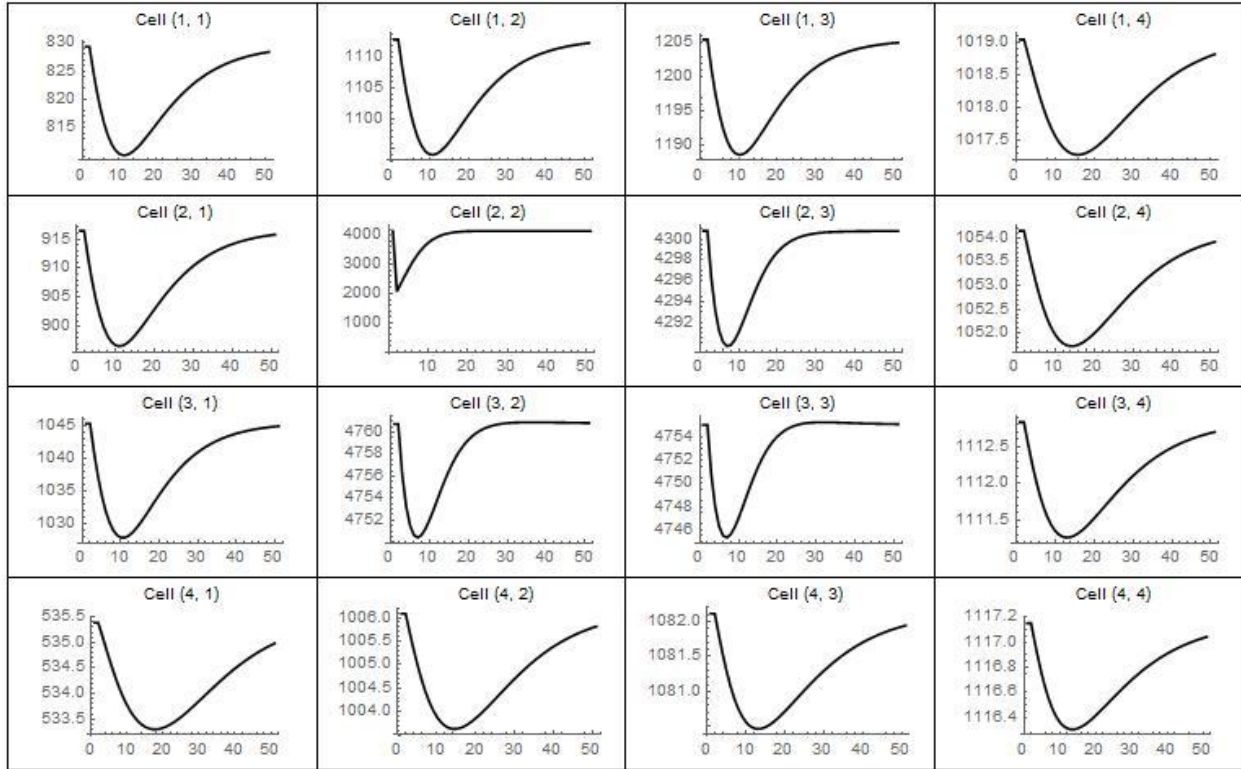
Notes. Snow water equivalent (SWE) uses average annual snowfall (inches) from Snow Course (SC) contour arc data between 1958 and 1972. These data were interpolated across space and converted from inches to SWE by dividing by 10. Openness is calculated using a 500m x 500m “moving window” and summing those cells that are grasslands or open conifer (deciduous forest, mixed forest and shrub scrub). Slope units are in decimal degrees and Euclidean distances were used for river and road distance calculations (measured in meters). Elk and wolf density effects on relative predation risk are omitted (set to zero). Our predation risk was then scaled linearly by a factor of 5 to match our predator-prey model visually to Kauffman et al. (2007) using consistent legend breaks.

Figure 4. Stylized Wolf-Elk Functional Response for Three Cell-Specific Landscape Types

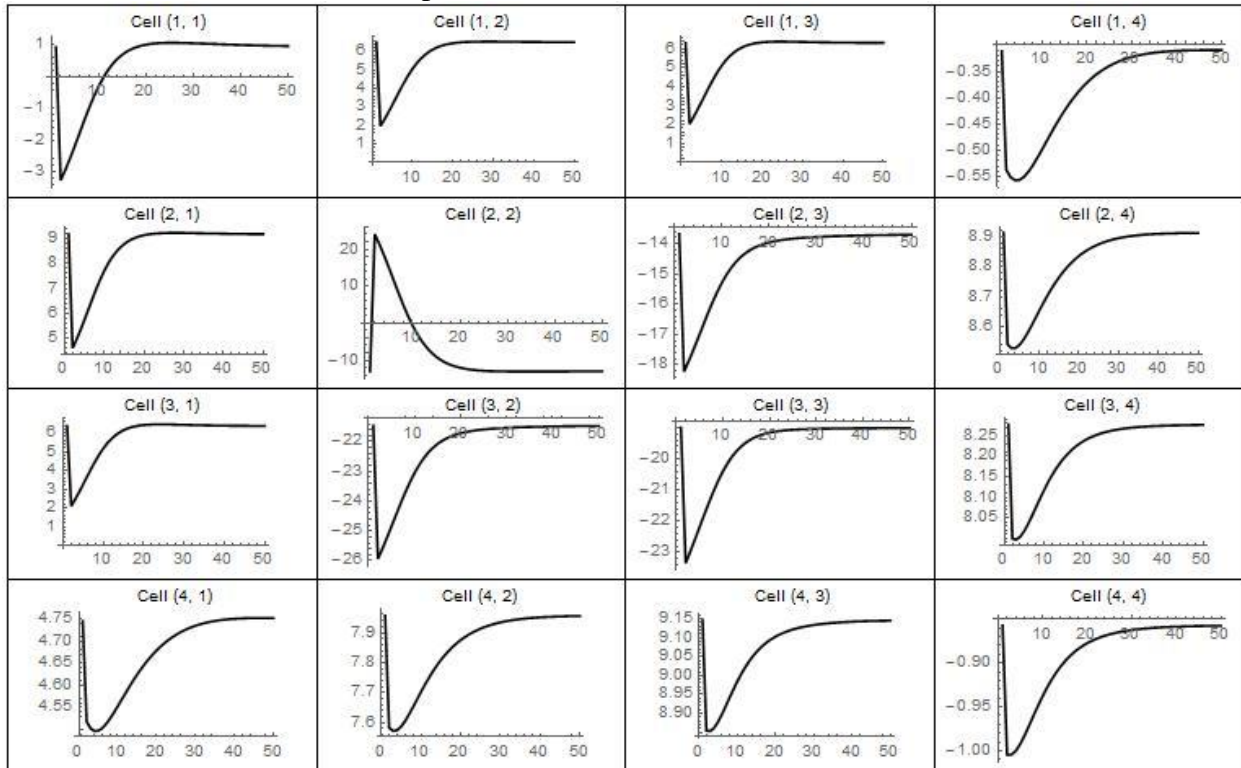


Notes. The Holling Type II functional responses (prey interference parameter  $m = 0$ ) are based on an attack rate of  $a = 1$  and a handling rate of  $h = 0.045$ . Cell #1 has landscape characteristics least favorable to elk predation with an RSF value of  $Exp(-0.5)$ ; cell #2 has landscape characteristics neutral to elk predation with an RSF value of  $Exp(0)$ ; and cell #3 has landscape characteristics most favorable to elk predation with an RSF value of  $Exp(0.5)$ .

