2015

Analysis of a Coupled *n*-Patch Population Model with Ceiling Density Dependence

Jason Callahan
St. Edward's University, jasonc@stedwards.edu

Richard Rebarber
University of Nebraska-Lincoln, rebarber@unl.edu

Eva Strawbridge
James Madison University, strawbem@jmu.edu

Brigitte Tenhumberg
University of Nebraska-Lincoln, btenhumberg2@unl.edu

Shenglan Yuan
LaGuardia Community College, CUNY, syuan@lagcc.cuny.edu

Callahan, Jason; Rebarber, Richard; Strawbridge, Eva; Tenhumberg, Brigitte; and Yuan, Shenglan, "Analysis of a Coupled *n*-Patch Population Model with Ceiling Density Dependence" (2015). *School of Biological Sciences: Faculty Publications*. 1011.
https://digitalcommons.unl.edu/bioscifacpub/1011

International Journal of Difference Equations
ISSN 0973-6069, Volume 10, Number 2, pp. 137–159 (2015)
`http://campus.mst.edu/ijde`

Analysis of a Coupled n-Patch Population Model with Ceiling Density Dependence

Jason Callahan
St. Edward's University
Department of Mathematics
Austin, TX 78704, USA
jasonc@stedwards.edu

Richard Rebarber
University of Nebraska-Lincoln
Department of Mathematics
Lincoln, NE 68588, USA
rebarber@unl.edu

Eva Strawbridge
James Madison University
Department of Mathematics
Harrisonburg, VA 22807, USA
strawbem@jmu.edu

Brigitte Tenhumberg
University of Nebraska-Lincoln
School of Biological Sciences
Lincoln, NE 68588, USA
btenhumberg2@unl.edu

Shenglan Yuan
LaGuardia Community College, CUNY
MEC Department
Long Island City, NY 11101, USA
syuan@lagcc.cuny.edu

Abstract

We consider a system of difference equations with ceiling density dependence to model the dynamics of a coupled population on an arbitrary, finite number of distinct patches where migration between all patches is possible. In this model, each patch possesses a separate carrying capacity, and the dynamics of the coupled population is governed by a linear model until the population of a patch reaches its capacity after which it remains at this maximum value. Further, we analyze the global attractors of this model and apply these results to an Arabian oryx metapopulation model with some patches protected and others unprotected from poaching.

AMS Subject Classifications: 39A30, 39A60, 92B05.
Keywords: Difference equations, global attractor, metapopulation, ceiling density dependence, positive system.

Received March 1, 2015; Accepted June 16, 2015
Communicated by Allan Peterson

1 Introduction

In many ecological examples, a population lives in a habitat that is separated into distinct geographical areas, called patches, between which the population can migrate. Such partial isolation could be due to natural or human-made factors (including geographical barriers such as rivers, valleys, highways, and pipelines) or resource availability (such as water or food source localization) [3,8,10,13]. A collection of such partially isolated subpopulations is called a *metapopulation*.

In this paper we outline the design and analysis of a mathematical model using difference equations with an arbitrary, finite number, n, of geographical patches where migration between all the patches is allowed. This is a generalization of the 2-patch model analyzed in [3] to n patches. Since patches differ in size and resource availability, they differ in the number of individual organisms that they can support. That is, each geographical patch has its own carrying capacity that its population may never exceed, called a *ceiling density dependence*. We describe the dynamics of such an n-patch model in three lemmas and two theorems in Section 3.

In [3], a justification was given for the use of a ceiling density dependence in the population dynamics of a 2-patch model, which is also valid for n patches. Since there is often a paucity of detailed knowledge regarding the density dependence of the population, expressing this nonlinearity in a function is generally impractical. Therefore, we make the assumption that population size in each patch increases like a linear model until that subpopulation reaches its respective carrying capacity. This is a commonly accepted approach and is incorporated in widely used, simulation-based population viability software such as RAMAS/METAPOP (Akcakaya [2]).

In the case with an arbitrary, finite number of patches, the location of the equilibria is necessarily more complicated than the 2-patch case. The determination and description of these equilibria is contained in Theorem 3.5 and three preceding lemmas. The proof of the global attractivity of some of the equilibria is markedly similar in the n-patch case to the 2-patch case, and these results are contained in Theorem 3.6, whose proof is similar to that of [3, Theorem 4.1] and is therefore given in the Appendix. Once we have the n-patch results, the consideration of more realistic metapopulations becomes possible. In Section 4, we apply our results to an Arabian oryx model with some patches protected from poaching and some patches unprotected.

2 Setup and Notation

Assume there are n patches for some positive integer n. In notation consistent with [3], we will denote the number or density of females in patch j at time $t \in \mathbb{N}$ by $N_{j,t}$, and the population vector at time t by

$$\vec{N}_t = [N_{1,t}, N_{2,t}, \ldots, N_{n,t}]^T .$$

The individual population in each patch cannot exceed the carrying capacity of that patch, and the vector of carrying capacities is

$$\vec{K} = [K_1, K_2, \ldots, K_n]^T \, .$$

Let $J = [r_{ij}]$ be the matrix that incorporates both the intra-patch dynamics (i.e., population growth and death rates) as well as the inter-patch dynamics (i.e., probabilities for moving from one patch to another in one time-step). In this paper, we will use the following standard notation.

- By $\vec{X} > \vec{Y}$ (or $\vec{X} \geq \vec{Y}$), we mean that each entry of $\vec{X}$ is greater than (or greater than or equal to) the corresponding entry of $\vec{Y}$.
- For $\vec{V}, \vec{W} \in \mathbb{R}^n$, $\min\{\vec{V}, \vec{W}\}$ is the vector with jth entry $\min\{V_j, W_j\}$.
- We denote the spectral radius of J by $\rho(J)$.

The time evolution of this system is then given by

$$\vec{N}_{t+1} = \min\{J\vec{N}_t, \vec{K}\} \tag{2.1}$$

where the minimum is taken to ensure the population in patch j never exceeds the corresponding carrying capacity K_j. Clearly, J is by necessity nonnegative, and we further assume that it is positive so that all patches in the metapopulation are connected to each other through migration.

We begin by investigating the location of the equilibria of this system. The only biologically relevant equilibria, $\vec{N}^*$, are nonnegative and satisfy

$$\vec{N}^* = \min\{J\vec{N}^*, \vec{K}\}. \tag{2.2}$$

In three lemmas and Theorem 3.5, we describe all such equilibria. While Theorem 3.5 is organized into cases based on how $\rho(J)$ compares to 1, these cases do in fact cover all possibilities of how $J\vec{K}$ compares to $\vec{K}$ as follows.

1. If $J\vec{K} \leq \vec{K}$ with at least one inequality strict, then $\rho(J) < 1$ by Lemma 3.2.
2. If $J\vec{K} = \vec{K}$, then $\rho(J) = 1$ by Lemma 3.3.
3. If $J\vec{K} \geq \vec{K}$ with at least one inequality strict, then $\rho(J) > 1$ by Lemma 3.4.
4. If some entries of $J\vec{K}$ are strictly less than those of $\vec{K}$ and some are strictly greater, then any of the above cases for $\rho(J)$ could occur.

In the next section a more specific version of this is proved.

3 The Equilibria

Definition 3.1. Let $\vec{N}_t = [N_{1,t}, \dots N_{n,t}]^T$. An equilibrium $\vec{N}^* = [N_1^*, \dots N_n^*]^T$ is called *globally attracting* if

$$\lim_{t\to\infty} \vec{N}_t = \vec{N}^*$$

for every $\vec{N}_0 \in \mathbb{R}_+^n \setminus \{\vec{0}\}$.

Before proceeding to our lemmas, we first note that $\vec{0}$ is trivially always an equilibrium.

