Wolf and Elk Management in a Spatial Predator-Prey Ecosystem

Wolves in Yellowstone National Park chase after an elk in deep snow. (Dan Stahler/NPS)

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Background

- Wolf reintroduction into Yellowstone National Park (94’-95’).

![Graph showing population trends of GYA Wolf and Elk](image-url)
Background


• August 31, 2012: Gray wolves lost protection in Wyoming.

• September 23, 2014: Wyoming wolf protection restored.

• New era of state-level management complicated by competing transboundary ecosystem services (viewing and hunting).

• Provisioning of those services are sensitive to landscape heterogeneity and various forms of management.
Tourism attributed to YNP wolves generates $35 million expenditures annually in Wyoming (Duffield et al. 2006).

In 2005, 44% of YNP visitors listed wolves as their most preferred species to view. Approximately 30% of visitors saw a wolf (Duffield et al. 2008).

In 2005, 14% of YNP visitors listed elk as their most preferred species to view. Between 85-93% of visitors saw elk (Duffield et al. 2008).

Annually, hunting generates approximately $132 million of in-state expenditure (Wyoming Game and Fish, 2013).
Research questions:

1. How does the spatial allocation and quantity of a reintroduction shape subsequent predator-prey population dynamics and provisioning of ecosystem services?

2. What implications does a refuge (national park) have on harvest management?

3. How does landscape heterogeneity, through its effect on predation risk, affect management decisions?
A spatial wolf-elk-livestock model of the Greater Yellowstone Ecosystem (GYE).

- Spatial (4x4 grid) Lotka-Volterra model with logistic elk growth and a predator-dependent (RD) functional response.

- Wolves and elk are hunted outside of YNP.

- Wolves and elk disperse following density-dependent forces using queen movement.

- Livestock are continually restocked to maintain constant outer-cell population levels.

- Wolf-elk ratio-dependent functional response augmented by resource selection function.
A spatial *wolf-elk-livestock* model of the Greater Yellowstone Ecosystem (GYE).
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RSF Landscape effects on predation risk (from Kauffman et al. 2007):

- Elk density.
- Wolf density.
- Distance to streams and roads (Euclidean distance calculations).
- Type of land cover (grassland, shrubs, forest, etc.).
- Slope.
- Snowfall.
A spatial *wolf-elk-livestock* model of the Greater Yellowstone Ecosystem (GYE).


Panel B. Our Spatial Predator-Prey Model
A spatial *wolf-elk-livestock* model of the Greater Yellowstone Ecosystem (GYE).
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Dispersion following Queen Contiguity:

**Elk:**
- Move away from high predation and hunting risk.
- Move towards better forage.

**Wolves:**
- Move away from hunting risk & intraspecific strife.
- Move towards elk, livestock & high predation success cells.
Ecosystem net benefit surface and optimal management (50-year planning horizon)

Discounted net benefits, measured in millions of dollars, are maximized by choosing a fixed combination of elk and wolf hunting rates subject to maintaining minimum viable GYE populations of wolves and elk.
Optimal harvest: Elk harvest (15.8% annually)
Optimal harvest: Wolf harvest (40.8% annually)
Implications of model for policy recommendations

- Analyze direct and indirect effects of population shocks at varying scales (local & global).

- Allows us to analyze how competing ecosystem services (i.e. hunting and wildlife viewing) are influenced by management across space and time.

- Evaluate the effects of spatial heterogeneity (i.e. landscape features that form predation risk) and management jurisdictions (i.e. YNP as a refuge) on optimal wildlife management.
Model reference: elk and wolf laws of motion.

\[ E_{t,pre}^{(i,j)} = (1 + g_{E,t}^{(i,j)} - p_{E,t}^{(i,j)})E_{t}^{(i,j)} - h_{E,t}^{(i,j)} \]

\[ W_{t,pre}^{(i,j)} = (1 + g_{W,t}^{(i,j)} - d_{W})W_{t}^{(i,j)} - h_{W,t}^{(i,j)} \]

- \( pre = \) Pre-dispersal state variable
- \( g_{E,t}^{(i,j)} = \) Rate of growth of elk.
- \( g_{W,t}^{(i,j)} = \) Rate of growth of wolves.
- \( p_{E,t}^{(i,j)} = \) Predation rate of wolves on elk.
- \( d_{W} = \) Natural death rate of wolves.
- \( h_{E,t}^{(i,j)} = \) Elk harvest.
- \( h_{W,t}^{(i,j)} = \) Wolf harvest.
Model reference: elk and wolf growth rates.

\[ g_{E,t}^{(i,j)} = r_E \left( 1 - \frac{E_t^{(i,j)}}{K^{(i,j)}} \right) \]

\[ g_{W,t}^{(i,j)} = \gamma \left( p_{E,t}^{(i,j)} E_t^{(i,j)} + p_{L,t}^{(i,j)} L_t^{(i,j)} \right) / W_t^{(i,j)} \]

