Beaver Dispersal

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July 18, 2015

1 Introduction

The beaver is the second largest rodent in the world, and the largest rodent in North America. Adult North American beavers weigh between 40 and 50 lbs on average, and have a total length of about 48 inches. These animals are specially adapted to depend on trees (timber) for survival. They eat bark, twigs, and tree leaves as well as herbaceous and aquatic vegetation. They prefer the tender bark at the tops of trees, and will carefully fell trees to access this choice food. Beavers also use logs, branches, and sticks to build the dams to create pond habitats and the lodges in which they live (Muller-Schwarze and Sun, 2003).

Beavers can have many positive effects on the area in which they live. Beaver ponds create habitat for many different species, and improve water quality in turbid waters. Adjacent land used for livestock will be more productive, and if beaver ponds and wetland areas are drained, the soil remaining will be very fertile (Huffaker et al., 1999, Muller-Schwarze and Sun, 2003).

Despite these benefits, beavers are often considered to be a nuisance, particularly on lands involved in the logging and timber industry, where both damage to trees and flooding are a problem. Though this may seem to be a trivial concern, beavers can in fact have a huge economic impact on an area. Estimated losses due to beavers include $2.4 billion in Mississippi from 1975 to 1985 , and $287,050 annually in a 6,296.4 sq. mi. area in central New York (Huffaker et al., 1992). Many land owners employ trapping to deal with the problem, but an effective solution is not as simple as trapping as many beavers as possible. Because it is nearly impossible to trap every single beaver, trapping in only particular areas creates a population vacuum, which beavers from neighboring properties continually migrate to (Huffaker et al., 1999). Trapping strategies must consider this, or else new beavers will simply migrate to the area in the future.

The social fence hypothesis offers an explanation of how small mammals move between adjacent land areas. Hestbeck (1982, 1988) and Stenseth (1986, 1988) have developed several mathematical formulations for the social fence hypothesis to describe the dynamics between two neighboring rodent populations. Stenseth's models describe two areas of land, an optimal and suboptimal patch, and their corresponding rodent populations. The population of rodents first flourishes in the optimal patch and then as the population density increases and social pressures increase, individuals disperse to the suboptimal patch. As the population in either area reaches the carrying capacity of the area, depletion of resources along with seasonal change can drive a population crash with limited survival on the optimal patch and no survival on the suboptimal patch, resetting the rodent population cycle.

Further, the "social fence" is the imagined barrier that exists between the two populations due to competition for resources. When both populations are high (relative to their respective carrying capacities), competition between groups is high, and little or no migration occurs. When one of the areas (the suboptimal patch initially) has a low population density, competition for resources within the high population area is greater than competition between the areas, so the social fence opens and migration can occur (Hestbeck, 1982, 1988).

In order to understand how two beaver populations interact under a nuisance beaver control program, Huffaker et al. (1992, 1999) use a modified version of the social fence hypothesis formulated by Stenseth (1988). Huffaker simplifies Stenseth's model with the assumption that both areas are equal in quality to beavers, and specifies that one of the areas is of economic value to humans. Areas that are valuable to humans may be residential or commercial property that are prone to damage by beavers. In this area, beavers are trapped to decrease property damage, opening the social fence barrier for new beavers to migrate into the trapped area.

Bhat, Huffaker and Lenhart also explore management scenarios in which two landowners both have an interest in controlling beaver but may or may not cooperate in their management efforts, and in which an association of interested landowners find greatest advantage in appointing a single manager Bhat et al. (1996). The two parcel model explored in this paper and the single manager scenario are both optimal control problems in which the objective is to minimize the combined cost of trapping and tree damage.

To address the question of what is the best trapping method to accomplish this objective, we consider both the population dynamics of neighboring beaver populations and the economic costs and benefits of the situation. We follow the paper, "Diffusing Nuisance-Beaver Populations," published by R. G. Huffaker, M. G. Bhat, and S. M. Lenhart in 1992, in which they use the social fence model developed by Hestbeck (1982, 1988) and Stenseth (1986, 1988) to describe cycles in neighboring populations of rodents, and combine it with the fisheries harvesting optimization model by Mesterton-Gibbons (1988) to create a bioeconomic model of beaver populations in a nuisance beaver control situation.

2 Methods

The following tables list the state variables and parameters used in the Huffaker et al. model. The abbreviations used are *hd* = head, *yr* = year, and *mi* = mile.