Lemma 3.2. *If $J\vec{K} \leq \vec{K}$ with at least one inequality strict, then $\rho(J) < 1$.*

Proof. Suppose $J\vec{K} \leq \vec{K}$ with at least one inequality strict, and let $\lambda = \rho(J)$. Since J is positive, by the Perron–Frobenius theorem, λ is an eigenvalue and has a eigenvector $\vec{v} = [v_1, v_2, \dots, v_n]^T > 0$. Let

$$r = \min_i \left\{ \frac{K_i}{v_i} \right\}$$

and reorder the entries so that $r = K_1/v_1$. Since $\vec{v}$ is an eigenvector of J and $r \neq 0$, $r\vec{v} \neq \vec{0}$ is also an eigenvector of J, so

$$\lambda r\vec{v} = Jr\vec{v} \tag{3.1}$$

where

$$r\vec{v} = \left[K_1, \frac{K_1}{v_1}v_2, \frac{K_1}{v_1}v_3, \dots, \frac{K_1}{v_1}v_n \right].$$

The first component of (3.1) is then

$$\lambda K_1 = r_{11}K_1 + \sum_{i=2}^{n} r_{1i}\left(\frac{K_1}{v_1}v_i\right) < r_{11}K_1 + \sum_{i=2}^{n} r_{1i}K_i$$

because by definition of r,

$$\frac{K_1}{v_1} \leq \frac{K_i}{v_i},$$

so

$$\frac{K_1}{v_1}v_i \leq K_i$$

for all $i = 1, \dots, n$. Moreover, one of these inequalities is strict because if all were equal, then $\vec{K}$ would be an eigenvector of J, which contradicts that at least one inequality of $J\vec{K} \leq \vec{K}$ is strict. From $J\vec{K} \leq \vec{K}$, we have

$$r_{11}K_1 + \sum_{i=2}^{n} r_{1i}K_i \leq K_1,$$

so $\lambda K_1 < K_1$, and $\lambda < 1$, i.e., $\rho(J) < 1$. □

Lemma 3.3. *If $J\vec{N}^* = \vec{N}^* \leq \vec{K}$, then $\rho(J) = 1$.*

Proof. By the Perron–Frobenius theorem, a positive matrix J has a positive leading eigenvalue $\lambda = \rho(J)$, which has the only nonnegative real eigenvector of J. Since $J\vec{N}^* = \vec{N}^*$ implies that 1 is an eigenvalue with a nonnegative eigenvector $\vec{N}^*$, 1 must be the leading eigenvalue, i.e., $\rho(J) = 1$. □

Lemma 3.4. *If $J\vec{K} \geq \vec{K}$ with at least one inequality strict, then $\rho(J) > 1$.*

Proof. Suppose $J\vec{K} \geq \vec{K}$ with at least one inequality strict, and let $\lambda = \rho(J)$. By the Perron–Frobenius theorem, λ has an eigenvector $\vec{v} = [v_1, v_2, \dots, v_n]^T > 0$. Let $r = \max_i \left\{ \frac{K_i}{v_i} \right\}$ and reorder the entries so that $r = \frac{K_1}{v_1}$. Since $\vec{v}$ is an eigenvector of J and $r \neq 0$, $r\vec{v} \neq \vec{0}$ is also an eigenvector of J. As before, the first component of (3.1) is

$$\lambda K_1 = r_{11}K_1 + \sum_{i=2}^{n} r_{1i}\left(\frac{K_1}{v_1}v_i\right) > r_{11}K_1 + \sum_{i=2}^{n} r_{1i}K_i$$

because by definition of r,

$$\frac{K_1}{v_1} \geq \frac{K_i}{v_i},$$

so

$$\frac{K_1}{v_1}v_i \geq K_i$$

for all $i = 1, \dots, n$. Moreover, one of these inequalities is strict because if all were equal, then $\vec{K}$ would be an eigenvector of J, which contradicts that at least one inequality of $J\vec{K} \geq \vec{K}$ is strict. From $J\vec{K} \geq \vec{K}$, we have

$$r_{11}K_1 + \sum_{i=2}^{n} r_{1i}K_i \geq K_1,$$

so $\lambda K_1 > K_1$, and $\lambda > 1$, i.e., $\rho(J) > 1$. □

Theorem 3.5. *Assume J has all positive entries and $\vec{K}$ is a positive vector.*

1. *If $\rho(J) < 1$, then $\vec{0}$ is a globally attracting equilibrium. By Lemma 3.2, this includes the case $J\vec{K} \leq \vec{K}$ with at least one inequality strict.*
2. *If $\rho(J) = 1$, then the only equilibria are $c\vec{v}$ for $0 \leq c \leq r$ where $\vec{v}$ is a positive eigenvector of J associated to the leading eigenvalue 1 and $r = \min_i \left\{ \frac{K_i}{v_i} \right\}$. By Lemma 3.3, this includes the case $J\vec{K} = \vec{K}$.*
3. *If $\rho(J) > 1$ and $J\vec{K} \geq \vec{K}$ with at least one inequality strict, then the only equilibria are $\vec{0}$ and $\vec{K}$.*

4. *If $\rho(J) > 1$ and some entries of $J\vec{K}$ are strictly greater than those of $\vec{K}$ and some strictly less, then the only nonzero equilibrium has some patches at capacity and some below. Specifically, every patch j with $(J\vec{K})_j < K_j$ has equilibrium below capacity. If we reorder the patches so that those with equilibria at capacity are first and those below capacity last, i.e., the capacity vector is $\vec{K} = [\vec{K}(1), \vec{K}(2)]^T$ and the nonzero equilibrium is $\vec{N}^* = [\vec{K}(1), \vec{N}^*(2)]^T$ where $\vec{N}^*(2) < \vec{K}(2)$, and write J in corresponding blocks*

$$J = \begin{bmatrix} J_{11} & J_{12} \\ J_{21} & J_{22} \end{bmatrix} \tag{3.2}$$

so that $J_{21}\vec{K}(1) + J_{22}\vec{N}^*(2) = \vec{N}^*(2)$, then $\vec{N}^*(2) = (I - J_{22})^{-1}J_{21}\vec{K}(1)$.

Proof. 1. If $\rho(J) < 1$, then as $t \to \infty$, $J^t \to 0$, so $\vec{N}_t \le J^t\vec{N}_0 \to \vec{0}$, i.e., $\vec{0}$ is globally attracting.

2. Now suppose $\rho(J) = 1$. By the Perron–Frobenius theorem, there exists a positive eigenvector $\vec{v}$ associated to the leading eigenvalue 1. Let $r = \min_i \left\{\frac{K_i}{v_i}\right\}$. Then, for $0 \le c \le r$, $Jc\vec{v} = c\vec{v} \le \vec{K}$, so $c\vec{v}$ is an equilibrium for $0 \le c \le r$. Suppose there exists another equilibrium $\vec{N}^* \ne c\vec{v}$ for $0 \le c \le r$. Let $s = \max_i \left\{\frac{N_i^*}{v_i}\right\}$ and reorder so that $s = \frac{N_1^*}{v_1}$. Clearly, $s\vec{v}$ is also an eigenvector of J associated to the leading eigenvalue 1, so the first component of $s\vec{v} = Js\vec{v}$ is

$$N_1^* = r_{11}N_1^* + \sum_{i=2}^{n} r_{1i}\left(\frac{N_1^*}{v_1}v_i\right) > r_{11}N_1^* + \sum_{i=2}^{n} r_{1i}N_i^* \tag{3.3}$$

because by definition of s,

$$\frac{N_1^*}{v_1} \ge \frac{N_i^*}{v_i},$$

so

$$\frac{N_1^*}{v_1}v_i \ge N_i^*$$

for all $i = 1, \ldots, n$. Moreover, one of these inequalities is strict because if all were equal, then $\vec{N}^*$ would be a multiple of v, a contradiction. But since $\vec{N}^*$ is an equilibrium, $\vec{N}^* = \min\{J\vec{N}^*, \vec{K}\}$, so $r_{11}N_1^* + \sum_{i=2}^{n} r_{1i}N_i^* \ge N_1^*$, and (3.3) yields the contradiction $N_1^* > N_1^*$. Thus, $c\vec{v}$ for $0 \le c \le r$ are the only equilibria in this case.

