Order of events matter: comparing discrete models for optimal control of species augmentation

Erin N. Bodine*, Louis J. Grossb and Suzanne Lenhartc

aDepartment of Mathematics and Computer Science, Rhodes College, 2000 N. Parkway, Memphis, TN 38112, USA; bDepartments of Ecology and Evolutionary Biology and Mathematics, University of Tennessee, Knoxville, TN 37996-1610, USA; cDepartment of Mathematics, University of Tennessee, 227 Ayres Hall, 1403 Circle Drive, Knoxville, TN 37996-1320, USA

(Received 29 February 2012; final version received 15 May 2012)

We investigate optimal timing of augmentation of an endangered/threatened species population in a target region by moving individuals from a reserve or captive population. This is formulated as a discrete-time optimal control problem in which augmentation occurs once per time period over a fixed number of time periods. The population model assumes the Allee effect growth functions in both target and reserve populations and the control objective is to maximize the target and reserve population sizes over the time horizon while accounting for costs of augmentation. Two possible orders of events are considered for different life histories of the species relative to augmentation time: move individuals either before or after population growth occurs. The control variable is the proportion of the reserve population to be moved to the target population. We develop solutions and illustrate numerical results which indicate circumstances for which optimal augmentation strategies depend upon the order of events.

Keywords: species augmentation; translocation; optimal control theory; discrete-time difference equations; comparing discrete-time order of events; mathematical modelling; ecological applications

AMS Subject Classification: 49J21; 49N90; 92D40; 65Q10

1. Introduction

Over the past three decades, much of ecological research has focused on biodiversity. Despite the efforts of many to protect and sustain certain species and ecosystems, there are still over 16,000 species considered threatened or endangered [12]. 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’ and has also been called ‘stocking reintroduction’ [7]. 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 have been virtually no systematically developed theoretical or practical tools for studying and predicting the impact of species augmentation.

*Corresponding author. Email: bodinee@rhodes.edu
Author Emails: gross@tiem.utk.edu; lenhart@math.utk.edu

ISSN 1751-3758 print/ISSN 1751-3766 online
© 2012 Erin N. Bodine
http://dx.doi.org/10.1080/17513758.2012.697197
http://www.tandfonline.com
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 [29]. 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 [28]. A 2006 population viability analysis (PVA) of ocelots (Leopardus pardalis) found that a combination of different recovery strategies, including augmentation, are needed to reduce ocelot extinction probability [14]. Other studies recommending augmentation as a means to promote species recovery and prevent extinction include [15,16,21,24,25,35].

Augmentation is related to the introduction, or reintroduction, of a species into an area not currently occupied by the species. Reintroduction can involve reestablishment of a population in a location it formerly occupied but from which it had been extirpated, or it could be a new introduction that might be in response to changes in environment. Climate change might lead to range shifts of species, and in some instances require active efforts to relocate or reintroduce populations to account for shifts in environmental conditions [31]. Though different in detail, the modelling approach we develop here can be used to address reintroduction.

In addition to such recommendations for augmentation, 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 in Montana for an augmentation effort [33]. 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 2007, it was reported that there was genetic evidence that at least one of the original transplanted bears had reproduced [19]. In 2009, it was confirmed that one translocated female and her offspring were still in the target release area [38]. 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 [22]. Since the augmentation effort, the panther population has increased roughly from 30 individuals to almost 100 and there is no evidence that individuals with Texas panther ancestry have inbreeding-related defects [11,22,26].

Despite the growing need and use of species augmentation as a conservation tool, very few mathematical results or practical tools have been developed to study and predict the impact of species augmentation. The models developed to describe and predict the outcome of species augmentation, though potentially applicable to a wider range of species, do not attempt to develop any general mathematical theory for augmentation and instead focus solely on one species. Pfab and Witkowski [25] constructed a PVA which compared four management strategies, one of which was augmentation for the critically endangered succulent plant species Euphorbia clivicola confined to only two known populations in the Northern Province of South Africa. Hearne and Swart [15] constructed a nonlinear differential equation model of the black rhinoceros (Diceros bicornis) in South Africa for which their simulations gave an indication of the number and age of animals which should be translocated to maximize the growth rate of the total rhino population in southern Africa. Prior to the 1995 Florida panther augmentation, Hedrick [16] developed a population genetics model to evaluate the potential for genetic restoration via augmentation and its specific applicability to the Florida panther case. This model was then used as one of the justifications to proceed with the Florida panther augmentation project. Rout et al. [30] developed a stochastic population model of the bridled nailtail wallaby (Onychogalea fraenata) and used decision theory and stochastic dynamic programming to determine an optimal translocation strategy of how many wallabies to augment each
population, given the state of each population, in order to maximize the benefit to the entire species.

Optimal control theory has been applied to systems of ordinary differential equations and discrete-time difference equations, modelling a variety of population scenarios. See, for example, [13] for a predator-prey system, [32] for a harvesting problem for bears in a park-forest scenario, and [37] for control of pests. See the books by Eisen [10], Lenhart and Workman [40], and Sethi and Thompson [34] for other examples. Hearne and Swart [15] developed a model for the optimal translocation of an age-structured black rhino population, where the strategies of maximizing the translocation rate and maximizing the growth of a newly established population are compared. We present the first application of optimal control theory to model species augmentation in discrete time.

The scientific interest and ecological importance of species augmentation as a conservation tool merits the development of a general mathematical control framework for species augmentation which will provide mathematical modelers, ecologists, and natural resource managers with theory and tools for analysing control strategies in augmented systems. The approach we develop here is based on discrete-time dynamic optimization methods with continuous state variables. There is an extensive literature on discrete-state space and discrete-time optimization which has been applied to many population biology and behavioral ecology situations [8], utilizing statistical decision theory with dynamic programming as the solution method. There has also been considerable development of mathematical programming approaches for spatial optimization in spatially gridded systems and discrete-time control options [17,18]. Spatial considerations of reserve design have rarely considered the temporal aspects of augmentation despite considerable effort to take account of the impacts of spatial heterogeneity on the success of the design [39]. Which modelling approach is most appropriate will depend upon the context of the particular conservation problem, and the impact on order of interactions on optimal policies may depend upon the modelling approach taken.

In a discrete-time model, the order of events is crucial. See the book by Caswell [6] (Section 2.4.2) for a discussion about the timing of events and model structure for discrete models. For the augmentation models presented here, we are illustrating the effect of the order of events on results from optimal control actions. Though optimal control has been applied to a variety of discrete-time models, this is one of the first which compares the effects of different underlying orders of events on optimal control strategies and state dynamics [23,41].

In this paper, we investigate the optimal augmentation of an endangered/threatened species population in discrete time, where there are two possible orders of events at each discrete-time step. The objective is to investigate general issues of timing of augmentation relative to major components of organism life history, such as reproductive or breeding season, rather than to develop a particular case study. Our numerical results demonstrate that a difference in the order of events can lead to qualitatively different augmentation strategies, and qualitatively different short-term and long-term dynamics of the population involved in the augmentation. Thus, life history constraints interact with constraints arising from feasible conditions to carry out augmentation in determining the impacts of augmentation programs.

