The Economics of Species' Migration When Space is the Thing that Moves:

An Application to Wildlife Disease Management

"It never occurred to me to think of SPACE as the thing that was moving!", Montgomery Scott ("Scotty"), after examining an equation for transporting an object across space (*Star Trek* 2009).

Richard Horan
Department of Agricultural, Food, and Resource Economics
Michigan State University; horan@msu.edu

David Finnoff
Department of Economics
University of Wyoming; finoff@uwyo.edu

Charles Sims
Department of Economics and Baker School of Public Policy
University of Tennessee-Knoxville, cbsims@utk.edu

Selected paper for presentation at the 2024 AAEA Meetings in New Orleans, LA.

We gratefully acknowledge funding from USDA-NIFA under award #2020-67023-33260, Michigan AgBioResearch, and USDA Hatch Project #1026133. The views here are the authors'.

Introduction

Many species, including wildlife and aquatic species as well as invasive pests and pathogens, are mobile and distributed unevenly across space. For such species, spatially-targeted species management strategies will most likely be efficiency-enhancing as well as more in line with extant, spatially-explicit management efforts. Bioeconomic modeling can guide management, but special models remain rare even though they were introduced some time ago (e.g., Sanchirico and Wilen 1999, 2005; Brock and Xepapadeas 2010, 2008; Smith et al. 2009; Horan et al. 2008; Horan and Shortle 1999; Wilen 2007).

The complexity of spatial bioeconomic models might limit their use. Two types of spatial ecological models dominate the literature. The first and most common is a metapopulation model (Keeling and Rohani 2008; van den Driessche 2008), which can be applied in either discrete or continuous time bioeconomic settings (e.g., Sanchirico and Wilen 1999, 2005; Smith et al. 2009; Horan et al. 2008). These models divide the landscape into distinct, heterogeneous “patches” that might differ by land use or resource availability, proximity to other patches, economic considerations, and economic and ecological linkages between patches. Each patch contains a sub-population whose members can move across adjacent patches in any given time period, often in response to relative resource availability (e.g., Sanchirico and Wilen 1999, Fig. 1). Dynamic optimization in these models can be challenging due to each sub-population being modeled as a separate state variable and with controls also being patch specific, resulting in a large number of states and controls over which to optimize over time.

Reaction-diffusion models (Keeling and Rohani 2008; Murray 2002; Wu 2008; Levin and Segel 1985) represent the second major type of spatial model used in bioeconomic analysis (Brock and Xepapadeas 2010, 2008; Smith et al. 2009; Wilen 2007). Space is continuous so that there are no patches and therefore no patch-specific states and controls. Rather, there is a single state variable for each wildlife population (e.g., the total numbers of each interacting species such as elk and deer, or categories of species such as healthy elk and diseased elk) whose value is a function of both a continuous time variable and a continuous spatial location variable. The same is true of each control variable. The equations of motion are partial differential equations with a diffusion term that determines movement across space. The diffusion term is based on the flux of individuals at a particular time and location, where flux can be a function of animal densities and local resource characteristics. This type of specification is in contrast to aspatial models based on simpler ordinary differential equations that only depend on time. Additional complexities involve net benefits being integrated over both time and space, and changes in the co-state variables optimally described by partial differential equations (Brock and Xepapadeas 2010, 2008; Smith et al. 2009).

The spatial component of reaction-diffusion models can be set up in one or two (or more!) dimensions, with each dimension having its own variable (e.g., vertical, horizontal). Bioeconomic analyses typically (or perhaps always) simplify matters by using a single space variable, modeling movement as a traveling or outward-expanding wavefront either along a line or as the uniform distance from a central, initial point within a circle (Smith et al. 2009; Brock and Xepapadeas 2010, 2008). The use of a single space variable is somewhat limiting, and it generally results in symmetric outcomes on either side of the initial location (e.g., Brock and Xepapadeas 2010, Figs. 3-5).

Metapopulation and reaction-diffusion models are particularly well-suited to species' movements in which some, but typically not all, population members move across a heterogeneous landscape. This includes the process of colonization, such as the spread/migration or invasion of pests and pathogens, as well as basic spatial interactions (Murray 2002; Wu 2008; van den Driessche 2008; Keeling and Rohani 2008; Flemming 1975). But other processes exist, such as long-distance seasonal migrations. In a setting with diffusion, long-distance movement may depend on non-local conditions such as those expected near the end of a long-used migratory path. Whereas local diffusion in the models described above are based on Fick's law to derive a diffusion term based on a second-order partial derivative (Wu 2008), the diffusion term in longer-range movement also involves a fourth-order partial derivative (Murray 2002; Leven and Segel 1985; Cohen and Murray 1981).

