UMAP

Modules in Undergraduate Mathematics and Its Applications

Published in cooperation with

The Society for Industrial and Applied Mathematics,

The Mathematical Association of America,

The National Council of Teachers of Mathematics,

The American Mathematical Association of Two-Year Colleges,

The Institute for Operations Research and the Management Sciences, and

The American Statistical Association.

Module 776

Small Mammal Dispersion

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Applications of Calculus to Biology and Ecology

INTERMODULAR DESCRIPTION SHEET: UMAP Unit 776

TITLE: Small Mammal Dispersion

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MATHEMATICAL FIELD: Differential equations

APPLICATION FIELD: Biology, ecology

TARGET AUDIENCE: Students in a course in differential equations

ABSTRACT: This module introduces students to the social fence hypothesis explaining small mammal migration between adjacent land areas. Students are shown how the hypothesis is formulated in the population ecology literature as a pair of autonomous differential equations, and then they are directed toward a modified version of the standard formulation leading to increased realism. The modified version is solved qualitatively with phase diagrams for a range of ecological circumstances. Students also gain experience working with the numerical phase-plane plotter Dynasys, which can be downloaded from the World Wide Web. The social fence hypothesis is presented within the real-world context of controlling beaver-related damage in a given area by trapping.

PREREQUISITES: Introduction to ordinary differential equations covering phase-plane solutions.

Tools for Teaching 1999, 19–37. Reprinted from *The UMAP Journal* 20 (1) (1999) 47–65.

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MODULES AND MONOGRAPHS IN UNDERGRADUATE MATHEMATICS AND ITS APPLICATIONS (UMAP) PROJECT

The goal of UMAP is to develop, through a community of users and developers, a system of instructional modules in undergraduate mathematics and its applications, to be used to supplement existing courses and from which complete courses may eventually be built.

The Project was guided by a National Advisory Board of mathematicians, scientists, and educators. UMAP was funded by a grant from the National Science Foundation and now is supported by the Consortium for Mathematics and Its Applications (COMAP), Inc., a nonprofit corporation engaged in research and development in mathematics education.

Paul J. Campbell	Editor
Solomon Garfunkel	Executive Director, COMAP

1. Introduction

Beavers (*Castor canadensis*) are the largest rodents in North America.[1] Adults are between three to four feet in length and weigh 30 to 60 pounds. Beavers possess a specialized digestive system that permits them to digest tree bark. They prefer the tender bark at the top of hardwood trees (i.e., maple, linden, birch, and poplar) and gain access to it by systematically gnawing at a tree's trunk until it falls over. Beavers also use felled trees to dam up slow moving streams and small rivers, thereby creating ponds that are an essential part of their habitat.

Beaver ponds create a wide range of potential environmental and agricultural benefits, including [Stuebner 1992]:

- habitat for a large number of wildlife species,
- improved water quality as sediment is allowed to settle out of turbid waters,
- improved productivity of adjacent land for livestock grazing, and
- fertile soils for agricultural production when drained.

Unfortunately, these potential benefits may come at what economists term an "opportunity cost." The opportunity cost of beaver ponds includes any environmental, aesthetic, or future commercial benefits trees were generating before being felled by beavers. Beavers may be deemed a public nuisance when the opportunity cost of their activities is thought to outweigh the benefits. In such case, the public might attempt to minimize beaver damage by controlling the population. For example, the North Carolina Legislature authorizes landowners to use any lawful method at any time to remove beavers destroying their property.

Trapping is generally the most effective means of controlling a beaver population whose primary damage in a given land area is felling trees. There have been many myopic attempts on a limited scale to trap and remove all beavers from a damaged area [Hill 1982]. However, experience from these attempted eradication efforts demonstrates that beavers from neighboring uncontrolled or lesser controlled areas tend to immigrate continually into the controlled area to fill the resulting population vacuum [Houston 1987].

Population ecologists have formulated the *social fence hypothesis* to explain how migration of small mammals between adjacent land areas might occur in general [Hestbeck 1982, 1988]. According to the hypothesis, individuals within a given area compete for vital resources, and when competition reaches a critical level, there is social pressure exerted on some individuals to depart (*within-group aggression*). For example, young beavers generally remain with the colony for only two years before departing to establish their own colonies.

[1] The information in this introduction was gleaned from the Web sites `http://ngp.ngpc.state.ne.us/wildlife/beaver.html`, `http://www.educ.wsu.edu/enviroed/beavers.html`, and `http://www.ces.ncsu.edu/nreos/wild/beavers.html` .