3. Next, suppose $\rho(J) > 1$ and $J\vec{K} \ge \vec{K}$ with at least one inequality strict. Clearly, $\vec{0}$ is an equilibrium, as is $\vec{K}$ because $J\vec{K} \ge \vec{K}$ implies $\min\{J\vec{K}, \vec{K}\} = \vec{K}$. Suppose

there exists a nonzero equilibrium $\vec{N}^* \leq \vec{K}$ with at least one inequality strict. Reorder the patches so that those at capacity are first and those below capacity last, i.e., $\vec{N}^* = [\vec{K}(1), \vec{N}^*(2)]^T$ and $\vec{K} = [\vec{K}(1), \vec{K}(2)]^T$ where $\vec{N}^*(2) < \vec{K}(2)$. By assumption $\vec{N}^*(2)$ is nonempty, and by Lemma 3.3, if $\vec{K}(1)$ were empty, then $\rho(J) = 1$, a contradiction, so both $\vec{N}^*(2)$ and $\vec{K}(1)$ are nonempty. Write J as in (3.2) so that

$$J_{21}\vec{K}(1) + J_{22}\vec{N}^*(2) = \vec{N}^*(2). \tag{3.4}$$

Since $J_{21}\vec{K}(1) > 0$, we have $J_{22}\vec{N}^*(2) < \vec{N}^*(2)$, so $\rho(J_{22}) < 1$ by Lemma 3.2 with $\vec{N}^*(2)$ in place of $\vec{K}$. This implies that $I - J_{22}$ is invertible, so, from (3.4), we have

$$(I - J_{22})^{-1}J_{21}\vec{K}(1) = \vec{N}^*(2). \tag{3.5}$$

Similarly, from $J\vec{K} \geq \vec{K}$, we have $J_{21}\vec{K}(1) + J_{22}\vec{K}(2) \geq \vec{K}(2)$, so

$$(I - J_{22})^{-1}J_{21}\vec{K}(1) \geq \vec{K}(2),$$

which, together with (3.5), yields $\vec{N}^*(2) \geq \vec{K}(2)$, a contradiction. Thus, $\vec{0}$ and $\vec{K}$ are the only equilibria in this case.

4. Finally, suppose $\rho(J) > 1$ and that some entries of $J\vec{K}$ are strictly greater than those of $\vec{K}$ and some strictly less. Patches j with $(J\vec{K})_j < K_j$ cannot have equilibria at capacity since for those patches $\min\{(J\vec{K})_j, K_j\} < K_j$. On the other hand, at least one patch for which $(J\vec{K})_j \geq K_j$ must have equilibrium at capacity for if not, Lemma 3.3 implies $\rho(J) = 1$, a contradiction. Thus, we reorder the patches so that those with equilibria at capacity are first and those below capacity last, i.e., $\vec{N}^* = [\vec{K}(1), \vec{N}^*(2)]^T$ and $\vec{K} = [\vec{K}(1), \vec{K}(2)]^T$ where $\vec{N}^*(2) < \vec{K}(2)$ and both $\vec{K}(1)$ and $\vec{N}^*(2)$ are nonempty. Write J as in (3.2) so that $J_{21}\vec{K}(1) + J_{22}\vec{N}^*(2) = \vec{N}^*(2)$. Since $J_{21}\vec{K}(1) > 0$, $J_{22}\vec{N}^*(2) < \vec{N}^*(2)$, so $\rho(J_{22}) < 1$ by Lemma 3.2 with $\vec{N}^*(2)$ in place of $\vec{K}$. This implies that $I - J_{22}$ is invertible, so, from above, we have $(I - J_{22})^{-1}J_{21}\vec{K}(1) = \vec{N}^*(2)$. Thus, $\vec{0}$ and $[\vec{K}(1), (I - J_{22})^{-1}J_{21}\vec{K}(1)]^T$ are the only equilibria in this case.

This concludes the proof. □

Theorem 3.6. *1. In Case (1) of Theorem 3.5, $\vec{0}$ is a globally attracting equilibrium.*

2. *In Case (2) of Theorem 3.5, there is no globally attracting equilibrium.*
3. *In Cases (3) and (4) of Theorem 3.5, the nonzero equilibrium is a globally attracting equilibrium.*

The proof of this theorem is similar to the proof of [3, Theorem 4.1], with some complications due to the arbitrary patch number. This proof is in the Appendix.

4 Example: an Arabian Oryx Metapopulation

In this section, we apply our model to an Arabian oryx (*Oryx leucoryx*) population living in six patches. The population is subject to poaching, and in the absence of protection, it is in asymptotic decline. We investigate what happens when one or two patches are protected, effectively changing the mortality in those patches. We use Theorem 3.5 to help determine to what degree the mortality must be lowered in order to maintain the largest possible population.

The entries of the matrix J are determined in terms of underlying life history parameters and with data from the relevant literature. All parameters refer to transitions from one time-step to the next where the step size is one year. Only females are counted in this model, with the implicit assumption that the sex ratio in the population stays fixed as time evolves. Moreover, this also implicitly assumes that matings are not limited by the number of males in the population. This assumption is justified in this example because a single male can mate with several females.

If the population in patch i is below the carrying capacity K_i, then the population dynamics in patch i are determined by a linear combination of individuals who survived and stayed in patch i from the previous time-step and individuals who migrated to patch i in the previous time-step. Let b be the probability that a given female in patch i gives birth to a single offspring, f the probability that the newborn is a female, m the probability of migration from one patch to another, and α the probability of surviving migration. In this example, we assume that these parameters are independent of the patch. Let μ_i be the probability of death in patch i; μ_i is naturally expected to be lower for protected patches. Then the jth component of the vector $J\vec{N}$ is

$$(J\vec{N})_j = \sum_{k=1}^{n} r_{jk} N_k$$

where, for $i, j = 1, \ldots, n$ with $j \neq i$,

$$\begin{aligned} r_{ii} &= (1-\mu_i)(1+bf)(1-m), \\ r_{ij} &= (1+bf)m\alpha. \end{aligned}$$

We assume that $r_{ij} > 0$ for all $i, j \in \{1, \ldots, n\}$ so that all patches in the metapopulation are connected to each other through migration.

We parameterize our model with data for Arabian oryx (*Oryx leucoryx*) from the literature. A summary of the range of vital rates published for this species are as follows. Under favorable conditions, females give birth to a single calf each year, which has a 75% [9] to 92.5% [14] chance of surviving the first year. Therefore, b is between 0.75 and 0.925, so we take $b = 0.8375$, the average of these two values. Additionally, the sex ratio is assumed to be $f = 0.5$ [9, 12, 14]. Annual mortality of adult Arabian oryx in captivity ranges from 4% to 15% [1, 9], so we choose the average, $\mu = 0.095$, for protected patches. For the unprotected patches, the mortality rate is assumed to increase up to 40% [12], so we take $\mu = 0.4$ for these. Following [5], we assume that 6% of each subpopulation migrates to other patches, so $m = 0.06/5$ since the migration is spread out over five other patches assuming this migration is spread equally. In [5], it is assumed that migration mortality is zero because subpopulations are connected through "safe" corridors. However, it is fair to assume that migration outside of corridors is risky, so in our model we set $\alpha = .5$, so migration mortality is $1 - \alpha = 0.5$.

