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OPTIMAL CONTROL APPLIED TO A MODEL FOR SPECIES AUGMENTATION

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Abstract. Species augmentation is a method of reducing species loss via augmenting declining or threatened populations with individuals from captive-bred or stable, wild populations. In this paper, we develop a differential equations model and optimal control formulation for a continuous time augmentation of a general declining population. We find a characterization for the optimal control and show numerical results for scenarios of different illustrative parameter sets. The numerical results provide considerably more detail about the exact dynamics of optimal augmentation than can be readily intuited. The work and results presented in this paper are a first step toward building a general theory of population augmentation, which accounts for the complexities inherent in many conservation biology applications.

1. Introduction.

Over the past three decades, a great deal of ecological research has focused on biodiversity. Despite the efforts of many to protect and sustain certain species and ecosystems, thousands of species are considered threatened or endangered [1]. One method of reducing species loss is to augment declining or threatened populations with individuals from captive-bred or stable, wild populations. This method is known as "species augmentation." Though the number of researchers calling for augmentation of threatened or endangered species has been increasing, and a handful of augmentation projects have been or are currently being carried out, there has been little effort to utilize mathematical theory to develop models for the dynamics of augmented populations and communities.

Recently, researchers working to conserve various species have begun to recommend species augmentation as a means to bring declining wild populations up to sustainable levels and to introduce greater genetic diversity to threatened and endangered populations. For example, a 2004 study of relative density and population size of a threatened grizzly bear population in Washington and British Columbia recommended augmentation after finding that natural recovery was highly unlikely [22]. A 1998 study of huemul deer species in South America recommended augmentation along with other conservation efforts to increase the range and total number of huemul, which had been reduced to a single population in Central Chile [21]. A 2006 population viability analysis (PVA) of ocelots (*Leopardus pardalis*)

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found that a combination of different recovery strategies, including augmentation, is needed to reduce ocelot extinction probability [8]. Other studies recommending augmentation as a means to promote species recovery and prevent extinction include [25, 17, 13, 10, 18, 9].

In addition to such recommendations for augmentation to conserve various threatened and endangered species, a handful of species augmentation projects have been executed and their level of success documented. Between July 1990 and October 1993, four female grizzly bears (*Ursus arctos horribilis*) of cub bearing age were captured in British Columbia and translocated to the Cabinet Mountains, Montana as an augmentation effort [24]. As of 2004, three of the four females were still within their target release area, but none of the three had produced any cubs. In 1995, eight female panthers (*Puma concolor*) were brought from Texas to augment the endangered Florida panther population in an effort to increase the low genetic diversity of the Florida panther population [14]. As of 2006, the panther population has increased from roughly 30 individuals to almost 100, and there is no evidence that individuals with Texas panther ancestry have inbreeding related defects [14, 5, 19].

Despite the growing need and use of species augmentation as a conservation tool, very few mathematical models or practical tools have been developed to study and predict the impact of species augmentation. The models developed for augmentation have mostly focused on a single particular species, though a more general approach could be broadly applicable. Models which employ the use of optimal control theory to predict the impact of species augmentation have been limited to a related problem of biocontrol to control agricultural pests.

Optimal control theory has been applied to systems of ordinary differential equations, modeling a variety of population scenarios. See for example, [6] a predator-prey system, [23] for a harvesting problem for bears in a park-forest scenario, and [26] for control of pests. See the books by Eisen [2] and Lenhart and Workman [27] for other examples. We present here the first application of optimal control to model augmentation. We call attention to the recent paper on optimization for a linear augmentation model with discrete time and stage structure (Hodgson *et al* [12]). We also call attention to the Hearne and Swart's model for the optimal translocation of an age-structured black rhino population [9] where the strategies of maximizing the translocation rate and maximizing the growth of a newly established population are compared.

In the next section, we develop a model and an optimal control formulation, and a characterization for the optimal control is found. In section 3, scenarios for different illustrative parameter sets are considered and the results discussed. The final sections present conclusions about control models for augmentation and discuss future extensions of this model.