Table 1: Table of parameters calculated from data by Huffaker et al. (1992)

Parameter (Units)	Description	Value
K_X $(\frac{hd}{mi^2})$	carrying capacity of area X	1.107
K_Y $(\frac{hd}{mi^2})$	carrying capacity of area Y	0.9963
R_X $(\frac{1}{yr})$	maximum net growth of X	0.335
R_Y $(\frac{1}{yr})$	maximum net growth of Y	0.3015
M $\left(\frac{hd}{\frac{mi^2}{yr}}\right)$	marginal dispersive rate with respect to $\frac{X}{K_X}$	0.3473
c $\left(\frac{\$hd}{(mi^2)^2}\right)$	trapping cost parameter	2.558
d_1 $\left(\frac{\$}{\frac{mi^2}{yr}}\right)$	maximum annual timber damage	47.87
d_2 $(\frac{hd}{mi^2})$	density causing 95% of max. annual damage	0.79
δ $(\frac{1}{yr})$	annual discount rate	0.056

Table 2: Table of state and control variables paraphrased from Huffaker et al. (1992)

Variable (Units)	Description
X $(\frac{hd}{mi^2})$	population density of controlled area (state)
Y $(\frac{hd}{mi^2})$	population density of uncontrolled area (state)
P $(\frac{1}{yr})$	per capita trapping rate of X at time t (control)

Baseline values of the parameters were collected by Huffaker et al. using data from various Wildlife Management Regions of the New York State Department of Environmental Conservation (Huffaker et al., 1992).

2.1 The Social Fence Model

To show how the two neighboring beaver populations interact, Huffaker et al. (1999) first describe the social fence model without trapping. For two beaver population densities (hd/mi^2) X and Y, the equations

$$\dot{X} = F_0(X)X - F_1(X,Y) \tag{1}$$

$$\dot{Y} = F_2(Y)Y + F_1(X,Y) \tag{2}$$

represent the annual total change in population density $(hd/mi^2/yr)$. The functions $F_0(X)$ and $F_2(Y)$ describe the proportional annual growth rates $(1/yr)$, and $F_1(X,Y)$ describes the dispersion flux. Thus the annual rate of change is equal to the difference between growth and dispersion. The proportional annual growth rates are given by:

$$F_0(X) = R_X(1 - X/K_X) \tag{3}$$

$$F_2(X) = R_Y(1 - Y/K_X) \tag{4}$$

with the parameters as described in Table 1.

If dispersion is set to zero, X and Y do not interact and $\dot{X}$ and $\dot{Y}$ reduce to a logistic growth model. Both populations will simply approach their carrying capacities, which are stable equilibrium points of the system.

The addition of the dispersion flux term $F_1(X,Y)$, allows populations to interact and migrate between areas. The dispersion flux term is given by:

$$F_1(X,Y) = M\left(\frac{X}{K_X} - \frac{Y}{K_Y}\right) \tag{5}$$

where M is a constant rate with units (hd/mi^2) and K_X and K_Y are the carrying capacities as described in Table 1.

2.2 Social Fence with Trapping

The social fence hypothesis as described above explains how two populations may approach their carrying capacities when individuals are allowed to disperse to an area that is less proportionately dense. Huffaker et al. (1999) add a trapping term to $\dot{X}$ that represents the rate of removal of beavers from the controlled area. Adding the trapping term results in the following system:

$$\dot{X} = F_0(X)X - F_1(X,Y) - PX \tag{6}$$

$$\dot{Y} = F_2(Y)Y + F_1(X,Y) \tag{7}$$

Here, P represents the annual per capita trapping rate of X $(1/yr)$. PX then gives the total number of beavers trapped each year.

2.3 Bioeconomic Model

Huffaker et al. (1992) use the social fence model and draw from the process of solving an optimal control problem used by Mesterton-Gibbons (1988) to develop their nuisance beaver control model.

To build the model, let

$$D(X) = \frac{d_1 X}{X + (0.052632)d_2} \tag{8}$$

be beaver inflicted damage in units of (dollars/square mile/year) and

$$C(X) = \frac{c}{X^2} \tag{9}$$

be the unit trapping cost, so

$$C(X)PX = \frac{c}{X^2}PX = \frac{cP}{X} \tag{10}$$

Note that $D(X)$ asymptotically approaches the maximum damage d_1 as X increases, representing increasing damage with increasing beaver population density. Note also that $C(X) \to \infty$ as $X \to 0$, representing increasing trapping effort and costs when beaver population density is low. When beaver density is high, or $X \to \infty$, then $C(X) \to 0$. This model does not allow for complete elimination of beavers in an area bordered by uncontrolled populations.