With this data, we obtain diagonal entries $r_{ii} = 0.841035$ for unprotected patches (which describe the intra-patch dynamics) and $r_{ii} = 1.26856$ for protected patches. The off-diagonal entries r_{ij} for $i \neq j$ are all 0.00849252 (which describe migration). For the six patches, we chose carrying capacities of 40, 60, 80, 100, 120 and 140 since the minimum viable population size is 100 [11] and for illustrative purposes, it is interesting to have a variety of viable and nonviable populations.

One patch protected: In this case, the leading eigenvalue of J is 1.2078949, so there is a positive asymptotically stable equilibrium $\vec{N}^*$, which can be obtained as follows. We rearrange the carrying capacity vector $\vec{K}$ so that the protected patch is K_1 (so $\mu_1 = 0.095$ and $r_{11} = 1.26856$); then $N_1^* = K_1$. If not, the vector $\vec{N}^*$ satisfies $J\vec{N}^* = \vec{N}^*$, which would mean, by the Perron–Frobenius theorem, that 1 is the leading eigenvalue of J, a contradiction. The remaining five entries of $\vec{N}^*$ are given by

$$\vec{N}^*(2) = (I - J_{22})^{-1} J_{21} K_1. \tag{4.1}$$

For instance, if the patch with capacity 140 is protected,

$$\vec{N}^* = [140, 9.512009, 9.512009, 9.512009, 9.512009, 9.512009]^T \tag{4.2}$$

while protecting a patch with capacity K_j leads to equilibrium $(K_j/140)\vec{N}^*$.

We obtain the same equilibrium for lower values of μ_1 and hence higher values of r_{11}. In fact, as long as the leading eigenvalue of J is greater than 1, the Perron–Frobenius theorem implies that $\vec{N}^*$ is given by (4.2) when protecting the 140-capacity patch. It is possible to use the *stability radius* (see, for instance, [6]) to conclude that if

$$r_{11} > 1 - J_{12}(I - J_{22})^{-1} J_{21} = 0.997115,$$

then $\rho(J) > 1$, and we find the same $\vec{N}^*$ as before. This means that if we protect one patch and

$$0 < \mu < 0.2886514$$

(that is, mortality in the protected patch is below approximately 28.86%), then the asymptotic population reaches its largest possible value.

In Figure 4.1, we simulate the system with $r_{11} = 1.26856$ (that is, $\mu = 0.095$), starting with a population of 10 in all patches. Note that it takes about 10 time-steps (years) for the protected population to reach its carrying capacity, while the unprotected patches get near their limit of 9.512009 by around 30 years. If we let $r_{11} = 1$ (close to the stability radius), it takes approximately 800 years to reach the same protected patch

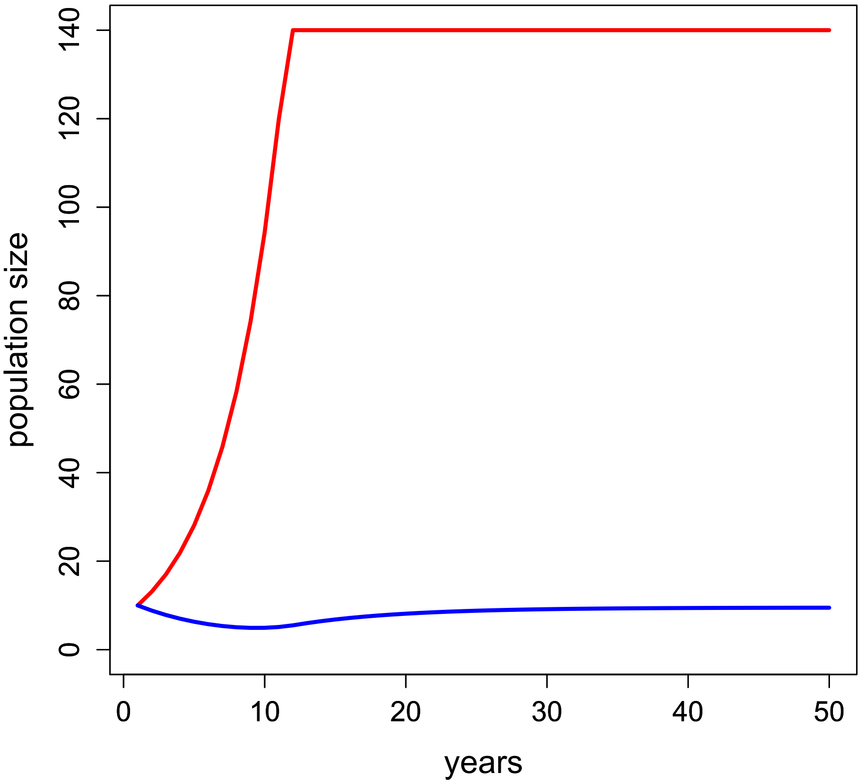

Figure 4.1: One patch protected ($r_{11} = 1.26856$). The upper curve is the population of the protected patch; the lower curve is the population the unprotected patches.

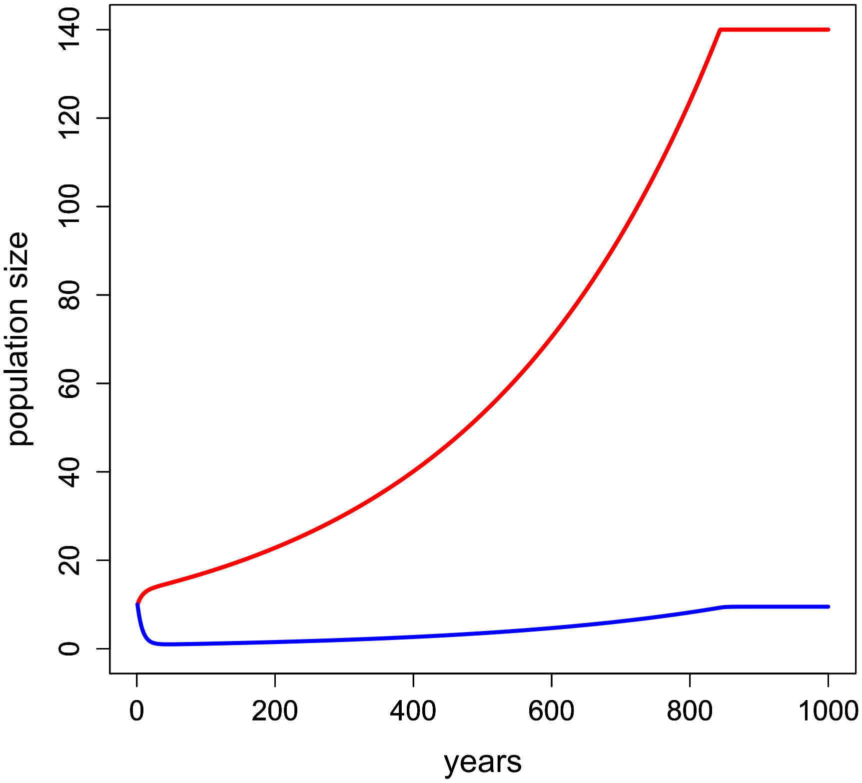

Figure 4.2: One patch partially protected ($r_{11} = 1$). The upper curve is the population of the protected patch; the lower curve is the population the unprotected patches.

equilibrium, and the other patches take approximately 850 years to get near their limit (Figure 4.2).

Two patches protected: If r_{11} and r_{22} are both raised sufficiently for $\rho(J) > 1$, then

$$K_j \le (J\vec{K})_j \qquad \text{for } j = 1, 2 \tag{4.3}$$

$$K_j > (J\vec{K})_j \quad \text{for } j = 3, 4, 5, 6 \tag{4.4}$$

where the $j = 1$ and $j = 2$ patches are the protected ones. This is true regardless of which of the two patches are protected. From the proof of Theorem 3.5, we see that (4.4) implies that $N_j^* < K_j$ for $j = 3, 4, 5, 6$ since $(J\vec{K})_j \ge (JN^*)_j$ for all j. However, we cannot conclude from (4.3) that $N_j^* = K_j$ for $j = 1, 2$. Since $\rho(J) > 1$, we can conclude that at least one $N_j^* = K_j$ for $j = 1, 2$; otherwise, the Perron–Frobenius theorem would be violated. Therefore, for either one or two patches, $N_j^* = K_j$.