2. **Optimal Control Model.**

Consider two populations of the same species: N, a target/endangered population, and R, a reserve population. We assume that, at the initial time, the endangered population is declining due to small population size, i.e. there is some critical population size below which the population declines to extinction. For the reserve population to be a viable source for harvesting individuals with which to augment the target population, it must be growing at the initial time, but it is also assumed to have a lower threshold for population growth that could be crossed due to over-harvesting. Therefore, each of these populations are assumed to grow according to a normalized Allee effect model, in which aK_N and

bK_R are the critical population sizes for growth for the target and reserve populations, respectively. The control u is the rate at which individuals are moved from the reserve population to the target population. Thus, the populations are modeled by the equations

$$\begin{aligned}\frac{dN}{dt} &= rN\left(1-\frac{N}{K_N}\right)\left(\frac{N}{K_N}-a\right)+uR\\ \frac{dR}{dt} &= sR\left(1-\frac{R}{K_R}\right)\left(\frac{R}{K_R}-b\right)-uR\end{aligned}$$

where r and s are the intrinsic growth rates of N and R, respectively, K_N and K_R are the carrying capacities of N and R, respectively, and aK_N and bK_R are the thresholds for population growth for N and R, respectively. Here we assume there is no net loss of population due to augmentation efforts.

Rescaling the two populations with respect to their carrying capacities ($x \equiv \frac{N}{K_N}$ and $y \equiv \frac{R}{K_R}$) gives

$$\begin{aligned}\frac{dx}{dt} &= rx(1-x)(x-a)+puy\\ \frac{dy}{dt} &= sy(1-y)(y-b)-uy\end{aligned}$$

where $p = K_R/K_N$, i.e. the ratio of the reserve carrying capacity to the target carrying capacity.

We assume the objective of augmentation is to maximize the target population at a given final time while minimizing the cost. This assumes there is cost associated with translocating an individual from the reserve population, and that it would be ideal to minimize this cost. We assume this cost to be a quadratic function of the fraction of translocated. We assume that the total population $(N + R)$ is to be maximized at the final time, with different relative weights applied to the reserve and target populations. We assume it is not as important to maximize the reserve population as it is the target population by the final time. Additionally, we assume that the target population x has an initial density x_0 below its minimum threshold for growth a, and that the reserve population y has an initial density y_0 above its minimum threshold for growth b. Thus, $x_0 < a$ and $y_0 > b$.

Thus, the optimal control formulation is

$$\max_{u\in U}\left[x(t_1)+By(t_1)-A\int_{t_0}^{t_1}u^2(t)dt\right]$$

where

$$U = \{u : [t_0, t_1] \to [0, 1] \mid u \text{ Lebesgue measurable}\}$$

and

$$\begin{aligned}x'(t) &= rx(1-x)(x-a)+puy,\ x(t_0)=x_0<a \qquad (1)\\ y'(t) &= sy(1-y)(y-b)-uy,\ y(t_0)=y_0>b \qquad (2)\end{aligned}$$

and a, b, t_0, t_1, x_0, y_0, r, s, A, and B are all non-negative constants and $0 \leq B \leq 1$. The objective functional seeks to maximize the two populations at the final time while minimizing the cost associated with translocating an individual from the reserve population to the target population. The weight factors, B and A, balance out the relative importance of the three terms. We assume the cost term is a nonlinear function of the control, and we use a quadratic cost to account for nonlinear increases in costs of translocation as the fraction translocated per unit time increase. We assume x_0, y_0, and A are positive.

Given $u \in U$, there exists a unique solution to the state system [16]. One can easily show that $y(t) \geq 0$ since y is a factor in each term of the right hand side of the differential equation (2). Then $x(t) \geq 0$ and the structure of the differential equations give upper bounds for the states. The convexity of the objective functional, the linearity of the differential equation in the control, and the compactness of the range values of the state variables combine to give the existence of an optimal control [4].