We examine management of a seasonally migrating herd. Herd-based migration is a unidirectional movement of an entire population across the landscape at any point in time, in contrast to more general notions of diffusion in multiple directions. Seasonal migration has received little attention in the bioeconomic literature, although it is vital for many populations and may provide a number of ecosystem services or dis-services (Albers et al. 2023). This population movement is based on seasonal changes in resource availability across the landscape, conditioned on the various land uses affecting relative resource abundance and habitat connectivity along preferred migration routes. These features, while important in traditional spatial models, are arguably more important here since physical connectivity is vital and animals generally have some, perhaps strong, fidelity to a particular path (Albers et al. 2023; Kindlmann and Burel 2008).

The herd movement of our seasonally migrating population allows us to model space in a novel manner that simplifies the dynamics relative to metapopulation and reaction-diffusion models. Specifically, we model the population only as a function of time, and space—or location—to be time-dependent so as to essentially move below the population's feet. This time-dependent change in location effectively transports the population over space, reflecting a notion of relativity between populations and space.

Our locational variables change over time in response to changes in relative resource abundance and land use drivers of movement that change as the location changes, similar to the flux term in a reaction-diffusion model. This formulation is less complex than other approaches, for at least two reasons. First, it involves only one extra state variable (location) relative to non-spatial models, assuming migration moves along a fixed path as is the case with species having high fidelity; it involves two extra state variables—vertical and horizontal—for species exhibiting less fidelity to a particular path. Second, our model relies on ordinary rather than partial differential equations. The approach extends Wilen's (2007) example where a species invasion is modeled by a single state variable indicating the area of infestation. Our approach models the locational state in greater detail while linking it to space-dependent population growth and ecological and land use drivers of movement.

A model of migration

We begin by focusing on the migration process, initially assuming there is no disease present in the population. Denote a species' population at time t by $N(t)$, with each population member at the same location at time t.[1] The location may change at each point in time and so we model two locational variables: $x(t)$ and $y(t)$ are the population's current horizontal (east-west) and vertical (north-south) locations, respectively. The set of locations arising during a particular time interval Δt, $\{(x(t), y(t)), \dots, (x(t+\Delta t), y(t+\Delta t))\}$, represents the particular migration route taken during that interval. The population state $N(t)$ is only a function of time, but it is implicitly location specific since the population and location variables move together over time so that each date corresponds to a particular location.

Let population growth at time t at location $(x(t), y(t))$ be given by

(1) $$\frac{dN(t)}{dt} = G\big(N(t), Q(x(t), y(t), q(t), t)\big) - h(t)N(t)$$

where $h(t)$ is the harvest rate, $G\big(N(t), Q(x(t), y(t), q(t), t)\big)$ is a density-dependent growth function and $Q(x(t), y(t), q(t), t)$ is a measure of habitat quality that we define broadly as resource or net energy availability at location $(x(t), y(t))$. Net population growth $G(\cdot)$ is increasing in habitat quality $Q(\cdot)$, $G_Q(\cdot) > 0$, with $G(\cdot)$ taking the usual shape with respect to $N(t)$. Specifically, we scale $Q(\cdot)$ to be

[1] Assuming many individuals can reside on a single point is not inconsistent with reaction-diffusion models where the population level at time t and location x is denoted by the continuous function $N(t, x)$. For instance, Murray (2002, p.403) presents an invasion example where $N(0,0) = Q > 0$. In contrast, if only one animal could be at any particular location at a given time, then $N(t, x) \in \{0,1\}$ and discontinuities would abound.

in population units so that it acts as the carrying capacity such that $G\big(0, Q(\cdot)\big) = G\big(Q(\cdot), Q(\cdot)\big) = 0$. We also assume $G_{NN}\big(N(t), Q(\cdot)\big) < 0$.

Habitat quality can be viewed as a production function that depends explicitly on the current location states $x(t)$ and $y(t)$ since resource availability is location specific. Habitat quality also depends on the date, t, since seasonal changes continuously influence habitat quality at each location. Quality could be increasing or decreasing in t depending on the current date. This effect could be modeled using an oscillatory relationship, described in other contexts by Murray (2002).

Habitat quality is also affected by a human choice $q(t)$, with $Q_q(\cdot) \equiv \frac{\partial Q}{\partial q} > 0$ (subscripts henceforth denote partial derivatives). Since elk feedgrounds lie along the migration path and represent the most important anthropogenic impact on habitat quality, we define $q(t)$ as supplemental feeding and restrict $q(t)$ to be non-negative.[2] As with the population state $N(t)$, control $q(t)$ (and other control variables) is implicitly location specific since each date corresponds to a particular location. Moreover, the location variables in the production function $Q(\cdot)$ ensure $q(t)$'s impact is location specific. To avoid intermittent corner solutions, we assume $q(t)$ can be strictly positive at all times, but that the largest incentives for $q(t) > 0$ will occur at a few particular locations.