If the two patches are fully protected so that $r_{11} = r_{22} = 1.26856$, then it is easy to verify numerically that both $N_1^* = K_1$ and $N_2^* = K_2$. The remaining four entries of $\vec{N}^*$ are given by (4.1). For example, if the protected patches are the ones with carrying capacity 80 and 60, then

$$\vec{N}^* = [80, 60, 8.906851, 8.906851, 8.906851, 8.906851]^T. \tag{4.5}$$

It is worth noting that while we are protecting the same number of individuals (approximately 140) as for (4.2), the total metapopulation size is lower (175.6 compared to 187.6) because the unprotected patches here have a lower asymptotic population than for (4.2). In Figure 4.3, we give a simulation of this system. We can obtain the same equilibrium population with lower levels of protection, provided $\rho(J) > 1$. For illustrative purposes, we will consider only protection so that $r_{11} = r_{22}$; that is, the same level of protection is provided in both patches. This way, we can control the degree of protection by one parameter. The convergence will be slower for lower protection levels; for instance, if $r_{11} = r_{22} = 1$, it takes approximately 150 years before the population levels off. The convergence is faster if the starting population is close to the limit; for instance, if the starting population is 50 in each patch, it takes only two years for the 60-capacity patch population to get to 60, and three years for the 80-capacity patch population to get to 80, while it takes around 30 years for the unprotected patches to reach their limits.

We can verify numerically that if

$$r_{11} = r_{22} \ge 0.98949,$$

then the asymptotic limit is still (4.5). When

$$0.98719 \le r_{11} = r_{22},$$

we see numerically that $\rho(J) < 1$, so the population dies off for that range of protection. In the narrow range

$$0.98719 \le r_{11} = r_{22} < 0.98948, \tag{4.6}$$

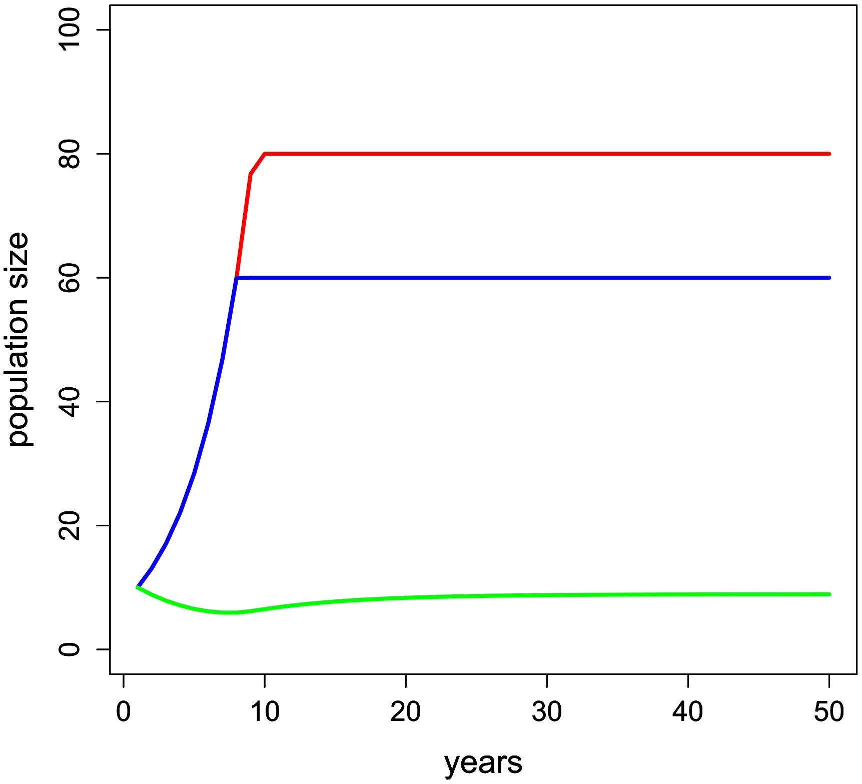

Figure 4.3: Two patches fully protected ($r_{11} = r_{22} = 1.26856$). The upper curve is the population of the 80-capacity patch, the middle curve is the population the 60-capacity patch, and the lower curve is the population of the unprotected patches.

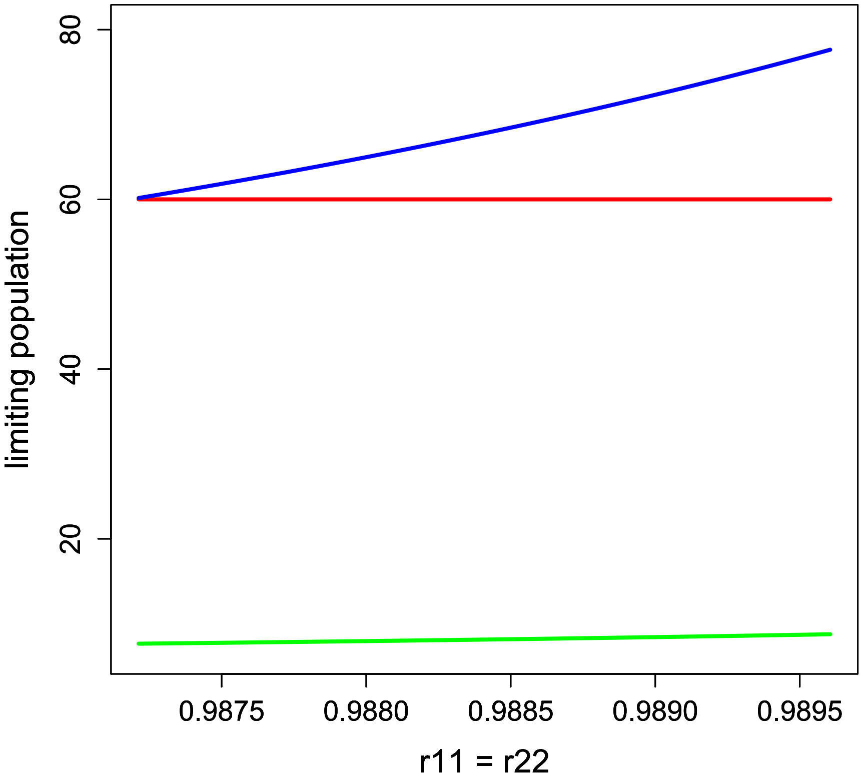

Figure 4.4: Population equilibria, N_i^*, values as a function of $r_{11} = r_{22}$. The upper curve is for the 80-capacity patch, the middle curve is for the 60-capacity patch, and the lower curve is for the unprotected patches.

we get a range of equilibria. In particular, the population in the patch with carrying capacity 60 converges to 60, but the population in the patch with carrying capacity 80 does not approach 80. To illustrate this, in Figure 4.4, we show N_1, N_2 and N_3 as functions of $r_{11} = r_{22}$ in the range (4.6). We see that the limiting population is extremely sensitive in this range, while out of this range the population is not at all sensitive. In Figure 4.5, we give a simulation of this system when $r_{11} = r_{22} = 0.988$, which is in this sensitive range. The convergence is extremely slow, taking over 2000 years to get near the limiting populations; this is to be expected because the leading eigenvalue of J is 1.00079, just a little above one. As we see, the limiting population of the 80-capacity patch is approximately 65, as predicted by Figure 4.5.

