

What are the benefits of delisting endangered species and who receives them?:  
Lessons from the gray wolf recovery in Greater Yellowstone

**Abstract.** This paper uses a spatial predator-prey model to provide insights into the complex and politically charged management of species recently removed from the federal endangered species list. The model is motivated by the recently delisted gray wolf with spatiotemporal dynamics between elk, wolves, hunters, cattle ranchers, and the tourism industry in the Greater Yellowstone Ecosystem. State wildlife managers set hunting rates for elk and wolves to maximize the discounted net benefits from tourism, hunting, cattle grazing, and non-use values that accrue to the area while ensuring a minimum viable wolf population meant to prevent extinction. We show that the cost of wolf conservation paid by residents and visitors to the area falls substantially after delisting. These cost savings arise by taking advantage of differences in habitats and economies across the region resulting in an unequal spatial distribution of wolves and of wolf hunting opportunities. The cost savings from delisting are reduced when a more even distribution of wolves and hunting opportunity is achieved, highlighting a bioeconomic equity-efficiency tradeoff. Finally, we show that current livestock compensation programs cannot decrease the discrepancy between state and federal management following delisting but propose a federally-funded alternative that can.

Keywords: Endangered Species Act, conservation, gray wolf, Yellowstone National Park, livestock depredation

*“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>

The number of species removed from the Endangered Species Act’s (ESA) protection has increased in recent years. Since the legislation’s inception in 1973, 58 species have recovered to warrant delisting of which 81 percent were delisted after 2000 and 69 percent were delisted from 2011 to 2019.<sup>2</sup> The recent increase in delistings is partly in response to critics of the ESA who cite the small number of delistings as proof of the legislation’s ineffectiveness (Doremus and Pagel, 2001; Landpap, Kerkvliet, and Shogren 2018). Delisting moves from a regime of full species protection to management for multiple objectives. Delisting also transfers management authority from the federal government back to states with some form of federal oversight such as minimum population mandates. Identifying when state incentives are aligned with the continued recovery of a previously listed species is becoming an increasingly important task as the number of delisted species grows. This paper is the first to consider the optimal economic management of a species that was recently removed from the endangered species list.

Economic research on endangered species has focused on the incentives for private landowners to make costly contributions to protect species habitat such as shifting the type or intensity of land use or permanently retiring land. This area of research, closely tied to the

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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> The data were retrieved on January 28<sup>th</sup>, 2020 from the U.S. Fish and Wildlife Service’s Environmental Conservation Online System (ECOS). This calculation includes both foreign and domestic species and defines species as a distinct population segment (DPS).

concept of private provision of a public good, has helped describe the economic forces that drive species to the brink of extinction (Brown and Shogren, 1998; Innes, Polasky, and Tshchirhart, 1998; Polasky and Doremus, 1998; Innes, 2000; Newburn, Brozovic, and Mezzatesta, 2011; Langpap and Wu, 2017) and identify incentive programs to encourage voluntary conservation when a species is listed (Smith and Shogren, 2002; Langpap, 2006; Langpap and Wu, 2004; Langpap and Kerkvliet, 2012). However, the incentive structure following delisting differs from the pre-listing context for two reasons. First, the tourism benefits generated by the continued presence of a previously endangered species may exceed the tourism benefits of that species prior to listing. If the enhanced tourism benefits of a recently delisted species are larger than the losses created by the species, states will find it in their own best interest to prevent local extinction. Second, prior to delisting, the federal government retains the authority to set a standard (i.e., a minimum viable population) that must be met following delisting but the obligation to meet the standard resides at the state level. This management setting is more akin to identifying cost-effective allocation of pollution control responsibility than voluntary provision of a public good. States will manage delisted species to minimize the impacts of that species on state residents while ensuring that any federal standard for species abundance is met. While the impacts of the ESA on landowners within an endangered species habitat are often acknowledged (Shogren et al., 1999), the cost savings from delisting as well as the winners and losers created by delisting remain unexplored.

Our analysis is motivated by the 2011 decision to delist gray wolves in the western United States. In 1973, the Northern Rocky Mountain (NRM) gray wolf was listed as an endangered species. The NRM population has exceeded minimum recovery goals ( $\geq 300$  wolves and  $\geq 30$  breeding pairs) since 2002 (U.S. Fish and Wildlife Service, 2004). By 2004, gray wolf

management in Idaho and Montana was transferred to the state level. These delisting decisions were subsequently overturned by U.S. District Courts effectively relisting the gray wolf. By 2012, the original rule delisting NRM wolves had been reinstated allowing wolf hunting in Montana, Idaho, and Wyoming. The delisting marked the first time that state wildlife agencies could jointly manage wolves and their primary prey, elk. In 2014, a federal judge relisted the gray wolf in Wyoming citing the federal government's reliance on "nonbinding promises to maintain a particular number of wolves when the availability of that specific numerical buffer was such a critical aspect of the delisting decision". This ended wolf hunting in Wyoming but not in Montana and Idaho. The decision to end wolf hunting in Wyoming was reversed by a three-judge U.S. Court of Appeals panel leading to the 2017 delisting of wolves in Wyoming. Similar to 2012 and 2013, Wyoming state wildlife agencies returned to joint management of wolves and their prey by reinstating hunting seasons starting in 2017.

Identifying the optimal management of a recently delisted species is akin to managing a multi-use species that at low densities is an asset worthy of preservation yet at high densities becomes an economic pest (Rondeau 2001). However, specific management of delisted species also requires an understanding of the spatial distribution of economic impacts from the delisted species since this distribution determines how states are impacted by the species and subsequently how they are managed following delisting. These distributional considerations require a spatial-dynamic modeling approach that considers species dispersal, habitat heterogeneity, and predator-prey interactions involving the delisted species. We integrate 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 involving wolves, elk and livestock, which are

depredated by wolves. Within the context of our spatial predator-prey model, we consider local habitat conditions, the cost of gray wolves on local livestock operations, the use (tourism and hunting) and non-use benefits of wolves and elk, and the impacts of management directly and indirectly on an apex predator and its primary prey.

Our spatial-dynamic model uncovers three general results about managing a recently delisted species. First, delisting can reduce the costs imposed on stakeholders within an endangered species habitat. However, the efficient management of a delisted species is characterized by an unequal allocation of conservation responsibility and cost savings from delisting across states and stakeholders. The cost savings of delisting arise by taking advantage of differences in habitat and state economies across the species range. States reliant on a sector that is negatively impacted by a delisted species will find it optimal to support lower populations than states that experience less adverse economic impacts. States with better habitat will find it advantageous to support larger populations to achieve federal population minimums at less cost. In our gray wolf example, delisting the gray wolf reduces the cost of wolf conservation incurred by stakeholders around Yellowstone National Park (YNP) by an average of \$1.88 million per year. By comparison, Duffield et al. (2008) find that visitor spending due to wolf presence in Montana, Wyoming, and Idaho is \$35.5 million per year. Using our model, it is optimal for Montana and Idaho to engage in the maximum amount of wolf hunting possible while it is optimal for Wyoming to engage in more moderate harvesting to ensure federal minimums are achieved. While the tourism sector is harmed by delisting, these losses are more than compensated by the increased benefits of livestock grazing and elk hunting.

Second, achieving a more equitable allocation of cost savings and a more even distribution of the species across its range comes at a cost. Faced with the inequities and localized extinctions

created by state-level management, the federal government may choose to set state-specific population mandates or to apply one-size-fits-all hunting limits to the states. These efforts lower the potential cost savings created by delisting leading to a bioeconomic equity-efficiency tradeoff. The reason is that these more equitable regulations limit the ability to take advantage of differences in habitat, predation rates, and economic sectors across the potential range of the delisted species. In our gray wolf example, imposing a state-specific wolf mandate instead of a single mandate for the entire Greater Yellowstone Experimental Population Area (GYEPA; an area that covers all of Wyoming, southern Montana, and southeastern Idaho) lowers the cost savings from delisting from \$1.88 to \$0.82 million per year – a 56 percent reduction. Imposing a single wolf hunting rate in all states leads to a similar equity-efficiency tradeoff.

Third, programs that compensate landowners for the costs of species conservation offer additional benefits when species have been delisted. When species are protected under the ESA, compensation programs primarily ease the burden on landowners. But when species are delisted and managed by states, compensating landowners eases economic incentives for states to actively reduce the population of the species through hunting. This shift in state incentives created by a compensation program can result in larger populations of the delisted species and reduce the need for federal oversight. However, these benefits only materialize if the compensation paid to landowners is sufficiently large and the portion of the program funded by the state is sufficiently small. The current program associated with gray wolves, which uses a mix of state and federal funds to compensate ranchers for the financial loss from livestock death and injured calves, offsets costs ranchers incur due to livestock depredation but not enough to change state hunting decisions and the wolf population. In contrast, a program that accounts for indirect predation costs (financial losses due to decreased weaning weights, decreased

conception rates, and increased cattle sickness) will be costly for the state but will eliminate Wyoming's incentive to hunt wolves resulting in a seven-fold increase in wolves in the GYEPA. Fully compensating ranchers also reduces the need for a federal minimum wolf mandate but only if the federal government or private organization (e.g., Defenders of Wildlife) fully funds the compensation program. With a federal or privately supported program that fully compensates ranchers for their losses, states have little incentive to promote wolf hunting since this hunting lowers non-use values and harms the tourism sector of the economy.

## Study Area

The model's spatial extent covers a portion of the Greater Yellowstone Ecosystem (GYE; Figure 1) using a  $4 \times 4$  grid with the interior cells representing YNP where hunting and grazing are not allowed and the 12 perimeter cells representing mostly U.S. Forest Service (FS) and private land where hunting and cattle grazing are allowed.<sup>3</sup> Although many definitions of the GYE extend beyond our grid, the  $4 \times 4$  grid captures the management tradeoffs between YNP, FS and private lands in a tractable manner.<sup>4</sup> Each cell on the grid is approximately 540,000 acres for a total 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

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<sup>3</sup> The  $4 \times 4$  grid was constructed manually in GIS. 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.

<sup>4</sup> We explicitly consider wolf populations that exist beyond our grid boundaries. The population of wolves that exist off the grid is calibrated to be consistent with existing data and the model following the re-introduction of wolves into YNP and central Idaho. See the appendix for details.

the area surrounding YNP, and are the primary prey of gray wolves (Smith et al., 2003). Our study area includes parts of the ranges of several elk herds including the Sand Creek, Blacktail, and Madison Valley herds in the eastern part of our study area, the Paradise Valley and Northern herds in the north, the Clarks Fork and Cody herds in the east, and the Jackson herd (one of the largest herds in North America) in the south (Middleton et al., 2019).

The gray wolf is also native but was hunted to extinction during the early-to-mid 1900's. Beginning in 1995, the gray wolf was reintroduced to the area and has recently recovered to the point that wolves have been legally hunted in the area surrounding YNP. At the end of 2015, the Greater Yellowstone Recovery Area (GYRA) contained an estimated 528 wolves (109 in Montana, 37 in Idaho, 382 in Wyoming) in 71 packs (18 in Montana, 5 in Idaho, 48 in Wyoming). States are currently managing wolves to remain above a minimum recovery goal of 100 wolves in the GYRA but outside 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. According to the USDA National Agricultural Statistics Service, there were over 266,000 head of cattle grazing in counties in our study area (147,472 in Montana, 36,446 in Idaho, 82,811 in Wyoming) in 2017. Cattle inventories in the study area have been stable over the past two decades.

### **Modeling abundance and movement of a delisted predator and its prey**

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. This constant stocking assumption is consistent with USDA National Agricultural Statistics Service data that indicates stable cattle inventories in the study area over the past two decades.

With the recent removal of the gray wolf from the federal endangered species list, wolf management in the GYE shifts from a regime of full species protection to management for multiple objectives. 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 service dependent activities (tourism, hunting, and cattle grazing) under various minimum wolf population mandates. Using these optimal strategies, we highlight the cost savings from delisting gray wolves as well as the states and stakeholder groups who benefit from the delisting.

### *Pre-dispersal laws of motion*

The landscape grid is subdivided into a set of discrete cells  $i = 1, \dots, 16$ . Time is discrete with  $t$  representing annual intervals.<sup>5</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  $i$  and are given

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<sup>5</sup> One drawback of annual intervals is that we are unable to model seasonal variations, such as elk migrating to lower elevations during the winter in search of forage or livestock grazing on public land during the summer and fall and private land the rest of the year. In future research, we intend to explore shorter time intervals that allow us to model seasonal effects such as migration, snowpack levels, and tourism.

respectively by  $W_t^i$ ,  $E_t^i$  and  $L_t^i$ . The management (control) variables in the system are elk and wolf hunting rates,  $h_E^i$  and  $h_W^i$ , where  $0 \leq h_E^i, h_W^i \leq 1$ . Based on hunting data from each state that shows annual wolves harvested are roughly a constant proportion of the respective populations, we specify proportional hunting such that total harvests are given by  $h_{E,t}^i = h_E^i \times E_t^i$  and  $h_{W,t}^i = h_W^i \times W_t^i$ . Hunting is not allowed in YNP so  $h_{E,t}^i = h_{W,t}^i = 0$  for  $i = 6, 7, 10$  and 11.

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

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

and

$$W_{t,pre}^i = (1 + g_{W,t}^i - d - lc)W_t^i - h_{W,t}^i \quad (2)$$

where  $g_{E,t}^i$  and  $g_{W,t}^i$  are the elk and wolf growth rates,  $F_{E,t}^i$  is the functional response (Hastings, 1997) that governs the number of elk killed per wolf,  $d$  is the natural mortality rate of wolves,  $lc$  is the rate of lethal control of nuisance wolves performed by wildlife agencies, and the state variables without the “pre” subscript indicate densities after dispersal.<sup>6</sup> Elk population growth is

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<sup>6</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  $p_{E,t}^i = F_{E,t}^i W_t^i / E_t^i$ . 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.

assumed to vary by cell and follows a logistic function with intrinsic growth rate  $r$  and a cell-specific carrying capacity  $K^i$  (Hastings, 1997) following<sup>7</sup>

$$g_{E,t}^i = r \left( 1 - \frac{E_t^i}{K^i} \right). \quad (3)$$

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

$$g_{W,t}^i = \gamma (F_{E,t}^i + F_{L,t}^i + \varphi), \quad (4)$$

where  $\gamma > 0$  is a scale parameter that translates caloric intake from prey into wolf growth,  $F_{L,t}^i$  is the functional response that governs the number of livestock killed per wolf, and  $\varphi$  is a constant that adjusts for other prey species not modeled here.