2. Optimal control of two models of species augmentation

We consider a system in which there are two populations of interest: \( N \), 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. For the reserve population to be a viable source from which to harvest individuals to augment the target population, it must be at equilibrium or growing at the initial time. Thus, in the absence of augmentation, the target and reserve populations
grow according to the logistic-type discrete difference equations

\[ N_{k+1} - N_k = rN_k \left( \frac{N_k}{K_N} - a \right) \left( 1 - \frac{N_k}{K_N} \right), \]  

\[ R_{k+1} - R_k = sR_k \left( \frac{R_k}{K_R} - b \right) \left( 1 - \frac{R_k}{K_R} \right) \]  

respectively, where \( N_k \) and \( R_k \) are the target and reserve population sizes at time step \( k \), \( r \) and \( s \) are the intrinsic growth rates of \( N \) and \( R \), respectively. The model is constructed such that, for \( N_k < aK_N \) and \( R_k < bK_R \), the endangered and reserve populations, respectively, are declining. This density-dependent population decline is known as the Allee effect.

2.1. The Allee effect

In the 1930s, Warder C. Allee wrote about the possibility of populations at low numbers having a positive relationship between any component of fitness and either the numbers or density of conspecifics [1,2,4,9,36]. Since then, this biological phenomenon has been referred to as the Allee effect. The general idea is that individuals in small populations will have lower reproduction and survival rates, but that these rates will increase with population size or density. The Allee effect is generally thought to disappear once population size or density is large enough and increased intraspecific competition (competition for resources among individuals within the population) occurs. The most obvious cause of the Allee effect in sexually reproducing species is the difficulty in finding mates at low-population sizes [4]. Other causes could be the necessity of a minimal group size for finding food, preventing predator attacks, and rearing offspring [4,9,36].

A distinction is made between what is known as a strong Allee effect and a weak Allee effect. Populations exhibiting a strong Allee effect have a critical population size or density, below which the growth rate of the population is negative and above which the population growth rate is positive. Populations exhibiting a weak Allee effect do not have this critical threshold [3].

Populations requiring augmentation are often populations small in size and on the decline. For endangered populations exhibiting a strong Allee effect, it is reasonable to assume that the populations are currently below some critical density and currently have a negative growth rate. If these populations could be augmented to be above the critical density, they would begin to grow on their own.

The underlying population model in Equations (1) and (2) is assumed to have both logistic growth and a strong Allee effect. For the remainder of this article, when we state that we are including the Allee effect, it is implied that we are using a strong Allee effect.

2.2. Order of events

In using discrete models, the order in which events take place is very important. For the underlying model described in Equations (1) and (2), there are two possibilities:

(I) At each time step, we harvest and augment, then let the populations grow;

(II) At each time step, we let the populations grow, then harvest and augment.

In some augmentation projects, it may be best to augment prior to the breeding season. In this case, the reserve population would be harvested and the target population augmented before the populations grow each year (i.e. prior to the breeding season an in Case I). Thus, in Case I, a single time step goes from just prior to the breeding season of 1 year to just prior to the breeding season of the next year. However, in other cases, wildlife managers may be limited to augmenting
when individuals become available, and this may result is a scenario more like Case II where the population is augmented after the breeding season. Thus, in Case II, a single time step goes from just after the breeding season in 1 year to just after the breeding season in the next year. These two different schemes for describing whether to augment before or after the breeding season are similar to the ‘postbreeding census’ and ‘prebreeding census’ schemes as described by Caswell [6].

We investigate how the change in the order will affect the optimal augmentation strategy and the short- and long-term population dynamics of both the target and reserve populations. In each case, we assume that the object of augmentation is to maximize the target population and the reserve population at a given final time \( T \), while minimizing the cost of translocating individuals from the reserve population to the target population. We assume that the total population \( (N + R) \) is to be maximized by the final time, with different relative weights applied to the reserve and target populations. We assume that it is not as important to maximize the reserve population as it is to maximize the target population at the final time. In each case, we have a vector of controls \( u = (u_0, \ldots, u_{T-1}) \), where \( u_k \) is the control applied (the fraction of the reserve population that is harvested and translocated to the target population) at time step \( k \).

### 2.3. Grow then augment

For this first model, we let the populations grow and then translocate individuals from the reserve population to the target population. Thus, the system in Equations (1) and (2) becomes

\[
N_{k+1} = N_k \left[ r \left( \frac{N_k}{K_N} - a \right) \left( 1 - \frac{N_k}{K_N} \right) + 1 \right] + u_k R_k \left[ s \left( \frac{R_k}{K_R} - b \right) \left( 1 - \frac{R_k}{K_R} \right) + 1 \right],
\]

\[
R_{k+1} = (1 - u_k) R_k \left[ s \left( \frac{R_k}{K_R} - b \right) \left( 1 - \frac{R_k}{K_R} \right) + 1 \right].
\]

Rescaling these two populations with respect to their carrying capacities \( x \equiv N_k/K_N \) and \( y \equiv R_k/K_R \) gives

\[
x_{k+1} = x_k [r(x_k - a)(1 - x_k) + 1] + pu_k y_k [s(y_k - b)(1 - y_k) + 1],
\]

\[
y_{k+1} = (1 - u_k) y_k [s(y_k - b)(1 - y_k) + 1],
\]

where \( p \equiv K_R/K_N \), that is, the ratio of the reserve carrying capacity to the endangered carrying capacity, and \( r \) and \( s \) are the intrinsic growth rates for the target and reserve populations, respectively. Thus, we have a vector for each state, \( x = (x_0, \ldots, x_T) \) and \( y = (y_0, \ldots, y_T) \), where \( x_k \) and \( y_k \) are the densities of the target and reserve populations, respectively, at time step \( k \), and the initial densities, \( x_0 \) and \( y_0 \), are known. Notice that since we are modelling population densities, we ignore issues that arise in discrete modelling with counting fractional individuals. 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 \( b \), that is, \( x_0 < a \) and \( y_0 > b \). Thus, the optimal control formulation is

\[
\max_{u \in U} \left[ x_T + By_T - \sum_{n=0}^{T-1} (A_1 u_n^2 + A_2 u_n) \right],
\]

where

\[
U = \{ u = (u_0, \ldots, u_{T-1}) | 0 \leq u_k \leq 0.9, k = 0, 1, \ldots, T - 1 \}
\]
As usual in discrete optimal control problems, the state vectors have one more component than the control vectors. Additionally, note that the maximum allowable value for $u_k$ is 0.9, indicating that at each time step, we can have no more than 90% of the entire reserve population at that time step.

We refer to the function being maximized as the objective functional, denoted

$$J(u) = x_T + By_T - \sum_{n=0}^{T-1} (A_1 u_n^2 + A_2 u_n).$$

Using this objective functional, we are maximizing the target population at the final time, minimizing the reserve population at the final time (but weighted by the constant $0 < B < 1$), and minimizing the cost associated with translocated individuals from the reserve population to the target population over the time steps $(0, 1, \ldots, T-1)$. The cost term $A_1 u_n^2$, which has quadratic dependence on $u_k$, accounts for nonlinear increases in the costs of translocation as the fraction translocated at a given time step increases. For example, the cost of labour to find and translocate suitable individuals may increase in a nonlinear fashion as more individuals are translocated at each time step since the time required to find one individual may increase nonlinearly as more individuals are sought per time step. The cost term $A_2 u_k$, which has linear dependence on $u_k$, accounts for linear increases in the costs of translocation as the fraction translocated at a given time step increases. For example, the cost of various supplies required to translocate one individual may be fixed, and thus this cost would increase linearly as the proportion of the reserve population being translocated per time step increased. Note that we assume $A_1 > 0$ and $A_2 \geq 0$.