Directional state variable $i \in \{x, y\}$ change over time based on the per animal marginal energy effects of moving in direction i. There are two energy impacts associated with movement. The first is a change in energy availability $Q(\cdot)$. Specifically, the per animal marginal energy effects of moving in direction i is $\frac{Q_i(\cdot)}{N(t)}$.[3] The term $\frac{Q_i(\cdot)}{N(t)}$ indicates the change in relative population density when moving from one location to another. This change influences movement in a manner consistent with many

[2] Control $q(t)$ could be a vector but we model it to be a scalar reflecting aggregate anthropogenic impacts at the location. Also, although we are assuming $q(t) \geq 0$, a more general model would define $q(t) > 0$ to represent a net improvement in habitat quality and $q(t) < 0$ to have the opposite effect.

[3] Human impacts on energy, $q(t)$, will also differ over space but mathematically this effect occurs in response to changes in time—which coincides with locational changes. Since $q(t)$ is fixed at time t when movement occurs, animals only respond to marginal changes in $Q(\cdot)$ that result from explicit directional changes.

metapopulation models (e.g., Sanchirico and Wilen 1999), given our assumption that the entire stock always resides in a single location. However, this is a second energy impact affecting movement.

The second energy impact is the explicit energy cost of movement. Let $M^i\big(i(t), j(t), b^i(t), t\big)$ represent the energy costs per animal per unit of moving in direction $i \in \{x, y\}$ given the current location $(i(t), j(t))$. Specifically, the herd cost of moving $di(t)$ units during the interval dt is $M^i(\cdot)N(t)\frac{di(t)}{dt}$. Variable $m^i(t)$ represents investments/land uses that increase ($m^i(t) > 0$) or reduce ($m^i(t) < 0$) barriers to movement in that direction so that $M^i_m\big(i(t), j(t), m^i(t), t\big) > 0$, and with the marginal value of these investments depending on the specific location. For simplicity, we focus on hazing as a control to restrict movement in a particular direction so that $m^i(t) \geq 0$. There may also be natural barriers that change seasonally, as represented by t. The marginal values in the *x* and *y* directions, $M^i_i\big(i(t), j(t), m^i(t), t\big)$, represent how the marginal energy costs change as animals move in a particular direction. Note that our assumptions here and above assume any changes in resource availability and movement costs are continuous across the landscape.[4]

Given these energy impacts of animal movement, directional state variable $i \in \{x, y\}$ changes over time based on the per animal marginal energy effects of moving in direction i, $\frac{Q_i(\cdot)}{N(t)}$, less the per animal energy costs of moving $M^i(\cdot)\frac{di(t)}{dt}$. The general equation of motion for direction i is therefore $\frac{di(t)}{dt} = \frac{Q_i(\cdot)}{N(t)} - M^i(\cdot)\frac{di(t)}{dt}$. This equation can be solved for:

(2a) $$\frac{dx(t)}{dt} = \alpha^x \frac{Q_x(x(t), y(t), q(t), t)}{N(t)[1 + M^x(x(t), y(t), m^x(t), t)]},$$

(2b) $$\frac{dy(t)}{dt} = \alpha^y \frac{Q_y(x(t), y(t), q(t), t)}{N(t)[1 + M^y(x(t), y(t), m^y(t), t)]},$$

[4] In reality $Q(\cdot)$ and $M^i_i(\cdot)$ are probably piecewise continuous functions, with particular land uses defined over a specific spatial domain.

where α^i represent the adjustment speed in direction $i \in \{x, y\}$. That movement is based on net energy gradients, which is consistent with flux mechanisms modeled in standard diffusion models (Cohen and Murray 1981). We assume $Q_{qx} < 0$: larger investments at current location diminish the marginal value of moving. This assumption is consistent with elk feeding efforts being used to truncate the elk migration path to prevent elk from moving on to ranches where cattle are put at risk of infection. Finally, larger marginal movement costs reduce movement, as expected.

Equations (2a,b) follow standard evolutionary adaptive dynamics models (Rice 2004) in which species' characteristics adjust to maximize their net fitness. Here the relevant characteristic that adjusts over time is the species' location. If we view net energy as fitness, then a steady state occurs when net fitness is maximized, i.e., $Q_i(\cdot) = 0$. However, a steady state will not arise in our case for more than a short period because the non-autonomous nature of net energy availability across space will cause continued movement. This evolutionary perspective is consistent with Taylor and Taylor (1977) that animals move across space to maximize net fitness, although this maximization is not typically modeled to follow an evolutionary-type process as it is here.