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

$$F_{E,t}^i = \frac{\alpha_E E_t^i}{1 + \alpha_E \mu_E E_t^i}, \quad (5)$$

where  $\alpha_E$  is the attack rate and  $\mu_E$  is the handling rate. Notice that equation (5) implies predation is proportional to predator density, which is consistent with the idea that predators only compete 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 depend on both elk and wolves,

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<sup>7</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.

$$F_{E,t}^i = \frac{a_E E_t^i}{(W_t^i)^{m_E} + a_E \mu_E E_t^i}, \quad (6)$$

where  $m_E \geq 0$  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 ( $m_E = 0$ ), the functional response collapses to the traditional Holling Type II response in equation (5). Here, we explore the properties of functional responses that are dependent on both predators and prey within a spatially explicit model of optimal management. There is a similar functional response to equation (6) for livestock with attack parameter  $a_L$ , handling parameter  $\mu_L$ , and predator interference parameter  $m_L$ .

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 (6). 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

$$\tilde{F}_{E,t}^i = F_{E,t}^i \times RSF(\mathbf{x}^i) \quad (7)$$

where

$$RSF(\mathbf{x}^i) = \text{Exp}(\boldsymbol{\beta}' \mathbf{x}^i), \quad (8)$$

and  $\mathbf{x}^i$  is a vector of landscape covariates including slope, aspect, openness, and snow water equivalent. 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.<sup>8</sup> 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 (5) and (6).

In Figure 4, we show the prey-dependent Type II spatial functional response for three different cell-specific levels of RSF.<sup>9</sup> The three cells 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 (8) with equations (2) and (4), we can write the pre-dispersal law of motion for wolves as

$$W_{t,pre}^i - W_t^i = \gamma \left( \frac{a_E E_t^i RSF(x^i)}{(W_t^i)^{m_E} + a_E \mu_E E_t^i} + F_L^i \right) W_t^i - (d + lc) W_t^i - h_{W,t}^i. \quad (9)$$

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<sup>8</sup> 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.

<sup>9</sup> The Holling Type II functional responses (prey interference parameter  $m_E = 0$ ) are based on an attack rate of  $a_E = 1$  and a handling rate of  $\mu_E = 0.045$ . 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  $Exp(0.5)$ .

Equation (9) shows the different mechanisms that influence local wolf populations before they begin the dispersal process, which we discuss next.

### *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. Because not every cell is connected to every other,  $\Phi_i$  represents the set of cells that are connected to cell  $i$ . 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. We also assume livestock remain on their cells and elk and wolves do not leave the grid (i.e., the grid has a reflecting boundary). This is also a reasonable assumption since wolves have already recolonized much of the GYEPA such that most of the movement of wolves across the grid is characterized by wolf pack territories that cover multiple cells.

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

$$E_{t+1}^i = \theta_{E,t}^i E_{t,pre}^i + \sum_{j \in \Phi_i} \theta_{E,t}^{i,j} E_{t,pre}^j \quad (10)$$

and

$$W_{t+1}^i = \theta_{W,t}^i W_{t,pre}^i + \sum_{j \in \Phi_i} \theta_{W,t}^{i,j} W_{t,pre}^j \quad (11)$$

where  $\theta_{E,t}^{i,j}$  and  $\theta_{W,t}^{i,j}$  measures the percent dispersal from cell  $j \neq i$  in period  $t$  into cell  $i$  in period  $t + 1$ . The first terms in (10) and (11) specify the number of elk and wolves that remain on cell  $i$ , where  $\theta_{E,t}^i$  and  $\theta_{W,t}^i$  are the residence rates on cell  $i$  in period  $t$ . Therefore, the fraction of elk and wolves that disperse to neighboring cells in period  $t$  is given by  $1 - \theta_{E,t}^i$  and  $1 - \theta_{W,t}^i$ , 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:

$$\theta_{species,t}^i = 1 - \text{Exp}(-\Lambda_{species,t}^i), \quad (12)$$

where  $\Lambda_{species,t}^i$  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, 2008a).

We assume the variable dispersal term for elk is given by

$$\Lambda_{E,t}^i = \left( \delta_E^i - \widehat{E}_{t,pre}^i - \widehat{F}_{E,t}^i \widehat{W}_t^i - \widehat{h}_{E,t}^i \right), \quad (13)$$

where  $\delta_E^i$  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 (13) is scaled to have a similar impact on dispersal near steady state. A negative sign in front of a variable in  $\Lambda_{E,t}^i$  specifies that elk will disperse away from cell  $i$  when the variable in cell  $i$  is higher than the average value across the grid. The first term,  $-\widehat{E}_{t,pre}^i$ , 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,  $-\widehat{F}_{E,t}^i \widehat{W}_t^i$ , represents dispersal to neighboring cells due to predation risk. Predation risk in cell  $i$  might increase because of higher wolf density or because the landscape is favorable to wolf-elk predation (Hebblewhite and Merrill, 2008b). The final term,  $-\widehat{h}_{E,t}^i$ , 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

$$\Lambda_{W,t}^i = \left( \delta_W^i - \widehat{W}_{t,pre}^i + \widehat{F}_{E,t}^i \widehat{W}_t^i - \widehat{h}_{W,t}^i + \widehat{L}_t^i \right). \quad (14)$$

Equation (14) is similar to equation (13) but is adjusted to reflect the fact that wolves are a predator. The term  $-\widehat{W}_{t,pre}^i$  captures inter-pack wolf competition rather than the abundance of forage (Lewis et al., 1997). As wolves prey on elk and livestock,  $\widehat{F}_{E,t}^i \widehat{W}_t^i$  and  $\widehat{L}_t^i$  have positive signs because wolves are drawn to cells with higher than average predation success.<sup>10</sup>

Equation (12) 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

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<sup>10</sup> In practice, wolf behavior within and between packs is sophisticated and highly territorial (Hochard and Finnoff, 2014, 2017). While most of this complexity is not included here for tractability, we do address the fact that wolf offspring routinely disperse to identify new territory and form breeding pairs (Gese and Mech, 1991). In our dispersal process the fixed component represents the territorial nature of wolves and the variable component represents new pack creation and dispersing pups.

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

$$\theta_{species,t}^{i,j} = (1 - \theta_{species,t}^i) \left( \frac{\Lambda_{species,t}^j}{\sum_{j \in \Phi_i} \Lambda_{species,t}^j} \right). \quad (15)$$

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 cell  $j$  relative to the other neighboring cells. The product of the two terms equals the overall fraction of animals that disperse in period  $t$  from cell  $i$  to neighboring cell  $j$ .<sup>11</sup>

#### *Model simulation under representative management*

To illustrate the spatiotemporal dynamics of the model, we assume elk and wolf hunting is occurring at a rate consistent with years in which wolf hunts were realized:  $h_E^i = h_{E,Actual} = 0.22$  and  $h_W^i = h_{W,Actual} = 0.24$  (see the Appendix for details on the hunting data and calibration procedure). We then introduce a one-time disturbance in the northwest corner of YNP (cell 6 of the grid) that reduces elk populations by 50%. The disturbance is hypothetical but could represent an extremely cold winter, disease outbreak, or management cull that significantly reduces the size of elk herds. Figure 5A shows the equilibrium and temporal dynamics of elk populations across the entire  $4 \times 4$  grid over a 50-year period. The long-run

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<sup>11</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 (12) and (15) is akin to selecting a functional form for a dispersal kernel.

equilibrium levels are given by the intersection with the vertical axis in period  $t = 1$ .<sup>12</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 6 fall suddenly by 50% from approximately 4,000 to 2,000 elk. With fewer elk in cell 6, 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 6 also increases through logistic growth being well below carrying capacity. As elk from neighboring cells disperse to cell 6, 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 visualize at the scale 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 axis at period  $t = 1$ . 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 6 and falls in neighboring cells after the disturbance. This reflects the fact that elk find cell 6 more attractive after the drop in the elk population and subsequent increase in forage.

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<sup>12</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.

Figure 6A shows how wolf densities change over time in response to the decline in elk in cell 6. In terms of spatiotemporal dynamics, wolf density in cell 6 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 6 and the surrounding area, which causes a prey shortage. Fewer elk, through the numeric response given in equation (3), imply that the wolf reproduction rates will not keep pace with natural death and hunting on outer cells.

### **Economically optimal wolf and elk management after delisting**

State resource managers within the GYE are concerned with balancing tourism revenues, hunting values, ranching profits, and non-use wolf values held by GYE residents while maintaining sustainable populations of elk and wolves above some minimum level at which irreversible and potentially large opportunity costs are imposed on the ecosystem. The four ecosystem-dependent benefits capture the joint production of consumptive use values (wolf hunting), non-consumptive use values (tourism), and non-use values generated by wolves (option value, bequest value, existence value), as well as detrimental impacts of wolves (elk hunting, cattle grazing) experienced by GYE residents. To provide clear comparisons between policies that affect the provisioning of the ecosystem services, each activity is enumerated in monetary terms. By monetizing the flows of ecosystem services, we can consistently compare variations in the provisioning of various services across time and space.

Let aggregate welfare within the GYE be given by the discounted sum of the four activities over time and space:

$$W = \sum_{t=0}^T e^{-\rho t} \left( \begin{array}{c} \pi_{hunt}(h_{E,t}, h_{W,t}) + \pi_{tour}(W_t^{GYE}) \\ + \pi_{nonuse}(W_t^{GYE}) + \pi_{lvstck}(W_t^{GYE}, L_t) - \eta C(W_t^{GYE}, L_t) \end{array} \right) \quad (16)$$

where  $\rho$  is society's discount rate,  $C$  is the compensation payments that ranchers receive for wolf predation, and  $\eta$  is the proportion of these compensation payments paid by the states. The first term within parentheses in equation (16) captures the net benefits from hunting, where  $h_{E,t}$  and  $h_{W,t}$  are the sums of hunted elk and wolves over all cells outside YNP. The second term within parentheses,  $\pi_{tour}(W_t^{GYE})$ , captures the net benefits realized from wolf-driven tourism in the GYE, where  $W_t^{GYE}$  is the aggregate number of wolves in the GYE. The third term,  $\pi_{nonuse}(W_t^{GYE})$ , capture the non-use values (i.e., option value, bequest value, existence value) held by GYE residents.<sup>13</sup> The fourth term,  $\pi_{lvstck}(W_t^{GYE}, L_t)$ , captures livestock net benefits measured as producer profits less predation losses plus compensation payments that ranchers receive for wolf predation. Equation (16) captures four of the most important economic activities in the GYE, but there are likely to be additional perturbations in ecosystem service provisioning 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 forage on 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.

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<sup>13</sup> Gray wolves 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). We assume these non-use values are a function of the total population of wolves based on recent research suggests the public places economic value on management that leads to gains in species abundance and not just changes in official conservation status designations (e.g., threatened vs. recovered)(Lewis et al., 2019). Because these values are difficult to measure, we consider the sensitivity of our results to non-use values held by GYE residents in Table A3.

The full spatio-dynamic problem maximizes equation (16) by choosing time-varying wolf and elk hunting rates while constraining wolf populations to remain above federally mandated minimum viable levels,  $\bar{W}$ .<sup>14</sup> This is similar to what happens when a species is ‘delisted’ under the ESA. The Euler equations include first-, second-, and higher-order population effects. First-order effects involve direct impacts on wolf populations from wolf hunting. Second-order effects involve indirect, future 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.

Consider the Euler equation for wolf hunting at time  $t$ :

$$\underbrace{\frac{\partial \Omega_t}{\partial h_{W,t}}}_{\text{first-order effects}} + \underbrace{e^{-\rho} \frac{\partial \Omega_{t+1}}{\partial h_{W,t}}}_{\text{second-order effects}} + \underbrace{\sum_{j=2}^{T-t} e^{-j\rho} \frac{\partial \Omega_{t+j}}{\partial h_{W,t}}}_{\text{higher-order effects}} = 0 \quad (17)$$

where

$$\begin{aligned} \Omega_t = & \pi_{\text{hunt}}(h_{E,t}, h_{W,t}) + \pi_{\text{tour}}(W_{t,\text{pre}}^{\text{GYE}}) + \pi_{\text{nonuse}}(W_{t,\text{pre}}^{\text{GYE}}) + \pi_{\text{lvstck}}(W_{t,\text{pre}}^{\text{GYE}}, L_t) \\ & - \eta C(W_{t,\text{pre}}^{\text{GYE}}, L_t). \end{aligned}$$

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 nearly intractable

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<sup>14</sup> We have also investigated optimal state-level hunting rates that consider the optimal behavior of neighboring states using a Nash equilibrium solution concept. Due to the small amount of dispersal between states at steady state, our results do not qualitatively change if we instead assume each state sets their own hunting rates.

for the current model. To allow an optimal solution, we make the common assumption (e.g., Hauser et al., 2006; Pastor, 2011) of proportional hunting at a fixed rate unless the populations fall below minimum viable levels, at which time hunting rates are set to zero. This allows hunting quotas to vary over time, but at a fixed proportion of the relevant species population.

Assuming a social discount rate of 3 percent, optimization is performed using a grid search across various fixed elk and wolf hunting rates to maximize the sum of discounted values of ecosystem service dependent activities over a  $T = 50$  year management horizon. The initial value ( $t = 1$ ) in equation (16) is given by the steady state using current elk and wolf hunting rates ( $h_{E,Actual} = 0.22$  &  $h_{W,Actual} = 0.24$ ) over the outer grid cells. Starting in period  $t = 2$ , the elk and wolf hunting 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 at increments of 0.01. The optimization is performed subject to the constraint that the total number of combined wolves in GYEPA must be equal to or greater than  $\bar{W} = 100$ , which is the stated recovery goal (U.S. Fish and Wildlife Service, 2004).<sup>15</sup> If either constraint binds over the planning horizon, we rule out the hunting strategy.