Using a generalization of Pontryagin’s maximum principle [27], we can derive the necessary conditions that an optimal control and corresponding state must satisfy. These conditions are similar to when the underlying states are described using ordinary differential equations. We then use the necessary conditions to derive a characterization of the optimal control. The following theorem assumes that there exists an optimal control, which is valid since we have bounded controls and states for a finite number of time steps.

**Theorem 2.1** Suppose $u^* = (u_0^*, u_1^*, \ldots, u_{T-1}^*)$ is an optimal control vector containing the optimal control value $u_k^*$ at each time step $k$ for the optimal control formulation given in Equations (7)-(10). Let $x^* = (x_0^*, x_1^*, \ldots, x_T^*)$ and $y^* = (y_0^*, y_1^*, \ldots, y_T^*)$ be the corresponding state solutions. Then, there exists adjoint variables $\lambda_x = (\lambda_{x,0}, \lambda_{x,1}, \ldots, \lambda_{x,T})$ and $\lambda_y = (\lambda_{y,0}, \lambda_{y,1}, \ldots, \lambda_{y,T})$ such that

$$\lambda_{x,k} = \lambda_{x,k+1}[-3r(x_k^*)^2 + 2r(1 + a)x_k^* + (1 - ra)],$$

(12)

$$\lambda_{x,T} = 1,$$

(13)

$$\lambda_{y,k} = [pu_k^* \lambda_{x,k+1} + (1 - u_k^*) \lambda_{y,k+1}][-3s(y_k^*)^2 + 2s(1 + b)y_k^* + (1 - sb)],$$

(14)

$$\lambda_{y,T} = B.$$  

(15)

Furthermore, the optimal control is represented by

$$u_k^* = \min \left\{ 0.9, \max \left\{ 0, \frac{-A_2 + (p \lambda_{x,k+1} - \lambda_{y,k+1})[sy_k(b - y_k)(1-y_k)+y_k]}{2A_1} \right\} \right\}.$$  

(16)
Proof Suppose \( u^* = (u^*_0, u^*_1, \ldots, u^*_T) \) is an vector of optimal controls with corresponding states \( x^* = (x^*_0, x^*_1, \ldots, x^*_T) \) and \( y^* = (y^*_0, y^*_1, \ldots, y^*_T) \). Using Pontryagin’s maximum principle for optimal control formulations with discrete-time difference state equations \([34,40]\), the Hamiltonian is formed

\[
H_k = -A_1 u^2_k - A_2 u_k + \lambda_{x,k+1} x_k [r(x_k - a)(1 - x_k) + 1] + pu_k y_k s(y_k - b)(1 - y_k) + 1]
\]

and the adjoint equations are constructed

\[
\lambda_{x,k} = \frac{\partial H_k}{\partial x_k} = \lambda_{x,k+1} \{-3r(x^*_k)^2 + 2r(1 + a)x_k + (1 - ra)\},
\]

\[
\lambda_{y,k} = \frac{\partial H_k}{\partial y_k} = [pu_k^* \lambda_{x,k+1} + (1 - u^*_k)\lambda_{y,k+1}] \{-3sy^*_k^2 + 2s(1 + b)y_k + (1 - sb)\},
\]

and the transversality condition gives \( \lambda_{x,T} = 1 \) and \( \lambda_{y,T} = B \). The Hamiltonian differentiated with respect to the control is

\[
\frac{\partial H_k}{\partial u_k} = -2A_1 u_k - A_2 + (p\lambda_{x,k+1} - \lambda_{y,k+1}) y_k [s(y_k - b)(1 - y_k) + 1].
\]

For the given objective functional, we maximize the Hamiltonian with respect to \( u_k \).

On the set \( \{k | 0 < u^*_k < 0.9\} \), \( \frac{\partial H_k}{\partial u_k} = 0 \) at \( u^*_k \). Thus,

\[
\frac{\partial H_k}{\partial u_k} = -2A_1 u_k - A_2 + (p\lambda_{x,k+1} - \lambda_{y,k+1}) y_k [s(y_k - b)(1 - y_k) + 1] = 0
\]

\[
\implies u^*_k = \frac{-A_2 + (p\lambda_{x,k+1} - \lambda_{y,k+1}) y_k [s(y_k - b)(1 - y_k) + 1]}{2A_1}
\]

When \( \frac{\partial H_k}{\partial u_k} < 0 \), then \( u^*_k = 0 \) and

\[
-A_2 + (p\lambda_{x,k+1} - \lambda_{y,k+1}) y_k [s(y_k - b)(1 - y_k) + 1] < 0
\]

\[
\implies \frac{-A_2 + (p\lambda_{x,k+1} - \lambda_{y,k+1}) y_k [s(y_k - b)(1 - y_k) + 1]}{2A_1} < 0
\]

since \( A_1 > 0 \).

When \( \frac{\partial H_k}{\partial u_k} > 0 \), then \( u^*_k = 0.9 \) and

\[
-2A_1 - A_2 + (p\lambda_{x,k+1} - \lambda_{y,k+1}) y_k [s(y_k - b)(1 - y_k) + 1] > 0
\]

\[
\implies \frac{-A_2 + (p\lambda_{x,k+1} - \lambda_{y,k+1}) y_k [s(y_k - b)(1 - y_k) + 1]}{2A_1} > 1.
\]

Combining the cases when \( u^*_k = 0, 0 < u^*_k < 0.9, \) and \( u^*_k = 0.9 \), we find the characterization of optimal control is

\[
u^*_k = \min \left\{ 0.9, \max \left\{ 0, \frac{-A_2 + (p\lambda_{x,k+1} - \lambda_{y,k+1}) [s(y_k - b)(1 - y_k) + y_k]}{2A_1} \right\} \right\}.\]

\[\square\]
2.4. Augment then grow

To model the scenario where we harvest and augment first and then let the populations grow, the results after augmentation, $N_k + u_k R_k$ and $R_k - u_k R_k$, are substituted into their respective growth functions (Equations (1) and (2)),

$$
N_{k+1} = (N_k + u_k R_k) \left[ r \left( \frac{N_k + u_k R_k}{K_N} - a \right) \left( 1 - \frac{N_k + u_k R_k}{K_N} \right) + 1 \right],
$$

$$
R_{k+1} = (R_k - u_k R_k) \left[ s \left( \frac{R_k - u_k R_k}{K_R} - b \right) \left( 1 - \frac{R_k - u_k R_k}{K_R} \right) + 1 \right].
$$