Disease Model

Suppose an elk herd is infected with brucellosis. This population is divided into three sub-populations based on disease status, $N(t) = S(t) + I(t)$, where $S(t)$ is the healthy but susceptible population and $I(t)$ is the brucellosis-infected population. Recovery is assumed not possible, for simplicity and because it is widely believed that brucellosis-infected elk remain infectious after symptoms dissipate (NAS 2017).

We assume each sub-population (or health class) exhibits logistic growth along without vertical disease transmission (i.e., mother-to-offspring).[5] This means reproduction from one health class does

[5] Brucellosis is known to be passed from mother to offspring (NAS 2017), but the degree to which this occurs is uncertain and so the process is seldom modeled.

not contribute to the other. Susceptible elk have a spatially-independent fertility rate of g_S, whereas fertility of infected elk is $g_I < g_S$ due to abortions or other physiological reasons. All elk have a natural, spatially-independent mortality rate of δ. The intrinsic growth rate of susceptible elk is therefore $r_S \equiv g_S - \delta$, and the intrinsic growth rate of infected elk is $r_I \equiv g_I - \delta$. The harvest mortality rate $h(t)$ is the same for both sub-populations since infected animals generally cannot be identified prior to the kill, making harvests non-selective in disease status (e.g., as in Fenichel and Horan 2007).

Disease transmission is density-dependent (NAS 2017) and given by the commonly used mass-action function $\beta(x(t), y(t), q(t), t)S(t)I(t)$. Here $\beta(x(t), y(t), q(t), t)$ is a transmission rate function that represents the average number of contacts by infectious animals times the rate at which these contacts produce infection (Barlow 1995). The transmission rate function depends on the current location since some locations naturally congregate animals more than others, leading to more contacts. It is also increasing in feedground investments $q(t)$ (i.e., $\beta_q(x(t), y(t), q(t), t) > 0$) since feedgrounds encourage animal congregation. We also model the transmission rate to depend on time since most transmission occurs during the birthing period when aborted fetuses are present. Finally, there is no disease mortality other than that which implicitly reduces the fertility rate of infected animals.

Given this specification, the sub-population dynamics are given by

(3a) $$\dot{S}(t) = [r_S S(t) + r_I I(t)]\left(1 - \frac{N(t)}{Q(x(t),y(t),q(t),t)}\right) - \beta(x(t), y(t), q(t), t)S(t)I(t) - h(t)S(t)$$

(3b) $$\dot{I}(t) = \beta(x(t), y(t), q(t), t)S(t)I(t) - h(t)I(t).$$

It is generally useful to work with the variable $N(t)$ rather than $S(t)$. We therefore use (3a,b) along with the relation $N(t) = S(t) + I(t)$ to derive the system

(4a) $$\dot{N}(t) = [r_S N(t) - \delta I(t)]\left(1 - \frac{N(t)}{Q(x(t),y(t),q(t),t)}\right) - h(t)N(t)$$

(4b) $$\dot{I}(t) = \beta(x(t), y(t), q(t), t)[N(t) - I(t)]I(t) - h(t)I(t).$$

An important concept in disease ecology is the host-density threshold, denoted $\widehat{N}(t)$. This is the host population level below which the infection begins to dissipate, i.e., $\dot{I}(t) < 0$ for $N(t) < \widehat{N}(t)$, due to the population density being small enough that too few infectious contacts are being made. The host-density population can be derived by setting $\dot{I}(t) = 0$ in (4b) and solving for $N(t)$ to yield

$$(5) \qquad \widehat{N}(t) \equiv \widehat{N}(I(t), x(t), y(t), q(t), h(t), t) \equiv I(t) + \frac{h(t)}{\beta(x(t), y(t), q(t), t)}.$$

This threshold is endogenous: it depends on the current infection level, the current location states, and the current controls $q(t)$ and $h(t)$. With no harvesting ($h(t) = 0$), then $\widehat{N}(t) = I(t)$ and the infected population increases whenever $N(t) > I(t)$, or alternatively when $S(t) > 0$. The threshold is increased when harvests occur: harvesting makes it more likely that the infected population will decline. Thresholds for pathogen invasion, when $I(t) = 0$, are often the focus of disease ecology. In a single-species susceptible-infected (SI) model such as ours, invasion thresholds are defined as the total mortality rate divided by the infectious contact rate (Anderson and May 1986). This is consistent with the second right-hand-side (RHS) term in our threshold definition (5), except that our threshold varies by location.

We can write (4b) in terms of threshold $\widehat{N}(\cdot)$:

$$(4c) \qquad \dot{I}(t) = \alpha^{I}(x(t), y(t), q(t), t)\big[N(t) - \widehat{N}(I(t), x(t), y(t), q(t), h(t), t)\big].$$

Here the force of infection, denote $\alpha^{I}(x(t), y(t), q(t), t) \equiv \beta(x(t), y(t), q(t), t)I(t)$, is the speed of adjustment. We adopt equations (4a.c) along with the spatial equations (2) to define our ecological dynamics. In what follows, we simplify matters by suppressing the time variable notation t from the state and control variables. We do, however, leave the time notation in functions where t arises as a separate argument.