However, as individuals attempt to depart, there is territorial pressure exerted against their departure by neighboring populations (*between-group aggression*). When within-group aggression exerted in area A is stronger than between-group aggression exerted in neighboring area B, the social fence is said to be open for individuals to migrate from A to B.

A single-shot eradication effort has the unintended consequence of opening the social fence to migration from uncontrolled to controlled areas by removing beavers in the controlled area who otherwise would exert between-group aggression against potential immigrants. Consequently, sustained trapping efforts are required to offset this continual migration so that the controlled population can be maintained at a desired fixed level through time. The exercises below investigate the long-term impacts of a range of multi-period sustained trapping strategies on the population densities of beavers in neighboring controlled and uncontrolled areas. The exercises are based on the following mathematical formulation of the social fence hypothesis.

2. Mathematical Formulation of the Social Fence Hypothesis

Consider first the mathematical formulation of the social fence hypothesis in the absence of trapping. Let X and Y represent nonnegative beaver population densities (in beavers/square mile) in neighboring areas, and let $\dot{X}$ and $\dot{Y}$ represent the associated annual net rates of change (in beavers/square mile/year) according to:

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

$$\dot{Y} = F_2(Y) + F_1(X,Y). \qquad \textbf{(2)}$$

The net rate of change in annual population in each area is equal to the difference between the rates of net growth (i.e., birth rate minus the death rate) and dispersion. Functions $F_0(X)$ and $F_2(Y)$ are net proportional annual growth rates for X and Y, respectively, with units 1/year and are given by:

$$F_0(X) = R_X\left(1 - \frac{X}{K_X}\right) \qquad \textbf{(3)}$$

$$F_2(X) = R_Y\left(1 - \frac{Y}{K_Y}\right), \qquad \textbf{(4)}$$

where the quantities R_X (1/year), K_X (beavers/square mile), R_Y (1/year), and K_Y (beavers/square mile) are nonnegative constants. As the population density X approaches zero in its area, the net proportional growth rate approaches R_X (i.e., $F_0 \to R_X$ as $X \to 0$), which is called the *intrinsic growth rate* (1/year). Alternatively, as X approaches K_X, the net proportional growth rate decreases toward zero (i.e., $F_0 \to 0$ as $X \to K_X$) due to the negative impacts of crowding.

Thus, K_X is the environmental carrying capacity for beavers in X's area. The parameters R_Y and K_Y are interpreted analogously in Y's area.

Exercise

1. Assume that $F_1(X, Y)$ is zero in **(1)**, so that the population X changes only in response to net growth, that is, $\dot{X} = F_0(X)X$. Graph this differential equation and indicate with directional arrows how X changes over time, for the two cases when $0 < X < K_X$ and when $X > K_X$ (e.g., an arrow pointing rightward indicates that X increases over time). Next, solve the differential equation and graph the solution. Explain how the solution satisfies the limits on $F_0(X)$ as X approaches zero and the carrying capacity, respectively.

The total dispersion flux term, $F_1(X, Y)$ (beavers/square mile/year), is a mathematical representation of the social fence hypothesis found in the mathematical ecology literature [Stenseth 1988]. This literature assumes that whenever $X > Y$, the within-group aggression exerted by X is greater than between-group aggression exerted by Y, and the net proportional annual migration rate, $F_1(X, Y)$, acts as a dispersive valve allowing beavers to migrate from X to Y, that is, $F_1 > 0$. Alternatively, whenever $Y > X$, the dispersive valve opens in the opposite direction ($F_1 < 0$) for beavers to migrate from Y to X. In short, operation of the social fence is tied to the population differential in the two areas. A functional form for $F_1(X, Y)$ satisfying these assumptions is

$$F_1(X, Y) = B(X - Y)X, \tag{5}$$

where $B > 0$ is a constant parameter with units $(\text{year})^{-1}(\text{beaver/square mile})^{-1}$.

Exercise

2. Assume that the population density of Y is much greater than that of X, that is, let $Y = 100$ and $X = 1$. Calculate the total dispersion flux $B(X - Y)X$ in terms of B. Now assume that Y is only marginally larger than X, that is, let $Y = 100$ and $X = 99$, and recalculate $F_1(X, Y)X$. Compare the total dispersion fluxes for both cases and discuss. Does the operation of the social fence as formulated by **(5)** make ecological sense?