Figure 5A. Predicted Elk Densities over the 4 × 4 GYE Grid



Panel 5B. Predicted Elk Net Dispersal Patterns over the 4 × 4 GYE Grid



Notes. The four central cells represent YNP where hunting of elk or wolves is not allowed. The 12 perimeter cells represent a mix of public and private land where hunting and cattle grazing are allowed. The driving shock is a one-time 50% reduction in the elk stock in cell (2,2), which is the northwest corner of YNP. Net dispersal refers to the number of elk dispersing into the given cells minus the number of elk dispersing out of the cell.

Figure 6A. Predicted Wolf Densities over the 4 × 4 GYE Grid

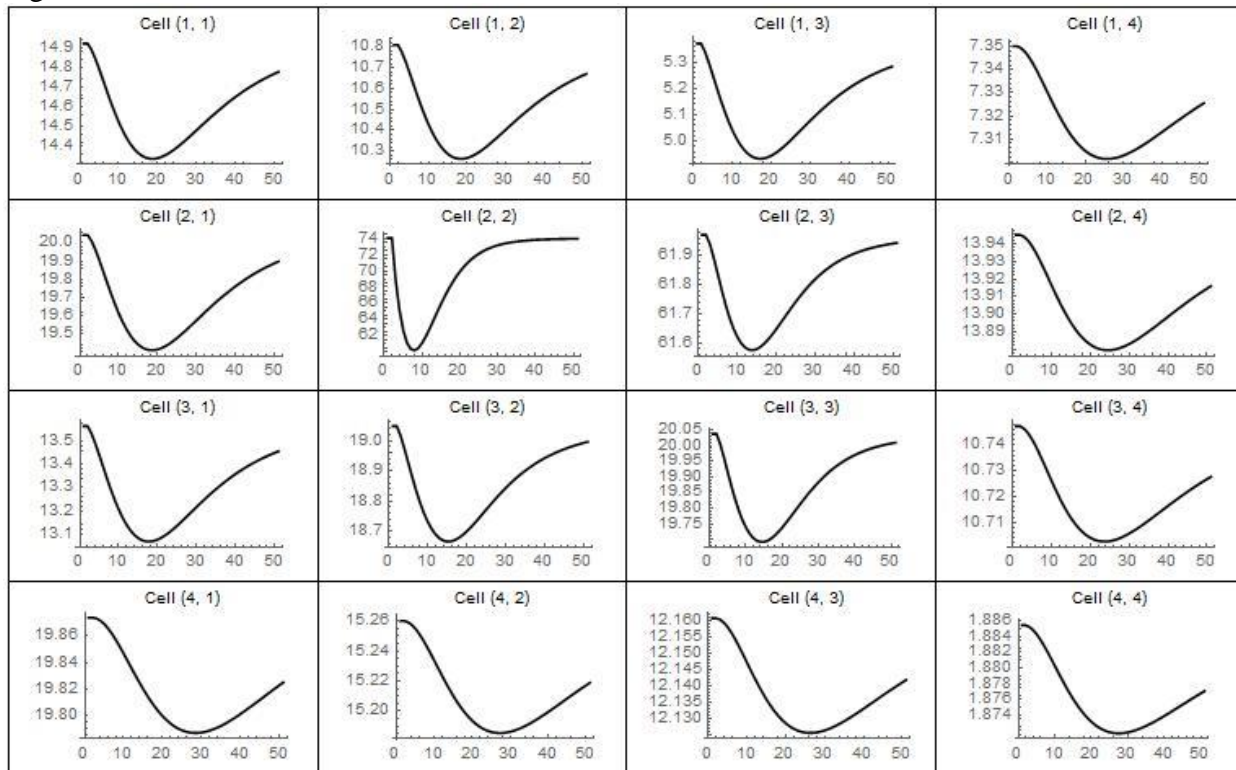
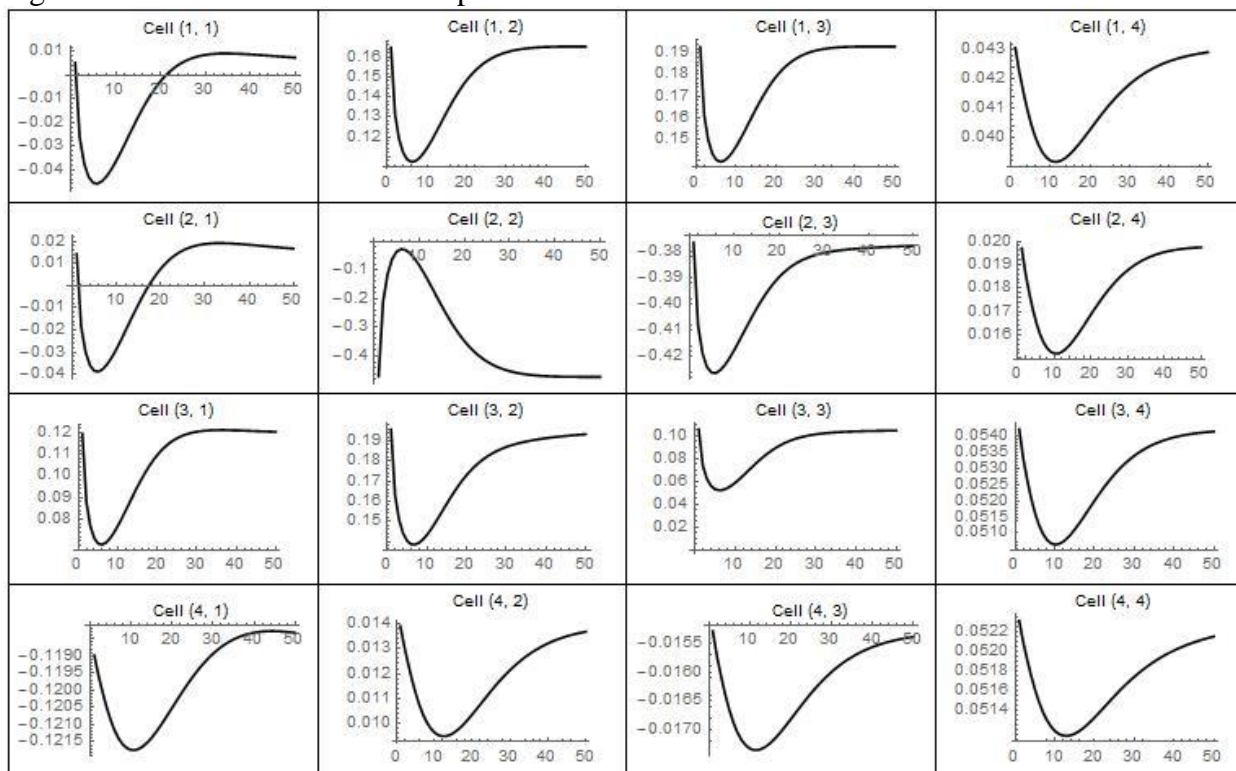
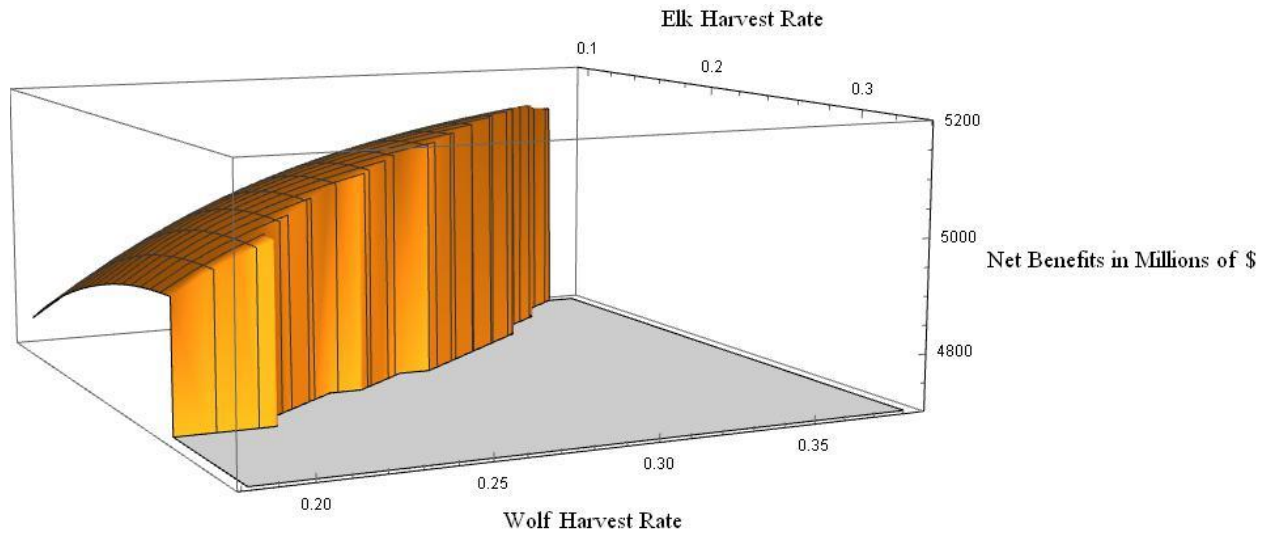