The model seeks to minimize the combined cost of damages and trapping $(D(X) + C(X)PX)$ of nuisance beavers to a landowner. The total cost over time is approximated by multiplying by $e^{-\delta t}$,

using continuous compounding at a discount rate to represent the cost over time to a landowner in present dollars. The total cost is found by integrating this function with respect to time. Since the function to be integrated does not depend on static values, but on component X of the dynamic system, this is not a simple integration, but an optimal control problem:

$$\text{Min}J(X,P) = \int_0^\infty e^{-\delta t}[D(X) + C(X)PX]dt \tag{11}$$

subject to the dynamic system developed in Section 1.2,

$$\dot{X} = F_0(X)X - F_1(X,Y) - PX \tag{12}$$

$$\dot{Y} = F_2(Y)Y - F_1(X,Y) \tag{13}$$

where

$$X(0) = X_0 \quad Y(0) = Y_0 \tag{14}$$

$$P^{min} \leq P \leq P^{max} \tag{15}$$

Solving the optimal control problems relies on Pontryagin's maximum principle (Pontryagin et al., 1962), which has been widely applied to economic questions (Dorfman, 1969) including harvest allocation (Conrad and Clark, 1987, Kaitala and Pohjola, 1988, Mesterton-Gibbons, 1988).

2.4 Non-Dimensionalization

Finally, Huffaker et al. (1992) scale all of the variables to obtain a non-dimensionalized model and simplify the analysis. The dimensionless variables and parameters are defined as follows:

Table 3: Table of dimensionless functions, variables and parameters

Functions	Variables	Parameters
$f_0(x) = r_x(1-x)$	$x = \frac{X}{K_X}$	$r_x = \frac{R_X}{\delta}$
$f_1(x,y) = m(x-y)$	$y = \frac{Y}{K_Y}$	$r_y = \frac{R_Y}{\delta}$
$f_2(y) = r_y(1-y)$	$p = \frac{P}{\delta}$	$m = \frac{M}{\delta K_X}$
$\tau = \delta t$	$k = \frac{K_X}{K_Y}$	
		$s_1 = \frac{d_1 K_X}{\delta c}$
		$s_2 = \frac{0.052632 d_2}{K_X}$

When the dimensionless variables are applied to the social fence model, the resulting system is

$$x' = \frac{dx}{dt} = x(1-x) - m(x-y) - px \tag{16}$$

$$y' = \frac{dy}{dt} = ry(1-y) + km(x-y) \tag{17}$$

Again using the substitutions in this table, the economic model system non-dimensionalizes to

$$\text{Min}J(x,p) = \int_0^\infty e^{-\tau}\left(\frac{s_1 x}{x+s_2} + \frac{p}{x}\right)d\tau \tag{18}$$

subject to

$$\frac{dx}{d\tau} = xf_0(x) - f_1(x,y) - px \tag{19}$$

$$\frac{dy}{d\tau} = yf_2(y) - kf_1(x,y) \tag{20}$$

$$x(\tau = 0) = x_0 \quad y(\tau = 0) = y_0 \tag{21}$$

$$p^{min} \leq p \leq p^{max} \tag{22}$$

The net present value of the non-dimensionalized problem is not J but actually $(\frac{c}{K_X})J$, but the minimum will not be changed by scalar multiplication, so $\min(\frac{c}{K_X})J = \min J$.

3 Mathematical Analysis

The goal of the model is to minimize total cost J over (dimensionless) time. We base our discussion of Huffaker et al.'s solution to their optimal control problem on the general description of optimal problems by Conrad and Clark (1987). Since there is no upper bound on time in this problem, it is an infinite horizon problem and we don't need to consider the future cost after a maximum time. To solve an optimal control problem of this form, we first need to form a Lagrangian expression and find the Hamiltonian, which is defined as the sum of the cost function and the products of each of the Lagrange multipliers with their state functions. We should substitute the Hamiltonian into the Lagrangian expression, then visualize a change in the control trajectory which causes corresponding changes in the state variable trajectories and Lagrangian expression. But for a minimum, the change in the Lagrangian must vanish for any change in the control variable, leading to the set of necessary conditions for a minimum in a system with initial conditions given:

$$\frac{\partial H(\cdot)}{\partial p(\tau)} = 0 \tag{23}$$

$$\frac{d\lambda_1}{d\tau} = -\frac{\partial H(\cdot)}{\partial x(\tau)} \tag{24}$$

$$\frac{d\lambda_2}{d\tau} = -\frac{\partial H(\cdot)}{\partial y(\tau)}. \tag{25}$$

So the key step to finding value of the control parameter needed to obtain a minimum is to set the partial derivative of the Hamiltonian with respect to the control parameter equal to zero.