Another problem with the formulation of the social fence hypothesis in **(5)** is that it unreasonably triggers migration in the situation where $X > Y$ but X exerts much less pressure on its carrying capacity than Y because $K_X \gg K_Y$. Competition for vital resources is less keen for X than for Y, implying that within-group aggression pressuring emigration from X's area should be less than between-group aggression exerted against immigration into Y's area. Under these circumstances, the dispersive value should be closed to migration from X to Y. An alternative formulation of the social fence hypothesis rectifying the above problems is:

$$F_1(X,Y) = M\left(\frac{X}{K_X} - \frac{Y}{K_Y}\right), \tag{6}$$

where M is a constant rate with units (beavers/square mile/year). Whenever X constitutes a larger fraction of its carrying capacity than Y (i.e., $X/K_X > Y/K_Y$), within-group aggression of X is assumed to be greater than between-group aggression, and $F_1(X,Y)$ acts as a dispersive valve allowing beavers to migrate from X to Y, that is, $F_1 > 0$.

3. The Social Fence Formulation with Trapping

Now assume that trapping occurs in X's area (i.e., the controlled area) but not in neighboring Y's area (i.e., the uncontrolled area). The modified rate equations are:

$$\dot{X} = F_0(X)X - F_1(X,Y) - PX \tag{7}$$

$$\dot{Y} = F_2(Y) + F_1(X,Y), \tag{8}$$

where $F_1(X,Y)$ is given by **(6)**, P (1/year) represents the per capita annual trapping rate of X, and PX represents the total beavers trapped each year. As trapping reduces the population pressure on carrying capacity in X's area, between-group aggression exerted by X against migration from Y decreases (all other things being equal), and the dispersive valve may open for individuals to migrate from uncontrolled population Y to controlled population X.

4. Dimensionless Rate Equations

The system of differential equations given by **(7)–(8)** can be simplified by making all variables and parameters dimensionless. Define dimensionless variables

$x = X/K_X$ (fraction of carrying capacity in the controlled area),

$y = Y/K_Y$ (fraction of carrying capacity in the uncontrolled area), and

$\tau = R_X t$ (dimensionless time variable).

Dimensionless parameters are

$m = M/R_X K_X$ (dimensionless dispersion parameter),

$p = P/R_X$ (dimensionless trapping parameter),

$r = R_Y/R_X$ (comparison of intrinsic growth rates in both areas), and

$k = K_X/K_Y$ (comparison of carrying capacities in both areas).

Exercise

3. Substitute these dimensionless quantities into **(7)–(8)** to show that the dimensionless model is:

$$x' = \frac{dx}{dt} = x(1-x) - m(x-y) - px \tag{9}$$

$$y' = \frac{dy}{dt} = ry(1-y) + km(x-y). \tag{10}$$

Note that the number of system parameters is reduced from six (R_X, R_Y, K_X, K_Y, M, P) to four (m, p, r, k).

We now analyze the solutions to the system **(9)–(10)** as the per capita trapping rate is increased from zero.

5. Zero-Trapping Dynamics

Consider first the population dynamics of X and Y when no trapping occurs in the tree-damaged area where X resides (i.e., $p = 0$ in **(9)**).

Setting **(9)** equal to zero yields the following implicit expression for the $x' = 0$ nullcline, which we will call $N_x(y)$:

$$x^2 - (1-m)x - my = 0. \tag{11}$$

The lack of an interaction term between x and y implies that $N_x(y)$ is a parabola in yx-space [Korn and Liberi 1978, 387] whose vertex occurs at a positive (negative) value of x when $(1-m)$ is positive (negative). The downward (upward) sloping branch of the parabola intersects the origin when $(1-m)$ is positive (negative).

Exercises

4. Set **(10)** equal to zero and solve for x in terms of y to derive the $y' = 0$ nullcline balancing net growth with diffusion each year in Y. Denote this nullcline by $N_y(y)$ and describe its graph.

5. Use the following baseline parameter values from a recent study [Huffaker et al. 1992] to plot the nullclines $N_x(y)$ and $N_y(y)$: $R_X = 0.335$, $R_Y = 0.3015$ ($r = 0.9$), $K_X = 1.107$, $K_Y = 0.9963$ ($k = 1.11$), and $M = 0.3473$ ($m = 0.937$).

6. The nullclines plotted in **Exercise 5** generate a dual steady-state configuration. One steady state occurs at the carrying capacities of X and Y (i.e., at $(x, y) = (1, 1)$) and the other occurs at the origin. Nullclines plotted with other parameter values can be shown to maintain these two steady states. The nullclines divide the phase plane into four regions called isosectors. Supply arrows indicating the directions of motion of x and y over time in each isosector.