Figure 6B. Predicted Wolf Net Dispersal Patterns over the 4 × 4 GYE Grid



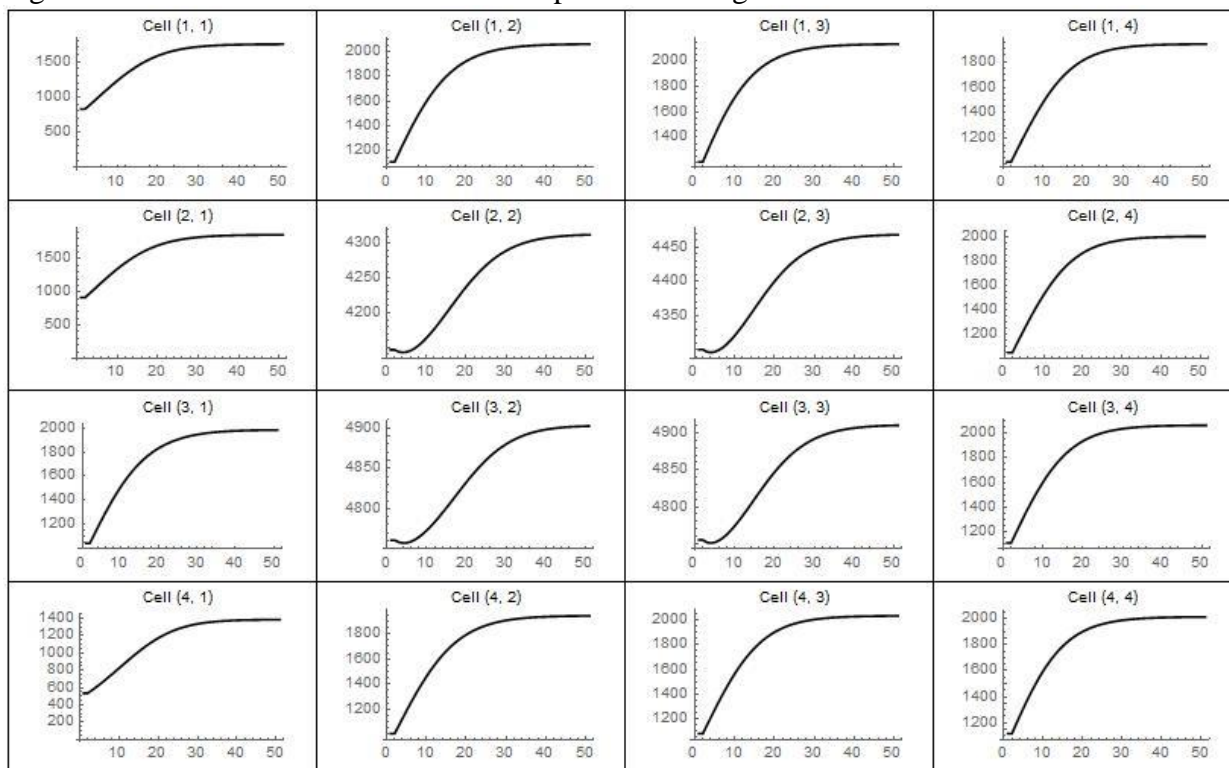
Notes. The four central cells represent YNP where hunting of elk or wolves is not allowed. The 12 perimeter cells represent a mix of public and private land where hunting and cattle grazing are allowed. The driving shock is a one-time 50% reduction in the elk stock in cell (2,2), which is the northwest corner of YNP. Net dispersal refers to the number of wolves dispersing into the given cells minus the number of wolves dispersing out of the cell.