Suppose u^* is an optimal control with corresponding states x^*, y^*. To characterize the optimal control using Pontryagin's Maximum Principle [20], the Hamiltonian and adjoint equations are constructed.

$$\begin{aligned} H &= -Au^2 + \lambda_x(rx(1-x)(x-a) + puy) + \lambda_y(sy(1-y)(y-b) - uy) && (3) \\ \lambda_x' &= -\frac{\partial H}{\partial x} = \lambda_x r\left(3(x^*)^2 - 2x^*(1+a) + a\right) && (4) \\ \lambda_y' &= -\frac{\partial H}{\partial y} = \lambda_y s\left(3(y^*)^2 - 2y^*(b+1) + b\right) - \lambda_x p u^* + \lambda_y u^*. && (5) \end{aligned}$$

The transversality condition gives $\lambda_x(t_1) = 1$ and $\lambda_y(t_1) = B$.

Next, the characterization of the optimal control is found. On the set $\{t \,|\, 0 < u^*(t) < 1\}$, we have

$$\begin{aligned} \frac{\partial H}{\partial u} &= -2Au + p\lambda_x y - \lambda_y y = 0 \text{ at } u^*(t) && (6) \\ \Rightarrow\ u^*(t) &= \frac{p\lambda_x(t) - \lambda_y(t)}{2A} y^*(t) && (7) \end{aligned}$$

When $\frac{\partial H}{\partial u} < 0$ at t, then $u^*(t) = 0$ and

$$[p\lambda_x(t) - \lambda_y(t)]\, y^*(t) < 0 \ \Rightarrow\ \frac{p\lambda_x(t) - \lambda_y(t)}{2A} y^*(t) < 0.$$

When $\frac{\partial H}{\partial u} > 0$ at t, then $u^*(t) = 1$ and

$$[p\lambda_x(t) - \lambda_y(t)]\, y^*(t) > 2A \ \Rightarrow\ \frac{p\lambda_x(t) - \lambda_y(t)}{2A} y^*(t) > 1.$$

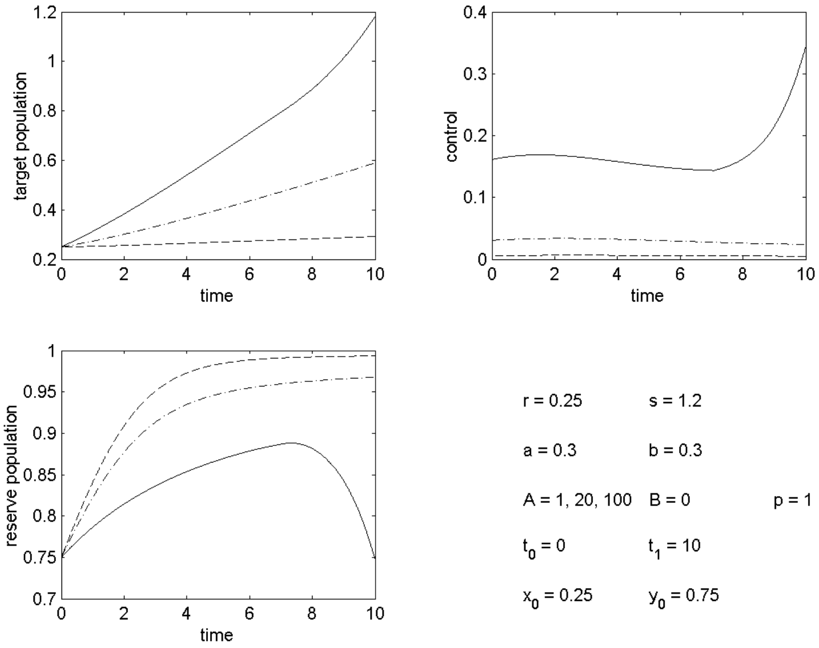
So, the characterization of the optimal control is

$$u^*(t) = \min\left\{1, \max\left\{\frac{p\lambda_x(t) - \lambda_y(t)}{2A} y^*(t), 0\right\}\right\}. \tag{8}$$