Similar patterns hold when we protect any two patches in this model: there is a range of $r_{11} = r_{22}$ for which the limiting population is zero, a range for which the limiting

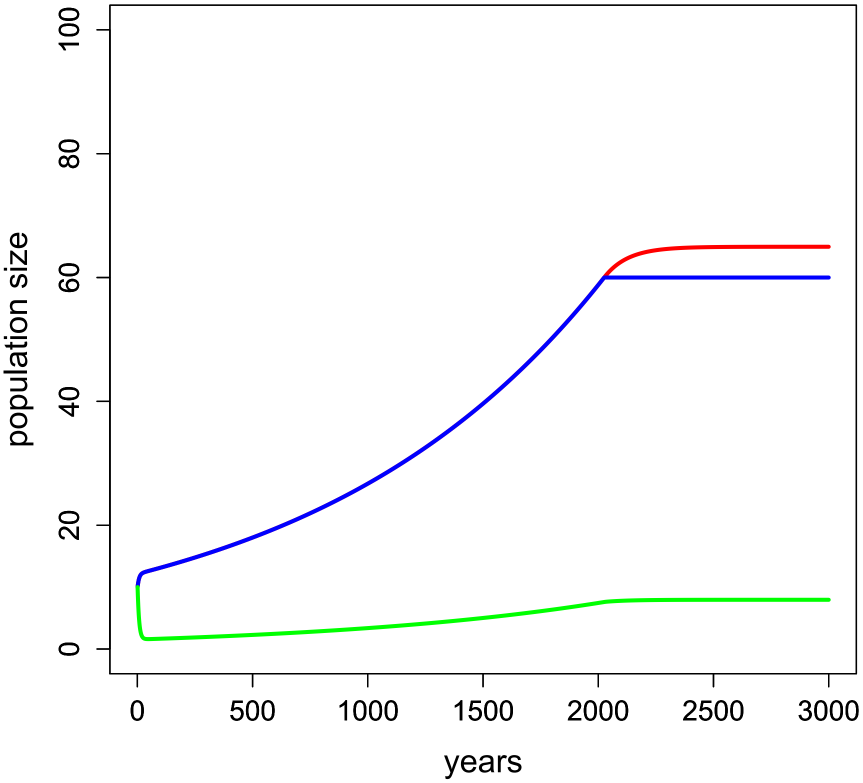

Figure 4.5: Two patches partially protected ($r_{11} = r_{22} = 0.988$). The upper curve is the population of the 80-capacity patch, the middle curve is the population the 60-capacity patch, and the lower curve is the population of the unprotected patches.

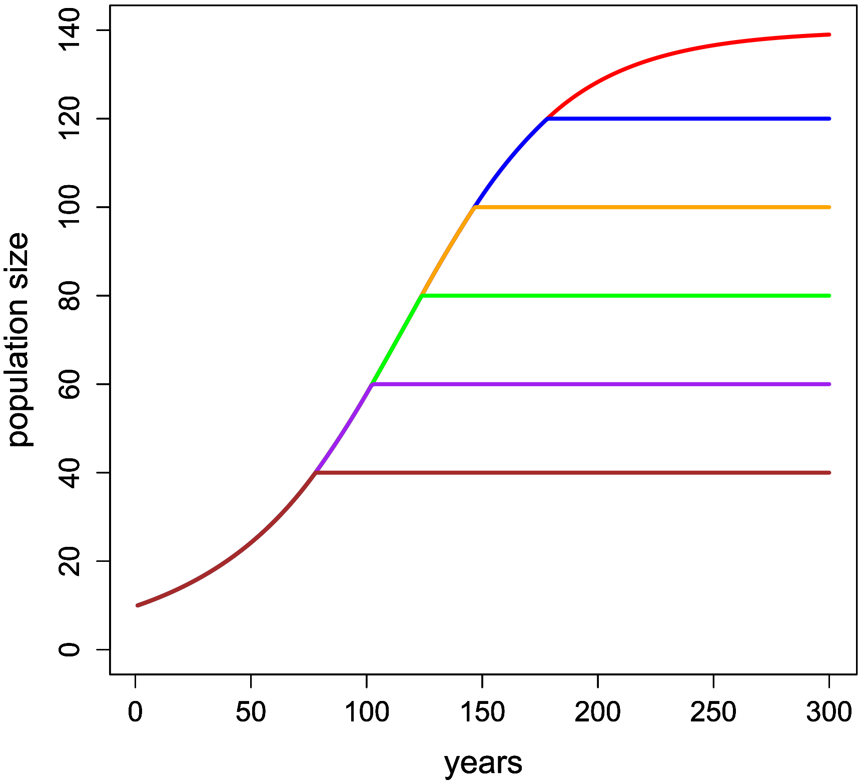

Figure 4.6: All patches protected with ($r_{jj} = 0.9757358$), the smallest protection of all patches which leads to every patch approaching capacity.

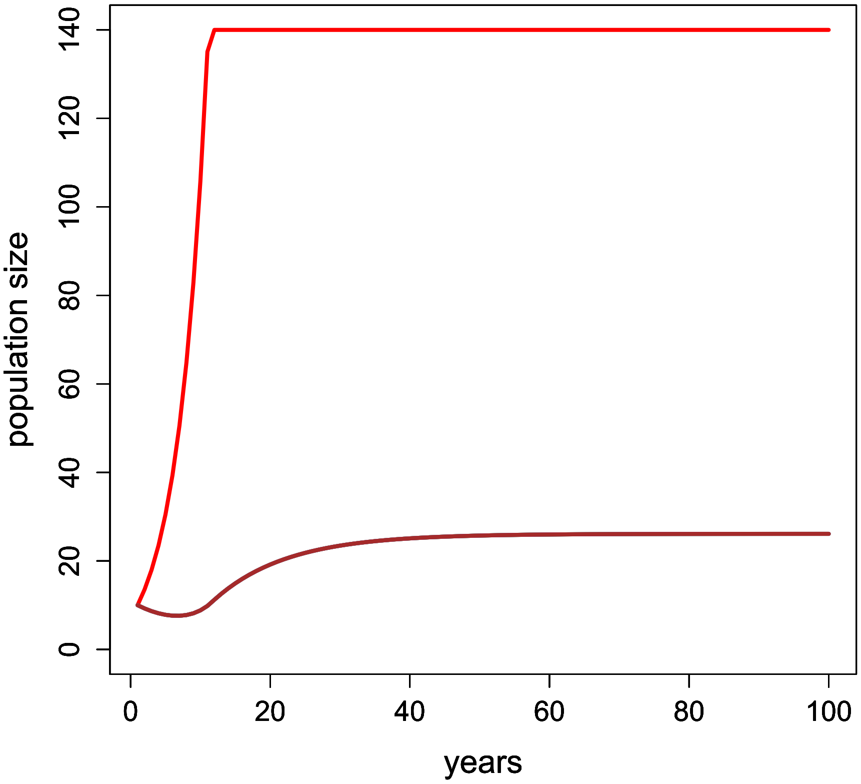

Figure 4.7: One patch protected ($r_{11} = 1.26856$), with migration survival at $\alpha = 1$. The upper curve is the population of the protected patch; the lower curve is the population the unprotected patches.

population has the carrying capacity of the two protected patches, and a narrow range in between where the population of the lower capacity protected patch is reached, but the other protected patch stays below the capacity.

If we protect all patches the same amount so that r_{jj} is constant at a value r, then when $r > 0.9575375$ ($\mu = 0.31689$), the spectral radius $\rho(J) > 1$ and the population is viable. When r is increased to 0.9757358 ($\mu = 0.30390$), all patches reach capacity, as shown in Figure 4.6, and this r is the lowest such r. This can also be seen by checking that $J\vec{K} > \vec{K}$. As 0.9757358 is increased from 0.9575375 to 0.9757358, the limiting population increases monotonically.