Figure 7. Ecosystem Net Benefit Surface and Optimal Management for the GYE

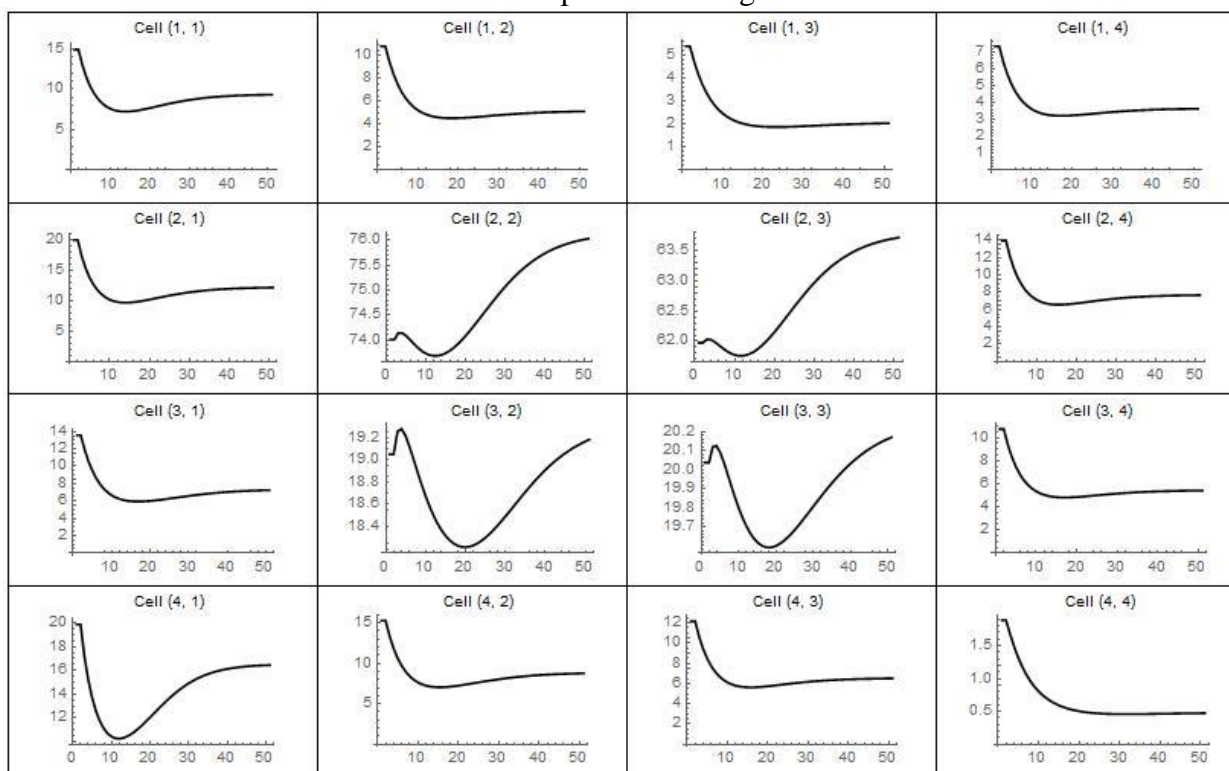


Notes. 'Net Benefits' are measured in millions of dollars. The optimal elk and wolf hunting rates are  $h_E^* = 0.16$  and  $h_W^* = 0.33$ . These are the fixed hunting rates that maximize the sum of discounted net benefits from ecosystem services over a 50-year period. The optimal value of the welfare function is \$5.15 billion. Ignoring discounting, this amounts to a positive net flow of benefits from ecosystem services (hunting, tourism and grazing profits less predation costs) equal to approximately \$103 million per year. The shaded gray area results in either elk or wolf populations falling below minimum allowable levels,  $\bar{E}$  and  $\bar{W}$ , and therefore are not considered optimal.

Figure 8A. Predicted Elk Densities with Optimal Hunting over the 4 × 4 GYE Grid



Panel 8B. Predicted Wolf Densities with Optimal Hunting over the 4 × 4 GYE Grid



Notes. The simulated time paths for elk and wolf densities start ( $t = 1$ ) at the current average hunting rates of 0.21 for wolves and 0.22 for elk. In period ( $t = 2$ ) and thereafter, hunting rates are set at the socially optimal levels of 0.16 for elk and 0.33 for wolves.