The optimal control can be numerically calculated under various parameter sets using a forward-backward sweep method [15] using 4^{th} order Runge-Kutta to solve the state equations (1) - (2) and their corresponding adjoint equations (4) - (5). The forward-backward sweep method makes an initial guess for u and then solves the state equations (1) - (2) forward in time using the Runge-Kutta method with the initial conditions (x_0 and y_0). Then, using the state values, the adjoint equations (4) - (5) are solved backwards in time using the Runge-Kutta method with the transversality conditions. At this point, the optimal control is updated using the characterization for the optimal control (8) and the values for the state and adjoint variables. This updated control replaces the initial control and the process is repeated until the successive iterates of control values are sufficiently close. The convergence of such an iterative method is based on the work of Hackbush [7]. Other examples using this method can be found in [23, 11, 3].

3. **Numerical Results.** In considering various parameter scenarios, the parameter constraints on x_0 and y_0, $x_0 < a$ and $y_0 > b$, must be included. For the examples here we take the minimum threshold for growth for both the target and reserve populations to be 0.3 (that is 30% of each populations' carrying capacity), and $x_0 = 0.25$ and $y_0 = 0.75$. Thus, the target population is starting just below its minimum threshold for growth and the reserve population is starting well above its minimum threshold for growth. Additionally, each scenario assumes that the intrinsic growth rate of the reserve population s is greater than the intrinsic growth rate of the target population r and in each scenario $r = 0.25$.

We first consider the impact of varying the cost of translocation, A. For the parameters listed in Figure 1 we vary the cost coefficient A and show the resulting optimal control and states. Notice that for high cost $A = 100$ (dashed line), the target population does not reach its minimum threshold for growth by the final time (i.e. $x(t_1) < a$). Thus, once augmentation has ceased (after the final time), the population will again start to decline. This illustrates the possibility of the cost of translocation being so high that, by the final time, the target population has not reached a density where it can sustain growth on its own. At the other extreme, with low cost coefficient $A = 1$ (solid line), the target population exceeds its carrying capacity by the final time (i.e. $x(t_1) > 1$). Thus, the target population has been over-augmented, and once augmentation has ceased, the population will decline to its carrying capacity. In this case, resources would have been wasted in over-augmenting the target population. This "over-augmenting" arises from a



$r = 0.25$ $s = 1.2$

$a = 0.3$ $b = 0.3$

$A = 1, 20, 100$ $B = 0$ $p = 1$

$t_0 = 0$ $t_1 = 10$

$x_0 = 0.25$ $y_0 = 0.75$

FIGURE 1. The solid line corresponds to $A = 1$, the dash-dot line to $A = 20$, and the dashed line to $A = 100$.

limitation of the model; there is no constraint in the model that limits augmentation once the target population reaches carrying capacity. This may arise however in cases for which carrying capacity is not easily estimated and there are benefits to having larger target populations.

For the second scenario, the time horizon is varied, with t_1 being 5, 10, or 20. In Figure 2, notice that for each final time, the target population is above the minimum threshold for growth by the final time, though only by a small amount in the case of $t_1 = 5$. Additionally, for $t_1 = 20$, over the last five years of the augmentation ($15 < t < 20$) the control increases again, and thus we see a slight decline in the density of the reserve population over those last five years.