Rescaling these two populations with respect to their carrying capacities ($x_k \equiv N_k/K_N$ and $y_k \equiv R_k/K_R$) gives

$$
x_{k+1} = (x_k + pu_k y_k) [r(x_k + pu_k y_k - a)(1 - x_k - pu_k y_k) + 1],
$$

$$
y_{k+1} = (y_k - u_k y_k) [s(y_k - u_k y_k - b)(1 - y_k + u_k y_k) + 1].
$$

where $p \equiv K_R/K_N$, that is, the ratio of the reserve carrying capacity to the endangered carrying capacity. Again, 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 $b$, that is, $x_0 < a$ and $y_0 > b$. Thus, the optimal control formulation is given by Equations (7) and (8), and for $k = 0, 1, \ldots, T - 1$

$$
x_{k+1} = (x_k + pu_k y_k) [r(x_k + pu_k y_k - a)(1 - x_k - pu_k y_k) + 1], \quad x_0 < a,
$$

$$
y_{k+1} = (y_k - u_k y_k) [s(y_k - u_k y_k - b)(1 - y_k + u_k y_k) + 1], \quad y_0 > b.
$$

Notice that the objective functional $J(u)$ is the same as the grow then augment model, see Equation (11). Again, we will assume $A_1 > 0$ and $A_2 \geq 0$.

In order to utilize Pontryagin’s maximum principle, the Hamiltonian, $H_k$, must satisfy the concavity condition

$$
\frac{\partial^2 H_k}{\partial u_k^2} \leq 0
$$

for all time steps $k$ [5]. Note that for the case of grow then augment, where the Hamiltonian is given by Equation (17), this condition is obviously satisfied since

$$
\frac{\partial^2 H_k}{\partial u_k^2} = -2A_1
$$

for all time steps $k$ and $A_1 > 0$.

Were we to use Pontryagin’s maximum principle to determine a characterization for the optimal control, we would have to construct the Hamiltonian function

$$
H_k = -A_1 u_k^2 - A_2 u_k + \lambda_{x,k+1} (x_k + pu_k y_k) [r(x_k + pu_k y_k - a)(1 - x_k - pu_k y_k) + 1] + \lambda_{y,k+1} (1 - u_k) y_k [s((1 - u_k) y_k - b)(1 - (1 - u_k) y_k) + 1],
$$

(26)
Thus, we can write the Hamiltonian as

\[ (x_k + pu_k y_k) [r(x_k + pu_k y_k - a)(1 - x_k - pu_k y_k) + 1] \]
\[ = -rx_k^2 + r(1 + a)x_k^2 + (1 - ra)x_k \]
\[ + [-3rx_k^2 + 2r(1 + a)x_k + (1 - ra)]pu_k y_k \]
\[ - [3rx_k - r(1 + a)]p^2 u_k^2 y_k^2 - rp^3 u_k^3 y_k^3. \]

Expanding the product after \( \lambda_{y,k+1} \) in Equation (26), we get

\[ (y_k - u_k y_k) [s(y_k - u_k y_k - b)(1 - y_k + u_k y_k) + 1] \]
\[ = -sy_k^2 + s(1 + b)y_k^2 + (1 - sb)y_k + [3sy_k^2 - 2s(1 + b)y_k^2 - (1 - sb)y_k]u_k \]
\[ - [3sy_k^2 - s(1 + b)y_k^2]a_k + su_k^3 y_k^3. \]

Thus, we can write the Hamiltonian as

\[ H_k = -A_1 u_k^2 - A_2 u_k + \lambda_{x,k+1} [-rx_k^2 + r(1 + a)x_k^2 + (1 - ra)x_k \]
\[ + [-3rx_k^2 + 2r(1 + a)x_k + (1 - ra)]pu_k y_k - [3rx_k - r(1 + a)]p^2 u_k^2 y_k^2 - rp^3 u_k^3 y_k^3] \]
\[ + \lambda_{y,k+1} [-sy_k^2 + s(1 + b)y_k^2 + (1 - sb)y_k + [3sy_k^2 - 2s(1 + b)y_k^2 - (1 - sb)y_k]u_k \]
\[ - [3sy_k^2 - s(1 + b)y_k^2]a_k + su_k^3 y_k^3] \] \quad (27)

Now, let

\[ f_{A,k}(x_k, y_k, \lambda_{x,k+1}, \lambda_{y,k+1}) = -rp^3 \lambda_{x,k+1} y_k^3 + s\lambda_{y,k+1} y_k^3, \]
\[ f_{B,k}(x_k, y_k, \lambda_{x,k+1}, \lambda_{y,k+1}) = A_1 + \lambda_{x,k+1} [3rx_k - r(1 + a)]p^2 y_k^2 + \lambda_{y,k+1} [3sy_k - s(1 + b)]y_k^2, \]
\[ f_{C,k}(x_k, y_k, \lambda_{x,k+1}, \lambda_{y,k+1}) = -A_2 + \lambda_{x,k+1} [-3rx_k^2 + 2r(1 + a)x_k + (1 - ra)]py_k \]
\[ + \lambda_{y,k+1} [3sy_k^2 - 2s(1 + b)y_k - (1 - sb)]y_k, \]
\[ f_{D,k}(x_k, y_k, \lambda_{x,k+1}, \lambda_{y,k+1}) = \lambda_{x,k+1} [-rx_k^2 + r(1 + a)x_k^2 + (1 - ra)x_k] \]
\[ + \lambda_{y,k+1} [-sy_k^3 + s(1 + b)y_k^2 + (1 - sb)y_k]. \]

Thus, we can rewrite the Hamiltonian as

\[ H_k = f_{A,k} u_k^3 - f_{B,k} u_k^2 + f_{C,k} u_k + f_{D,k} \] \quad (28)

The second derivative of the Hamiltonian at time step \( k \) with respect to the control at time step \( k \) using the form of the Hamiltonian given in Equation (28) is

\[ \frac{\partial^2 H_k}{\partial u_k^2} = 6f_{A,k} u_k - 2f_{B,k}. \] \quad (29)

Since we cannot guarantee that

\[ \frac{\partial^2 H_k}{\partial u_k^2} \leq 0 \]

for all parameter sets, we cannot utilize Pontryagin’s maximum principle for this particular control problem. See [5] for an example in which the optimal control does not maximize the Hamiltonian with respect to the controls due the lack of concavity. Thus, we turn to alternative numerical methods to solve our optimal control problem.
3. Numerical methods

3.1. Grow then augment

The optimal control can be numerically calculated under various parameter sets using a discrete-time version of the forward–backward sweep method. An initial guess is made for the vector of optimal controls, \( u = (u_0, u_1, \ldots, u_{T-1}) \). Using the initial guess for \( u \), we then solve for \( x = (x_0, x_1, \ldots, x_T) \) and \( y = (y_0, y_1, \ldots, y_T) \) using Equations (9) and (10) and the given initial conditions \( x_0 \) and \( y_0 \). Then, using the vectors \( u, x, \) and \( y \), we solve for \( \lambda_x = (\lambda_{x,0}, \lambda_{x,1}, \ldots, \lambda_{x,T}) \) and \( \lambda_y = (\lambda_{y,0}, \lambda_{y,1}, \ldots, \lambda_{y,T}) \) using Equations (12) and (14) with transversality conditions \( \lambda_{x,T} = 1 \) and \( \lambda_{y,T} = B \). At this point, the optimal control is updated using the characterization for the optimal control, Equation (16), and the vectors for the state and adjoint variables. This updated control replaces the initial control and the process is repeated until the successive iterates of control vectors are sufficiently close. See the book by Kelley [20] for iterative methods for discrete control problems.