Huffaker et al. modeled their solution process after a fisheries harvest model by Mesterton-Gibbons (1988). Under Pontryagin's maximum principle the Hamiltonian for the dispersal model is:

$$H(x,y,\lambda_1,\lambda_2,\tau) = e^{-\tau}\left[\frac{s_1 x}{x+s_2} + \frac{p}{x}\right] + \lambda_1\left[xf_0(x) - f_1(x,y) - px\right] + \lambda_2\left[yf_2(y) + kf_1(x,y)\right] \tag{26}$$

$$\frac{d\lambda_1}{d\tau} = -\frac{\partial H}{\partial x} \tag{27}$$

$$\frac{d\lambda_2}{d\tau} = -\frac{\partial H}{\partial y}, \tag{28}$$

where λ_1 and λ_2 are Lagrange multipliers representing the incremental change in total cost from an incremental change in trapping, and the derivatives of λ form the adjoint system. Next they defined new functions with bioeconomic significance

$$W_1 = e^{\tau}\lambda_1 \tag{29}$$

$$W_2 = e^{\tau}\lambda_2 \tag{30}$$

$$\eta(x,\tau,W_1) = \frac{\partial H}{\partial p} = e^{-\tau}\left(\frac{1}{x} - xW_1\right). \tag{31}$$

W_1 represents the marginal discounted total cost associated with each trapping increment, and η is used to determine which trapping rate should be used for an optimal solution.

$$\eta(x,\tau,W_1) = 0 \tag{32}$$

is the minimum condition, and represents the singular path solution for trapping values, where discounted marginal trapping costs balance and do not exceed the discounted marginal benefits of avoided timber damage.

In the Hamiltonian, the p terms are all first degree, so H is linear in terms of the control variable p. From initial conditions off of the singular path (but where the singular path is reachable from the initial conditions) the optimal approach is usually either asymptotic, or the most rapid approach path (MRAP). For the MRAP, landowners should use a "bang-bang" control, choosing either the maximum or minimum trapping rate to drive the system as quickly as possible to the singular path (Conrad and Clark, 1987).

Let p^{opt} be the optimum trapping rate and $p^{\star}(x,y)$ be the trajectory of trapping rates that maintains the system on the singular path.

$$p^{opt} = \begin{cases} 0 & \text{if} \quad \eta(x,\tau,W_1) < 0 \\ p^{\star}(x,y) & \text{if} \quad \eta(x,\tau,W_1) = 0 \\ p^{max} & \text{if} \quad \eta(x,\tau,W_1) > 0 \end{cases} \tag{33}$$

To find $p^{\star}$, Huffaker et al. rewrote the Hamiltonian, using W_1 and W_2, as

$$H = \eta(x,\tau,W_1)p + e^{-\tau}\left\{\frac{s_1 x}{x+s_2} + W_1\left[xf_0(x) - f_1(x,y)\right] + W_2\left[yf_2(y) + kf_1(x,y)\right]\right\} \tag{34}$$

and substituted the adjoint system into the derivatives with respect to τ of W_1 and W_2 to obtain a new adjoint system

$$\frac{dW_1}{d\tau} = W_1\left[1 - z_1(x) + p\right] - kf_{1_x}W_2 + \frac{p}{x^2} - \frac{s_1 s_2}{(x+s_2)^2} \tag{35}$$

$$\frac{dW_2}{d\tau} = f_{1_y}W_1 + W_2[1 - z_2(y)], \tag{36}$$

where functions $z_1(x)$, $z_2(x)$ consolidate terms for notational convenience and f_{0_x}, f_{1_x} are the first derivatives of f_0, f_1 with respect to x and f_{2_y}, f_{1_y} are the first derivatives of f_2, f_1 with respect to y.

We corrected some typographical errors and propose the modified functions

$$z_1(x) = \frac{dx}{d\tau} f_0(x) + x f_{0_x} - f_{1_x} \tag{37}$$

$$z_2(x) = \frac{dy}{d\tau} f_2(y) + y f_{2_y} + k f_{1_y}. \tag{38}$$

Huffaker et al. substituted the modified adjoint system into the first and second derivatives with respect to τ of $\eta(x,\tau,W_1)$ to obtain

$$\frac{d\eta}{d\tau} = e^{-\tau}\left[\Gamma_1(x,y)W_1 + \Gamma_2(x)W_2 - \Gamma_3(x)\right] \tag{39}$$

$$\frac{d^2\eta}{d\tau^2} = e^{-\tau}\left[A(x,y,W_1,W_2)p - B(x,y,W_1,W_2)\right] \tag{40}$$

using the substitutions given in Table 4, which we have not checked.