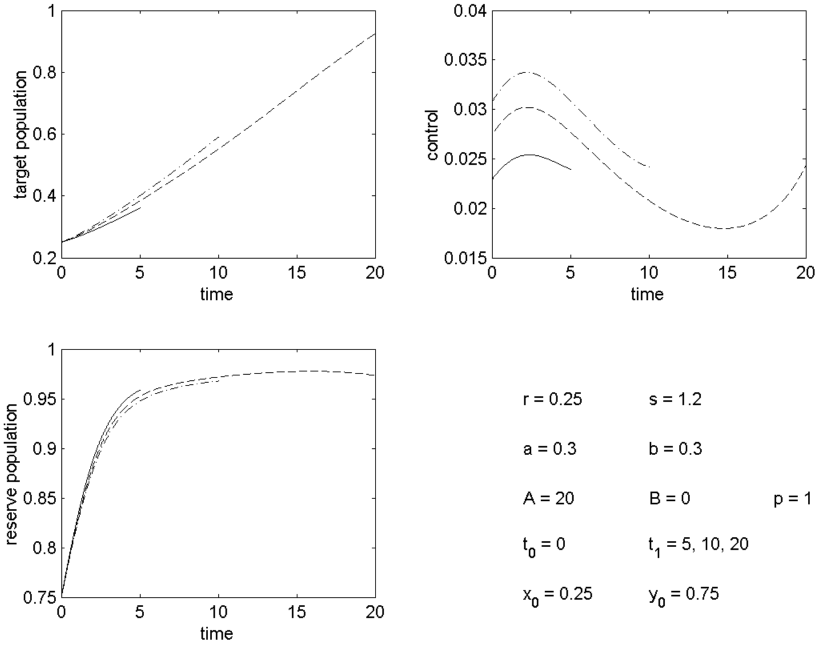


FIGURE 2. The solid line corresponds to $t_1 = 5$, the dash-dot line to $t_1 = 10$, and the dashed line to $t_1 = 20$.

In the third scenario, the ratio of the intrinsic growth rates of the target and reserve populations is varied by allowing the value of s to vary in $\{0.3, 0.9, 1.5\}$. For each value of s, Figure 3 shows that the target population is well above its minimum threshold for growth by the final time. When the value of s is higher, the reserve population is able to grow more quickly at the beginning of the time interval and achieve a higher population density by the end of the time interval. For $s = 0.3$, there is very little increase in the reserve population size over the entire time period. This is due to the fact that most of the growth in the reserve population is counter-balanced by the translocation of individuals to the target population.

In the fourth scenario all parameters are the same as in the third scenario with a lower cost of augmentation ($A = 1$). Note in Figure 4, that by the final time, for $s = 0.9$ and $s = 1.5$, $x > 1$. Thus, the target population has been over-augmented.

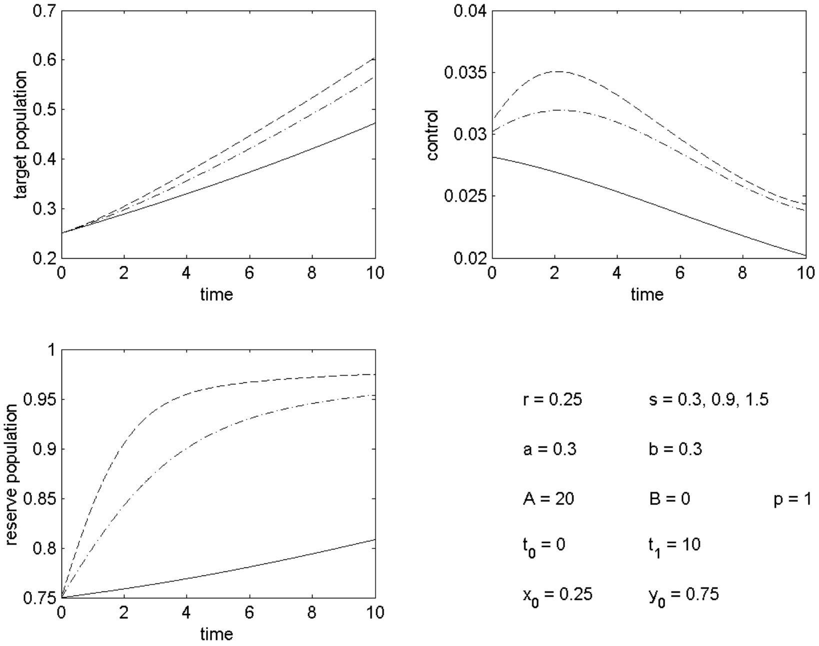


FIGURE 3. The solid line corresponds to $s = 0.3$, the dash-dot line to $s = 0.9$, and the dashed line to $s = 1.5$.