Figure 7 shows the ecosystem welfare surface (from equation (16)) across various elk and wolf hunting rates when the rates are uniformly applied (i.e., “one-size-fits-all” management strategy) across all cells in the grid. The shape of the welfare surface reveals several interesting features of optimal management in this case. First, welfare is single-peaked with respect to elk hunting rates. Low elk hunting rates reduce hunting benefits, while high elk hunting rates

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<sup>15</sup> The stated recovery goal of 100 wolves pertains to all of the GYEPA, not just the portion on our grid. To adjust for this fact, we scale up the number of wolves in each non-YNP cell in a manner that is proportional to the number of wolves off the grid in each state. See the appendix for further details.

adversely impact wolf populations (and thus tourism, wolf hunting benefits, and existence value) in addition to lowering the number of available elk to hunt in the long run. A lower elk hunting rate (about 0.13) and moderate wolf hunting rate (about 0.64) generates the highest social welfare. Second, the welfare surface exhibits thresholds where certain combinations of elk and wolf hunting rates cause the federal minimum 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 wolf populations to fall below minimum levels and trigger a federal wolf hunting moratorium. The proximity of the threshold and optimum ( $h_E^* = 0.13$  and  $h_W^* = 0.65$ ) highlights the need for the federally imposed minimum population levels.<sup>16</sup> States have an incentive to maintain a population of wolves only if the federal government imposes significant penalties on the states for failing to maintain a healthy population. Third, the direction of the ridge in the welfare surface reveals a 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.

The optimal steady-state hunting strategy, given the federal mandate of no less than 100 wolves in the GYEPA, is presented in the third row of Table 1.<sup>17</sup> The optimal strategy calls for

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<sup>16</sup> The proximity of the threshold and the optimum also illustrates how 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 hunting rates to lower the risk of a federally imposed moratorium, in the event that the ecosystem experiences an unanticipated disturbance.

<sup>17</sup> The second row of Table 1 considers the removal of wolf minimums and shows that in the absence of some protections, it is optimal to hunt wolves aggressively in all states and drive all remaining wolves into YNP. However, as YNP habitat alone cannot fulfill the GYEPA recovery criteria, we do not consider it as the optimal scenario. Also, note steady-state wolf populations on the grid are less than the GYEPA wolf minimums in Table 1. This is due to wolves that exist off the grid but within the GYEPA and is explained in more detail in the Appendix, Section A.2.

stark differences in the optimal wolf hunting rates across the states due to the spatial configuration of the GYEPA in relation to state boundaries and the heterogeneity within the GYEPA – a primary contribution of our spatially explicit model. The optimal hunting strategy involves very aggressive hunting in Montana and Idaho ( $h_{W,MT}^* = 1.0$  and  $h_{W,ID}^* = 1.0$ ) with a more modest hunting rate in Wyoming. The shift from the current hunting rates to the new optimal hunting rates increases elk populations across the grid (see Figure 8A) while aggregate wolf populations fall (see Figure 8B).<sup>18</sup>

However, the new optimal hunting rates also cause the distribution of wolves to change so that all wolves are concentrated in Wyoming and YNP. Figures 9A and 9B show the spatial and temporal patterns of elk and wolves in response to the shift from the current hunting rates 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, the elk population declines in YNP, but over time the elk population increases 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 9B shows that the increases in wolf hunting in Montana and Idaho from  $h_W = 0.24$  to  $h_{W,MT}^* = h_{W,ID}^* = 1$  where all wolves present are hunted. The heavy hunting pressure in all states directs the (remaining) wolves to seek refuge in the portions of YNP with less competition from existing wolves (cells 7, 10, and 11). But the park is unable to sustain these higher wolf numbers and eventually the wolf population falls below the level experienced before the switch in management regimes. This reduction and spatial shift in the wolf population has the added benefit of resulting in less livestock predation and conflict with ranchers while only marginally decreasing the level of wolf-driven tourism.

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<sup>18</sup> The simulated aggregate time paths for elk and wolf densities start ( $t = 1$ ) at the current average hunting rates of 0.24 for wolves and 0.22 for elk. In period ( $t = 2$ ) and thereafter, hunting rates are set at the socially optimal levels.

These results suggest that the GYEPA recovery goal would be most efficiently met by allowing aggressive hunting practices on the Idaho and Montana portions of the grid. There are several reasons for this. First, a small portion of the GYEPA is in Idaho. Driving local wolf populations to such low levels over this small portion of the GYEPA reduces conflicts with ranchers and elk hunters without severely limiting the ability to maintain 100 wolves over the whole GYEPA. The vast majority of the GYEPA is in Montana and Wyoming. However, wolf-stakeholder conflicts are more pronounced in Montana than in Wyoming. The Montana portion of our grid contains approximately 25 percent more livestock than the Wyoming portion of the grid and more areas with above average wolf-elk predation risk. Since the cost of wolf conservation is relatively high in Montana and the habitat in the Wyoming is capable of supporting 100 wolves, the entirety of wolf conservation is focused on the Wyoming portion of the GYEPA. However, we expect wolf conservation in Idaho and Montana would become necessary with a more stringent recovery criteria (e.g., 300 wolves in the GYEPA instead of 100).

The sum of discounted net benefits from the optimal hunting rates is \$12.65 billion over the  $T = 50$  period after delisting (Table 1). However, the spatial and temporal patterns in Figure 9 illustrate how these net benefits are unequally distributed across space and stakeholder groups within the region due to differences in composition of state economies. Over 30 percent of these discounted net benefits accrue to ranchers while only 1 percent of the discounted net benefits accrue to hunters.

*Cost savings from delisting*

While listing the gray wolf imposes costs on residents of the GYE through restrictions on wolf hunting and increased risk of livestock depredation, delisting should reduce these costs by lowering these restrictions. To determine how delisting increases welfare within the study area, we first consider a wolf hunting moratorium ( $h_w = 0$ ) to identify welfare if gray wolves remain listed for the next 50 years.<sup>19</sup> Results are presented in the first row of Table 1. With no wolf hunting, steady state wolf populations increase in all states relative to optimal state management post-delisting; particularly in Montana and Wyoming. By prohibiting wolf hunting, the flow of ecosystem service provisioning for wolf tourism increases. However, these gains are more than offset by the decreased flow of ecosystem service provisioning for cattle grazing and elk hunting.

The cost savings from delisting are presented in Table 2. Comparing the results of the wolf hunting moratorium to the optimal wolf hunting strategy following delisting, we find that delisting reduces the cost of wolf conservation in the GYE (increases welfare) by an average of \$1.88 million per year (\$94 million over the  $T = 50$  year study period). While the tourism sector and non-use wolf values are harmed by delisting, these losses are more than offset by the increased flow of net benefits from livestock grazing and hunting. The vast majority of the net benefits from delisting (85 percent) accrue to ranchers.

A key result of the analysis is that delisting does not completely eliminate the cost of wolf conservation since the GYEPA must still maintain at least 100 wolves. To estimate the cost of achieving this 100-wolf minimum, we consider a case where states are allowed to choose wolf hunting rates without the 100-wolf minimum restriction in the GYEPA (a scenario which can be thought of as replicating the past classification of wolves as a nuisance predator). Results are presented in the second row in Table 1. Without the minimum population restriction, states find

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<sup>19</sup> In this listed scenario we also assume the compensation program is fully funded by the federal government or private NGOs (e.g., Defenders of Wildlife).

it optimal to heavily hunt wolves. While the tourism sector is harmed by aggressive hunting, these losses are more than compensated by the increased flow of net benefits from livestock grazing and elk and wolf hunting. Thus, federal oversight is necessary in our baseline scenario to preserve a viable population of gray wolves in our study area. Achieving 100 wolves in the GYEPA costs stakeholders in the study area on average  $(\$12,693-\$12,653)/50 = \$800,000$  per year. Thus, delisting reduces the cost of wolf conservation imposed on residents by  $\$1.88/(\$1.88+\$0.8) = 70$  percent.

#### *Bioeconomic equity-efficiency tradeoffs*

The unequal distribution of conservation responsibility and cost savings from delisting arises because the federally mandated wolf minimum applies to the entire GYEPA. Under a GYEPA mandate, the spatial flexibility results in a large degree of wolf hunting in Montana and Idaho and an uneven distribution of wolves across the GYEPA. To achieve a more equitable allocation of cost savings from delisting or a more even distribution of wolves across the GYEPA, the federal government may choose to set state-specific wolf mandates or to apply a one-size-fits-all wolf hunting rate across the three states that border YNP. The former would more evenly distribute conservation responsibility and thus wolves across the grid while the latter would more equitably allocate hunting opportunities across the states. The optimal harvest rates for these more equitable delisting strategies are presented in the fourth and fifth rows of Table 1 while the efficiency implications can be seen in Table 2.

If the federal government were to require the 100-wolf minimum in the GYEPA be proportionally distributed across the three states based on area, the cost savings achieved by delisting falls by 56 percent to \$820,000 per year. Thus, the GYE savings from delisting are

reduced by \$1.06 million per year if the responsibility for meeting the minimum wolf mandate is shared across all three states. The one-size-fits-all wolf hunting rate results in a similar reduction (55 percent reduction) in cost savings from delisting and a similar equity-efficiency tradeoff. Thus, efforts to spread the benefits of delisting and the responsibility for wolf conservation more equitably (and more evenly allocate wolves across the GYE) comes at the cost of efficiency. More equitable recovery goals and hunting strategies limit the ability to take advantage of spatial flexibility in management that comes with differences in habitat, predation rates, and economic sectors across the GYE.

#### *Livestock depredation compensation programs*

The results in the previous section assume ranchers are only compensated for the direct predation cost of wolves (i.e., the financial loss from livestock death and injured calves) and state and federal governments equally share the cost of these programs ( $\eta = 0.5$ ). However, there is considerable debate surrounding the effectiveness of these programs (Ravenelle and Nyhus, 2017). While generally popular among rural residents in wolf territory, there is little evidence that these programs increase tolerance toward wolves (Naughton-Treves et al., 2003). Recent research also suggests that compensation based on direct predation costs is too low since it omits indirect predation risk costs such as decreased weaning weights, decreased conception rates, and increased cattle sickness (Steele et al., 2013; Ramler et al., 2014).

To investigate the viability of depredation programs, we consider two alternative scenarios. In the first, the compensation program is terminated and ranchers are no longer compensated for the losses due to livestock death and injured calves. In the second, the compensation program is extended to account for indirect predation costs (i.e., full predation

compensation). Following Ramler et al. (2014), indirect cost of wolf-livestock predation is 7.5 times the direct costs. Results are presented in Table 3.

Eliminating the compensation program will reduce livestock profits (and total GYE welfare) by an average of only \$80,000 per year (\$4 million over the 50-year time horizon in our study). Direct compensation is not large enough to reduce the states' incentives to lower wolf populations in the GYEPA and its elimination does not change the states' optimal wolf hunting rates. Eliminating the compensation program financially harms ranchers and results in the same number and geographic distribution of wolves as the case where direct compensation is paid. In contrast, extending the compensation program to account for both direct and indirect predation costs result in a more uneven distribution of wolves across the GYEPA. Importantly, the incentive to hunt wolves in Wyoming is eliminated since ranchers are compensated for the full cost of wolf conservation. While the inclusion of indirect predation costs increases total compensation program costs by an average of \$880,000 per year (\$44 million over 50 years), these programs are welfare enhancing for the states since they increase livestock profits, non-use wolf values, and tourism revenues.

Paying full compensation to ranchers also reduces the need for a federal minimum wolf mandate but only if the compensation program is fully funded by the federal government or NGOs. The last three lines in Table 3 show that paying full compensation to ranchers does not eliminate the incentive for states to hunt wolves to extinction in the absence of a wolf minimum. However, a federally or privately funded compensation program that pays ranchers both direct and indirect predation costs (the largest costs inflicted by wolf conservation) does eliminate the incentive for states to hunt wolves and eliminates the need for the federal minimum wolf mandate. Since ranchers are fully compensated for their losses and states don't pay this

compensation, there is little incentive for states to engage in high levels of wolf hunting. While these compensation programs may not increase tolerance for wolves among GYE residents (Naughton-Treves et al., 2003), they do reduce the economic incentive for states to actively engage in hunting wolves. If the present value cost of administering and enforcing the minimum wolf mandate were larger than the \$20 million in indirect predation costs, it may be preferable for the federal government or NGOs to pay ranchers the indirect predation cost and suspend any regulatory oversight.

## **Conclusion**

Some of the most contentious conservation issues involve human-wildlife conflicts. Managing these conflicts in an era where an increasing number of species are being removed from the endangered species list will require an improved understanding of both the biological and social science drivers of these conflicts. The delisting of gray wolves in the GYE is a prime example. While human-wolf conflicts are influenced by several factors that extend beyond the costs and benefits considered in this study (Farrell, 2017), there is a growing need to better understand how the economic incentives to conserve these species change when management shifts from the federal government with a sole focus on preservation to states with a focus on multiple and often competing objectives. We illustrate a bioeconomic approach (i.e., resource selection functions can be combined with a spatially explicit predator-prey model) to better understand the local economic benefits that come from delisting a species. Three key results emerge from our investigation into the optimal management of a wolf-elk-livestock ecosystem following delisting of wolves around Yellowstone National Park.

First, delisting endangered species reduces the costs imposed on landowners that harbor those species. However, these cost savings and the responsibility for wolf conservation will vary across space meaning that states and stakeholders do not equally share in the benefits created by delisting a species. Spatial heterogeneity creates an inherent challenge for wildlife management and often yields optimal harvesting rates that vary considerably across space (Sanchirico and Wilen, 1999; Smith et al., 2009; Epanchin-Niell and Wilen, 2012). Our findings illustrate how incorporating spatial heterogeneity brings a degree of flexibility that increases the cost savings produced by delisting a species yet leads to an unequal allocation of these cost savings and an uneven distribution of the recovered species.

Second, states charged with the management of recently delisted species must negotiate an equity-efficiency tradeoff. Efforts to achieve a more equitable allocation of conservation responsibility and cost savings from delisting reduces the benefits of delisting. In other words, efforts to more equally share the welfare pie actually decrease the size of the pie. If states or the federal government wish to more equally share the cost savings achieved by delisting or evenly distribute a recently delisted species within its former habitat, they should look to foster Pareto improving agreements between states or stakeholders negotiated after a species is delisted. Such ecosystem service net benefit sharing rules could relax the bioeconomic equity-efficiency tradeoffs facing states following the delisting.