Table 4: Functions used by Huffaker et al. to solve for $p^\star(x,y)$

$\Gamma_1(x,y) = f_1 + x^2 f_{0_x} - x f_{1_x}$
$\Gamma_2(x,y) = k x f_{1_x}$
$\Gamma_3(x,y) = \frac{1}{x}\left(1 + f_0 - \frac{1}{x} f_1\right) - \frac{s_1 s_2 x}{(x+s_2)^2}$
$w_1 = W_1(x,y) = \frac{1}{x_2}$
$w_2 = W_2(x,y) = \left(\frac{1}{x_2 \Gamma_2}\right)\left(\Gamma_3 x^2 - \Gamma_1\right)$
$A(x,y) = w_1\left(\Gamma_1 - x\Gamma_{1_x}\right) - w_2 x \Gamma_{2_x} + x\Gamma_{3_x} + \frac{\Gamma_1}{x^2}$
$B(x,y) = w_1\left[z_1\Gamma_1 - f_{1_y}\Gamma_2 - (x f_0 - f_1)\Gamma_{1_x} - (y f_2 + k f_1)\Gamma_{1_y}\right]$
$\quad + w_2\left[k f_{1_x}\Gamma_1 + z_2\Gamma_2 - (x f_0 - f_1)\Gamma_{2_x}\right]$
$\quad \frac{s_1 s_2 \Gamma_1}{(x+s_2)^2} - \Gamma_3 + (x f_0 - f_1)\Gamma_{3_x} + (y f_2 + k f_1)\Gamma_{3_y}$
$\psi_1(x,y) = \Gamma_{2_x}\left(3\Gamma_1 - x\Gamma_{1_x} - x^2\Gamma_3 + x^3\Gamma_{3_x}\right)$
$\psi_2(x,y) = \Gamma_{2_x}\left\{\Gamma_1\left[x(z_1 - z_2) - 2(x f_0 - f_1) + x^2\Gamma_3 - \Gamma_1 + \frac{s_1 s_2 x^3}{(x+s_2)^2}\right]\right.$
$\quad \left. - \Gamma_{2_x} x(y f_2 + k f_1)\Gamma_{1_x} + x^3(z_2 - 1)\Gamma_3 - x^2 f_{1_y}\Gamma_{2_x} + x^3(y f_2 + k f_1)\Gamma_{3_y}\right\}$

Huffaker et al. note that $\eta(x,W_1,\tau) = 0$ along the singular path implies $\frac{d\eta}{d\tau}$ and $\frac{d^2\eta}{d\tau^2}$ must vanish, which we have not verified. They set $\eta = 0 = \frac{d\eta}{d\tau}$ to solve for W_1 and W_2 in terms of x and y, then solved $\frac{d^2\eta}{d\tau^2} = 0$ for the optimal control rule

$$p^\star(x,y) = \frac{\beta(x,y)}{\alpha(x,y)} = \frac{\left[x f_0(x) - f_1(x,y)\right]\psi_1(x,y) + \psi_2(x,y)}{x\psi_1(x,y)} \tag{41}$$

4 The Optimal Trapping Strategy

The optimal trapping rate, p^{opt}, defined in equation 33, gives the three trapping rates that will lead to the most cost-effective trapping solution. As seen in the previous section, setting the necessary conditions to minimize total costs defines a singular path solution and its corresponding optimal feedback control rule for trapping, $p^{\star}(x,y)$. The two extreme trapping cases provide most rapid approaches to the cost-minimizing singular path. This means landowners should use the minimum trapping rate ($p^{opt} = 0$) when the marginal discounted trapping costs are larger than the discounted benefits of trapping in terms of the total damage costs prevented. Similarly, the maximal trapping rate ($p^{opt} = p^{max}$) should be used when damages outweigh trapping costs. Examining the phase planes associated with the extreme trapping cases illustrates how these serve as most-rapid-approaches to the singular path. Juxtaposing these trajectories with the singular path will graphically explain the mechanism of the optimal trapping strategy.