Economic Model

Denote the total benefits from elk harvests by the increasing, concave function $B(hN)$, which is uniform across space.[6] Harvest costs, which are also spatially uniform, are assumed independent of the elk population since elk move in large herds. Specifically, costs are cqN, where $c > 0$ is a parameter representing the unit cost of hunting (e.g., see Conrad and Clark's 1997 model of schooling fisheries).

Damages from cattle infection are $D(x, y, I)$, which is increasing and convex in I. We assume $D(0,0, I) = 0$, where location (0,0) is the mountaintop and the furthest point from the cattle ranches. We model damages as continuous in the location variables, with $D_x(0,0, I) \geq 0$ and $D_y(0,0, I) \geq 0$. At other locations, the partials with respect to the location variables depend on the current location. Note that damages do not depend directly on feeding or hazing, as they might in aspatial models (e.g., Horan and Wolf 2005; Fenichel and Horan 2007). However, since feeding and hazing occur over time at different locations, these controls do ultimately affect damages.

Denote supplemental feeding costs by wq, where w is the per-unit cost of feeding. Hazing costs are given by $0.5v\Delta^2$, with $v > 0$ being a hazing cost parameter and $\Delta = \sqrt{(m^x)^2 + (m^y)^2}$ being the hazing distance. The cost parameters w and v do not vary spatially, but feeding and hazing activities will vary spatially (since choices at any time t coincide with the spatial location at time t) in response to spatial incentives generated by the ecological dynamics and the spatially-explicit damage function. The final economic consideration is the discount rate, which we denote by ρ.

An economically efficient management strategy then solves the problem

(5) $$\max_{h,q,m^x,m^y} \int_0^\infty \left[B(hN) - chN - D(x, y, I) - wq - 0.5v[(m^x)^2 + (m^y)^2]\right] e^{-\rho t} dt$$

$$s.t. (2), (4), \quad N(0) = N_0, I(0) = I_0, x(0) = x_0, y(0) = y_0.$$

The current value Hamiltonian for problem (5) is

[6] Although animals' disease status is unknown during the hunting stage (making hunting non-selective with respect to disease status), we assume disease status is verified after the animal is killed via either close direct observation or testing. But even with this information, the willingness to pay for brucellosis-infected elk is the same as for healthy animals since humans are generally not at risk from brucellosis.

(6) $$H = B(hN) - chN - D(x,y,I) - wq - 0.5v[(m^x)^2 + (m^y)^2]$$
$$+\lambda_N \left[[r_S N - \delta I] \left(1 - \frac{N}{Q(x,y,q,t)}\right) - hN \right]$$
$$+\lambda_I \left[\alpha^I(x,y,q,t)\left[N - \widehat{N}(I,x,y,q,h,t)\right] \right] + \lambda_x \left[\alpha^x \frac{Q_x(x,y,q,t)}{N[1+M^x(x,y,m^x,t)]} \right] + \lambda_y \left[\alpha^y \frac{Q_y(x,y,q,t)}{N[1+M^y(x,y,m^y,t)]} \right]$$

where λ_j is the co-state variable associated with state variable $j \in \{N, I, x, y\}$ (co-states are functions of time, with subscripts being indices rather than partial derivatives). We expect $\lambda_I < 0$ since infected elk impose social costs. The positive hunting value of elk means co-state λ_N is likely positive, unless a sufficient number of the total population are infected.

The first order condition with respect to the harvest rate is

(7a) $$\frac{\partial H}{\partial h} = 0 \;\; \rightarrow B_h(hN) - c = \lambda_N + \lambda_I \underbrace{\alpha^I(x,y,q,t)\widehat{N}_h(I,x,y,q,h,t)/N}_{=I/N}$$

where the second equation has been derived after applying a bit of algebra to the condition $\frac{\partial H}{\partial h} = 0$, including dividing by N. The left-hand side (LHS) of this equation is the current-period marginal net benefits of harvesting. The right-hand side (RHS) is the marginal net intertemporal costs of harvesting, which is equivalently the foregone marginal intertemporal net benefits of conservation, in terms of the impacts to elk dynamics affecting future periods. We focus on the marginal benefit interpretation as it is more intuitive. The non-selectivity of hunting means there are two dynamic impacts: one for the overall population and one for the infected population. We expect the first RHS impact to have a positive marginal value, i.e., $\lambda_N > 0$.