Finally, our results illustrate how the federal government could use indemnity payments or compensation programs to ensure states don't undermine the recovery of a delisted species. Delisting transfers management authority from the federal government back to states with some form of federal oversight. The most common form of federal oversight are minimum population mandates. Compensation programs, if sufficiently generous and funded by the federal

government or NGOs, can be used to diminish a state's incentive to draw down populations of recently delisted species and lessen the need for federally mandated minimum viable populations. Thus, while federal intervention is needed to ensure delisted species don't need to be eventually relisted, federal mandates that prescribe minimum population levels are not the only tool available to federal agencies. Additional work on monitoring and enforcement of these compensation programs (i.e., distinguishing wolf depredations from other sources of livestock loss; false reports of wolf depredations by ranchers) will be needed to fully assess the tradeoffs between these two conservation tools.

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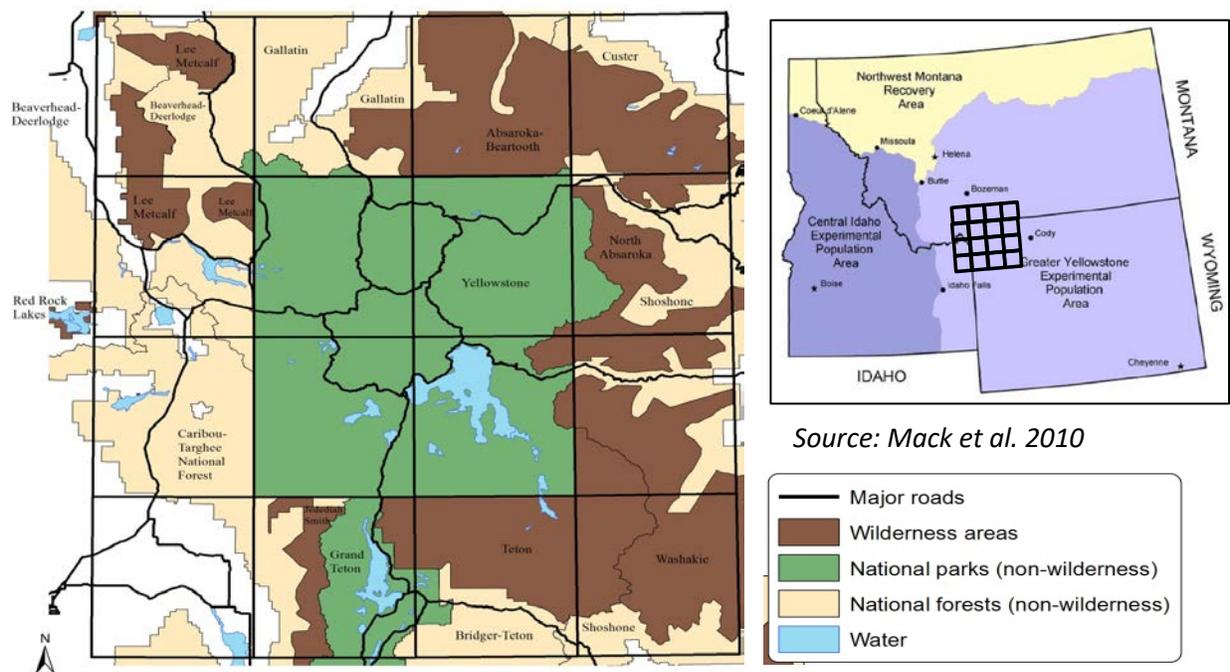
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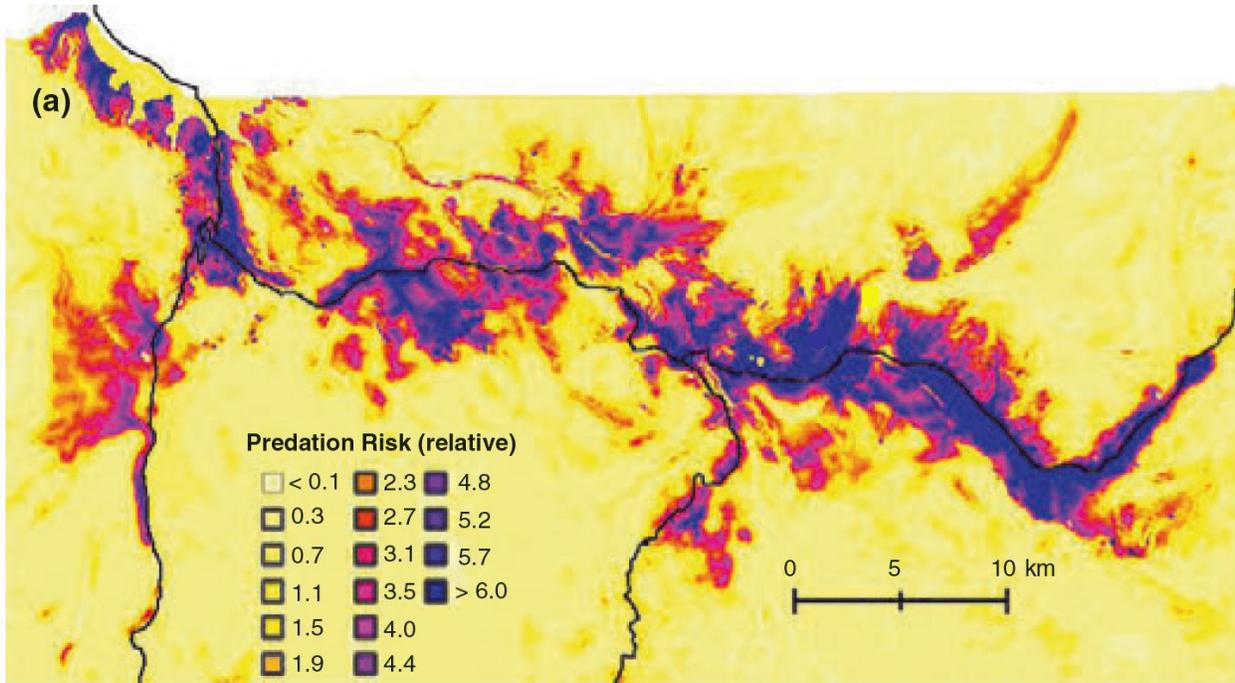
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Source: Mack et al. 2010

Figure 1. Greater Yellowstone Ecosystem 4 × 4 Grid

Panel A. Kauffman et al. (2007)



Panel B. Our Spatial Predator-Prey Model

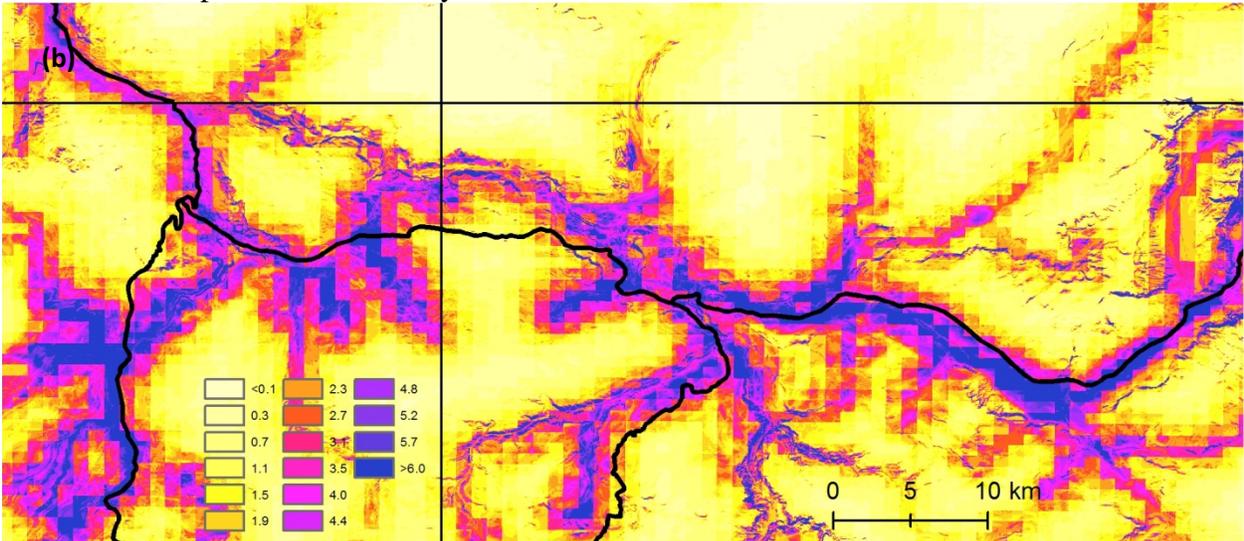


Figure 2. Comparison of relative risk (a value of 1 denotes average risk) of wolf predation on elk on Yellowstone's Northern Range

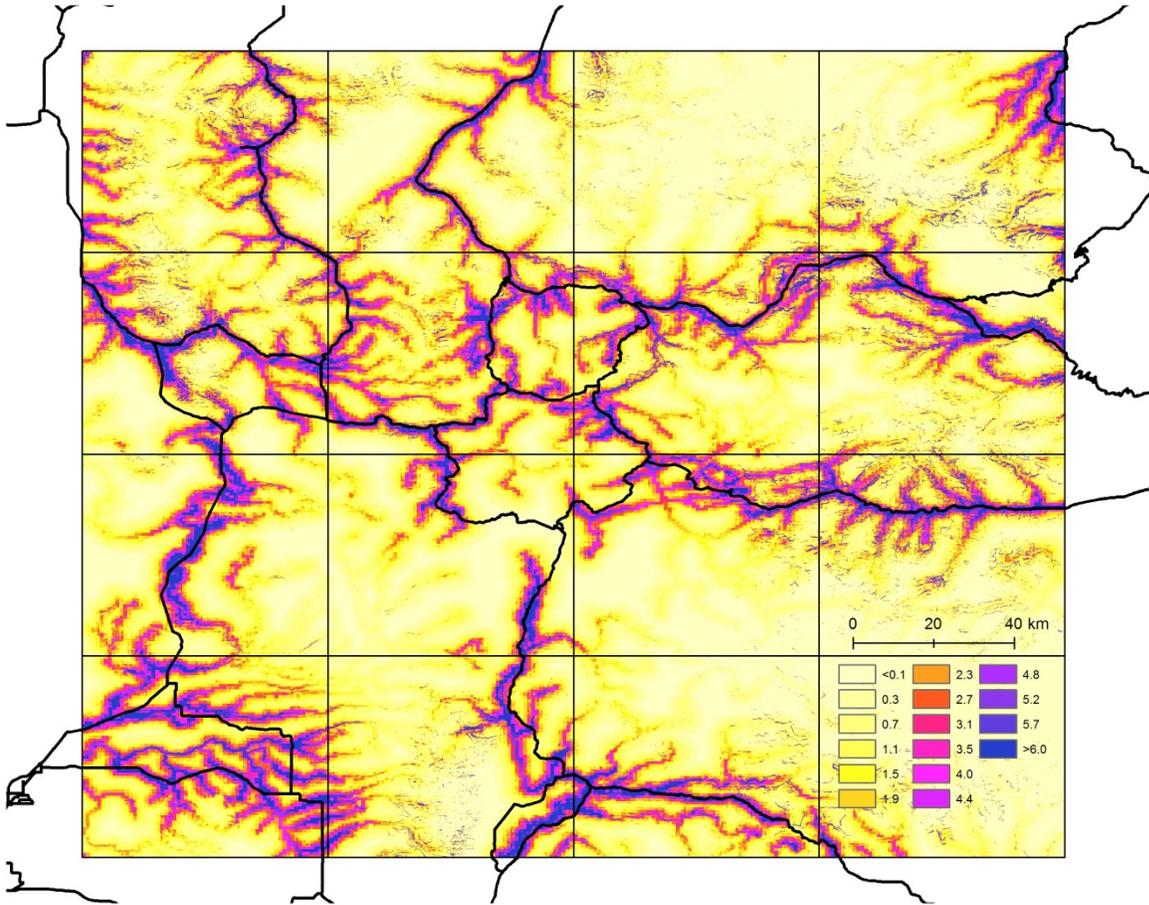


Figure 3. Spatial variation in relative risk (a value of 1 denotes average risk) of wolf predation on elk for the entire  $4 \times 4$  grid