4.1 Naturally-regulated phase plane ($p^{opt} = 0$)

The dimensionless system of differential equations describing the beaver populations is detailed in section 2.4. Letting $p = 0$ in this system illustrates the dynamics of the population when both populations are allowed to grow naturally in the absence of trapping. Setting x' and y' equal to 0 yields the following nullclines:

$$x^2 - (1 - m - p)x - my = 0 \tag{42}$$

$$ry^2 - y(r - km) - kmx = 0 \tag{43}$$

These nullclines are graphed in Figure 1. The alternative yx-plane is used because x is the dependent variable. A decrease in the x population will therefore be seen as a downward change on the vertical axis, instead of the "backward" change that would result if the x-direction was horizontal. When juxtaposing the three trapping cases, using the yx-plane also better matches the language of the optimal trapping strategy.

Equilibrium points occur where the nullclines intersect. For the naturally-regulated phase-plane, equilibrium points occur at the origin and at $(1,1)$. The stability of these points is analyzed by calculating the eigenvalues from the following Jacobian matrix.

$$J = \begin{bmatrix} 2x - (1 - m - p) & -m \\ -km & 2ry \end{bmatrix} \tag{44}$$

Using the parameter values to solve for the eigenvalues results in the two eigenvalues $\lambda = -0.95, -2.92$. for the point (1,1) and $\lambda = 0.95, -1.03$ for the origin. These eigenvalues indicate that there is a stable point at (1,1) and a saddle point at the origin. Example trajectories are illustrated in Figure 2.

4.2 Maximal trapping phase plane ($p^{opt} = p^{max}$)

The dynamics of the maximal trapping phase plane can be analyzed by following the same procedure. The equations for the nullclines and Jacobian will still be the same except that $p^{opt} = p^{max}$. The eigenvalues result in a saddle point at the origin and a stable equilibrium point at (0.15,0.05). The nullclines with trajectories are illustrated in Figure 3.

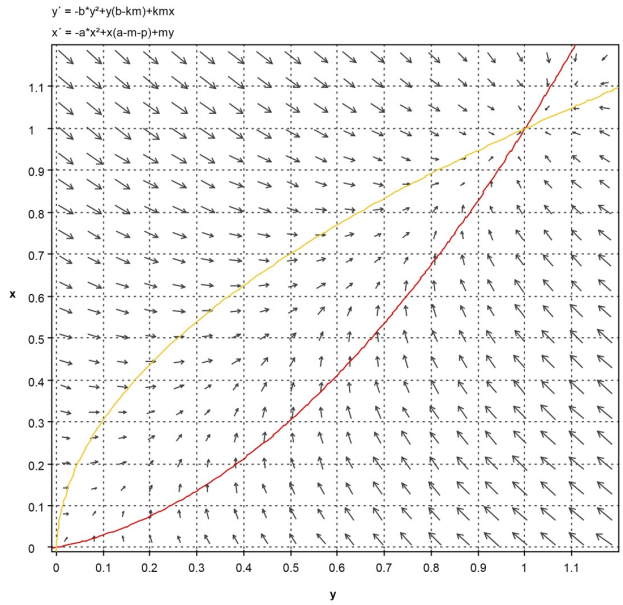

Figure 1: Nullclines for the Zero Trapping Case. Parameters used: $rx = 5.98$, $ry = 5.38$, $k = 1.11$, $m = 6.2$, $p = 0$.