Figure 9A. Aggregate Elk Time Path from Optimal Management over 50 Years

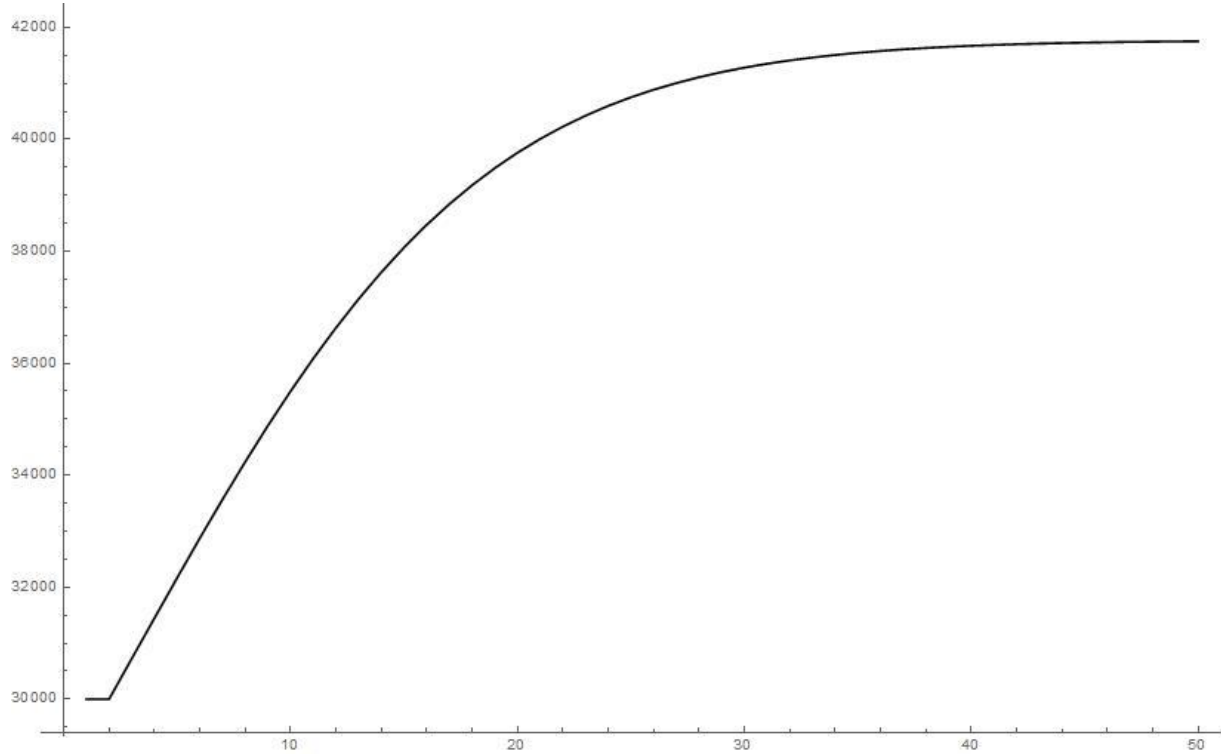
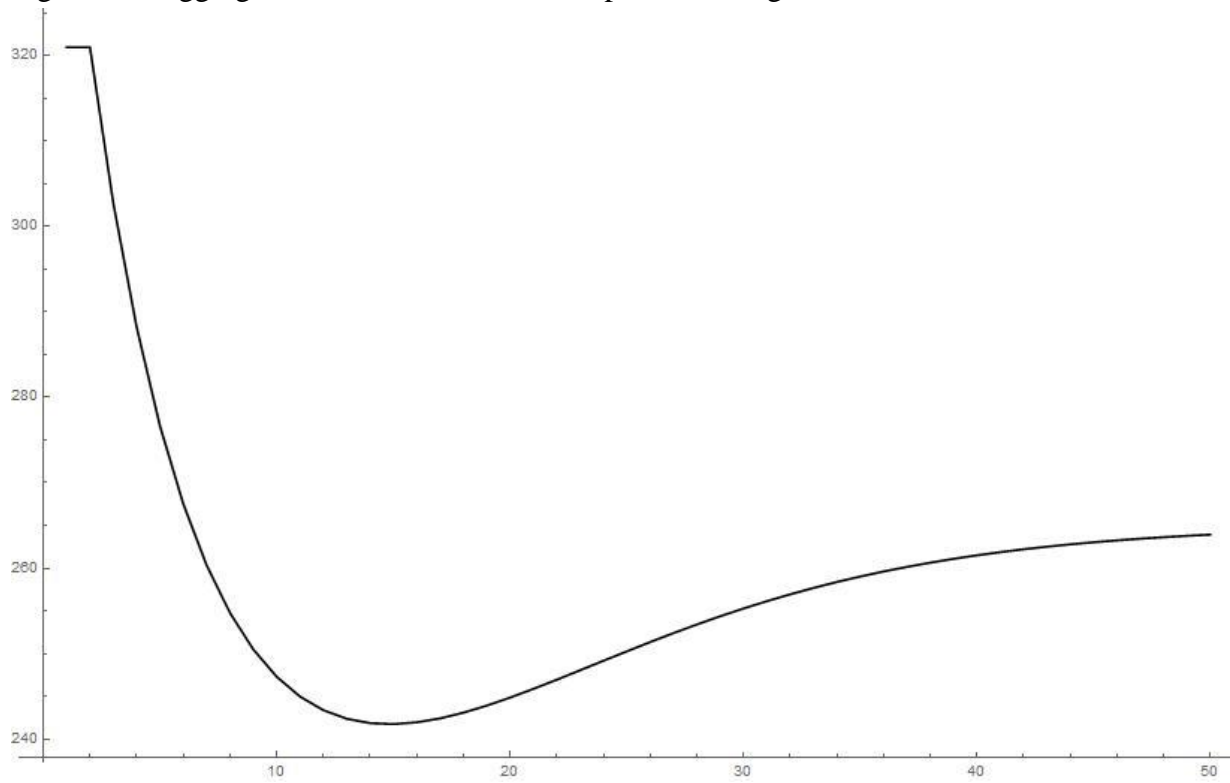


Figure 9B. Aggregate Wolf Time Path from Optimal Management over 50 Years



Notes. The simulated aggregate time paths for elk and wolf densities start ( $t = 1$ ) at the current average hunting rates of 0.21 for wolves and 0.22 for elk. In period ( $t = 2$ ) and thereafter, hunting rates are set at the socially optimal levels of 0.16 for elk and 0.33 for wolves.

Table 1. Optimal Federal Wolf Hunting Rates

Management Strategy	Wolf Harvest Rates			Discounted Ecosystem Benefits over a 50-year Planning Horizon (Millions of \$\$)
	ID	MT	WY	
Rates uniform across states	0.33	0.33	0.33	\$5,151
Rates varied by state (w/ spatially <b>heterogeneous</b> elk predation risk; $\beta' \neq 0$ )	0.91	0.33	0.28	\$5,162
Rates varied by state (w/ spatially <b>homogeneous</b> elk predation risk; $\beta' = 0$ )	0.94	0.27	0.32	\$5,124

Notes. Elk hunting rates are fixed at  $h_E = 0.16$ , which is the optimal rate under federal management with uniform hunting rates across states. Discount rate is set at 1% per year.



Table 2. Sensitivity Analysis for Optimal “One-Size-Fits-All” Federal Wolf Hunting Rates

Change in Parameter Value or Functional Form	Optimal Elk Hunting Rate	Optimal Wolf Hunting Rate	Ecosystem Benefits (\$ millions)
Baseline specification	$h_E^* = 0.16$	$h_W^* = 0.33$	\$5,151
Tourism component of welfare function is linear in wolf population	$h_E^* = 0.10$	$h_W^* = 0.15$	\$6,062
Higher wolf-livestock predation rate ( $\bar{p}_L = 0.05$ )	$h_E^* = 0.13$	$h_W^* = 0.24$	\$4,231
Minimum viable population restrictions ( $\bar{E} = 0.9E_{SS}$ ; $\bar{W} = 0.9W_{SS}$ )	$h_E^* = 0.17$	$h_W^* = 0.25$	\$5,064
Spatially homogeneous functional response ( $\beta' = 0$ )	$h_E^* = 0.15$	$h_W^* = 0.32$	\$5,121
No predator interference in functional response ( $m = 0$ )	$h_E^* = 0.14$	$h_W^* = 0.32$	\$5,227
Add non-use value for wolves ( $\alpha_{non-use} = \$81,000$ )	$h_E^* = 0.16$	$h_W^* = 0.33$	\$6,179
Higher indirect cost of wolf-livestock predation ( $20 \times$ direct costs)	$h_E^* = 0.16$	$h_W^* = 0.33$	\$4,914
Shorter time horizon ( $T = 25$ years)	$h_E^* = 0.16$	$h_W^* = 0.33$	\$2,882
Higher social discount rate ( $\rho = 0.05$ )	$h_E^* = 0.16$	$h_W^* = 0.33$	\$2,439
Highly responsive dispersion ( $5 \times$ response to dispersion factors in eqs. (14) and (15))	$h_E^* = 0.17$	$h_W^* = 0.33$	\$5,139
Lower social value for each harvested wolf ( $\alpha_W = \alpha_E = \$1,785$ )	$h_E^* = 0.16$	$h_W^* = 0.33$	\$5,122
Longer time horizon ( $T = 100$ years)	$h_E^* = 0.16$	$h_W^* = 0.33$	\$8,294
No social discounting ( $\rho = 0$ )	$h_E^* = 0.16$	$h_W^* = 0.33$	\$6,521
Differential residence rates ( $\bar{\theta}_W^{(i,j) \rightarrow (i,j)} = 0.99$ ; $\bar{\theta}_E^{(i,j) \rightarrow (i,j)} = 0.8$ )	$h_E^* = 0.20$	$h_W^* = 0.36$	\$5,210
Minimum viable population restrictions ( $\bar{E} = 0.6E_{SS}$ ; $\bar{W} = 0.6W_{SS}$ )	$h_E^* = 0.19$	$h_W^* = 0.38$	\$5,212
Higher elk carrying capacity ( $K_E^{(i,j)} = 100,000/16$ )	$h_E^* = 0.19$	$h_W^* = 0.41$	\$5,152