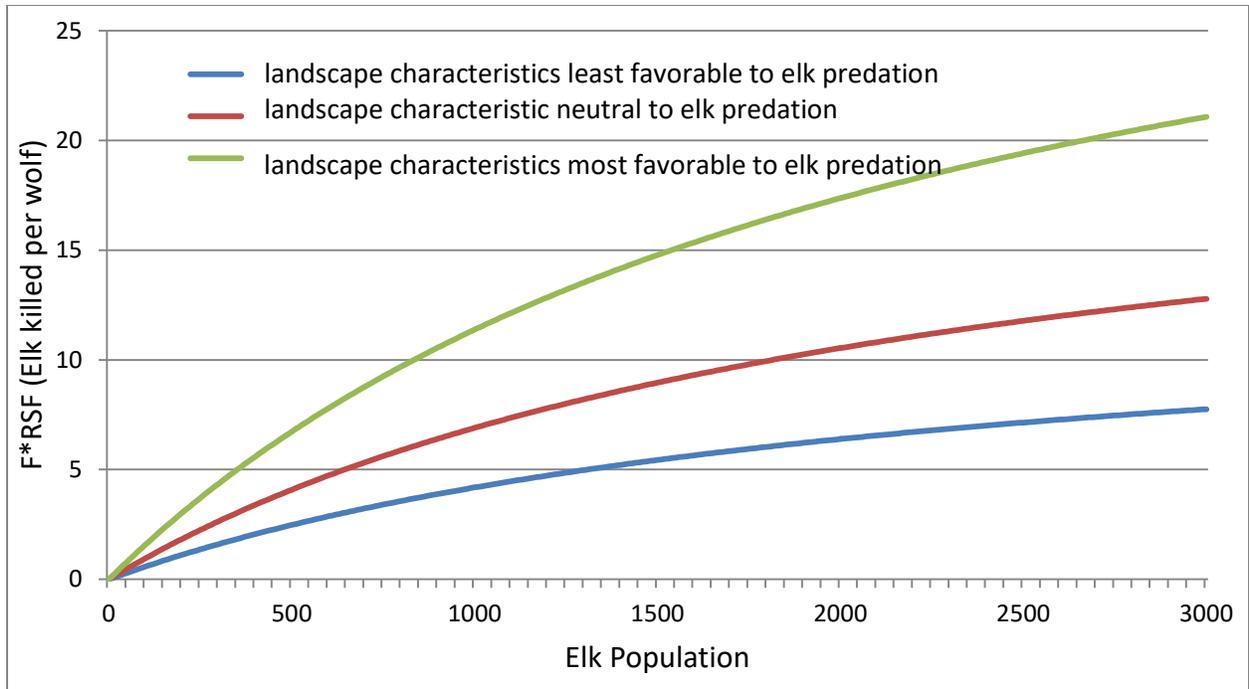
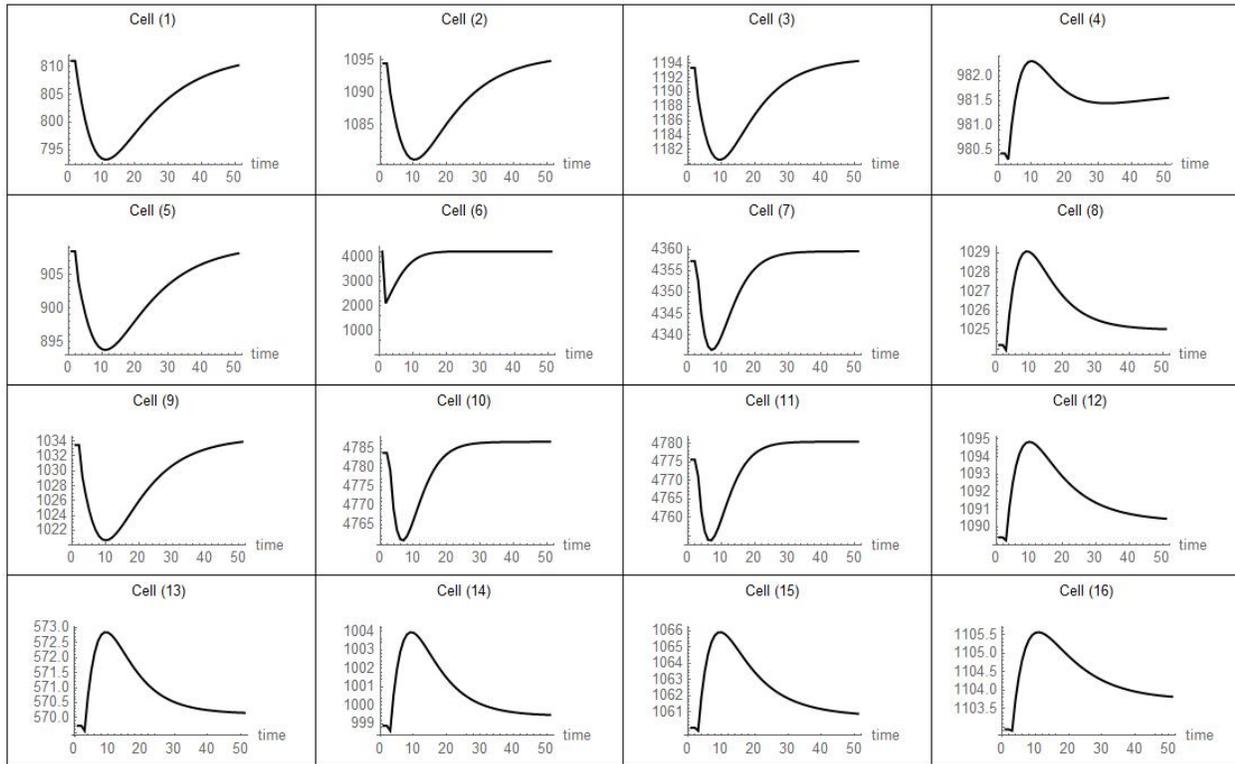


Figure 4. Stylized Wolf-Elk Functional Response for Three Cell-Specific Landscape Types

Panel A. Predicted Elk Populations over the  $4 \times 4$  Grid



Panel B. Predicted Elk Net Dispersal Patterns over the  $4 \times 4$  Grid

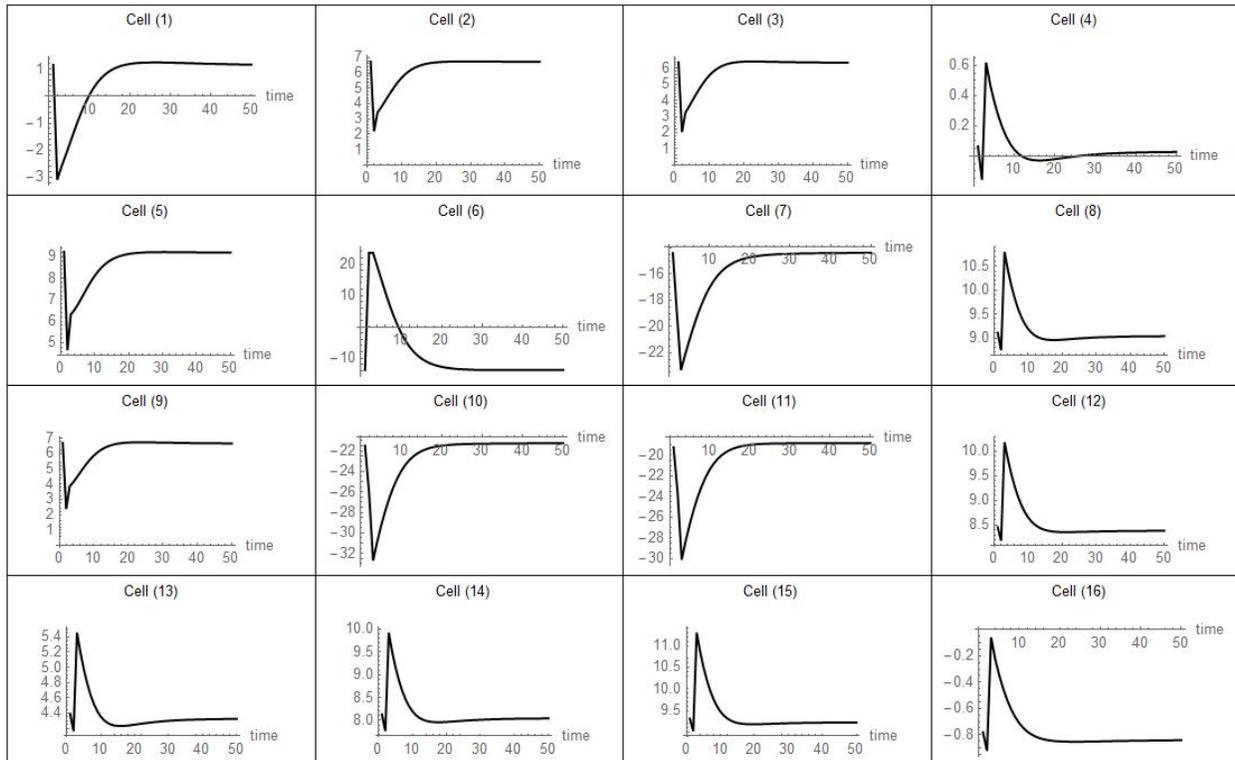
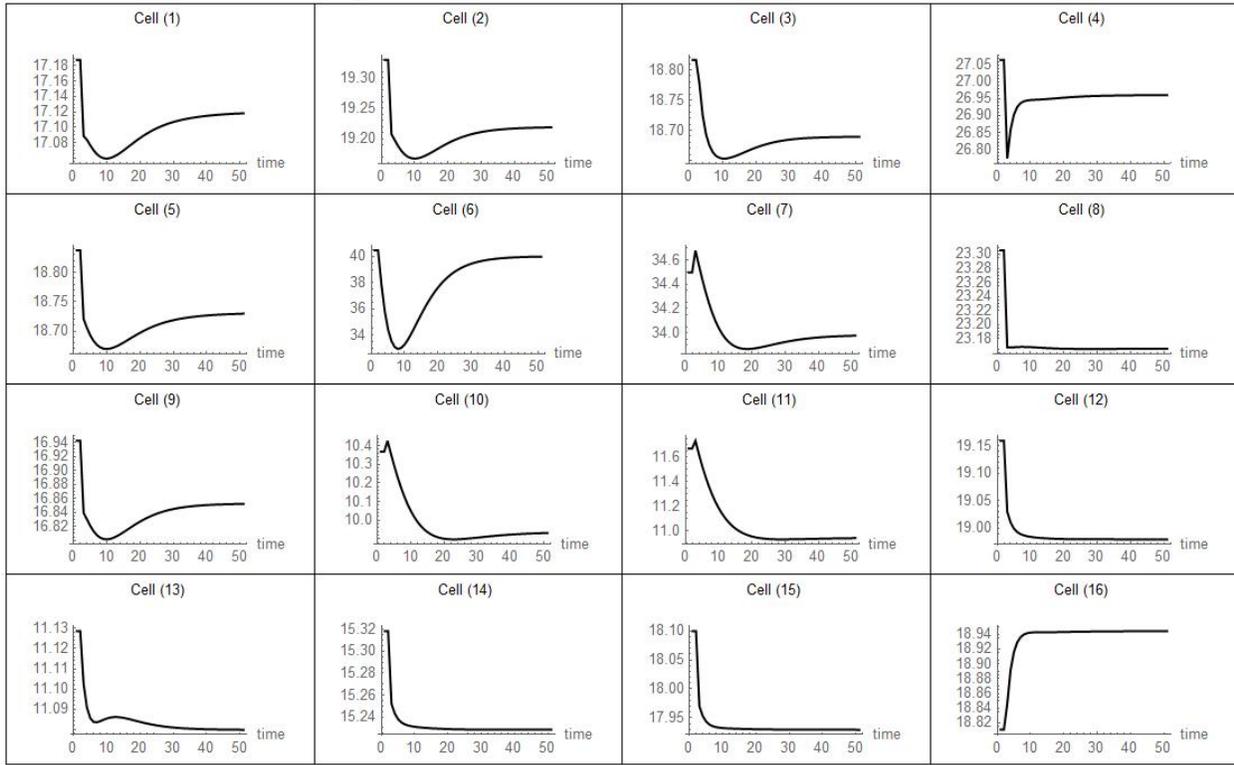


Figure 5. Simulated spatio-temporal elk dynamics in response to a one-time reduction in the elk stock in the northwest corner of YNP (cell #6)

Panel A. Predicted Wolf Populations over the  $4 \times 4$  Grid



Panel B. Predicted Wolf Net Dispersal Patterns over the  $4 \times 4$  GYE Grid

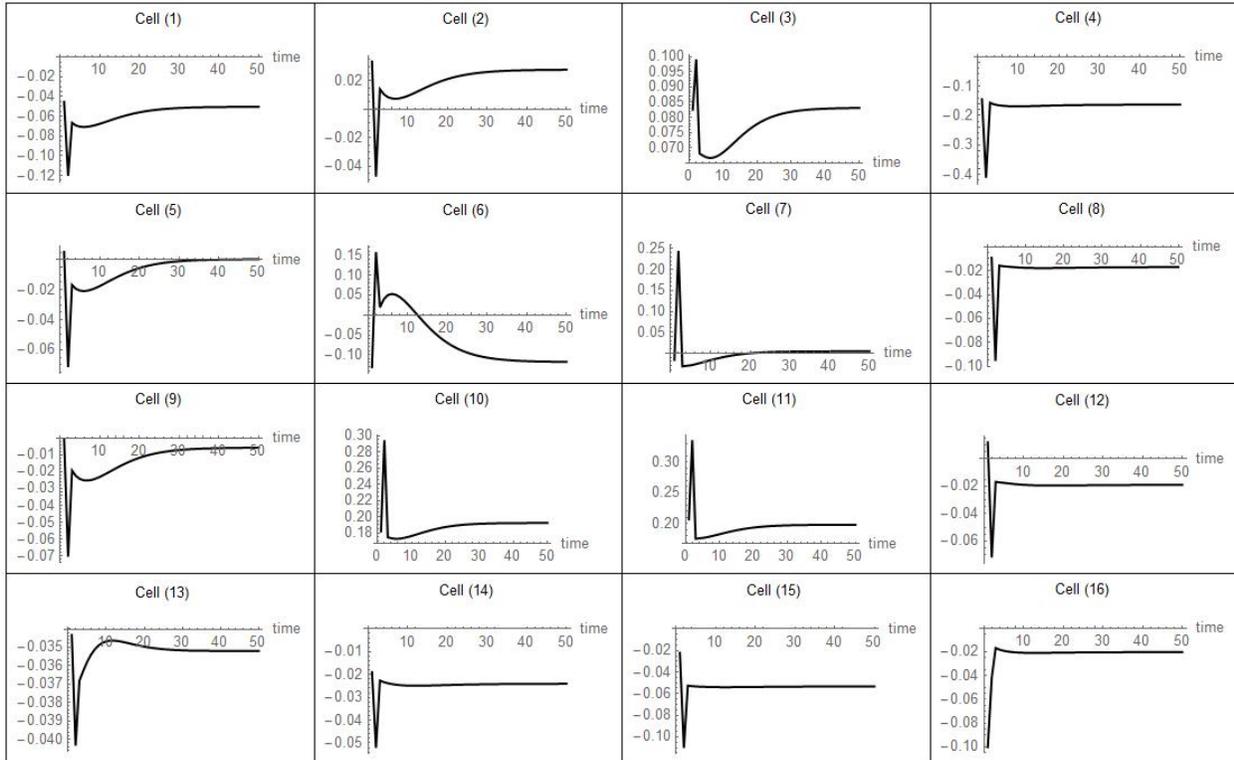


Figure 6. Simulated spatio-temporal wolf dynamics in response to a one-time reduction in the elk stock in the northwest corner of YNP (cell #6)