7. Calculate the relevant eigenvalues to show that the equilibrium at the origin is a saddle point. Calculate the relevant eigenvalues to show that the equilibrium at the carrying capacities is a stable node. Draw in solution trajectories consistent with this information.

8. Use a computer program to generate numerically the phase diagram for the baseline parameters. One such program that you can download from the World Wide Web is DynaSys at `http://www.sci.wsu.edu/idea/software.html`.

Figure 1 is helpful in understanding the dynamics associated with various isosectors of the phase plane. The figure denotes the net proportional growth rate for x from **(9)** as $f_0 = (1 - x)$ and the net proportional growth rate for y from **(10)** as $f_2 = r(1 - y)$. Three dashed lines are superimposed on the nullclines from **Exercise 6** to divide phase space further into six regions. The regions bounded by the lines $x = 1$ and $y = 1$ (II and III) are characterized by positive net proportional growth rates for both populations, since each is below carrying capacity. Regions above $x = 1$ (I, IV, and V) produce negative net proportional growth rates for x, since the population is above carrying capacity. Regions to the right of $y = 1$ (IV, V, and VI) produce negative growth rates for y, since the population is above carrying capacity. The dashed line running from the origin through the nullclines at carrying capacity is the zero-dispersion line (zdl), which sets the dispersion flux term $f_1 = m(x - y)$ equal to zero since $x = y$. Population levels above the zdl (Regions I, II, and VI) open the social fence for migration from x to y, while levels below (Regions III, IV, and V) reverse the migratory flux.

Consider, for example, the dynamics in region II, which is bounded above by $x = 1$ and below by the zdl. Growth rates are positive for both populations, since each is below carrying capacity. The social fence is open for migration from x to y, since population levels are above the zdl. Thus, x enjoys a positive net proportional growth rate but suffers emigration losses. Initial levels of x above $N_x(y)$ initially decrease over time, because emigration losses are greater than growth each period. However, once x falls below $N_x(y)$, the growth rate overwhelms the emigration rate and the population begins to increase. Conversely, positive net proportional growth rates work together with immigration gains to increase y.

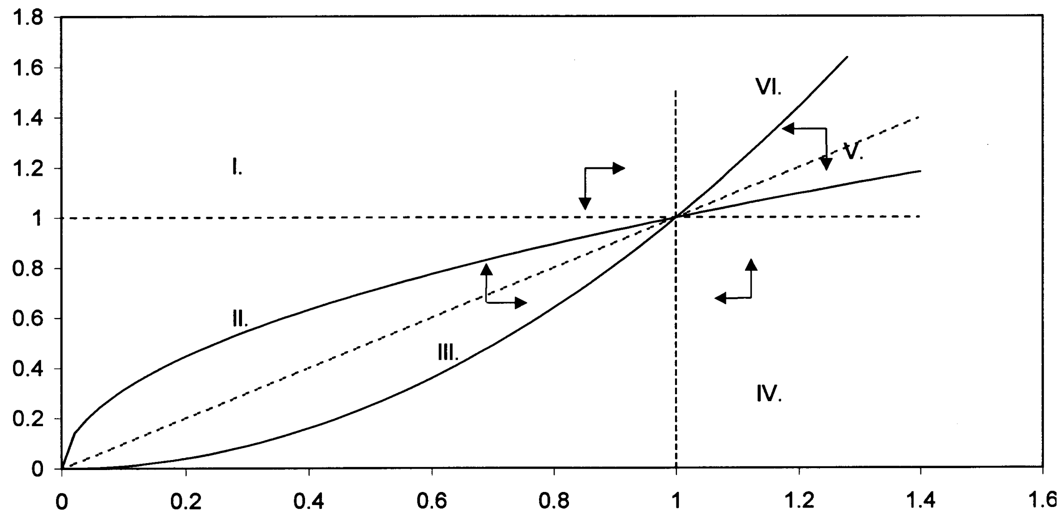


Figure 1. The zero-trapping plane ($p = 0$) with directions of motion from various isosectors. The plot is divided into regions by the dotted lines. Each region is labeled using roman numerals:

I. $f_0 < 0, f_2 > 0$, beavers migrate from x to y;
II. $f_0 > 0, f_2 > 0$, beavers migrate from x to y;
III. $f_0 > 0, f_2 > 0$, beavers migrate from y to x;
IV. $f_0 > 0, f_2 < 0$, beavers migrate from y to x;
V. $f_0 < 0, f_2 < 0$, beavers migrate from y to x;
VI. $f_0 < 0, f_2 < 0$, beavers migrate from x to y.