Notes. Unless otherwise stated, ecosystem benefits are summed over a 50-year planning horizon and discounted at a 1% rate per year. The baseline specification has the following features: (i) predator interference is  $m = 0.825$ ; (ii) spatially heterogeneous functional response  $\beta' \neq 0$ ; (iii) minimum viable population restrictions are  $\bar{E} = 0.75E_{SS}$  &  $\bar{W} = 0.75W_{SS}$ ; (iv) tourism component of welfare function depends on the natural logarithm of the aggregate wolf population; (v) social value for each harvested wolf is  $\alpha_W = \$28,921 > \alpha_E$ ; (vi) indirect cost of wolf-livestock predation is 7.5 times the direct costs; (vii) elk carrying capacity is  $K_E^{(i,j)} = 80,000/16$ ; (viii) wolf-livestock predation rate is  $\bar{p}_L = 0.01$ ; (ix) time horizon is  $T = 50$  years; and (x) social discount rate is  $\rho = 0.01$ .

## Appendix. Model calibration

Calibration of the spatial predator-prey model to the GYE was conducted by selecting values for parameters that are consistent with the available data on animal populations, economic values, the GYE landscape characteristics, and the existing literature on wolf-elk-livestock ecosystems. All remaining unknown parameters are identified by solving a steady-state version of the spatial predator-prey equations and an equal number of external restrictions. This is a standard calibration methodology in the macroeconomic literature on optimal policy in dynamic economic systems (Kydland and Prescott, 1982).

Table A1 shows the parameters, definitions, values, and methods of calibration. The three methods used to select the parameter values are called: ‘Data’, ‘Literature’, and ‘Model’. In the ‘Data’ method, we use observed data to choose parameter values by matching the parameters or variables in the model directly to the data. The ‘Literature’ method takes parameter values from related journal articles and reputable websites. In the ‘Model’ method, we rely on the equilibrium structure of the model and use observed data to solve for internally consistent parameter values.

### A.1 Welfare and management parameters

We select a social discount rate of  $\rho = 0.01$ , which is lower than often used in policy studies, and chosen to encourage intergenerational foresight and species conservation. Moore et al. (2004) advocate for social discount rates of 3.5% or lower, while Caplin and Leahy (2004) state that most intergenerational studies choose social discount rates that are too high.

Social welfare in equation (1) includes three ecosystem services: hunting, tourism and livestock profits. Hunting ecosystem services are assumed to take the form:

$$\pi_{\text{hunting}}(h_{E,t}, h_{W,t}) = \alpha_E h_{E,t} + \alpha_W h_{W,t} \quad (\text{A.1})$$

where  $\alpha_E$  and  $\alpha_W$  are dollars per harvested elk and wolf, respectively. In the absence of estimated demand curves for harvests of these species, we assume the values are invariant over time, space, or number harvested. Values of  $\alpha_E$  and  $\alpha_W$  are calculated from the estimates in the literature that represent the social value per elk or wolf harvested. For elk, we use the inflation-adjusted maximum willingness to pay (WTP) estimate for elk hunting in Montana, U.S.A. (Park et al., 1991). The mean WTP value (in 2014 dollars) from Table 4 in Park et al. (1991) is \$357 per trip. Dividing this number by a 0.2 success rate for MT elk hunts (Wright et al., 2006), provides the calibrated value of  $\alpha_E = \$1,785$  in Table A1. For wolves, we multiply the average of 7.4 recreation days per hunter (Wyoming Game and Fish, 2013) by an estimate of \$45.50 value per recreation day (Walsh et al., 1992) and then divide by the average 0.02 success rate for wolf hunts (Wyoming Game and Fish, 2014). This produces the value of  $\alpha_W = \$28,921$  per wolf harvested in Table A1.<sup>19</sup>

The value of wolf-driven tourism is taken from Duffield et al. (2008). Duffield et al. (2008) use 2005 survey data and estimate that the presence of wolves in YNP contributed \$35.5 million of direct expenditures in Idaho, Montana and Wyoming. To link changes in wolves to tourism revenues we specify a relationship that is linear when wolves are at their steady state values and nonlinear out of steady state. The specific relationship depends on the aggregate GYE wolf population,  $W_t^{GYE}$ :

$$\pi(W_t^{GYE}) = \alpha_0 + \alpha_{\text{tourism}} \ln(W_t^{GYE}), \quad (\text{A.2})$$

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<sup>19</sup> Although we treat it as fixed, the average success rate of 0.02 for wolf hunting is likely to vary year-to-year with the density of wolves. Also, the marginal value of each harvested wolf is much larger than the marginal value of each harvested elk. The primary reason for this is that the success rate for wolf hunting is much lower than that of elk so that each harvested wolf is associated with substantially more hunter recreation days. In a later section of the paper, we investigate the sensitivity of our results to  $\alpha_W$ .

where  $\alpha_0 = \alpha_{tourism}(W^{GYE} - \ln(W^{GYE}))$  so that the total contribution of wolves to tourism revenues is equal to  $\alpha_{tourism}W^{GYE}$  in steady state and varies in a diminishing fashion with the wolf population out of steady state. Other functional forms are investigated later in the paper. The contribution per wolf to tourism expenditures in the steady state,  $\alpha_{tourism}$ , is calculated by dividing the \$35.5 million estimated by Duffield et al. (2008) by the population of wolves in the GYE. Using an estimate of 321 wolves within our GYE grid, we find that, on average, each wolf contributes approximately  $\alpha_{tourism} = \$111,000$  to tourism expenditures in the GYE area.