3.2. Augment then grow

Due to the fact that we cannot utilize Pontryagin’s maximum principle, we must resort to a numerical method that directly maximizes the objective functional,

\[
J(u) = x_T + By_T - \sum_{n=0}^{T-1}(A_1 u_n^2 + A_2 u_n).
\]

We discretize the range of the control and search for the control that maximizes \( J \). To accomplish this, we first define how fine the control space \( U \) will be discretized. Recall, each \( u_k \) must be in the interval \([0, 0.9]\), for \( k = 0, \ldots, T - 1 \). Let \( n \) be the number of discrete values of \( u_k \) in the interval \([0, 0.9]\), and let

\[
h = \frac{0.9 - 0}{n - 1} = \frac{0.9}{n - 1}.
\]

Thus, given an \( n \), the possible discrete values for \( u_k \) are given in the set

\[
U_{\text{mesh}} = \{0, h, 2h, 3h, \ldots, (n-2)h, 0.9\}.
\]

Next, evaluate the objective functional for all possible permutations of the components of \( u \). If, for example, \( T = 5 \) and \( n = 10 \), then

\[
u = (u_0, u_1, u_2, u_3, u_4),
\]

and there are \( 5^{10} = 9,765,625 \) possible permutations for \( u \). Note, the objective functional depends not only on \( u \), but also on \( x_T \) and \( y_T \). Thus, given a permutation of \( u \), we first solve for \( x_T \) and \( y_T \) using Equations (23) and (24), respectively. Then, using \( x_T \), \( y_T \), and \( u \), we evaluate \( J(u) \). In evaluating the objective functional for each \( u \), we can determine which \( u \) maximizes the objective functional. For this numerical method, the vector \( u \) that maximizes the objective functional will be referred to as the optimal control. For a problem with more time steps or a much finer mesh for \( U_{\text{mesh}} \), a more efficient numerical algorithm will be needed.

4. Numerical results

In considering various parameter scenarios, the parameter constraints \( x_0 < a \) and \( y_0 > b \) must be included. For the examples included here, we take the minimum threshold for growth for both the
target and reserve populations to be 0.3 (that is 30\% of each population’s carrying capacity) with $x_0 = 0.25$ and $y_0 = 0.7$. 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. For each of the following scenarios, we use the parameters $a = 0.30, b = 0.30, x_0 = 0.25, y_0 = 0.70, p = 1$ and vary the values of the parameters $r, s, A_1, A_2,$ and $B$. Additionally, in each the scenarios, we assume $T = 5$, where the units of $T$ correspond to the length of time from the start of one breeding season to the start of the next breeding season. We do not attempt here to display an exhaustive analysis of all parameter sets, but instead to highlight parameter scenarios for which the different order of events in the two models (grow then augment vs. augment then grow) can lead to different qualitative outcomes.

Finally, in each of the scenarios where the population is modelled by the augment then grow model, we let $n = 19$ which corresponds to $h = 0.05$, and thus

$$U_{\text{mesh}} = \{0, 0.05, 0.10, \ldots, 0.85, 0.90\}.$$ 

Since we are considering small population sizes, it is reasonable to consider 5\% increments of $u_k$. For a small population, moving some small percentage (< 5\%) would correspond to moving one individual. Furthermore, since we are looking for qualitative results, requiring a finer mesh for $U_{\text{mesh}}$ is unnecessary.

### 4.1. Scenario 1: Qualitatively different optimal augmentation strategies

In the first parameter scenario we considered, we let $a = 0.30, b = 0.30, r = 0.30, s = 0.70, p = 1, x_0 = 0.25, y_0 = 0.70, A_1 = 0.10, A_2 = 0.50,$ and $B = 0.25$ (Figure 1). Thus, in this scenario some of the cost of augmentation is quadratic with respect to the control ($A_1 = 0.10$), while some of the cost is linear ($A_2 = 0.50$). Additionally, the value of $B = 0.25$ indicates that it is 25\% as important to maximize the reserve population at the final time as it is to maximize the target population at the final time.

Figure 1(a) shows the target and reserve populations, along with the optimal control at each time step when the grow then augment model is used. Note that the values for the optimal control in this scenario (grow then augment) are

$$u = [0.10 \ 0.10 \ 0.10 \ 0.09 \ 0.09],$$

and thus a low level of augmentation occurs at each time step. For time steps $k = 0, 1,$ and 2, 10\% of the reserve population is translocated to the target population, and at time steps $k = 3$ and 4, 9\% of the reserve population is translocated. This maintained low level of augmentation is enough to augment the target population such that it rises above its minimum threshold for growth, $a = 0.3$ (see dashed black line in Figure 1(a)) by $k = 1$, and above 60\% of its carrying capacity by the final time $T = 5$.

Figure 1(b) shows the target and reserve populations, along with the optimal control at each time step when the augment then grow model is used. Note that the values for the optimal control in this simulation (augment then grow) are

$$u = [0.00 \ 0.00 \ 0.00 \ 0.50 \ 0.00],$$

and thus the only augmentation occurs at time step $k = 3$ when 50\% of the reserve population is translocated to the target population. As with the grow then augment simulation (Figure 1(a)), we see that the augmentation leads to both the target and reserve populations being above their minimum thresholds for growth ($a = b = 0.30$) at the final time.
Figure 1. Simulations for the discrete optimal control of augmentation where the population (a) grows and then is augmented at each time step and (b) the populations is augmented before growth in each time step. In both simulations, the parameters are $a = 0.30, b = 0.30, r = 0.30, s = 0.70, p = 1, x_0 = 0.25, y_0 = 0.70, A_1 = 0.10, A_2 = 0.50$, and $B = 0.25$. The graphs on the left show the density of the target (red) and reserve (blue dashed) populations at each time step. The graphs on the right show the proportion of the reserve population used to augment the target population at each time step. Note that the values for the optimal control are (a) $u = [0.10 0.10 0.10 0.09 0.09]$ and (b) $u = [0.00 0.00 0.00 0.50 0.00]$. (a) Grow then augment and (b) augment then grow.

When we compare the optimal controls for Figure 1(a) and (b), we find that they are qualitatively different. When the underlying model allows the population to grow before augmenting at each time step, the qualitative optimal control strategy in this parameter scenario is to maintain a low level of augmentation at each time step. However, when the underlying model augments the population before population growth occurs in each time step, the qualitative optimal control strategy in this parameter scenario is to only augment at one time step, $k = 3$. Thus, this parameter set demonstrates that a difference in the order of events of the underlying model for the optimal control formulation, can lead to qualitatively different optimal control strategies. It should be noted that when many other parameter scenarios were explored, the majority of them led to optimal control strategies which were generally qualitatively similar. However, there was no obvious parameter trend or parameter threshold to indicate when the optimal strategies would be qualitatively similar or different.
4.2. Scenario 2: Qualitatively different short-term population dynamics post augmentation

In the second parameter scenario we considered, we let $a = 0.30$, $b = 0.30$, $r = 0.25$, $s = 1.20$, $p = 1$, $x_0 = 0.25$, $y_0 = 0.70$, $A_1 = 1$, $A_2 = 0$, and $B = 0$ (Figure 2). Thus, in this scenario, the cost of augmentation is strictly quadratic with respect to the control ($A_1 = 1$), with none of the cost being linear ($A_2 = 0$). Additionally, the value of $B = 0$ indicates that there is no importance given to maximizing the reserve population at the final time.