- \( g_{E,t}^{(i,j)} \) = Elk growth rate.
- \( g_{W,t}^{(i,j)} \) = Wolf growth rate.
- \( r_E \) = Elk intrinsic growth rate.
- \( K_E^{(i,j)} \) = Elk carrying capacity.
- \( \gamma \) = Scale parameter \((\gamma > 0)\).
- \( p_{E,t}^{(i,j)} \) = Predation rate of wolves on elk.
- \( p_{L,t}^{(i,j)} \) = Predation rate of wolves on livestock.
Model reference: elk and wolf predation risk.

\[ p_{E,t}^{(i,j)} = \frac{F_{E,t}^{(i,j)} W_t^{(i,j)}}{E_t^{(i,j)}} \]

\[ p_{L,t}^{(i,j)} = \frac{F_{L,t}^{(i,j)} W_t^{(i,j)}}{L_t^{(i,j)}} \]

- \( F_{E,t}^{(i,j)} \) = Wolf functional response to elk.
- \( F_{L,t}^{(i,j)} \) = Wolf functional response to livestock.

\[
F_{E,t}^{(i,j)} = \frac{aE_t^{(i,j)}}{\left(W_t^{(i,j)}\right)^m + ahE_t^{(i,j)}}
\]

\[
F_{L,t}^{(i,j)} = F_L^{(i,j)}
\]

- \(a\) = Attack rate.
- \(h\) = Handling rate.
- \(m\) = Degree of predator interference.
- \(F_L^{(i,j)}\) = Cell specific restocking constant.

\(m = 0.394\). When \(m = 0\) Holling type-II; \(m = 1\) ratio-dependent.

\[
RSF \left( x^{(i,j)} \right) = \text{Exp} \left[ \beta' x^{(i,j)} \right]
\]

\[
\tilde{F}_{E,t}^{(i,j)} = \frac{F_{E,t}^{(i,j)}}{RSF \left( x^{(i,j)} \right)}
\]

- \( RSF \) = Resource selection function.
- \( x^{(i,j)} \) = Vector of landscape covariates.
- \( \beta' \) = Vector of landscape risk coefficients.

When \( \beta' = 0 \), no landscaped-induced risk, collapses to traditional functional response.
Model reference: wolves combined law of motion.

\[
W_{t,pre}^{(i,j)} - W_{t}^{(i,j)} = \gamma \left[ \frac{aE_{t}^{(i,j)} \text{RSF} \left( x^{(i,j)} \right)}{\left( W_{t}^{(i,j)} \right)^{m}} + ahE_{t}^{(i,j)} \right] W_{t}^{(i,j)} + F_{L,t}^{(i,j)} W_{t}^{(i,j)} - d_{w} W_{t}^{(i,j)} - h_{W,t}^{(i,j)}
\]
Model reference: dispersal across cells.

\[
\theta_{\text{species},t}^{(i,j)\rightarrow(i,j)} = 1 - \exp(\tau_{\text{species}} - \delta_{\text{species}} \Lambda_{\text{species},t}^{(i,j)})
\]

- \(\theta_{\text{species},t}^{(i,j)\rightarrow(i,j)}\) = Probability an individual for a given species remains in the same cell.
- \(\tau_{\text{species}}\) = Fixed dispersal.
- \(\Lambda_{\text{species},t}^{(i,j)}\) = Variable dispersal.
- \(\delta_{\text{species}}\) = Relative strength of variable dispersal.
Model reference: variable dispersal of wolves and elk.

\[ \Lambda_{E,t}^{(i,j)} = -\hat{E}_{t,pre} - \hat{p}_{E,t} - \hat{h}_{E,t} \]

\[ \Lambda_{W,t}^{(i,j)} = \left( \begin{array}{c} \text{Repelled away from wolves and hunting} \\ -\hat{W}_{t,pre} - \hat{h}_{W,t} \end{array} \right) + \left( \begin{array}{c} \text{Attracted to livestock, elk and favorable predation.} \\ \hat{p}_{E,t} + \hat{L}_{t} + \hat{E}_{t,pre} \end{array} \right) \]
Model reference: parameters.

- $m = \text{predator interference} = 0.394$.
- $\delta_E = \text{elk variable dispersal} = 1$
- $\delta_W = \text{wolf variable dispersal} = 1$
- $h = 0.045 = \text{handling rate (Garrott et al. 2007)}$.
- $d_W = \frac{1}{14} = \text{natural death rate for wolves}$.
- $r_E = 0.28 = \text{intrinsic rate of growth for elk}$. 
Model reference: restrictions & calibrated parameters.

Restrictions:

- $\bar{p}_L = 0.01 =$ Average livestock predation rate.
- $\bar{\theta}_E = 0.99 =$ Portion of elk not migrating per period.
- $\bar{\theta}_W = 0.99 =$ Portion of wolves not migrating per period.
- $GYE = 30,000 =$ Number of elk in GYE.
- $GYW = 321 =$ Number of wolves in GYE.

Calibrated parameters:

- $\gamma = 0.035 =$ Scale parameter on wolf growth.
- $a = 0.002 =$ Attack rate.
- $\tau_E = -8.892 =$ Elk fixed-dispersal.
- $\tau_W = -4.456 =$ Wolf fixed-dispersal parameter.