6. Positive Trapping Dynamics

Consider now the impact of trapping some portion of x each year. The system of differential equations governing the evolution of neighboring beaver populations under these circumstances is **(9)–(10)**, with p set at fixed rate p_f. Assume that p_f represents a 100% annual trapping rate (i.e., $P = 1$ and $p = P/R_X = 2.985$) and that all other parameters are held at the baseline values given in **Exercise 5**. The nullcline for the uncontrolled population y remains the same as in the zero-trapping case.

Setting **(9)** equal to zero with $p = p_f$ yields the following implicit expression for the $x' = 0$ nullcline $N_x(y)$:

$$x^2 - (1 - m - p_f)\, x - my = 0. \qquad \textbf{(12)}$$

The nullcline $N_x(y)$ is a parabola whose vertex occurs at a positive (negative) value of x when $(1 - m - p_f)$ is positive (negative). The downward (upward) sloping branch of the parabola intersects the origin when $(1-m-p_f)$ is positive (negative). Increasing the fixed trapping rate from zero shifts $N_x(y)$ downward. The nullcline $N_y(y)$ remains the same as in the zero-trapping case.

Exercises

9. Plot $N_x(y)$ and $N_y(y)$ for the baseline parameters and describe the resulting steady-state configuration. How does this configuration differ from that in the zero-trapping case? Does trapping open the social fence for sustained migration from y to x given the baseline parameter values?

10. Do the necessary eigenvalue analysis to determine the stability of all non-negative steady states, and draw in solution trajectories.

11. Use a computer program to generate the phase diagram for the baseline trapping scenario.

Table 1 shows the impact, on the positive steady-state levels of the controlled and uncontrolled populations, of the per capita trapping rate, P. In the table,

- X and Y are the dimensional controlled and uncontrolled population variables,
- x and y are their respective dimensionless counterparts measuring population pressure exerted on carrying capacity,
- $F_0(X)X$ and $F_2(Y)Y$ are their respective total sustained annual growth rates,
- $F_1(X,Y) < 0$ is sustained annual migration from Y to X, and
- PX is the total sustained annual trapping rate of X.

The annual growth functions are defined in **(3)–(4)** and the annual migration function is defined in **(5)**.

Table 1.
Effect of the per capita trapping rate P on population levels.

	P				
	0	0.25	0.5	0.75	1.0
X	0.072	0.610	0.295	0.141	0.072
Y	0.205	0.720	0.480	0.313	0.205
x					
y					
$F_0(X)X$					
$F_2(Y)Y$					
$F_1(X,Y)$					
PX					

Exercise

12. Do the required calculations to complete the table and generate the following plots using this information: First, plot x and y against P. Next, plot the total sustained annual trapping and migration rates against P. Finally, plot the total sustained annual growth rates of X and Y against P. Use these plots to explain why the total sustained annual trapping rate, PX, first increases and then decreases in response to increasing sustained per capita trapping rates, P.

7. Discussion

Landowners suffering beaver-related tree damage have several options. One extreme is to take no control action, which allows beavers to approach their environmental carrying capacity in the tree-damaged area. A landowner might be willing to forego control action if tree damage is outweighed by the many benefits provided by beaver ponds.

The other extreme is to attempt to eradicate beavers in the tree-damaged area with a single-shot trapping effort. This option may be futile because of the migratory behavior of neighboring beaver populations. The recently formulated social fence hypothesis explains the migratory behavior of small mammal populations as the ecological analogue of osmosis: Animals from a superior habitat are posited to diffuse through a social fence to a less densely populated habitat until the pressure to depart ("within-group aggression") is equalized with the pressure exerted against invasion ("between-group aggression"). According to this hypothesis, a landowner succeeding in removing the entire beaver population from an area in the short term unintentionally creates a population vacuum that is filled by migrating beavers from surrounding areas in the longer term. The specter of continual immigration into the controlled area justifies a sustained trapping strategy that offsets this sustained migration, so that the controlled population can be maintained at some fixed level through time.