Figure 2(a) shows the target and reserve populations, along with the optimal control at each time step when the grow then augment model is used. Note that the values for the optimal control

![Figure 2(a)](image1)

**Figure 2.** Simulations for the discrete optimal control of augmentation where the population (a) grows and then is augmented at each time step and (b) the population is augmented before growth in each time step. In both simulations, the parameters are $a = 0.30$, $b = 0.30$, $r = 0.25$, $s = 1.20$, $p = 1$, $x_0 = 0.25$, $y_0 = 0.70$, $A_1 = 1$, $A_2 = 0$, and $B = 0$. The graphs on the left show the density of the target (red) and reserve (blue dashed) populations at each time step. The graphs on the right show the proportion of the reserve population used to augment the target population at each time step. Note that the values for the optimal control are (a) $u = [0.13 \ 0.14 \ 0.16 \ 0.21 \ 0.34]$ and (b) $u = [0.10 \ 0.10 \ 0.15 \ 0.20 \ 0.30]$. (a) Grow then augment and (b) augment then grow.
in this scenario (grow then augment) are

\[ u = [0.13\ 0.14\ 0.16\ 0.21\ 0.34], \]

and thus the augmentation starts at a low level and slowly rises over each of the time steps. This optimal augmentation strategy is such that the target population is augmented such that it rises above its carrying capacity by the final time, that is, \( x_T > 1 \). We refer to this type of strategy as ‘over-augmenting’ the target population. This is likely due to the relatively high intrinsic growth rate of the reserve population (\( s = 1.2 \)). Since the reserve population is able to sufficiently replace harvested individuals at each time step, the density of the reserve population remains high, and thus the total number of individuals translocated at each time step is large; large enough to over-augment the target population by the final time.

Figure 2(b) shows the target and reserve populations, along with the optimal control at each time step when the augment then grow model is used. Note that the values for the optimal control in this simulation (augment then grow) are

\[ u = [0.10\ 0.10\ 0.15\ 0.20\ 0.30], \]

that is, at time steps \( k = 0, 1 \), 10\% of the reserve population is translocated to the target population, at time steps \( k = 2, 3, 4 \), 15\%, 20\%, and 30\%, are translocated, respectively. Thus, like in Figure 1(a), we see that the optimal augmentation strategy is to start augmenting at a low level and slowly increase the level of augmentation over each of the time steps. This optimal augmentation strategy leads to both the target and reserve populations being above their minimum thresholds for growth (\( a = b = 0.30 \)) at the final time. However, for this underlying model (augment then grow), the target population is not over-augmented, that is, \( a < x_T < 1 \).

When we compare the optimal controls for Figure 2(a) and (b), we find that, though the optimal augmentation strategies are qualitatively similar, they lead to different short-term population dynamics after the final time \( T = 5 \). When the underlying model is to grow then augment, at the final time, the target population is above its carrying capacity and the reserve population is above its minimum threshold for growth but below its carrying capacity. Thus, if it is still appropriate to model the populations using the underlying population model given in Equations (1) and (2), then for time steps beyond \( T = 5 \), the target population will decline towards its carrying capacity, while the reserve population increases towards its carrying capacity. However, when the underlying model is augment then grow, at the final time, both the target and reserve populations are between their minimum threshold for growth and their carrying capacities. Thus, for time steps beyond \( T = 5 \), both the target and reserve populations will grow towards their carrying capacity. Thus, we see this difference in short-term dynamics given the order of events at each time step in the underlying model. In one case, we will see a small decline in the target population after the augmentation strategy is implemented (grow then augment), and in the other case, we will see the target population to continue to increase after the optimal augmentation strategy is implemented (augment then grow).

### 4.3. Scenario 3: Qualitatively different long-term population dynamics post augmentation

In the third parameter scenario we considered, we let \( a = 0.30,\ b = 0.30,\ r = 0.25,\ s = 0.30,\ p = 1,\ x_0 = 0.25,\ y_0 = 0.70,\ A_1 = 1,\ A_2 = 0,\ \text{and}\ B = 0 \) (Figure 3). Thus, in this scenario, all the parameters are the same as in the previous scenario, except the intrinsic growth rate of the reserve population which has been lowered to \( s = 0.30 \). Therefore, in this parameter scenario, the reserve population will not be able to replace harvested individuals as quickly as in the previous parameter scenario when \( s = 1.20 \).
Figure 3. Simulations for the discrete optimal control of augmentation where the population (a) grows and then is augmented at each time step and (b) the populations is augmented before growth in each time step. In both simulations, the parameters are \(a = 0.30, b = 0.30, r = 0.25, s = 0.30, p = 1, x_0 = 0.25, y_0 = 0.70, A_1 = 1, A_2 = 0,\) and \(B = 0.\) The graphs on the left show the density of the target (red) and reserve (blue dashed) populations at each time step. The graphs on the right show the proportion of the reserve population used to augment the target population at each time step. Note that the values for the optimal control are (a) \(u = [0.19\ 0.18\ 0.18\ 0.18\ 0.18]\) and (b) \(u = [0.20\ 0.20\ 0.20\ 0.15\ 0.15]\). (a) Grow then augment and (b) augment then grow.

Figure 3(a) shows the target and reserve populations, along with the optimal control at each time step when the grow then augment model is used. Note that the values for the optimal control in this scenario (grow then augment) are

\[ u = [0.19\ 0.18\ 0.18\ 0.18\ 0.18], \]

and thus a low to moderate level of augmentation occurs at each time step. Specifically, at time step \(k = 1,\) 19% of the reserve population is translocated to the target population, and at each remaining time step, 18% is translocated. This optimal augmentation strategy leads to the target population being above its minimum threshold but below its carrying capacity by the final time,
that is, $a < x_T < 1$. However, for this parameter scenario, the optimal augmentation strategy leads to the reserve population being at its minimum threshold for growth at the final time, that is, $y_T = b$.

Figure 3(b) shows the target and reserve populations, along with the optimal control at each time step when the augment then grow model is used. Note that the values for the optimal control in this simulation (augment then grow) are

$$u = [0.20 \ 0.20 \ 0.20 \ 0.15 \ 0.15],$$

and thus a low to moderate level of augmentation occurs at each time step with the amount decreasing for time steps $k = 3, 4$. This optimal augmentation strategy leads to the target population being above its minimum threshold but below its carrying capacity by the final time, that is, $a < x_T < 1$. However, for this parameter scenario, the optimal augmentation strategy leads to the reserve population being below its minimum threshold for growth at the final time, that is, $y_T < b$.