Also, notice that for $s = 0.3$ the reserve population is very close to its minimum threshold for growth by the final time. If the same scenario is run, except with $b = 0.4$, the results are quantitatively very similar, however the reserve population is below its minimum threshold for growth of $b = 0.4$. In this latter case, after the augmentation has taken place, the reserve population will decline to extinction. Thus, if the cost of augmentation is very low, it is possible that by the final time the reserve population has been "over-harvested," in that it will not naturally be able to increase its population density. This effect on the reserve population can be counteracted by increasing the value of B.

In prior scenarios the value of B has been set to zero, which means the objective function is not affected by the size of the reserve population at the final time. It may be necessary to increase B in order to prevent the reserve population from falling below its minimum threshold for growth by the final time. In the fifth scenario, $B = 0.75$ (all other parameter values are the same as in the fourth scenario). Thus, it is 75% as important to maximize the reserve population at the final time as it is to maximize the target population by the final time. In Figure 5 notice that the reserve population, for each value of s, is now well above the minimum threshold for growth, as is expected when increasing the value of B. Also notice that the target population, for $s = 0.9$ and $s = 1.5$, is still above a density of 1 by the final time, so there is still over-augmenting.

Figure 6 shows the effect of changing the ratio of the carrying capacities, p. Notice for $p = 0.1$ virtually no augmentation takes place, and that $x(t_1) < a$, so the target population will decline again after augmentation is completed. This

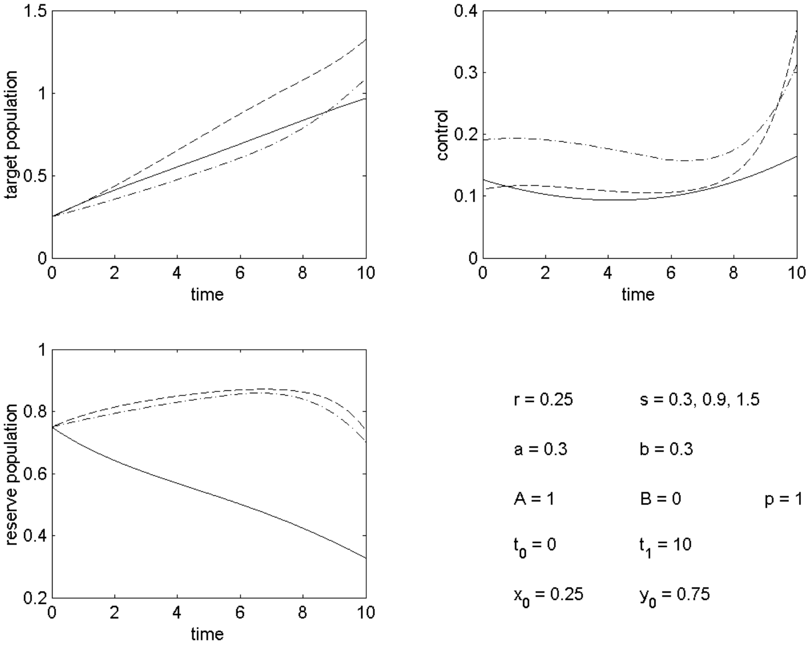


FIGURE 4. The solid line corresponds to $s = 0.3$, the dash-dot line to $s = 0.9$, and the dashed line to $s = 1.5$.