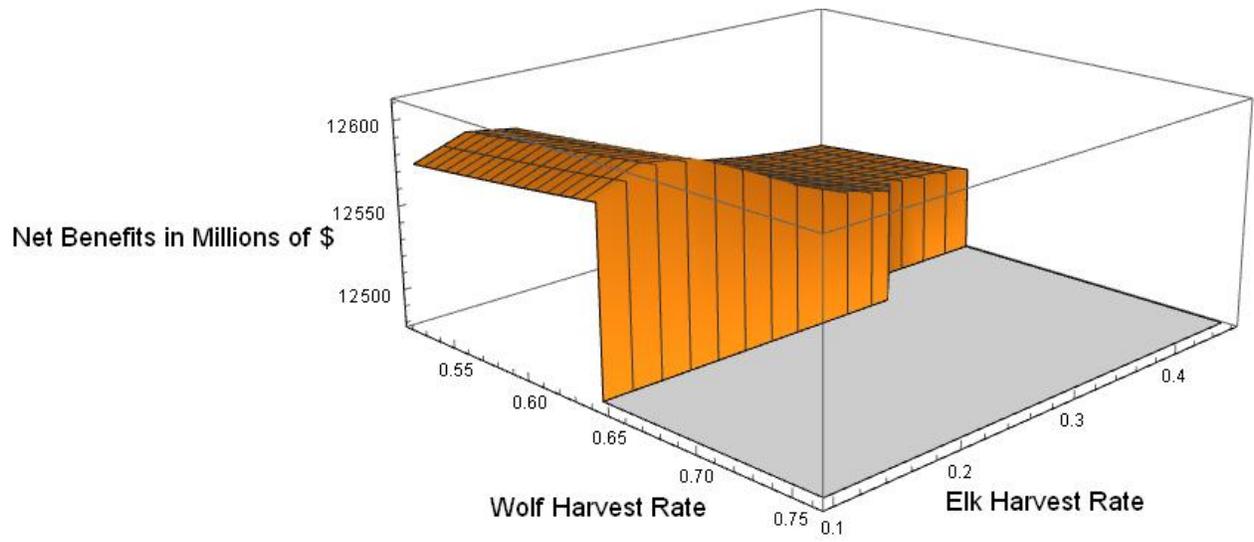


Figure 7. Ecosystem Net Benefit Surface for One-Size-Fits-All Hunting Rates

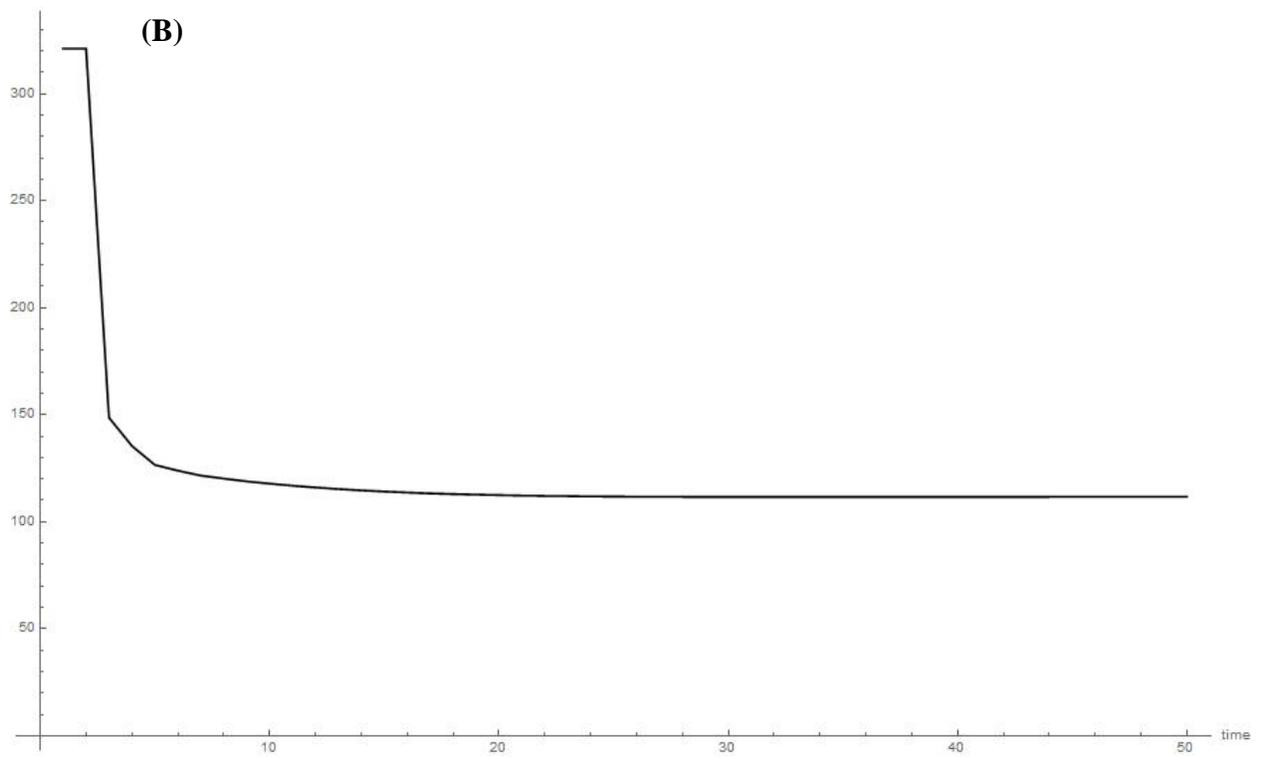
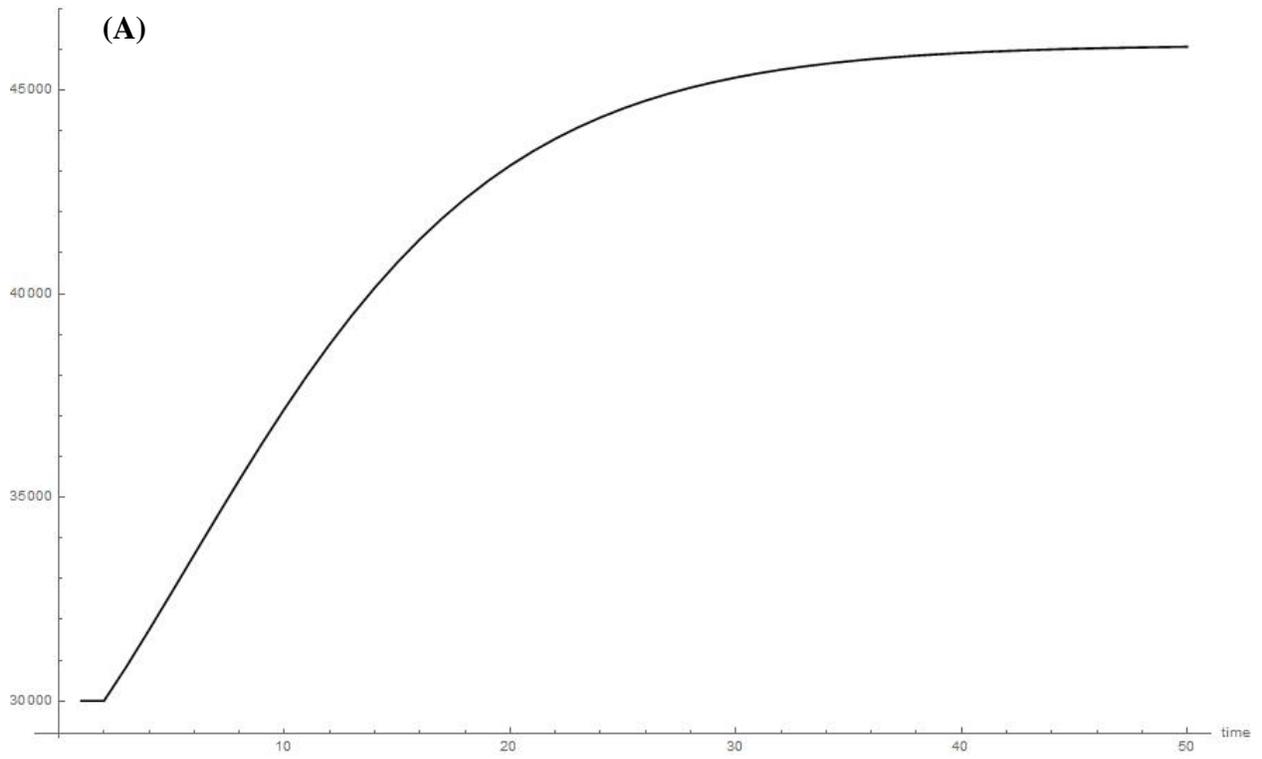
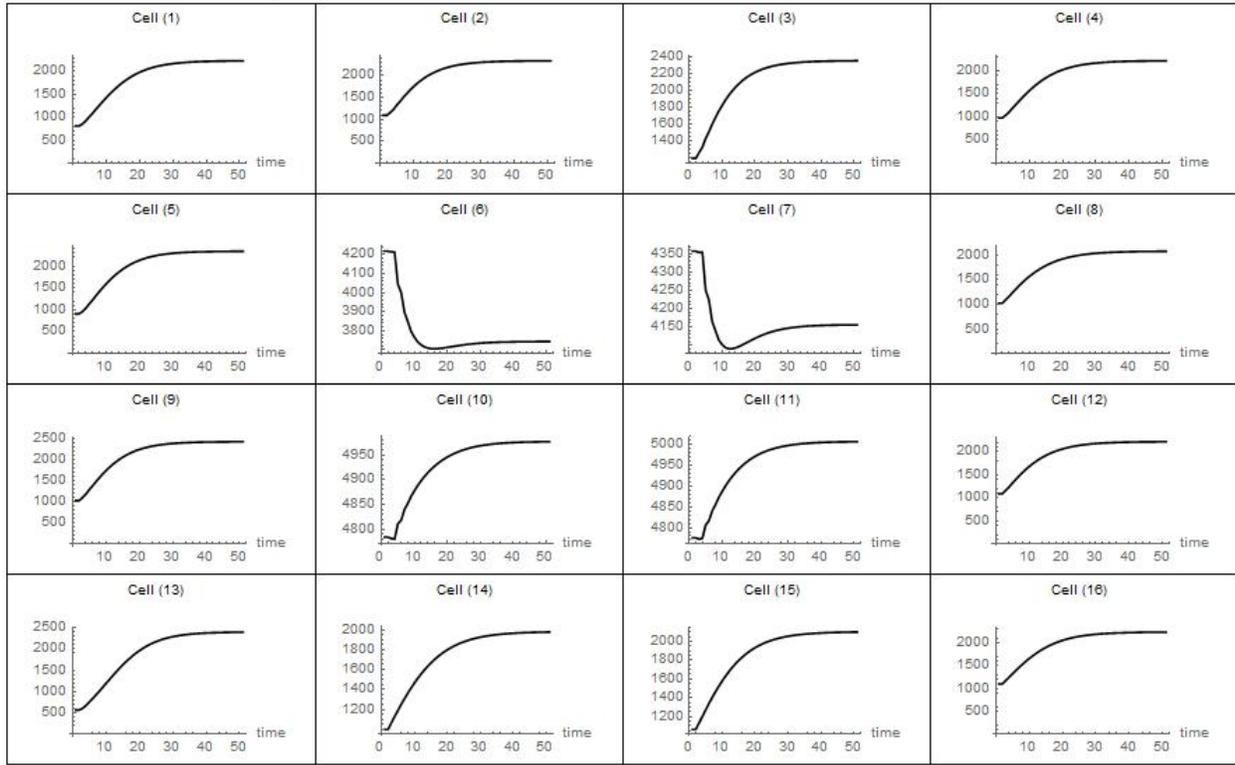


Figure 8. Aggregate (A) Elk and (B) Wolf Population Time Paths from Optimal Management over 50 Years

A. Predicted Elk Populations over the  $4 \times 4$  Grid



Panel B. Predicted Wolf Populations over the  $4 \times 4$  Grid

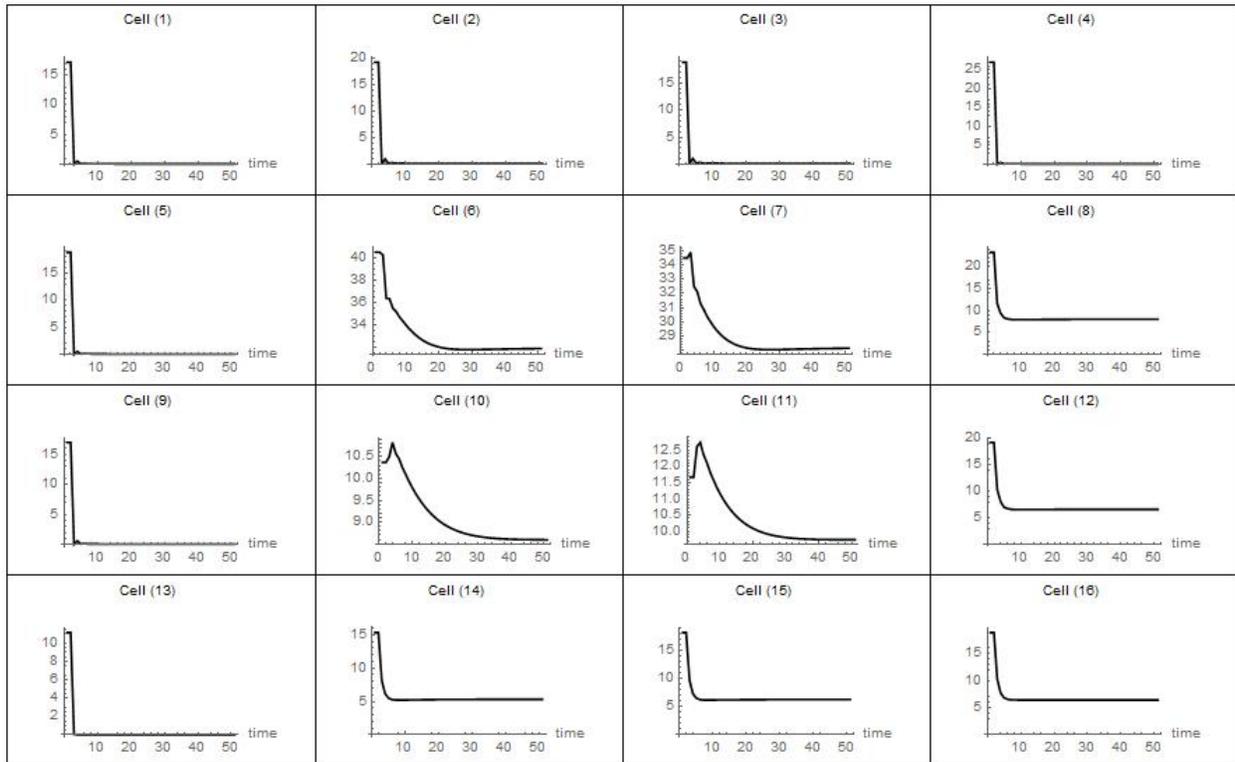


Figure 9. Predicted (A) Elk and (B) Wolf Populations with Optimal Hunting over the  $4 \times 4$  Grid