When we compare the optimal controls for Figure 3(a) and (b), we find that, though the optimal augmentation strategies are qualitatively similar, they lead to different long-term population dynamics and different population outcomes after the final time $T = 5$. If we assume that the underlying population model given in Equations (1) and (2) holds for each population after the period of augmentation ($k = [0, 1, 2, 3, 4, 5]$), then we can analyse the long-term dynamics of each population after the final time $T = 5$. When the underlying model during augmentation is to grow then augment, at the final time, the target population is between its minimum threshold for growth and its carrying capacity, while the reserve population is at its minimum threshold for growth. Thus, the target population will continue to increase to its carrying capacity, while the reserve population remains at the equilibrium $y = b$, its minimum threshold for growth. However, when the underlying model during augmentation is to augment then grow, at the final time, the target population is between its minimum threshold for growth and its carrying capacity, while the reserve population is below its minimum threshold for growth. Thus, the target population will continue to increase to its carrying capacity, while the reserve population declines to extinction. Therefore, depending on the order of events at each time step, this parameter scenario may lead to the reserve population being maintained at its minimum threshold for growth or may lead to the reserve population becoming extinct – two very different population outcomes.

5. Conclusions and future directions

The three parameter scenarios explored in Section 3 illustrated three ways in which having a different order of events in the underlying population model of the optimal control formulation can lead to qualitatively different results.

The scenarios in Figure 1 demonstrate how qualitatively different optimal augmentation strategies arise. When many other parameter scenarios were explored, the majority of them led to optimal control strategies which were qualitatively similar. However, there was no obvious parameter trend or parameter threshold to indicate when the optimal strategies would be qualitatively similar or different. Thus, for natural resource managers considering implementing species augmentation, it is important that they know which order of events best describes the populations they are considering augmenting, how they plan to perform the augmentation, and to then carefully explore different parameter scenarios.

The scenarios in Figure 2 demonstrate how order of events can lead to a difference in the short-term dynamics of the target population. The optimal control formulation presented here allowed for the possibility of over-augmenting the target population. When natural resource managers
are considering different augmentation strategies, it may be more financially prudent to seek a strategy which does not over-augment the target population, as this could be viewed as a waste of resources. One possible extension of this optimal control formulation would be to impose a condition which did not allow for the target population to be augmented above $x_k = 1$ for any given $k$. Imposing a condition of this type would resolve the issue of over-augmenting the target population, but would likely lead to qualitatively different optimal control strategies.

The scenarios in Figure 3 demonstrate how order of events can lead to a difference in the long-term dynamics of the reserve population. Note that the optimal control formulation did not place a restriction on harvesting individuals from the reserve population. The only parameter controlling the proportion harvested from the reserve population was $B$, the weight which indicated the relative importance of maximizing the reserve population with respect to the target population. A possible extension of this optimal control formulation would be to impose a condition so that the reserve population cannot be harvested below its minimum threshold for growth, that is, $y_k > b$ for all $k$. This condition would remove the possibility of the reserve population becoming extinct, however, there may be a trade-off in some parameter scenarios where the target population can then not be sufficiently augmented such that it rises above its minimum threshold for growth by the final time. Additionally, we would expect this condition to lead to qualitatively different optimal control strategies.

The methods we utilized to obtain results on the impact of order of events on optimal augmentation can readily be extended to situations involving more complex life histories. The assumptions we made were constrained to whether population growth (e.g. birth pulses) occurred before or after augmentation. This is directly connected to considerations of demographic structure and decisions about what age or size groups to translocate, seasonal aspects of birth pulses, and the sexual status of those being translocated. There are no inherent modelling constraints in extending our approach to incorporate expanded life history considerations, though the solution techniques would become more elaborate. Similarly, our emphasis here was on augmentation rather than reintroduction. Our approach inherently allows for consideration of reintroduction (or introduction if the species had not previously been present at the new location) by allowing for a time and magnitude for translocation of an initial population to the new location (i.e. $x_0 = 0$).

The methods we develop here can readily be expanded to incorporate alternative criteria for optimization. We considered only final time maximization of the target and reserve populations accounting for costs of translocation throughout the final time period. This inherently assumes that there is public concordance on a time horizon over which the planning process for conservation of the species should be considered. It is possible that such concordance is not possible and therefore an optimization criteria that incorporates benefits for target populations at various times would be appropriate. This expansion of the control methodology we developed is straightforward though potentially more computationally demanding. Another consideration we do not include is the possibility of a major external (to the model) event, such as a disease outbreak or a major storm, which could significantly reduce the target or reserve population. While this could be framed in a stochastic model, and develop risk assessments for recovery from such events, this would require explicit assumptions about the probability distributions for catastrophic event occurrences that may well be difficult to obtain. Model analysis could readily be expanded to incorporate probability of such events in a stochastic control framework, though the analysis then becomes considerably more complex and a variety of trade-offs would need to be incorporated in the optimization criteria. This would typically take into account a mean–variance trade-off for mean population sizes minus a ‘cost’ associated with high variance in population sizes. Alternatively, one could investigate a model in which the control represents the number of individuals to be translocated. Perhaps, integer programming would be an alternate reasonable solution technique to consider [17,18].
Finally, the optimization approach we consider here is intended to provide a basis for comparison of the impacts of alternative population management schemes relative to the ‘best’ that might be feasible to accomplish. Managers developing augmentation schemes would typically have a limited set of possibilities under consideration, due to many constraints that are not reflected in our model. We do not incorporate the many constraints on effort and funding that limit feasible conservation actions. These constraints would be expected to vary considerably with particular species and circumstances, and incorporating them would involve development of a more realistic, and less general framework. What our methods provide is the ability to compare how timing impacts augmentation and estimates of how far from ‘optimal’ a particular more constrained augmentation program might be.

Acknowledgements

The authors thank Simon Levin for his inspiration over many years to foster the development and application of mathematical methods in both fundamental and applied ecology. This work was supported in part by funding from the National Science Foundation through award IIS-0427471 to the University of Tennessee. This work was assisted by attendance by E.N.B. as a short-term Visitor and for S.L. and L.J.G. through support at the National Institute for Mathematical and Biological Synthesis, an Institute sponsored by the National Science Foundation, the US Department of Homeland Security, and the US Department of Agriculture through NSF Award #EF-0832858, with additional support from The University of Tennessee, Knoxville.