means that when the carrying capacity of the reserve population is only 10% of the carrying capacity of the target population there are not enough individuals in the reserve population to effectively augment the target population (i.e., have $x(t_1) > a$). However, further numerical simulations show that for all other parameter values remaining the same, a value of $p > 1.2$ was sufficient to guarantee that $x(t_1) > a$. Thus, it is possible to have a reserve population with a much smaller carrying capacity and still have effective augmentation of the target population. Notice also that when $p = 0.7$ the target population is over-augmented. In this scenario the cost of augmentation A was set to a low value of 1. If the cost of augmentation is raised, larger and larger values of p are needed to ensure $x(t_1) > a$. For example, with all other values remaining the same, if $A = 20$, a value of $p > 0.48$ is needed to guarantee that $x(t_1) > a$, and if $A = 100$, a value of $p > 1.05$ is needed to guarantee that $x(t_1) > a$.

The sets of results described above by no means exhausts the possible sets of scenarios that could be shown. However, numerous scenarios covering the breath of the biologically feasible parameter space were conducted, and the results shown above display the gamut of dynamical results collected from all the scenarios tested.

4. **Conclusions.** Several important conclusions about the continuous control of species augmentation can be drawn from this model. First, high cost of augmentation can prevent moving sufficient numbers of individuals to the target population in order for the target population to be above its minimum threshold for growth by the final time. Additionally, a low p value can exacerbate this effect; having a lower

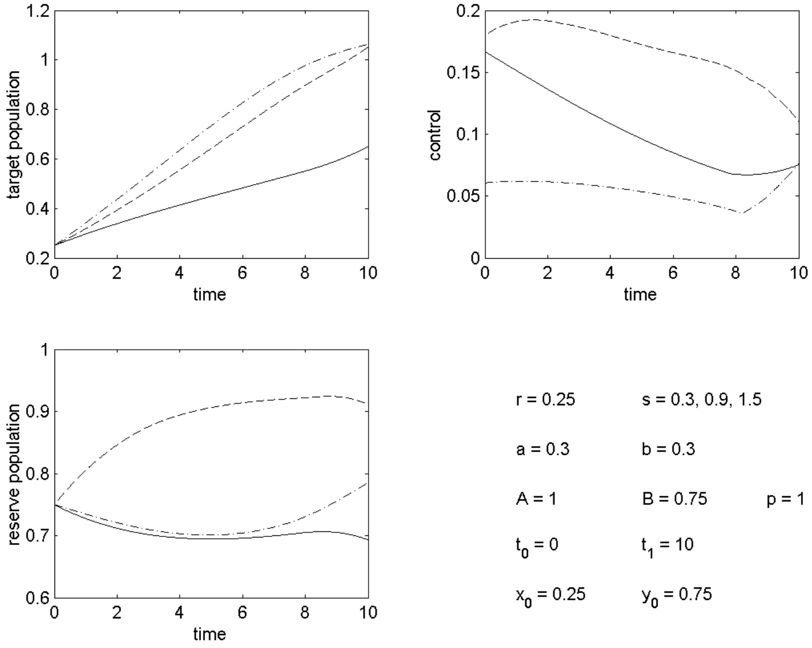


FIGURE 5. The solid line corresponds to $s = 0.3$, the dash-dot line to $s = 0.9$, and the dashed line to $s = 1.5$.

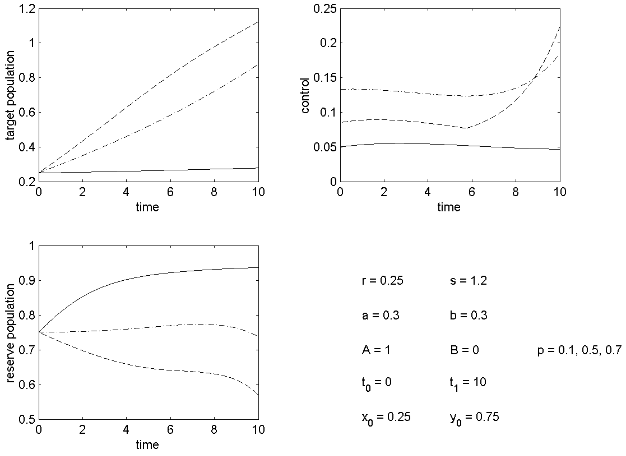


FIGURE 6. The solid line corresponds to $p = 0.1$, the dash-dot line to $p = 0.5$, and the dashed line to $p = 0.7$.