Finally, we investigate what happens if the probability α that migration will be successful is increased. This will increase r_{ij} for $i \neq j$, while leaving the diagonal of J alone. As expected, this will increase the population in the unprotected patches. For instance, if one patch is protected, as in Figure 4.1, but α is increased to its biological limit $\alpha = 1$, the resulting population behaves as in Figure 4.7, with the protected patch reaching the capacity of 140, while the other patches have limit 26.12034, compared with 9.512009 when $\alpha = 0.5$.

5 Conclusions

We have studied a coupled population model for an arbitrary, finite number of patches where the model is linear in a patch until the patch's carrying capacity is reached. This is a reasonable approximation for a wide range of models where there is a dearth of data preventing determination of the nonlinear function describing density dependence. Moreover, it is shown in [4] that the asymptotic behavior of a density dependent system is strongly dependent on the functional form for the nonlinearity. Hence, we impose as few assumptions on the nonlinearity as possible. For this model, when $\rho(J) \neq 1$, the results are as one would expect: if $\rho(J) < 1$, the origin is globally attracting, while if $\rho(J) > 1$, some patches will have populations approaching their carrying capacity. The example illustrates what we expect is a typical situation: when $\rho(J)$ is sufficiently larger than 1, the globally attracting equilibrium $\vec{N}^*$ is not at all sensitive to the life history parameters, but there is a small range of parameters for which $\rho(J) > 1$ and the globally attracting equilibrium is sensitive to the life history parameters. This latter situation corresponds to $\rho(J)$ being slightly larger than 1, which also corresponds to very slow convergence; Theorems 3.5 and 3.6, combined with numerical tests, give a way of economically improving life history parameters (e.g., mortality) to get the best possible globally attracting equilibrium since, past a certain point, any improvement in the life history will not improve the asymptotic behavior.

Acknowledgements

This work began at the American Institute of Mathematics (AIM) and Institute for Computational and Experimental Research in Mathematics (ICERM) Research Experiences for Undergraduate Faculty (REUF) program supported by the National Science Foundation (NSF) through DMS 1239280. REUF continuation funding was provided by AIM's research program SQuaREs (Structured Quartet Research Ensembles). Richard Rebarber was also partially funded by NSF Grant DMS-1412598.

References

[1] M. Z. Abu Jafar and C. Hays–Shahin, *Reintroduction of the Arabian oryx into Jordan*, pages 35–40 in A. Dixon and D. Jones, editors, *Conservation biology of desert antelopes*, Christopher Helm, London, 1988.

[2] H. R. Akcakaya, RAMAS Metapop: Viability Analysis for Stage Structured Metapopulations. Version 4.0. Setauket, NY, Applied Biomathematics, 2002.

[3] E. Eager, M. Herbert, E. Hellwig, F. Hernandez, R. Rebarber, B. Tenhumberg, and B. Wigianto, *Global attracting equilibria for coupled systems with ceiling density dependence*, Int. J. Difference Equ. 8(2) (2013), 179–193.

[4] E. Eager, R. Rebarber, and B. Tenhumberg, *Choice of density-dependent seedling recruitment function effects predicted transient dynamics: A case study with Platte thistle*, Theoret. Ecol. 5(2) (2012), 387–401.

[5] O. Gilad, W. E. Grant, and D. Salz, *Simulated dynamics of Arabian Oryx (Oryx leucoryx) in the Israeli Negev: Effects of migration corridors and post-reintroduction changes in natality on population viability*, Ecol. Model. 210 (2008), 169–178.

[6] D. Hinrichsen and A. Pritchard, *Mathematical Systems Theory I: Modelling, State Space Analysis, Stability and Robustness*, Springer, Heidelberg, 2005.

[7] U. Krause and P. Ranft, *A limit set trichotomy for monotone nonlinear dynamical systems*, Nonlinear Anal. 19(4) (1992), 375–392.

[8] R. Lande, S. Engen and B. E. Saether, *Stochastic population dynamics in ecology and conservation*, Oxford University Press, Oxford, 2003.

[9] G. M. Mace, *The genetic status of the Arabian oryx and the design of cooperative management programmes*, pages 58–74 in A. Dixon and D. Jones, editors *Conservation biology of desert antelopes*, Christopher Helm, London, 1988.

[10] T. Münkemüller and K. Johnst, *Compensatory versus over-compensatory density regulation: Implications for metapopulation persitence in dynamic landscapes*, Ecol. Model. 197 (2006), 171–178.

[11] D. Saltz, *A long-term systematic approach to palnning reintroductions: the Persian fallow deer and the Arabian Oryx in Israel*, Anim. Conserv. 1 (1998), 245–252.

[12] J. A. Spalton, M. W. Lawrence, and S. A. Brend, *Arabian oryx reintroduction in Oman: successes and setbacks*, Oryx 33 (1999), 168–175.

[13] J. H. Vandermeer and D. E. Goldberg, *Population ecology: first principles*, Princeton University Press, Princeton, 2003.

[14] J. C. Vie, *Reproductive biology of captive Arabian oryx (Oryx leucoryx) in Saudi Arabia*, Zoo Biol. 15 (1996), 371–381.

6 Appendix: Proof of Theorem 3.6

The proofs in this appendix are similar to those in [3] with some modifications to account for n patches as opposed to 2. Parts 1 and 2 of Theorem 3.6 follow immediately from Theorem 3.5. The remainder of this Appendix is devoted to outlining the proof of Part 3 of Theorem 3.6, so we assume that $\rho(J) > 1$. In this proof, we use the notation that if $\vec{x} \in \mathbb{R}^n$ and $a \in \mathbb{R}$, then $\vec{x} < a$ means that all entries of x are less than a. Similar interpretation is used for $\vec{x} \leq a$, $\vec{x} > a$, and $\vec{x} \geq a$. Also, we define $\mathbb{R}_+$ as the nonnegative real numbers.

We write the system (2.1) as

$$\vec{N}_{t+1} = G(\vec{N}_t). \tag{6.1}$$

Given a system

$$\vec{N}_{t+1} = F(\vec{N}_t), \tag{6.2}$$

we may guarantee global attractivity if certain conditions are satisfied on the map F.

Definition 6.1. A map $F : \mathbb{R}^n_+ \to \mathbb{R}^n_+$ is sublinear if, for all $0 < \lambda < 1$ and $x \in \mathbb{R}^n_+$ such that $x > [0,0]^T$, it follows that $\lambda F(x) < F(\lambda x)$. F is a monotone map if for all $x, y \in \mathbb{R}^n_+$ such that $x \leq y$, it follows that $Fx \leq Fy$.

The long-term dynamics of difference equations which are monotone and sublinear maps can be stated concisely as follows.

Theorem 6.2 (See [7])**.** *Let $F : \mathbb{R}^n_+ \to \mathbb{R}^n_+$ be a monotone, sublinear, and continuous operator over $\mathbb{R}^n_+$. Let*

$$P = \operatorname{int} \mathbb{R}^n_+ = \{[x_1, \ldots, x_n]^T \in \mathbb{R}^n \mid x_1 > 0, \ldots x_n > 0\}.$$

Precisely one of the following three cases holds:

1. *Each nonzero orbit of* (6.2) *in P is unbounded.*

2. *Each orbit of* (6.2) *in P is bounded with at least one limit point not contained in P.*

3. *Each nonzero orbit of* (6.2) *in P converges to a unique fixed point of P.*

We would prefer to replace P with $\mathbb{R}^n_+ \setminus \{\vec{0}\}$ since here we want to be able to consider initial populations which start with the population in only some of the patches. This is not a mathematical issue for our system since a population starting in $\mathbb{R}^n_+ \setminus \{\vec{0}\}$ will be in P during the second time-step.