References

[1] W.C. Allee, Animal Aggregations: A Study in General Sociology, University of Chicago Press, Chicago, 1931.
[2] W. Allee, The Social Life of Animals, William Heinemann, London, 1938.
[3] L. Berec, E. Angulo, and F. Courchamp, Multiple Allee effects and population management, Trends Ecol. Evol. 22 (2007), pp. 185–191.
[4] D.S. Boukal and L. Berec, Single-species models of the Allee effect: Extinction boundaries, sex ratios and mate encounters, J. Theoret. Biol. 218 (2002), pp. 375–394.
[5] M.D. Canon, C.D. Cullum, Jr., and E. Polak, Theory of Optimal Control and Mathematical Programming, McGraw-Hill Series in Systems Science, McGraw-Hill, New York, 1970.
[6] H. Caswell, Matrix Population Models, Sinauer Associates, Sunderland, MA, 2001.
[7] S.M. Cheyne, Wildlife reintroduction: Considerations of habitat quality at the release site, BMC Ecol. 6 (2006).
[8] C.W. Clark and M. Mangel, Dynamic State Variable Models in Ecology: Methods and Applications, Oxford Series in Ecology and Evolution, Oxford University Press, 2000.
[9] F. Courchamp, T. Clutton-Brock, and B. Grenfell, Inverse density dependence and the Allee effect, Trends Ecol. Evol. 14 (1999), pp. 405–410.
[10] M. Eisen, Mathematical Methods and Models in the Biological Sciences, Prentice Hall, Englewood Cliffs, NJ, 1988.
[11] Florida Fish and Wildlife Conservation Commission, Annual report on the research and management of florida panthers: 2005–2006, Tech. rep., Fish and Wildlife Research Institute & Division of Habitat and Species Conservation, Naples, Florida, USA, 2006, available at http://www.panther.state.fl.us/news/pdf/PantherAR2005_2006.pdf.
[12] Global Environmental Outlook 4: Environment for Development Report, Tech. rep., United Nations Environmental Programme, 2007, available at http://www.unep.org/geo/GE04/report/GE04_Report_Full_en.pdf.
[13] B. Goh, G. Leitmann, and T. Vincent, Optimal control of a prey-predator system, Math. Biosc. 19 (1974), pp. 263–286.
[14] A.M. Haines, M.E. Tewes, L.L. Laack, J.S. Horne, and J.H. Young, A habitat-based population viability analysis for ocelots (Leopardus pardalis) in the United States, Biol. Conservat. 132 (2006), pp. 424–436.
[15] J. Hearne and J. Swart, Optimal translocation strategies for saving the black rhino, Ecol. Model. 59 (1991), pp. 279–292.
[16] P.W. Hedrick, Gene flow and genetic restoration: The florida panther as a case study, Conservat. Biol. 9 (1995), pp. 996–1007.
[17] J. Hof and M. Bevers, Spatial Optimization for Managed Ecosystems, Columbia University Press, New York, 1998.
[18] J. Hof and M. Bevers, Spatial Optimization in Ecological Applications, Columbia University Press, New York, 2002.
[19] W.F. Kasworm, M.F. Proctor, and C. Servheen, Success of grizzly bear population augmentation in Northwestern Montana, J. Wildlife Manag. 71 (2007), pp. 1261–1266, available at http://www.forestry.umt.edu/research/MFCES/programs/GrizzlyBearRecovery/Kasworm.
[20] C. Kelley, Iterative Methods for Optimization, SIAM, Philadelphia, 1999.
[21] N. Kingston, S. Waldren, and N. Smyth, Conservation genetics and ecology of Angiopteris chauliodonta Copel. (Marattiaceae), a critically endangered fern from Pitcairn Island, South Central Pacific Ocean, Biol. Conservat. 117 (2004), pp. 309–319.
[22] D. Land, M. Cunningham, M. Lotz, and D. Shindle, *Florida panther annual report 2004-05*, Tech. rep., Florida Fish and Wildlife Conservation Commission, Tallahassee, Florida, 2005, available at http://myfwc.com/panther/news/pdf/2003-2004PantherGeneticRestorationAnnualReportFinal9-28-04.pdf.

[23] S. Lenhart and P. Zhong, *Investigating the order of events in optimal control of integrodifference equations*, in Systems Theory: Modeling, Analysis and Control, A.E. Jal, L. Affi, and E.H. Zerrik, eds., Presses Universitaires de Perpignan, Perpignan, France, 2009, pp. 89–100.

[24] D. Maes, W. Vanreusel, W. Talloen, and H. Van Dyck, *Functional conservation units for the endangered Alcon Blue Butterfly Maculinea Alcon in Belgium (Lepidoptera: Lycaenidae)*, Biol. Conservat. 120 (2004), pp. 229–241.

[25] M. Pfaf and E. Witkowski, *A simple population viability analysis of the critically endangered Euphorbia clivicola R.A. Dyer under four management scenarios*, Biol. Conservat. 96 (2000), pp. 263–270.

[26] S.L. Pimm, L. Dollar, and O.L.J. Bass, The genetic rescue of the Florida panther, Anim. Conservat. 9 (2006), pp. 115–122.

[27] L. Pontryagin, V. Boltyanskii, R. Gamkrelize, and E. Mishchenko, *The Mathematical Theory of Optimal Processes*, Wiley, New York, 1967.

[28] A. Povlititis, *Characteristics and conservation of a fragmented population of huemul Hippocamelus bisulcus in central Chile*, Biol. Conservat. 86 (1998), pp. 97–104.

[29] K.A. Romain-Bondi, R.B. Wielgus, L. Waits, W.F. Kasworm, M. Austin, and W. Wakkinen, *Density and population size estimates for North Cascade grizzly bears using DNA hair-sampling techniques*, Biol. Conservat. 117 (2004), pp. 417–428.

[30] T. Rout, C. Hauser, and H.P. Possingham, *Minimise long-term loss or maximise short-term gain? Optimal translocation strategies for threatened species*, Ecol. Model. 201 (2007), pp. 67–74.

[31] I. Rozdilsky, J. Chave, S. Levin, and D. Tilman, *Towards a theoretical basis for ecosystem conservations*, Ecol. Res. 16 (2001), pp. 983–995.

[32] R.A. Salinas, S. Lenhart, and L.J. Gross, *Control of a metapopulation harvesting model for black bears*, Nat. Resource Model. 18 (2005), pp. 307–321.

[33] C. Servheen, W.F. Kasworm, and T.J. Thier, *Transplanting grizzly bears Ursus arctos horribilis as a management tool – Results from the cabinet mountains, Montana, USA*, Biol. Conservat. 71 (1995), pp. 261–268.

[34] S.P. Sethi and G.L. Thompson, *Optimal Control Theory: Applications to Management Science and Economics*, Kluwer Academic Press, 2000.

[35] A. Sinclair, P. Nantel, and P. Catling, *Dynamics of threatened goldenseal populations and implications for recovery*, Biol. Conservat. 123 (2005), pp. 355–360.

[36] P. Stephens, W. Sutherland, and R. Freckleton, *What is the Allee effect?* Oikos 87 (1999), pp. 185–190.

[37] K. Wickwire, *Mathematical models for the control of pests and infectious diseases: A survey*, Theor. Popul. Biol. 11 (1977), pp. 182–238.

[38] L. Willcox, *Grizzly bears: Taking stock of 2009, and a bear prayer for 2010*, Switchboard: Natural Resources Defense Council Staff Blog, 2009, available at http://switchboard.nrdc.org/blogs/lwillcox/grizzly_bears_taking_stock_of.html.

[39] J. Williams, C. ReVelle, and S. Levin, *Spatial attributes and reserve design models: A review*, Environ. Model. Assess. 10 (2005), pp. 161–162.

[40] J.T. Workman and S. Lenhart, *Optimal Control Applied to Biological Models*, Chapman & Hall/CRC, London, 2007.

[41] P. Zhong and Lenhart, *Optimal control of a harvesting problem in integrodifference equations with growth-harvesting-dispersal order*, Discrete Contin. Dyn. Syst., Ser. B 17 (2012), pp. 2281–2298.