Profits associated with cattle grazing on public land outside YNP,  $\pi_{livestock}(W_t^{GYE}, L_t)$ , are calculated by number of cattle stocked  $L_t$  and a cattle price of \$1.70 per pound<sup>20</sup>, an average weight gain of 697.4 pounds (Hussain and Tschirhart, 2013), and a grazing fee of \$1.35 per month per cow.<sup>21</sup> Ranchers are assumed to graze cattle over four summer months. There are two consequences of cattle predation by wolves. The opportunity cost of a cow killed by wolf predation is the lost profits plus an additional cost equal to 7.5 times the direct opportunity cost. The additional cost is primarily due to lower weaning rates of calves (Ramler et al., 2014). This is a more conservative estimate of the additional cost than reported in Steele et al. (2013).

Lastly, we calculate the current elk and wolf hunting rates across the three states. The 2012 hunting rates are calculated as the total elk and wolves harvested in the 12 cells outside YNP as a fraction of the relevant populations. In 2012, there were 3,172 elk harvested in the 12 cells surrounding YNP. We assume an elk population of approximately 14,500 outside YNP, which implies an average hunting rate of  $h_E = 0.22$ .<sup>22</sup> In 2012, there were 47 wolves harvested outside

<sup>20</sup> <http://usda.mannlib.cornell.edu/usda/nass/AgriPric//2010s/2014/AgriPric-12-30-2014.txt>.

<sup>21</sup> <http://www.fs.fed.us/news/releases/blm-and-forest-service-announce-2014-grazing-fee>.

<sup>22</sup> The average hunting rate for elk is calculated from 2012 harvest surveys reported on the Fish and Game websites for ID, MT and WY (<http://fishandgame.idaho.gov/>; <http://fwp.mt.gov/>; <https://wgfd.wyo.gov/web2011/home.aspx>). Approximate elk populations are taken from published data on the website of the National Park Service (<http://www.nps.gov/yell/learn/nature/elkinfo.htm>).

YNP and an estimated wolf population of 226. This produces an average wolf hunting rate of  $h_W = 0.21$ .<sup>23</sup>

## A.2 Populations

The population of cattle outside YNP is calculated using a stocking rate of 17.87 head of cattle per section (640 acres) and the percent of forage area per cell.<sup>24</sup> This results in approximately 78,000 head of cattle in the GYE.

Determining populations of elk in the GYE is complicated as boundaries and total area within the GYE are not well defined. The GYE has been estimated to cover anywhere from 18,750 to 28,000 square miles.<sup>25</sup> Since our  $4 \times 4$  GYE grid covers only 13,500 square miles, elk and wolves may disperse on and off the grid but remain within the GYE boundaries. In equilibrium, we assume the dispersal onto the grid and “leakage” off the grid exactly offset. In addition, the data on elk populations across the entire GYE are imprecise. Using available sources, we assume the annual average elk population is restricted to be 30,000 in the equilibrium.<sup>26</sup>

In contrast, the location and count of wolves in the GYE has been closely tracked since their re-introduction in 1995. We use the available data (see footnote 23) to restrict the steady-state population on the GYE grid to equal 321 wolves. This is our estimate of the number of wolves residing on the GYE grid in 2011.

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<sup>23</sup> The data on wolf harvesting rates and wolf populations are taken from the Rocky Mountain Wolf Recovery 2012 Interagency Annual Report (<http://www.fws.gov/mountain-prairie/species/mammals/wolf/annualrpt12/index.html>).

<sup>24</sup> The percent of forage area per cell is the share of land cover containing shrubs, grasslands and pasture hay using the 2011 national land cover dataset (Jin et al., 2011).

<sup>25</sup> <http://www.nps.gov/yell/naturescience/>.

<sup>26</sup> <http://www.nps.gov/yell/naturescience/elk.htm>.

### A.3 Predation parameters

Skalaski and Gilliam (2001) have advocated for the use of functional responses that depend on both prey and predators, as opposed to the traditional Holling type II functional response that depends only on prey density. Equation (7) allows us to vary from prey density predation responses ( $m = 0$ , Holling type II) to ratio-dependent functional response ( $m = 1$ ) advocated by Hebblewhite (2013). To calibrate  $m$ , we introduce wolf populations into the model in the same locations and at the same numbers as the actual 1994-1995 YNP re-introduction. The model is then run for 18 periods and a value of  $m$  is selected that matches the 2011 wolf population across the entire GYE, not just our grid. The year 2011 is selected because it was the last year wolves in the GYE were under Federal protection. We use the entire GYE wolf population because wolves had yet to re-establish in areas outside our grid. Figure A1 shows the actual and simulated path for the aggregate GYE wolf populations in the wolf re-introduction exercise.

The estimate from this calibration exercise is  $m = 0.825$ , which implies a significant amount of predator interference. Average livestock predation outside YNP is fixed, but it is allowed to vary across the 12 outside cells of the GYE. The total number of cattle lost to wolf depredation in the northwest portion of Wyoming, U.S.A. is 300 (USDA, 2013), and our estimate of cattle stocked on public lands in Wyoming cells outside YNP is 33,000 head. This results in an average predation rate of approximately  $\bar{p}_L = 0.01$ . The constant functional response for wolf-cattle predation is calibrated at  $F_L = 4.818$ , which implies that each wolf kills approximately 5 cows or calves per year. The attack rate in equation (7) for wolf-elk functional response is calibrated at  $a = 0.008$  and the handling rate  $h = 0.045$  is taken from Garrott et al. (2007). Finally, the vector of coefficients on the landscape covariates (i.e., distance to roads, distance to streams/rivers, slope, snow, elk density, and wolf density) is taken from Table A1 in Kauffman et al. (2007).

#### A.4 Growth and death parameters

The GYE elk carrying capacity,  $K_E^{(i,j)}$ , is difficult to estimate. We specify a total carrying capacity of 80,000 elk (White and Garrott, 2005) and divide them evenly across the 16 cells in the GYE grid. The intrinsic growth rate for elk from equation (4) is  $r_E = 0.28$  (Boyce, 1995), while the average lifespan of a gray wolf in the wild is approximately 7 years.<sup>27</sup>

To calibrate the numeric response scale factor,  $\gamma$ , we use a combination of external restrictions and the equilibrium (i.e., steady-state) conditions following the ‘Model’ method of Table A1. We impose three external restrictions:  $\Sigma_{(i,j)} E^{(i,j)} = 30,000$ ,  $\Sigma_{(i,j)} W^{(i,j)} = 321$ ,  $\bar{p}_L = 0.01$ ; and use them to solve for three unknown parameters ( $\gamma$ ,  $a$ ,  $F_L$ ). The external restrictions and their data sources are described in greater detail below. This procedure leads to an estimate of the scale parameter of  $\gamma = 0.06$ . Using equation (5), this implies that average wolf growth will be 6% when the consumption of prey (i.e., the number of elk and livestock) is equal to the population of wolves.