The second RHS term indicates the marginal value with respect to the infected population depends on the marginal impact of hunting on the threshold $\widehat{N}(\cdot)$. From (5), harvesting has a positive marginal impact on the threshold, i.e., $\widehat{N}_h(\cdot) > 0$. This is costly since a larger threshold means the pathogen is more likely to spread for any given a particular population level N.

The net effect of the RHS terms is ambiguous. If the marginal pathogen effect is small, then conservation is more valuable and this implies the LHS is positive under an optimal strategy. The opposite is true if the marginal pathogen effect is large, as society would find it optimal to incur current-period costs (i.e., a negative LHS term) to reduce the population and therefore infectious contacts. The first order condition with respect to feeding is

(7b) $$\frac{\partial H}{\partial q} = 0 \rightarrow \; w = \lambda_N \left[[r_S N - \delta I] \frac{N}{Q(x,y,q,t)^2} Q_q(x,y,q,t) \right]$$

$$+\lambda_I \underbrace{\left[\alpha_q^I(x,y,q,t)\left[N - \widehat{N}(I,x,y,q,h,t)\right] + \alpha^I(x,y,q,t)\left[-\widehat{N}_q(I,x,y,q,h,t)\right] \right]}_{=\beta_q(x,y,q,t)I[N-I]}$$

$$+\lambda_x \frac{\alpha^x}{N[1+M^x(x,y,m^x,t)]} Q_{xq}(x,y,q,t) + \lambda_y \frac{\alpha^y}{N[1+M^y(x,y,m^y,t)]} Q_{yq}(x,y,q,t).$$

The LHS of the second equation is the current-period marginal cost of feeding. The RHS is the marginal net intertemporal benefit of feeding in terms of the impacts to elk dynamics. The non-selectivity of feeding means there are two aspatial dynamic impacts—one for the overall population and one for the infected population—as well as two spatial impacts.

We expect the first RHS impact to have a positive marginal value since feeding enhances habitat quality ($Q_q > 0$) and therefore elk productivity, with the total elk population generally being valuable ($\lambda_N > 0$). The second RHS term indicates that feeding affects both the speed of adjustment and the threshold. The marginal speed of adjustment is positive ($\alpha_q(\cdot) = \beta_q(\cdot)I$), but whether this generates a cost or a benefit depends on whether the infection level is increasing ($N > \widehat{N}(\cdot)$, a cost) or decreasing ($N < \widehat{N}(\cdot)$, a benefit). The threshold impact of feeding is negative ($-\widehat{N}_q(I,x,y,q,h,t) = -\frac{h}{\beta(x,y,q,t)^2}\beta_q$), which is a cost because a reduction in $\widehat{N}(\cdot)$ means the infection level is more likely to increase for any given N. The net effect is that the sign of the second RHS term is negative since $\beta_q(x,y,q,t) > 0$, $N > I$, and $\lambda_I < 0$. This means feeding has a costly infection impact.

The last two RHS terms represent the marginal impact of feeding on elk movement. Here $\alpha^i \frac{Q_{xq}(x,y,q,t)}{N[1+M^x(x,y,m^x,t)]} < 0$ for $i \in \{x, y\}$, meaning that feeding reduces movement in either direction. Whether this imposes costs associated with movement impacts in a particular direction $i \in \{x, y\}$ depends on the sign of λ_i. If $\lambda_i > 0$ then movement in direction i would be beneficial but feeding reduces that movement, imposing a cost. The opposite is true when $\lambda_i < 0$. As mentioned earlier, feeding does affect new cattle infections by truncating the migration path. The damage impacts do not arise explicitly in condition (7b), but they are implicit via the last two terms—specifically through the sign and magnitude of λ_i.

Finally, consider the first order condition for hazing animals in direction i, m^i. The condition for an interior solution is

(7c) $$\frac{\partial H}{\partial m^i} = 0 \rightarrow \ vm^i = \lambda_i \frac{\alpha^i}{N\left[1+M^i(i,j,m^i,t)\right]^2}\left[-M_m^i\left(i,j,m^i,t\right)Q_i(i,j,q,t)\right].$$

The LHS of the second equation in (7c) is the marginal cost of hazing. The RHS is the marginal net intertemporal benefit of hazing in direction i, in terms of the impacts to elk movement dynamics. The RHS must be positive for any hazing investments in direction i to be optimal. For instance, λ_i the term $M_m^i\left(i,j,m^i,t\right) \equiv \frac{dM^i}{dm^i}$ is positive as hazing makes movement in direction $i \in \{x, y\}$ more costly. If $Q_i(i,j,q,t) > 0$ (i.e., movement leads to better habitat quality) then $-M_m^i\left(i,j,m^i,t\right)Q_i(i,j,q,t) < 0$: hazing reduces access to better habitat quality. Other things equal, this is impact beneficial if $\lambda_i < 0$, i.e., if movement in direction i is socially costly such as when movement increases transmission risks among elk or from elk to cattle.