We investigated the impact of sustaining various fixed per capita annual trapping rates. We applied those to steady-state beaver populations, in neighboring controlled and uncontrolled areas, by solving a mathematical model of the social fence hypothesis, using baseline parameters taken from a recent study. We found that:

- In the absence of trapping, both populations tend toward their respective carrying capacities.
- As the sustained per capita trapping rate increases from zero to relatively low levels, the steady-state population in the controlled area is driven to smaller fractions of its carrying capacity. This opens the social fence to increasing sustained migration from the uncontrolled to the controlled area and also—due to less crowding—increases the sustained net proportional growth rate

in the controlled area. These additions to the population must be offset by trapping an increasing total number of beavers so that controlled population is sustainable at lower steady states. The steady-state population in the uncontrolled area is also driven to smaller fractions of its carrying capacity, due to emigration losses.

- As the sustained per capita trapping rate increases to relatively high levels, the steady-state populations in both areas continue to exert decreasing pressure on their respective carrying capacities. The total number of beavers that need to be trapped annually to sustain these decreasing steady-state levels declines, due to decreased migratory and growth pressures in the controlled area. Migratory pressure drops, because the social fence begins to close a bit, due to decreasing gaps between the pressures exerted on carrying capacity in the controlled and uncontrolled areas. Growth pressures drop, because the steady-state populations in the two areas decrease to the extent that their net proportional growth rates begin to decline.

In light of these results:

> *Should a landowner adopt a relatively low or high sustained per capita trapping rate?*

The answer depends on the underlying biological and economic circumstances. Economists would expect a rational landowner to adopt a trapping rate that results a steady-state controlled population defined by the following characteristic:

> Marginally decreasing the steady-state population by annually trapping one more beaver would generate sustained trapping costs outweighing sustained benefits measured as avoided tree damage.

All other things being equal, the economically optimal steady-state controlled population is expected to be relatively low (reflecting a relatively high sustained per capita trapping rate) when beavers cause significantly more tree damage than they cost to trap, even at low population levels. See Huffaker et al. [1992] for an extended discussion of this question.

8. Solutions to the Exercises

1. See **Figure 2**. The solution of the differential equation is

$$X(t) = \frac{1}{1 + ce^{-rt}},$$

where c is a constant depending on the initial conditions; this function is graphed in **Figure 3**.

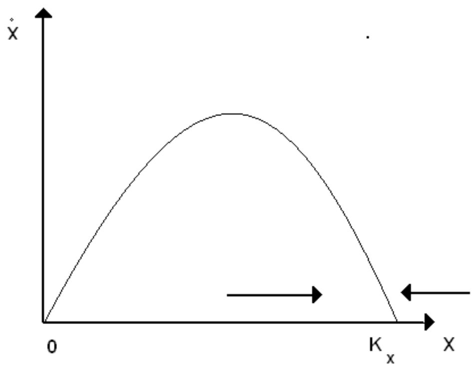


Figure 2. Graph of **(1)** when $F_1(X) = 0$.

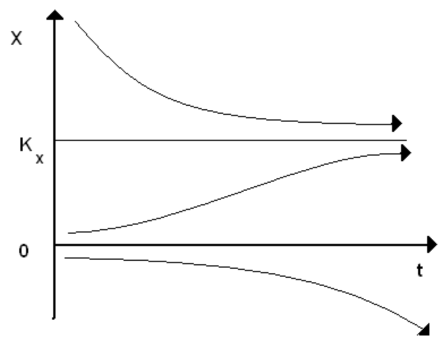


Figure 3. Graph of solutions to **(1)** for various initial conditions.

2. For $Y = 100$, $X = 1$: $F_1(X,Y) = B(1 - 100)(1) = -99B$.
For $Y = 100$, $X = 99$: $F_1(X,Y) = B(99 - 100)(99) = -99B$.

The problem with the formulation of the social fence in **(5)** is that it can generate the above result, where the same number of beavers migrate annually from Y to X regardless of whether the population differential between the two is large or small.

3. $N_y(y) = \dfrac{1}{km}\left[ry^2 - (r - km)y\right].$

See **Figure 4** for graphs for the two cases $r - km > 0$ and $r - km < 0$.

6. See **Figure 5**.

7. See **Figure 6**. The eigenvalues are:
for $(x,y) = (0,0)$: 0.953864, -1.03093;
for $(x,y) = (1,1)$: -0.951343, -2.92573.

9. The origin remains a steady-state solution, but trapping drives the interior steady state below carrying capacity for both populations. Trapping opens the door to sustained migration from Y to X, given the baseline parameters.