ratio of the carrying capacity of the reserve to the target population necessitates having a lower cost in order to optimally augment the target population such that it is above its minimum threshold for growth by the final time. If, in fact, the target population does not reach its minimum threshold for growth by the final time, then additional future augmentations may be required to prevent the population from going extinct. Additionally, the combination of a low cost of translocation and a low intrinsic growth rate of the reserve population could cause the reserve population to fall below its threshold for population growth by the final time. However, this can be counteracted in the optimal control solution by increasing the importance of having a large reserve population by the final time (i.e., increase the value of B). All of the above conclusions conform to intuition. However, our results provide considerably more detail about the exact dynamics of optimal augmentation than can be readily intuited.

One of the drawbacks of this model is that it does not provide a constraint to prevent over-augmenting the target population. In Figures 4, 5, and 6, we see that it is possible for the optimal augmentation strategy to continue augmenting the target population even after its density has increased past 1, i.e., above its carrying capacity. Once the augmentation is complete the target population will fall back down to its carrying capacity and remain there. Thus, over-augmenting is not cost effective as it requires the translocation of "extra" individuals from the reserve population. Possible modifications to prevent excess cost due to over-augmenting include stopping augmentation once the target population has been over augmented (i.e. $u(t) = 0$ when $x(t) \geq 1$), or placing a final time condition on the target population (i.e. $x(t_1) = 1 - \delta$ where $0 \leq \delta << 1$).

Our model places no restriction on what proportion of the reserve population can be translocated to the target population. However, it may be unreasonable to allow all the individuals in the reserve population to be moved. Thus, another reasonable modification is to consider a constraint that ensures the reserve population will be above its minimum threshold for growth by the final time, i.e. $y(t_1) \leq b$, or will be maintained above this throughout the entire period. Our model was for control in continuous time of species augmentation. However, in practice, species augmentation often happens in a discrete manner, moving individuals to the target population at discrete times. A discrete-time formulation of optimal augmentation presents somewhat different mathematical challenges, in part due to the fact that there are constraints associated with the time scale of allowed augmentation that may not match with the time scales of population growth (typically annual for many mammal species). We are unaware of any comparisons of continuous versus discrete time optimal control applied in a population management context, and the introduction of discrete-time may well lead to complex underlying model behavior as occurs for example in the discrete logistic model.

Associated with optimal augmentation strategies are the numerous issues which arise from introduction of more detailed assumptions about the underlying populations. Conclusions about population behavior may be quite different when complications such as population demographic structure and genetics are incorporated. We expect that expansion to include these aspects of population structure, though leading to quantitative population analyses that may be more readily applicable, would no doubt lead to more complex optimal strategies that may not be readily feasible (there would be controls associated with each population age class for example). So additional feasibility constraints might have to be placed on the control space. A quite different set of models would be necessary if the community-level aspects of augmentation strategies were to be considered. Optimal augmentation following our above results may be singularly unsuccessful if the augmented population were prey for a predator population with density-dependent impacts on the prey. This could arise for example if, once augmented, the prey population was in sufficiently high density as to lead to predator switching, perhaps due to an enhanced search image of the predator for this prey species now occurring at higher density. Similar problems may arise if the augmented population was the predator in the system, or if competitive interactions were involved. Thus, the work presented here is simply a first-step toward building a general theory of population augmentation which accounts for the complexities inherent in many conservation biology applications. One challenge in developing this theory is to account for the practical constraints faced by natural system managers in carrying out augmentation.

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