Four adjoint conditions, one for each state variable, are also necessary for the optimal solution. The first adjoint condition is for the state variable N:

(8a) $$\rho = \left[r_s\left(1 - \frac{2N}{Q(x,y,q,t)}\right) - \delta\frac{I}{Q(x,y,q,t)}\right] - \frac{-\lambda_I}{\lambda_N}\alpha^I(x,y,q,t)$$

$$-\frac{\lambda_x}{\lambda_N}\left[\alpha^x \frac{Q_x(x,y,q,t)}{N^2[1+M^x(x,y,m^x,t)]}\right]-\frac{\lambda_y}{\lambda_N}\left[\alpha^y \frac{Q_y(x,y,q,t)}{N^2[1+M^y(x,y,m^y,t)]}\right]+\frac{\dot{\lambda}_N}{\lambda_N}.$$

The LHS of (8a) is the rate of return to outside investments and therefore serves as the opportunity cost of conservation (i.e., forgoing harvest-related benefits). The RHS is the return to conservation. The first RHS term is the marginal reproduction from having more elk. This return is reduced by elk abortions. The second RHS term is an infection cost (since $-\lambda_I > 0$), reducing the return to conservation, as having more elk increases infectious contacts and therefore the chance the disease spreads at the rate of $\alpha^I(x,y,q,t)$.

The third and fourth RHS terms are the rate of return impacts of a larger elk population on elk movement. A larger population reduces marginal habitat quality per elk, reducing movement. This is costly, reducing the rate of return, when movement is valuable ($\lambda_x > 0$) and increases access to better habitat quality ($Q_x(x,y,q,t) > 0$).[7] Otherwise the return is negative. The final RHS term is the capital gain or loss from having more elk: the proportional rate at which the marginal value of elk increases, making conservation more valuable, or declines to make conservation less valuable.

The adjoint condition associated with infection is

(8b) $$\rho = \frac{D_I}{-\lambda_I} + \frac{\delta\left(1-\frac{N}{Q(x,y,q,t)}\right)}{-\lambda_I} + \frac{\alpha^I(x,y,q,t)\hat{N}_I(I,x,y,q,h,t)}{-\lambda_I} - \frac{\dot{\lambda}_I}{-\lambda_I}$$

Here the LHS is the opportunity cost of reallocating resources to disease control. The RHS is the return from disease control. This return reflects the marginal costs of increased disease, and so the return to disease control represents an avoidance of those costs. The first RHS term is the return from avoiding the marginal damages from infection. The second RHS term is the return from avoiding infection-related abortions. The third RHS term simply equals $\frac{\alpha^I(x,y,q,t)}{-\lambda_I} > 0$, which is the return from preventing an increase in the threshold (which would make spread of the disease more likely). The final term is the

[7] Mathematically the return is also reduced when movement is not valuable ($\lambda_x < 0$) and would decrease access to better habitat quality ($Q_x(x,y,q,t) < 0$). However, in a given time period, it does not make sense that λ_x and Q_x

capital gain or loss from having more infections. For instance, since $\lambda_I < 0$, disease control yields benefits, increasing the return, when leaving a larger infected stock causes λ_I to fall ($\dot{\lambda}_I < 0$) and increase the marginal cost of infection.

The final adjoint conditions are associated with space. We present the condition for x, noting that the condition for y is symmetric.

(8c) $$\rho = \frac{\lambda_N}{\lambda_x}[r_S N - \delta I]\left(\frac{N}{Q(x,y,q,t)^2} Q_x(x,y,q,t)\right) + \frac{-\lambda_I}{\lambda_x}\widehat{N}_x(I,x,y,q,h,t)$$
$$+ \sum_{i\in\{x,y\}} \frac{\lambda_i}{\lambda_x}\left[\alpha^x \frac{[1+M^x(x,y,m^x,t)]Q_{xx}(x,y,q,t) - M_x^x(x,y,m^x,t)Q_x(x,y,q,t)}{N[1+M^x(x,y,m^x,t)]^2}\right] + \frac{\dot{\lambda}_x}{\lambda_x}$$

The LHS of (8c) is the rate of return from elk moving in the x direction. Here it is not possible to sign all of the terms since the benefits of moving are most likely to be seasonal and therefore time dependent. However, we do see that the return depends on the habitat quality impacts of movement on reproduction, the disease threshold impacts of movement, and the net marginal drivers of movement (i.e., habitat quality and movement cost impacts), and a capital gain or loss term.

Numerical Example

The next step in our analysis is to develop a numerical example. This is being developed from the parameters and resource selection functions (which govern animal movement) used in Maloney et al. 2020).