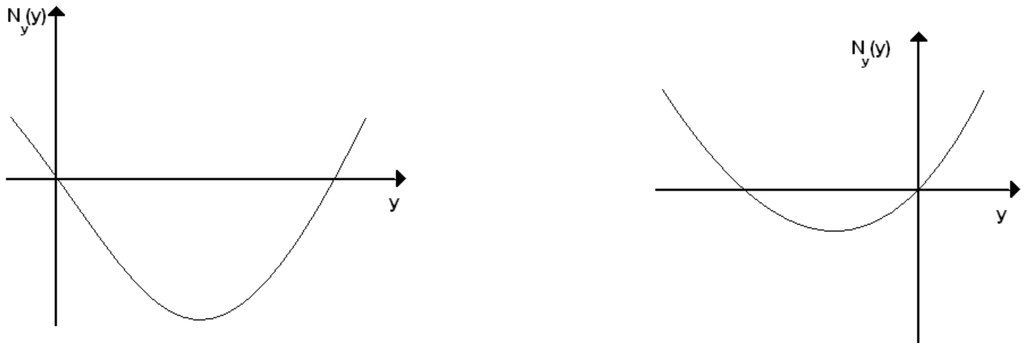


Figure 4. Graph of $N_y(y)$ for **a)** $r - km > 0$. **b)** $r - km < 0$.

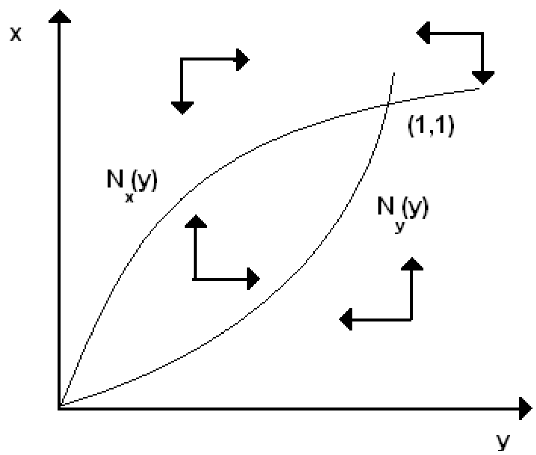


Figure 5. Solution to **Exercise 6**.

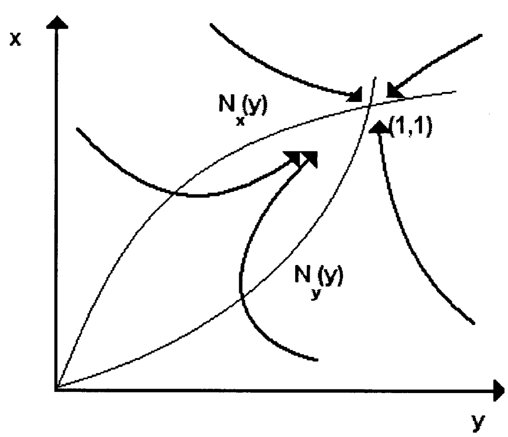


Figure 6. Solution to **Exercise 7**.

10. See **Figure 7**. The eigenvalues are:
for $(x, y) = (0, 0)$: 0.174641, -3.22671;
for $(x, y) = (0.21, 0.061)$: -0.177817, -3.38225.

12. See **Table 2** and **Figure 8**. See the **Discussion** section of the Module for explanation of why the total sustained annual trapping rate, PX, first increases and then decreases in response to increasing sustained per capita trapping rate, P.

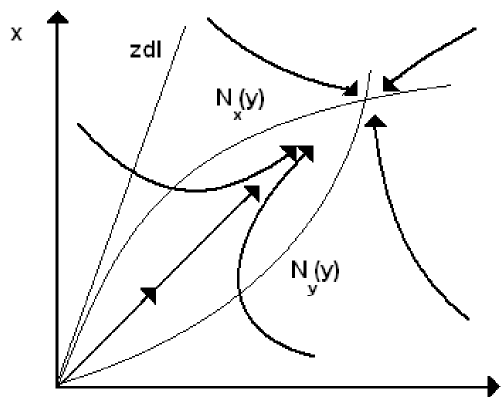
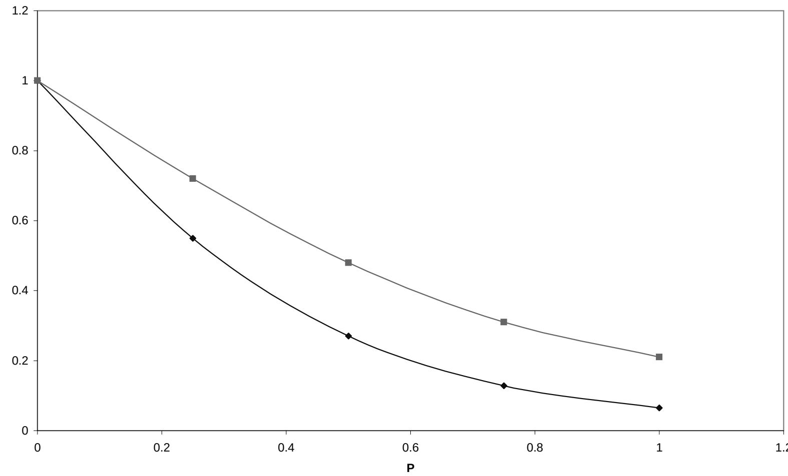