**Table 1. Optimal Wolf and Elk Hunting Rates and the Distribution of Net Benefits Across Stakeholders**

	Wolves - Hunting Rates (Steady-State Grid Population)			Elk - Hunting Rates (Steady-State Grid Population)			Components of 50-yr Discounted Net Benefits (Millions \$)					
	ID	MT	WY	ID	MT	WY	Livestock Profits	Wolf Non-use Values	Hunting	Tourism	State Depredation Compensation	Total
<b>Listed</b>	0.00 (84)	0.00 (281)	0.00 (262)	0.13 (3,915)	0.14 (10,635)	0.15 (10,142)	\$3,834	\$7,519	\$132	\$1,074	\$0	\$12,559
<b>Delisted:</b>												
No wolf minimum	1.00 (0)	1.00 (0)	1.00 (0)	0.16 (4,623)	0.18 (11,079)	0.17 (10,821)	\$3,995	\$7,463	\$171	\$1,066	-\$2	\$12,693
100 wolf minimum in the GYEPA	1.00 (0)	1.00 (0)	0.53 (33)	0.15 (4,827)	0.16 (11,476)	0.15 (10,615)	\$3,954	\$7,481	\$153	\$1,069	-\$4	\$12,653
100 wolf minimum distributed across states in GYEPA	0.48 (13)	0.59 (25)	0.70 (14)	0.14 (4,012)	0.15 (10,599)	0.15 (10,984)	\$3,912	\$7,485	\$141	\$1,069	-\$7	\$12,600
One-size-fits-all hunting rate	0.64 (7)	0.64 (22)	0.64 (20)	0.15 (3,942)	0.15 (10,696)	0.15 (10,843)	\$3,913	\$7,484	\$141	\$1,069	-\$6	\$12,601

Notes: The steady-state wolf populations on the grid are sometimes less than the GYEPA wolf minimums. This is due to wolves that exist off the grid but within the GYEPA and is explained in more detail in the Appendix, Section A.2.

**Table 2. Average Annual Cost Savings from Delisting (Millions \$)**

Management Strategy	Total	Allocation of cost savings across stakeholder groups			
		Ranchers	Hunters	Wolf Non-use Values	Tourism
100 wolf minimum in the GYEPA	\$1.88	\$2.40	\$0.42	-\$0.76	-\$0.10
100 wolf minimum distributed across states in GYEPA	\$0.82	\$1.56	\$0.18	-\$0.68	-\$0.10
One-size-fits-all hunting rate	\$0.84	\$1.58	\$0.18	-\$0.70	-\$0.10

**Table 3. Impact of Depredation Compensation Programs on Optimal Wolf and Elk Hunting Rates and the Distribution of Net Benefits Across Stakeholders**

	Wolves - Hunting Rates (Steady State Population)			Elk - Hunting Rates (Steady State Population)			Components of 50-yr Discounted Ecosystem Benefits (Millions \$)					
	ID	MT	WY	ID	MT	WY	Livestock Profits	Wolf Non-use Values	Hunting	Tourism	State Depredation Compensation	Total
<b>100 wolf minimum in the GYEPA</b>												
no predation compensation	1.00 (0)	1.00 (0)	0.53 (33)	0.15 (4,827)	0.16 (11,476)	0.15 (10,615)	\$3,946	\$7,481	\$153	\$1,069	\$0	\$12,649
direct predation compensation	1.00 (0)	1.00 (0)	0.53 (33)	0.15 (4,827)	0.16 (11,476)	0.15 (10,615)	\$3,954	\$7,481	\$153	\$1,069	-\$4	\$12,653
full predation compensation	1.00 (0)	1.00 (0)	0.00 (258)	0.15 (4,779)	0.16 (11,179)	0.15 (9,731)	\$4,017	\$7,503	\$148	\$1,072	-\$48	\$12,692
<b>No wolf minimum</b>												
direct predation compensation	1.00 (0)	1.00 (0)	1.00 (0)	0.16 (4,623)	0.18 (11,079)	0.17 (10,821)	\$3,995	\$7,463	\$171	\$1,066	-\$2	\$12,693
full predation compensation	1.00 (0)	1.00 (0)	1.00 (0)	0.15 (4,922)	0.18 (11,100)	0.16 (11,609)	\$4,017	\$7,462	\$171	\$1,066	-\$12	\$12,704
full predation compensation not paid by states	0.00 (84)	0.00 (281)	0.00 (262)	0.13 (3,915)	0.14 (10,635)	0.15 (10,142)	\$4,017	\$7,519	\$132	\$1,074	\$0	\$12,743

Notes: Discount rate is set at 3% per year.

## **Online Supplemental Appendix. Model calibration**

Calibration of the spatial predator-prey model was conducted by selecting values for parameters that are consistent with the available data on animal populations, economic values, the GYEPA 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 academic (i.e., journal articles) and gray literature. In the ‘Model’ method, we rely on the equilibrium structure of the model and use observed data to solve for internally consistent parameter values. The ‘Model’ method for calibration is described further in Section A.5. Since there is considerable uncertainty in several of these parameters, a sensitivity analysis is provided in Section A.7

### **A.1 Welfare and management parameters**

Following recommendations by the Office of Management and Budget (OMB 2003), we select a social discount rate of  $\rho = 0.03$ . 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 (16) includes four ecosystem services: hunting, tourism, livestock profits, and non-use values from wolves. Hunting ecosystem services are assumed to take the form:

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

where  $\alpha_E$  and  $\alpha_W$  are dollars per hunted elk and wolf, respectively, and  $\sigma$  is the fraction of wolf hunters that are primarily hunting elk. It is common for elk hunters to purchase a wolf tag in case they have the opportunity to shoot a wolf. If  $\sigma = 0$ , then the two hunting groups are independent of one another. If  $\sigma = 1$ , then there is only really one group of hunters that are hunting both elk and wolves and it will be important not to double count the hunting benefits. In the absence of estimated demand curves for hunting of these species, we assume the values are invariant over time, space, or number hunted. Values of  $\alpha_E$  and  $\alpha_W$  are calculated from the estimates in the literature that represent the social value per elk or wolf hunted. 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 2012 dollars) from Table 4 in Park et al. (1991) is \$342 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, 2013). This produces the value of  $\alpha_W = \$28,921$  per wolf harvested in Table A1.<sup>20</sup>

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<sup>20</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.

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. While the Duffield study does not indicate what portion of these direct expenditures occur on our grid, it is reasonable to assume that most of the direct expenditures occur in the gateway communities surrounding YNP. For exposition we assume all direct expenditures occur on our grid. 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,  $W_t^{GYE}$ :

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

where  $\alpha_0 = \alpha_{tour}(W^{GYE} - \ln(W^{GYE}))$  so that the total contribution of wolves to tourism revenues is equal to  $\alpha_{tour}W^{GYE}$  in steady state and varies in a diminishing fashion with the wolf population out of steady state. The contribution per wolf to tourism expenditures in the steady state,  $\alpha_{tour}$ , 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 grid, we find that, on average, each wolf contributes approximately  $\alpha_{tour} = \$111,000$  to tourism expenditures in 2005 dollars. Using a 2% cost-of-living adjustment, this translates to  $\alpha_{tour} = \$127,500$  in 2012 dollars.

Profits associated with cattle grazing on public land outside YNP,  $\pi_{lvstck}(W_t^{GYE}, L_t)$ , are calculated by number of cattle stocked  $L_t$  and a 2012 cattle price of \$1.22 per pound<sup>21</sup>, an

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<sup>21</sup> Source: USDA Livestock, Poultry & Grain Market News Division, LM\_CT185 Iowa/Minnesota Monthly Weighted Average Cattle Report - Negotiated Purchases

average weight gain of 697.4 pounds (Hussain and Tschirhart, 2013), and a grazing fee of \$1.35 per month per cow.<sup>22</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 hunted 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>23</sup> In 2012, there were 116 wolves harvested outside YNP in the GYEPA. Applying the percentage of wolf packs on our grid and assuming that wolf harvests are uniformly distributed across packs, this implies 54 wolf harvests on our grid. Using an estimated wolf population of 224 on the grid, this produces an average wolf hunting rate of  $h_W = 0.24$ .<sup>24</sup>

The non-use value of wolves is difficult to estimate, both because of uncertainty associated with the average value per person and which households should count. We specify a modest annual existence per person of approximately five cents per wolf for the 3.175 million residents

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<sup>22</sup> <http://www.fs.fed.us/news/releases/blm-and-forest-service-announce-2014-grazing-fee>.

<sup>23</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 (<https://www.nps.gov/yell/learn/nature/elk.htm>). To our knowledge, there are no scientific estimates of elk populations for our grid area. Therefore, we vary this elk population estimate in the sensitivity analysis.

<sup>24</sup> The data on wolf hunting rates and wolf populations are taken from the Rocky Mountain Wolf Recovery 2012 Interagency Annual Report ([https://www.fws.gov/mountain-prairie/es/species/mammals/wolf/annualrpt12/tables/FINAL\\_Table2b-c\\_YNP\\_GYA\\_2012.pdf](https://www.fws.gov/mountain-prairie/es/species/mammals/wolf/annualrpt12/tables/FINAL_Table2b-c_YNP_GYA_2012.pdf)).

of ID, MT and WY. This amounts to an approximate maximum willingness to pay of \$1 per person per month in the three state region for wolf existence on the grid. In Section A.7, we check to see if the main results are robust when there is no wolf existence value.

## **A.2 Populations and Population Restrictions**

The population of cattle outside YNP is calculated using a stocking rate of 41.24 head of cattle per section (640 acres) and the percent of forage area per cell.<sup>25</sup> This results in approximately 180,000 head of cattle on our GYE grid.

Determining populations of elk on the grid and in the GYEPA is complicated. Since our  $4 \times 4$  GYE grid covers only 13,500 square miles, elk and wolves exist off the grid but remain within the GYEPA boundaries. In equilibrium, we assume the dispersal onto the grid and movement 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 24) to restrict the steady-state population on the grid to equal 321 wolves. This is our estimate of the number of wolves residing on the grid at the beginning of 2012. The total number of wolves estimated in the entire GYEPA is 497, which includes the 97 wolves in YNP, state cells within our grid, and state GYEPA lands off the grid.

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<sup>25</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., 2013). Using a stocking rate of 3.88 acres per animal unit month (Reid, 2017) translates to a 4-month stocking rate per section of  $(4 \text{ months}) \times (640 \text{ acres}) / (3.88 \text{ acres/AUM}) = 41.24$  cows per section over the 4-month period.

<sup>26</sup> <https://www.nps.gov/yell/learn/nature/elk.htm>.

The optimization procedure to maximize discounted future ecosystem benefits is performed subject to the population restriction that the total number of combined wolves in the GYEPA must be equal to or greater than  $\bar{W} = 100$ , which is the stated goal for the GYEPA (U.S. Fish and Wildlife Service, 2004). We also consider a case where the  $\bar{W} = 100$  restriction is proportionally allocated to states based on the state's area in the GYEPA. However, the stated recovery goals include wolves that are in the GYEPA but off the grid. To account for this fact, we adjust the population grid restrictions downward because the grid only covers a portion of the GYEPA. In 2012, there were 321 wolves on the grid and 497 in the GYEPA. The estimate of wolves on the grid is found by overlaying our grid on maps of wolf pack locations. The first step is to distribute the 176 wolves off the grid to the three states using established maps of wolf pack locations<sup>27</sup>. Then the portion of wolves on the grid for each state in 2012 are calculated:  $\frac{37}{50} = 74\%$  for Idaho,  $\frac{88}{137} = 64\%$  for Montana, and  $\frac{99}{311} = 32\%$  for Wyoming. In other words, the portion of wolves on our grid (relative to the population of wolves in the portion of the state in the GYEPA) is 32% for Wyoming, 64% for Montana, and 74% for Idaho. These proportions are then used to scale down the wolf population restrictions for management in each state. Scaling the 100/3 uniform state restriction to the grid cells in each state implies that the minimum grid populations in ID, MT and WY are approximately 25, 21, and 11, respectively. For the centralized 3-state management regime, these grid minimum population levels for each state are aggregated together to produce a minimum wolf population of 57 wolves on the grid.

### A.3 Predation parameters

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<sup>27</sup> [https://www.fws.gov/mountain-prairie/es/species/mammals/wolf/annualrpt12/figures/Final\\_Fig1\\_NRM.pdf](https://www.fws.gov/mountain-prairie/es/species/mammals/wolf/annualrpt12/figures/Final_Fig1_NRM.pdf)

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 (6) allows us to vary from prey density predation responses ( $m_E = 0$ , Holling type II) to ratio-dependent functional response ( $m_E = 1$ ) advocated by Hebblewhite (2013). To calibrate  $m_E$ , 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  $m_E$  is selected that matches the beginning-of-year 2012 wolf population across the entire GYEPA, not just our grid. The period up through 2012 was selected because it was the period where wolves in the GYEPA were under Federal protection. We use the entire GYEPA 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 GYEPA wolf populations in the wolf re-introduction exercise.

The estimate from this calibration exercise is  $m_E = 0.825$ , which implies a significant amount of predator interference. The attack rate in equation (6) for wolf-elk functional response is calibrated using the model (see Section A.5) at  $a_E = 0.008$  and the handling rate  $\mu_E = \frac{16.39}{365} = 0.045$  is taken from Garrott et al. (2007). As described in the main text, the wolf-elk functional response is modified in equation (9) to be spatially explicit. The vector of coefficients on the landscape covariates (i.e., distance to roads, distance to streams/rivers, slope, snow, elk density, and wolf density) for the resource selection function is taken from Table A1 in Kauffman et al. (2007).

The average livestock predation rate outside YNP is fixed, but it is allowed to vary across the 12 outside cells of the GYE grid. The total number of cattle lost to wolf depredation in the northwest agricultural district of Wyoming, U.S.A. is 300 (USDA, 2013), and our estimate of cattle stocked on public lands in Wyoming cells outside YNP is approximately 76,500 head.