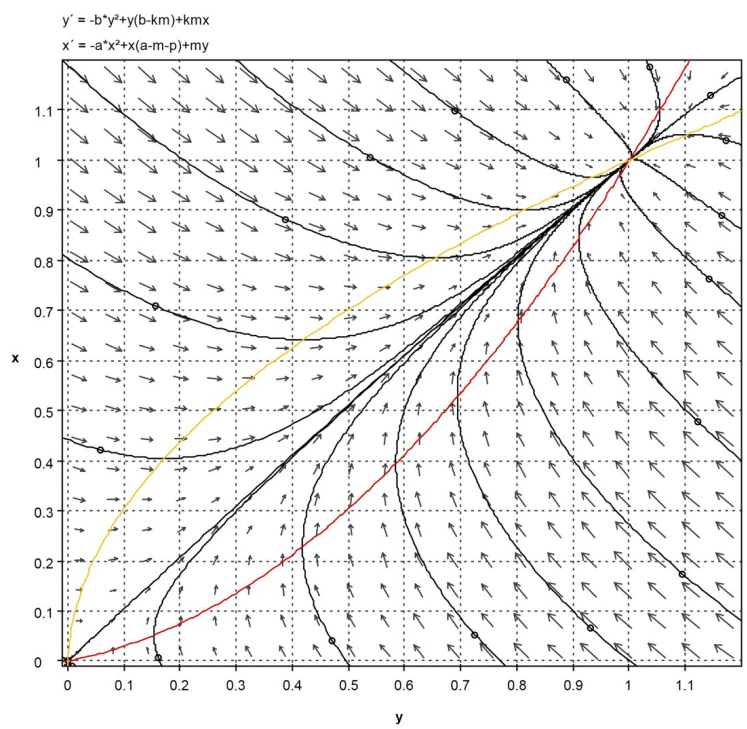

Figure 2: Nullclines and Trajectories for Zero Trapping.

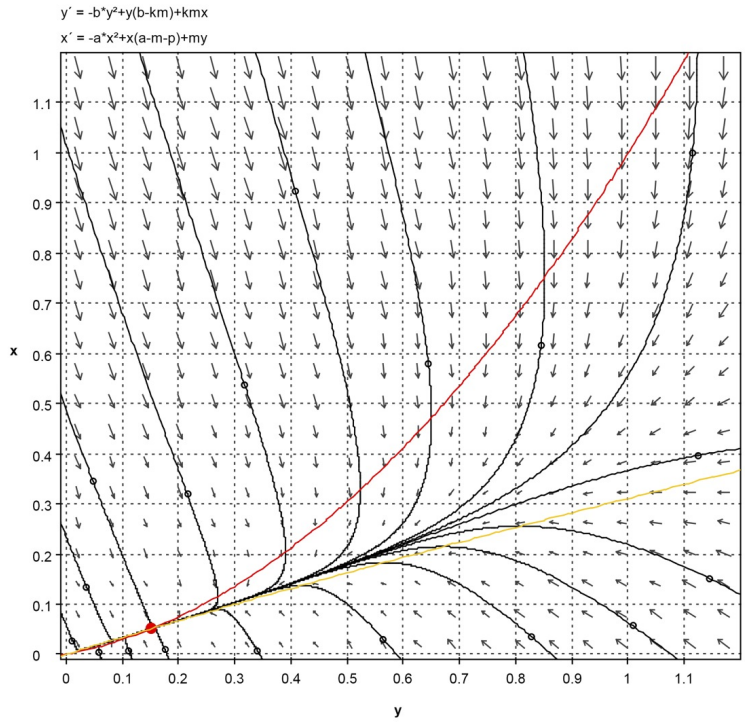

Figure 3: Nullclines and Trajectories for Maximal Trapping. Parameters same as previous figures except $p = 17.86$.

4.3 Singular phase plane ($p^{\star}(x,y)$)

The dynamics of the singular phase plane are not as easy to derive. Here, the trapping parameter, $p^{opt} = p^{\star}(x,y)$, depends on x and y and requires several layers of substitution to get the fully defined function. The singular phase plane found by Huffaker et al. (1992) is similar to Figure 4.

The thickened portion of the graph is the desired singular path that will minimize the total cost of trapping and damages. Off of this path, the x population may either shoot upwards over time or become cyclic. Due to the unstable dynamics off of the singular path, a landowner should use one of the other trapping scenarios ($p^{opt} = 0$ and $p^{opt} = p^{max}$) as the most rapid approach to the singular path. Once this path is reached, $\eta = 0$ and the optimal feedback trapping rule, $p^{\star}(x,y)$, should be used to minimize costs.

Figure 5 shows the singular path and two trajectories representative of the minimum and maximum trapping dynamics. If the current population of beavers is below the singular path, the minimum trapping rate will bring the population up to the singular path (e.g. starting below and to the left, following p^{min} brings the population up to point a, where the trapping rate should shift to $p^{\star}(x,y)$ for the singular path). Similarly, starting above the singular path, p^{max} should be used to bring the population to point b on the singular path, where shifting the rate to $p^{\star}(x,y)$ will keep the population on the cost-effective singular path.

Using the baseline parameters in Table 1 specific to regions of New York , the optimal sustained population for parcel X is 59% of the carrying capacity and 75% for parcel Y. The corresponding optimal sustained annual trapping rate is 22%.