#### A.5 Dispersal parameters

There is limited evidence in the literature on the dispersal parameters for wolves and elk.<sup>28</sup> For simplicity, we set  $\bar{\theta}_E^{(i,j) \rightarrow (i,j)} = \bar{\theta}_W^{(i,j) \rightarrow (i,j)} = 0.99$ , so that in steady state the two species are relatively stationary.<sup>29</sup> To ensure these conditions are satisfied, the ‘Model’ method is used to

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<sup>27</sup> <http://www.californiawolfcenter.org/learn/wolf-facts/>.

<sup>28</sup> Some of the wolves in the GYE are fit with GPS collars so that their movement can be tracked. In theory, this data could be used to more accurately calibrate the dispersal parameters. However, state agencies have not released this data to the public.

<sup>29</sup> Given our dispersal functional form in equation (13), a positive amount of equilibrium dispersal is necessary unless  $\delta_{species}^{(i,j)} \rightarrow \infty$ . We have experimented with other high values for the residence rates (i.e.,  $\bar{\theta}_E^{(i,j) \rightarrow (i,j)}$ )

solve for the necessary cell-specific values of  $\delta_E^{(i,j)}$  and  $\delta_W^{(i,j)}$ . This implies that when the GYE is in equilibrium, nearly all elk and wolves remain in their local cell. Out of equilibrium, the dispersal rates can vary by cell depending on local conditions. We now turn to our policy simulations.

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and  $\bar{\theta}_W^{(i,j) \rightarrow (i,j)}$ ) and our main results are not qualitatively affected. Elk are more migratory than wolves, who tend to be more territorial (Mao et al., 2005; Kauffman et al., 2007). In our sensitivity analysis that follows, we allow the equilibrium residence rate to be higher for wolves than for elk.

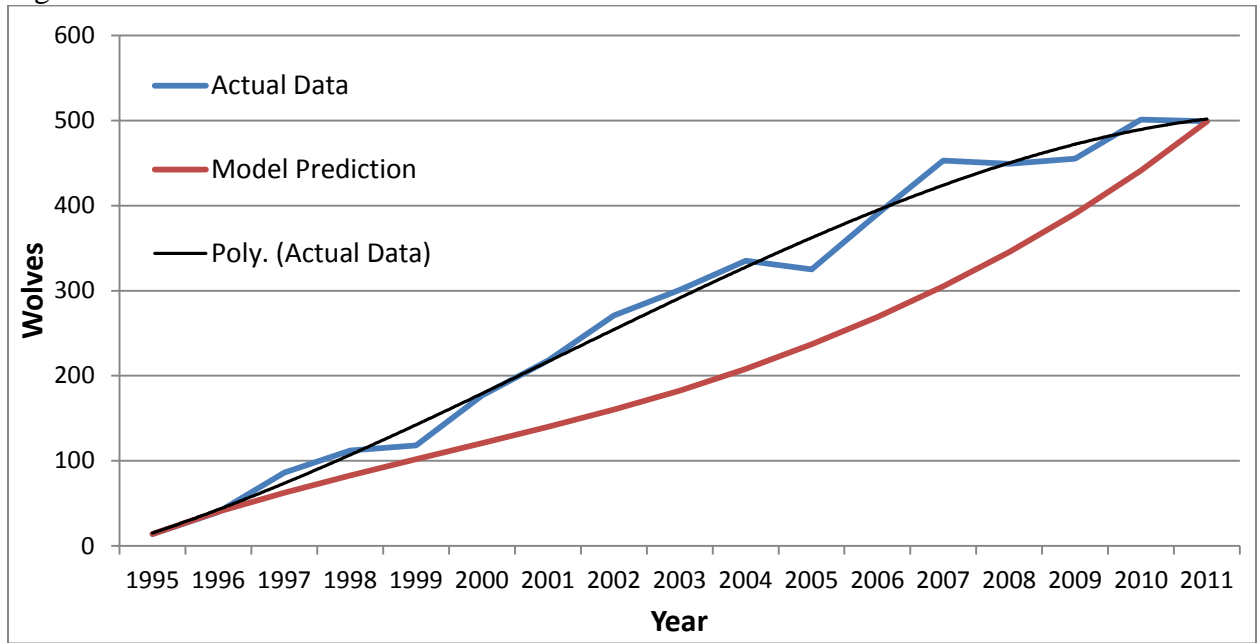


Table A1. Calibrated Parameter Values

Parameter	Definition	Parameter Value	Calibration Method
<b>WELFARE AND MANAGEMENT</b>			
$\rho$	Social discount rate	0.01	Literature
$\alpha_E$	Weight on elk hunting (\$/elk harvested)	\$1,785	Literature
$\alpha_W$	Weight on wolf hunting (\$/wolf harvested)	\$28,921	Literature
$\alpha_{tourism}$	Weight on wolf-driven tourism (\$/wolf)	\$111,000	Literature
$h_E$	Hunting rate for elk	0.216	Data
$h_W$	Hunting rate for wolves	0.208	Data
<b>GROWTH, DEATH &amp; LEAKAGE</b>			
$K_E^{(i,j)}$	Elk carrying capacity	80,000/16	Literature
$r_E$	Intrinsic elk growth rate	0.28	Literature
$d_W$	Wolf natural death rate	1/7	Literature
$\gamma$	Numeric response scale factor	0.060	Model
<b>PREDATION</b>			
$m$	Predator interference parameter	0.825	Model
$\bar{p}_L$	Average livestock predation on outer cells	0.01	Literature
$F_L$	Fixed wolf-cattle functional response	4.818	Model
$a$	Attack rate for wolf-elk functional response	0.008	Model
$h$	Handling rate for wolf-elk functional response	0.045	Literature
$\beta'$	Vector of resource selection coefficients	vector of values	Literature
<b>DISPERSAL</b>			
$\bar{\theta}_E^{(i,j) \rightarrow (i,j)}$	Cell-specific elk residence rate*	0.99	Model
$\bar{\theta}_W^{(i,j) \rightarrow (i,j)}$	Cell-specific wolf residence rate*	0.99	Model
<b>POPULATIONS</b>			
$\bar{L}$	Average number of cattle on outer cells	6,514	Data
$\Sigma_{(i,j)} E^{(i,j)}$	Total number of elk on the GYE grid	30,000	Literature
$\Sigma_{(i,j)} W^{(i,j)}$	Total number of wolves on the GYE grid	321	Literature

Notes. Calibration Methods: ‘Data’ refers to specification of the parameter value based on the available data. ‘Literature’ refers to specification of the parameter value based on published research and reputable online resources. ‘Model’ refers to specification of the parameter value by solving for the parameter values that are consistent with external restrictions (discussed in the text) and the structure of the model. \*The steady-state residence rates are set at their values by using the model to solve for the implied values of  $\delta_E^{(i,j)}$  and  $\delta_W^{(i,j)}$ .

Figure A1. Actual and Simulated Time Paths for Wolf Re-Introduction into the GYE



Notes. Solid black line is a fitted third-order polynomial trend line to the actual GYE wolf population profile.