Assuming most of the wolf predation events occur on the more heavily wolf populated area around YNP and on our grid, the livestock predation rate is approximately  $\frac{300}{76,500} = 0.4\%$  or  $\bar{p}_L = 0.004$ . Since the livestock kills from wolves is reported from an agricultural survey, the predation numbers may be overstated. The confirmed cattle predation numbers from the U.S. Fish & Wildlife Service is 47 kills for Wyoming. This implies a livestock predation rate of approximately  $\frac{47}{75,000} = 0.063\%$  or  $\bar{p}_L = 0.00063$ . However, these are only confirmed kills so it is likely an underestimate of true predation. We choose a livestock predation rate of 0.5% or  $\bar{p}_L = 0.005$  but explore other values in the sensitivity analysis.

Given the lack of data, we set the wolf-livestock predator interference parameter to be the same as that of elk (i.e.,  $m_L = m_E = 0.825$ ). The handling rate for livestock depredation is  $\mu_L = \frac{6}{365} = 0.016$  is taken from moose data (Zimmermann et al., 2015), and the attack rate is calibrated using the model (see Section A.5) at  $a_L = 0.006$ .

Wolves that are confirmed to kill livestock are often subject to lethal control either by U.S. Fish and Wildlife officials or state game agencies (Kompaniyets and Evans, 2017). Although our model does not allow us to identify specific wolves that kill livestock, we do calibrate the model such that a fixed proportion of wolves are subject to lethal control each year. The lethal control rate we use is 11.5%. This rate is calculated by taking 2012 lethal control figures for wolves in each state (USFWS, 2013, Tables 2b and 2c), adjusting for the proportion likely on the grid, and then dividing by the population of non-YNP wolves on the grid:

$$lc = \frac{(43 \times 0.32) + (13 \times 0.64) + (5 \times 0.74)}{(321 - 97)} = 0.115.$$

#### A.4 Growth and death parameters

The GYEPA elk carrying capacity,  $K^i$ , is difficult to estimate. White and Garrott (2005) report a total carrying capacity of 80,000 elk for the Northern Yellowstone elk herd. We assume a similar carrying capacity applied throughout our grid and divide it evenly across the 16 cells in the grid. The intrinsic growth rate for elk from equation (3) is  $r = 0.28$  (Boyce, 1995), while the average lifespan of a gray wolf absent lethal control and hunting is approximately 7 years (MacNulty et al., 2009; Young and Goldman 1944). The numeric response scale factor,  $\gamma$ , and the numeric response fixed factor,  $\varphi$ , are calibrated using the model to  $\gamma = 0.034$  and  $\varphi = 0.019$ . Using equation (4), this implies that average wolf growth will be 3.4% when the consumption of prey 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  $\bar{\theta}_E^{i,j} = \bar{\theta}_W^{i,j} = 0.99$ , 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 solve for the necessary cell-specific values of  $\delta_E^i$  and  $\delta_W^i$ . This implies that when the grid 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.

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<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 (12), a positive amount of equilibrium dispersal is necessary unless  $\delta_{species}^i \rightarrow \infty$ . We have experimented with other high values for the residence rates (i.e.,  $\bar{\theta}_E^{i,j}$  and  $\bar{\theta}_W^{i,j}$ ) 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.

## A.6 Calibration procedure using the model

We use a combination of external restrictions and the equilibrium (i.e., steady-state) conditions following the ‘Model’ method of Table A1. We impose four external restrictions:  $\sum_i E^i = 30,000$ ,  $\sum_i W^i = 321$ ,  $\sum_{i \in YNP} W^i = 97$ , and  $\bar{p}_L = 0.005$ . These four conditions along with all the system-wide equations are used to solve for the four unknown parameters ( $\gamma$ ,  $\varphi$ ,  $a_E$ ,  $a_L$ ) and the equilibrium values for wolves and elk in each cell.

## A.7 Sensitivity analysis

In this section, we investigate whether our results are robust to changes in key parameter values or assumptions regarding functional forms. Tables A2 and A3 summarize the changes in the severity of the equity-efficiency tradeoffs (in % reduction) and percentage of cost savings that accrue to ranchers under the one-size-fits-all regime when we change the ecological parameters and assumptions (Table A2) and the economic parameters and assumptions (Table A3).

We consider twenty variations of the model to ensure the results are not driven by particular parameter value or specification. Most of the changes in the ecological parameters and assumptions continue to result in ranchers receiving the greatest portion of the cost savings and produce an equity-efficiency tradeoff. The two starkest exceptions are the case where the wolf-livestock predation rate is low and the case with no predator interference in the functional response. When the wolf-livestock predation rate is sufficiently low, the major cost of wolf conservation (livestock depredation) is so low that states only want to engage in a small amount

of wolf hunting. With minimal hunting and livestock depredation, the welfare under the listed and delisted regimes are similar. In fact, states are actually worse off under delisting because they are responsible for a portion of the livestock compensation (\$2 million) whereas the federal government or an NGO is responsible for livestock compensation under the listed regime. The small welfare difference between the listed and delisted regimes minimizes the cost savings from delisting and the equity-efficiency tradeoff. Thus, our results may not persist if the economic impacts of the species are sufficiently small. This result is of little practical importance since the most policy-relevant and contentious delisting cases involve species with significant economic impacts.

No predator interference in the function response lessens the equity-efficiency tradeoff but does not eliminate it. This result is partly related to the fact that wolf conservation is concentrated in Wyoming in our efficient hunting strategy. With predator interference, wolves get in their own way and reduce predation risk so there is less predation costs and the efficient welfare is higher. Without predator interference, all the wolves in Wyoming lead to a high predation risk and lower welfare leading to welfare in the efficient hunting strategy that is closer to the welfare under the one-size-fits-all hunting strategy. The similarities in welfare between the efficient and one-size-fits-all hunting strategies minimizes the equity-efficiency tradeoff.

In addition, our results are robust to changes in the economic parameters and assumption. The equity-efficiency tradeoff ranges from 37 to 103 percent and ranchers consistently capture 88 to 136 percent of the cost savings from delisting.

Table A1. Calibrated Parameter Values

Parameter	Definition	Parameter Value	Calibration Method
<b>WELFARE AND MANAGEMENT</b>			
$\rho$	Social discount rate	0.03	Literature
$\alpha_E$	Weight on elk hunting (\$/elk harvested)	\$1,743	Literature
$\alpha_W$	Weight on wolf hunting (\$/wolf harvested)	\$28,249	Literature
$\sigma$	Fraction of wolf hunters that primarily hunt elk	1	
$\eta$	Proportion of compensation paid by states	0.5	
$\alpha_{tour}$	Weight on wolf-driven tourism (\$/wolf)	\$127,000	Literature
$h_E$	Hunting rate for elk	0.216	Data
$h_W$	Hunting rate for wolves	0.241	Data
$lc$	Lethal control rate for wolves	0.115	Data
<b>GROWTH, DEATH &amp; DISPERSAL</b>			
$K^i$	Elk carrying capacity	80,000/16	Literature
$r$	Intrinsic elk growth rate	0.28	Literature
$d$	Wolf natural death rate	1/7	Literature
$\varphi$	Numeric response fixed factor	0.019	Model
$\gamma$	Numeric response scale factor	0.034	Model
$\bar{\theta}_E^{i,j}$	Cell-specific elk residence rate*	0.99	
$\bar{\theta}_W^{i,j}$	Cell-specific wolf residence rate*	0.99	
<b>PREDATION</b>			
$m_E = m_L$	Predator interference parameter	0.825	Model
$\bar{p}_L$	Average livestock predation on outer cells	0.005	Literature
$a_E$	Attack rate for wolf-elk functional response	0.008	Model
$a_L$	Attack rate for wolf-cattle functional response	0.00123	Model
$\mu_E$	Handling rate for wolf-elk functional response	0.045	Literature
$\mu_L$	Handling rate for wolf-cattle functional response	0.016	Literature
$\beta'$	Vector of resource selection coefficients	vector of values	Literature
<b>POPULATIONS</b>			
$\bar{L}$	Average number of cattle on outer cells	15,033	Data
$\Sigma_i E^i$	Total number of elk on the GYE grid	30,000	Literature
$\Sigma_i W^i$	Total number of wolves on the GYE grid	321	Literature
$\Sigma_{i \in YNP} W^i$	Total number of wolves in YNP	97	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  $\delta_E^i$  and  $\delta_W^i$ .

Table A2. Sensitivity Analysis for Economically Optimal Management – Ecological Parameters and Assumptions

Change in Parameter Value or Functional Form	Overall delisting cost savings with 100 wolf minimum			Ranching: Cost savings from delisting	
	Efficient	OSFA	% Reduction	Total	% of Overall
Baseline specification	\$1.88	\$0.84	55%	\$2.40	128%
Higher wolf-livestock predation rate ( $\bar{p}_L = 0.01$ )	\$4.78	\$3.12	35%	\$5.37	102%
Lower wolf-livestock predation rate ( $\bar{p}_L = 0.001$ )	-\$2	-\$2	0%	\$0	0%
No predator interference in functional response ( $m_E = m_L = 0$ )	\$9.53	\$9.38	1.6%	\$9.38	93%
Differential residence rates ( $\bar{\theta}_W^{i,j} = 0.99$ ; $\bar{\theta}_E^{i,j} = 0.8$ )	\$2.17	\$1.14	48%	\$2.38	98%
Spatially homogeneous functional response ( $\beta' = 0$ )	\$1.60	\$0.83	48%	\$2.30	125%
Higher elk population ( $E = 33,000$ )	\$2.11	\$0.98	54%	\$2.39	101%
Lower elk population ( $E = 27,000$ )	\$1.15	\$0.64	44%	\$2.08	152%
Highly responsive dispersion ( $2 \times$ response to factors in eqs. (13) and (14))	\$1.82	\$0.87	52%	\$2.20	107%
Higher elk carrying capacity ( $K^i = 100,000/16$ )	\$2.36	\$1.14	52%	\$2.42	92%
Lower elk carrying capacity ( $K^i = 60,000/16$ )	\$1.28	\$0.56	56%	\$2.29	149%

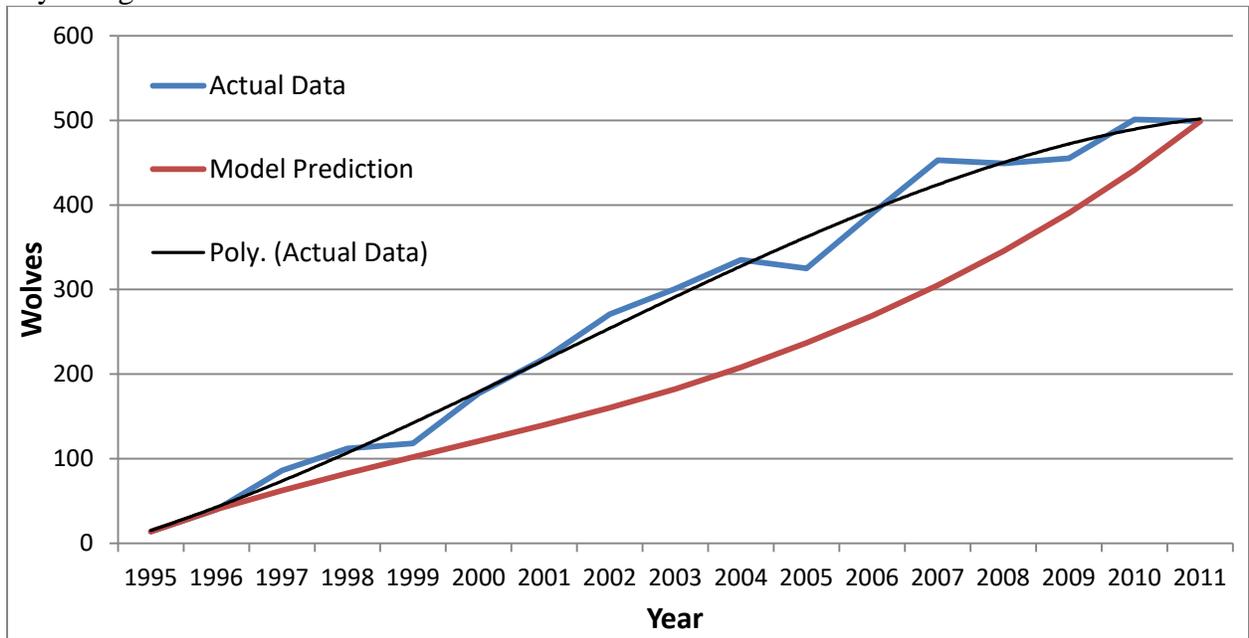
Notes. The baseline specification parameter values are shown in Table A1.

Table A3. Sensitivity Analysis for Economically Optimal Management – Economic Parameters and Assumptions

Change in Parameter Value or Functional Form	Overall delisting cost savings with 100 wolf minimum			Ranching: Cost savings from delisting	
	Efficient	OSFA	% Reduction	Total	% of Overall
Baseline specification	\$1.88	\$0.84	55%	\$2.40	128%
Higher minimum viable wolf population restrictions ( $\bar{W} = 125$ )	\$1.60	\$0.74	54%	\$2.17	136%
Lower minimum viable wolf population restrictions ( $\bar{W} = 75$ )	\$2.74	\$0.99	64%	\$2.41	88%
50% of wolf hunters separate group from elk hunters ( $\sigma = 0.5$ )	\$2.74	\$1.75	37%	\$2.41	88%
Zero non-use value for wolves ( $\alpha_{non-use} = \$0$ )	\$2.64	\$1.54	42%	\$2.41	91%
Higher indirect cost of wolf-livestock predation ( $20 \times$ direct costs)	\$5.86	\$3.44	41%	\$6.41	109%
Higher stocking rate for livestock (60 cows per section)	\$3.14	\$1.76	44%	\$3.71	118%
Lower stocking rate for livestock (20 cows per section)	\$0.80	-0.02	103%	\$0.89	111%
No lethal control of predating wolves ( $lc = 0$ )	\$1.83	\$0.88	52%	\$2.00	109%
Higher social discount rate ( $\rho = 0.05$ )	\$1.27	\$0.55	57%	\$1.65	130%
Lower social discount rate ( $\rho = 0.01$ )	\$2.97	\$1.33	55%	\$3.76	127%

Notes. The baseline specification parameter values are shown in Table A1.

Figure A1. Actual and Simulated Time Paths for Wolf Re-Introduction into Idaho, Montana, and Wyoming



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