References

Albers, H.J., K. Kroetz, C. Sims, A.W. Ando, D. Finnoff, R.D. Horan, R. Liu, E. Nelson, and J. Merkle (2023). Where, When, What, and Which? Using Characteristics of Migratory Species to Inform Conservation Policy Questions. *Review of Environmental Economics and Policy*. 17: 111-131.

Anderson, R.M. and R.M. May 1986. The Invasion, Persistence, and Spread of Infectious Diseases within Animal and Plant Communities. *Philosophical Transactions of the Royal Society of London B.* 314: 533-570.

Barlow, N.D. (1995). Critical Evaluation of Wildlife Disease Models. In *Ecology of Infectious Diseases in Natural Populations* (B.T. Grenfell and A.P. Dobson, eds.). Cambridge University Press: Cambridge. U.K.

Brock, W. and A. Xepapadeas (2010). Pattern Formation, Spatial Externalities and Regulation in Coupled Economic-Ecological Systems. *Journal of Environmental Economics and Management.* 59: 149-164.

Brock, W. and A. Xepapadeas (2008). Diffusion-Induced Instability and Pattern Formation in Infinite Horizon Recursive Optimal Control. *Journal of Economic Dynamics & Control*. 32: 2745-2787.

Cohen, D.S. and J.D. Murray (1981). A Generalized Diffusion Model for Growth and Dispersal in a Population. *Journal of Mathematical Biology* 12: 237-249.

Conrad, J.W. and C.W. Clark. (1997). *Natural Resource Economics: Notes and Problems,* New York: Cambridge University Press.

Fenichel, E.P. and R.D. Horan (2007). Jointly-Determined Ecological Thresholds and Economic Tradeoffs in Wildlife Disease Management. *Natural Resource Modeling* 20: 511-547.
Flemming 1975

Horan, R.D., J.F. Shogren, and B. Gramig (2008). Wildlife Conservation Payments to Address Habitat Fragmentation and Disease Risks. *Environment and Development Economics* 13: 415-439.

Horan, R.D., and J.S. Shortle (1999). Optimal Management of Multiple Renewable Resource Stocks: An Application to Minke Whales. *Environmental and Resource Economics* 13: 435-458.

Horan, R.D. and C.A. Wolf (2005). The Economics of Managing Infectious Wildlife Disease. *American Journal of Agricultural Economics* 87: 537-551.

Keeling, M.J., and P. Rohani (2008). *Modeling Infectious Diseases in Humans and Animals*. Princeton University Press: Princeton.

Kindlmann, P. and F. Burel (2008). Connectivity Measures: A Review. *Landscape Ecology* 23: 879-890.

Levin, S.A. and L.A. Segel (1985). Pattern Generation in Space and Aspect. *SIAM Review* 27: 45-67.

Maloney, M., J. Merkle, D. Aadland, D. Peck, R.D. Horan, K. Monteith, T. Winslow, J. Logan, D. Finnoff; C. Sims, and B. Schumaker. 2020. Chronic Wasting Disease Undermines Efforts to Control the Spread of Brucellosis in the Greater Yellowstone Ecosystem. *Ecological Applications*, 30(6): e02129.

Murray, J.D. 2002. *Mathematical Biology I: An Introduction*. Springer: New York.

National Academies of Sciences, Engineering, and Medicine. 2017. *Revisiting Brucellosis in the Greater Yellowstone Area*. Washington, DC: The National Academies Press.

Rice, S.H. (2004). *Evolutionary Theory: Mathematical and Conceptual Foundations*. Sunderland, MD: Sinauer.

Sanchirico, J.N. and J.E. Wilen (2005). Optimal Spatial Management of Renewable Resources: Matching Policy Scope to Ecosystem Scale. *Journal of Environmental Economics and Management* 50: 23-46.

Sanchirico, J.N. and J.E. Wilen (1999). Bioeconomics of Spatial Exploitation in a Patchy Environment. *Journal of Environmental Economics and Management*. 37: 129-150.

Smith, M.D., J.N. Sanchirico, J.E. Wilen. (2009). The Economics of Spatial-Dynamic Processes: Applications to Renewable Resources. *Journal of Environmental Economics and Management* 57: 104-121.

Taylor, L.R. and R.A.J. Taylor (1977). Aggregation, Migration and Population Mechanics. *Nature* 265:415–421.

van den Driessche, P. (2008). Spatial Structure: Patch Models. In *Mathematical Epidemiology* (F. Brauer, P. van den Driessche, and J. Wu, eds.). Springer: Verlag.

Wilen, J.E. (2007). Economics of Spatial-Dynamic Processes. *American Journal of Agricultural Economics* 89: 1134-1144.

Wu, J. (2008). Spatial Structure: Partial Differential Equations Models. In *Mathematical Epidemiology* (F. Brauer, P. van den Driessche, and J. Wu, eds.). Springer: Verlag.