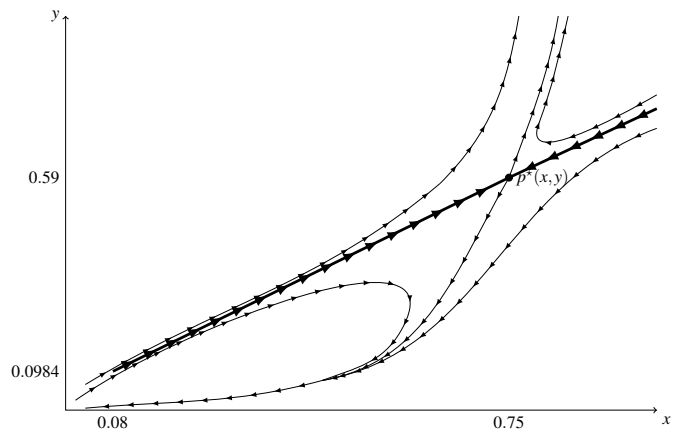

Figure 4: Singular Phase plane under $p^\star(x,y)$. The dark portion is the optimal singular path.

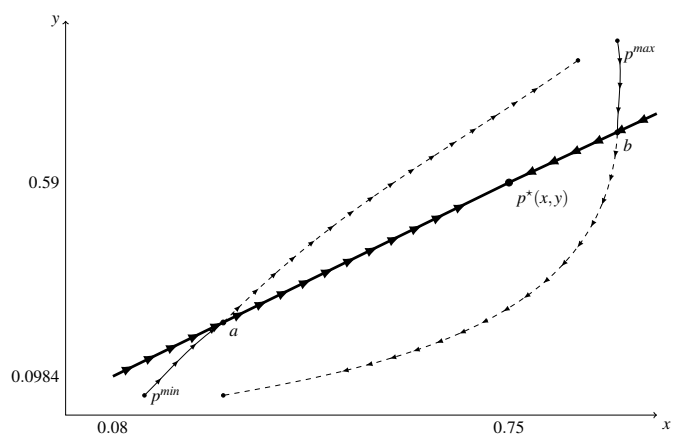

Figure 5: Optimal trapping sequences. Below the singular path, using p^{min} will drive the population up to the path at point a. Above singular levels, using p^{max} will drive the population to point b. Once singular levels are reached, using the optimal trapping rule, $p^\star(x,y)$, will minimize total costs.

5 Discussion

Beavers have the potential to cause major damage and significant economic losses. The current methods of dealing with nuisance beaver populations are relatively ineffective and inconsistent. One option landowners have is to take no action and allow the beaver population to approach the natural carrying capacity of an area. This strategy works well if the damages caused by beavers are lower than the cost of trapping them. The other option landowners resort to is a single-shot attempt to exterminate all beavers on their property. However, the effort is futile as the population vacuum allows nearby beaver populations to migrate to their property.

The ideas of the social fence hypothesis and Pontryagin's maximum principle provide tools to find a solution to the economic losses caused by beavers. Similar to the process of osmosis, the Social Fence Hypothesis describes how animals in one habitat will diffuse through a social fence into an area that is less densely populated in order to equalize the population's social and logistic pressures. Trapping continuously creates an area that has a lower population density compared to nearby uncontrolled areas. This will always attract new migrants as long as beavers are able to travel to the controlled area. In order to decrease the beaver population and associated damages, landowners must utilize a trapping strategy mindful of the trade-offs between the costs of trapping and the money saved by avoiding beaver damage.

The strategy outlined in this paper minimizes total costs of trapping and damage using Pontryagin's Maximum Principle and methods of optimal control. The result is a strategy where landowners must leave some beavers untrapped in order to prevent further invasion through the social fence. Following the strategy requires using a suitable extreme trapping rate to drive the population to stable cost-minimizing levels. If beaver populations are below that of calculated singular levels, landowners will let the beaver population grow naturally until the cost-minimizing singular levels are reached. If beaver populations and damages are higher than singular levels, landowners will use a maximal trapping rate until singular levels are reached. Once singular levels are reached, the optimal trapping rule should be used in order to bring the population to a cost effective steady state.

The optimal trapping rule $p^\star$ is a complicated function that most landowners would be unable to use directly. Even in a software implementation requiring numerical inputs for parcel specific parameters, individual landowners may have difficulty obtaining estimates for those values. Instead, it is more appropriate for professional managers or advisers from a central agency to calculate site specific trapping rates. In cases where neighboring landowners share a common interest in control of an animal population, the centralized manager scenario is most efficient (Bhat et al., 1996, Skonhoft and Armstrong, 2005). Regardless of specific interests or philosophy of landowners, using the optimal trapping rule under a central manager seems to be the most economically beneficial to all parties, effectively minimizing damages caused by beavers and creating new trapping and management jobs.

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