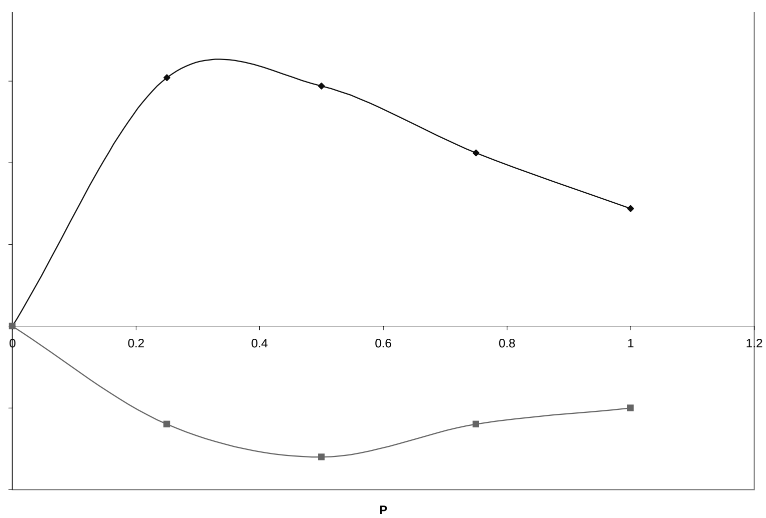
Figure 7. Solution to **Exercise 10**.

Table 2.
Effect of P on population levels.

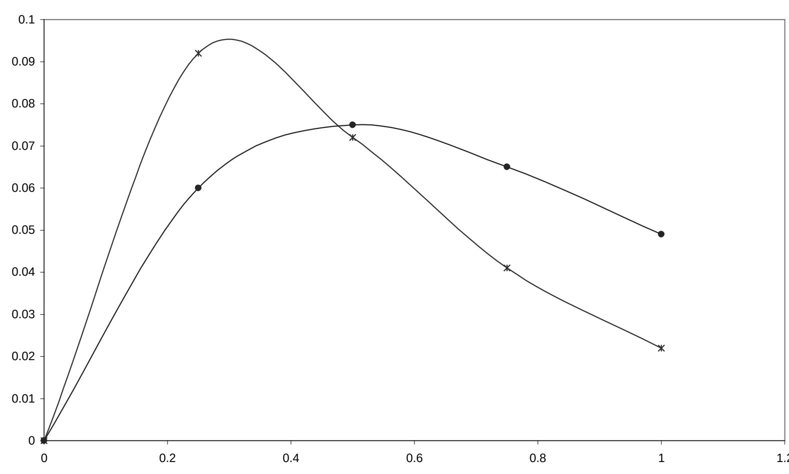
P	0	0.25	0.5	0.75	1.0
X	0.072	0.610	0.295	0.141	0.072
Y	0.205	0.720	0.480	0.313	0.205
x	1	0.550	0.270	0.128	0.065
y	1	0.720	0.480	0.310	0.210
$F_0(X)X$	0	0.092	0.072	0.041	0.022
$F_2(Y)Y$	0	0.060	0.075	0.065	0.049
$F_1(X, Y)$	0	−0.060	−0.080	−0.060	−0.050
PX	0	0.152	0.147	0.106	0.072



a) Graphs of y (upper) and x (lower) vs. P.



b) Graphs of PX (upper) and $F_1(X,Y)$ (lower) vs. P.



c) Graphs of $F_0(X)X$ (lower at $P = 1$) and $F_2(Y)Y$ (higher at $P = 1$) vs. P.

Figure 8. Solution to **Exercise 12**.

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