As with the 2-patch case in [3], our operator G is not sublinear. Hence, we cannot directly apply this theorem to (6.1). However, it is again possible to construct a sequence of monotone, sublinear maps $\{G_m\}_{m\in\mathbb{N}}$ that will converge to our operator G from below. As a result, we may use the global attractivity properties of this approximating sequence, each with its own attractor, to draw conclusions about the global attractivity for the nonzero equilibrium of our model system (6.1).

Theorem 6.3. *There exists maps $G_m : \mathbb{R}^n_+ \to \mathbb{R}^n_+$, $m \in \mathbb{N}$, such that G_m is monotone and sublinear and $G_m \to G$ uniformly on R^n_+. Furthermore, (G_m) is increasing in the sense that for every $\vec{x} \in \mathbb{R}^n_+$ and $k > m$, $G_k(\vec{x}) > G_m(\vec{x})$.*

This result is [3, Theorem 3.3], where the result is proved in $\mathbb{R}^2$, and the proof is identical for $\mathbb{R}^n$. In the proof, scalar-valued functions $g_m(z, a) = \min\{z, a\}$, for scalar z and a, are constructed such that

$$G_m(\vec{x}) = [g_m((J\vec{x})_1, K_1), \ldots, g_m((J\vec{x})_n, K_n)]^T.$$

Let $\vec{x}_{m,t}$ solve

$$\vec{x}_{m,t+1} = G_m(\vec{x}_{m,t}). \tag{6.3}$$

From the proof of [3, Theorem 3.3] we also have

$$\frac{d}{dz} g_m(z, K) \mid_{z=0} = 1$$

for any $K > 0$ and $m \in \mathbb{N}$, so the Jacobian of G_m at $\vec{0}$ is J. We are further restricting ourselves to the case with $\rho(J) > 1$, so $\vec{0}$ is not globally attractive. By the definition of G_m and g_m, we know that $G_m(\vec{x}) \leq \vec{K}$ for all $\vec{x} \in \mathbb{R}^n_+$. Hence, the trajectories of (6.3) are bounded by $\vec{K}$. By Theorem 6.2, the system (6.3) has a unique globally attractive equilibrium in P. Since there is not a single attractor for all G_m, we will denote each attractor for the respective G_m by $\vec{x}_m$.

We must now show that the sequence $(\vec{x}_m)_{m\in\mathbb{N}}$ is nondecreasing. Let $\hat{x} \in P$ and $k, m \in \mathbb{N}$ with $k > m$, so

$$\vec{x}_k = \lim_{t\to\infty} \vec{x}_{k,t} \text{ where } x_{k,t+1} = G_m(x_{k,t}) \text{ and } x_{k,0} = \hat{x}$$

$$\vec{x}_m = \lim_{t\to\infty} \vec{x}_{m,t} \text{ where } x_{m,t+1} = G_m(x_{m,t}) \text{ and } x_{m,0} = \hat{x}.$$

By Theorem 6.2, we know that $G_k(\vec{x}) > G_m(\vec{x})$ for all $\vec{x} \in \mathbb{R}^m_+$. Therefore, by induction, we find that $\vec{x}_{k,t} \geq \vec{x}_{m,t}$ for all $t \in \mathbb{N}$ and, consequently, $\vec{x}_k \geq \vec{x}_m$.

Because $(\vec{x}_m)_{m\in\mathbb{N}}$ is a nondecreasing, bounded sequence in $\mathbb{R}^n$, it converges to some $\tilde{x} \in \mathbb{R}^n_+$. Given $\epsilon > 0$ and any norm, $\|\cdot\|$, on $\mathbb{R}^n$, there exists $M \in \mathbb{N}$ such that $\|G(\vec{x}) - G_m(\vec{x})\| < \epsilon$ for all $m > M$ and $\vec{x} \in \mathbb{R}^m_+$ by Theorem 6.2. Since $G_m(\vec{x}_m) = \vec{x}_m$,

$$\|G(\vec{x}_m) - \vec{x}_m\| = \|G(\vec{x}_m) - G_m(\vec{x}_m)\| < \epsilon$$

for all $m > M$. With $m \to \infty$ and the continuity of G, we have $G(\tilde{x}) = \tilde{x}$. In the cases of interest here, the only fixed points of G are $\vec{0}$ and $\vec{N}^*$. Moreover, since the sequence $(\vec{x}_m)$ is increasing, we have $\tilde{x} = \vec{N}^*$. In particular, this yields

$$\lim_{m\to\infty} \vec{x}_m = \vec{N}^*. \tag{6.4}$$

Now write $\vec{N}^* = [\vec{K}(1), \vec{N}^*(2)]^T$ as in the statement of Theorem 3.5, and decompose $\vec{x}_m$ analogously as $[\vec{x}_m(1), \vec{x}_m(2)]^T$. From (6.4), for $\epsilon > 0$, there must exist $M > 0$ such that

$$0 < \vec{K}(1) - \vec{x}_m(1) < \epsilon/2 \tag{6.5}$$

for all $m > M$. Let $m_0 > M$ and $\hat{x} \in P$. Consider

$$\vec{N}_{t+1} = G(\vec{N}_t), \quad \vec{N}_0 = \hat{x}$$

with the vector $\vec{N}_t = [\vec{N}_t(1), \vec{N}_t(2)]^T$ and

$$\vec{x}_{m_0,t+1} = G_{m_0}(\vec{x}_{m_0,t}), \quad \vec{x}_{m_0,0} = \hat{x} \tag{6.6}$$

where $\vec{x}_{m_0,t} = [\vec{x}_{m_0,t}(1), \vec{x}_{m_0,t}(2)]^T$. Because $G_{m_0}(\vec{x}) \leq G(\vec{x})$ for all $\vec{x} \in \mathbb{R}^n_+$, it follows that

$$\vec{x}_{m_0,t}(1) \leq \vec{N}_t(1) \tag{6.7}$$

for all $t \in \mathbb{N}$. The system (6.6) has an equilibrium $[\vec{x}_{m_0}(1), \vec{x}_{m_0}(2)]^T$, so there must exist $T > 0$ such that

$$|\vec{x}_{m_0,t}(1) - \vec{x}_{m_0}(1)| < \epsilon/2 \tag{6.8}$$

for all $t > T$. By combining the equations (6.5), (6.7), and (6.8), we find $|\vec{N}_t - \vec{K}(1)| < \epsilon$ for $t > T$, which shows that

$$\lim_{t\to\infty} \vec{N}_t(1) = \vec{K}(1). \tag{6.9}$$

Specifically, if $\rho(J) > 1$ and $J\vec{K} \geq \vec{K}$, then $\vec{N}^* = \vec{K}$ is a globally attracting equilibrium.

If $\vec{N}^* \neq \vec{K}$, then, by Theorem 3.5,

$$\vec{N}^* = [\vec{K}(1), (I - J_{22})^{-1} J_{21} \vec{K}(1)]^T$$

where

$$\rho(J_{22}) < 1. \tag{6.10}$$

Recall that $\vec{N}_t(2)$ satisfies

$$\vec{N}_{t+1}(2) = \min\{J_{21}\vec{N}_t(1) + J_{22}\vec{N}_t(2), \vec{K}(2)\}.$$

Let $\vec{M}_t$ have the same dimension and initial state as $\vec{N}_t(2)$ satisfying

$$\vec{M}_{t+1} = J_{21}\vec{N}_t(1) + J_{22}\vec{M}_t. \tag{6.11}$$

By construction, $\vec{N}_t(2) \leq M_t$. It follows from (6.9), (6.10), (6.11), and the standard discrete-time variation of parameters formula that

$$\lim_{t\to\infty} \vec{M}_t = (I - J_{22})^{-1}J_{21}\vec{K}(1).$$

By the assumptions of the decomposition, $(I - J_{22})^{-1}J_{21}\vec{K}(2) \leq \vec{K}(1)$, so

$$\lim_{t\to\infty} \vec{N}_t(2) \leq \lim_{t\to\infty} \vec{M}_t \leq \vec{K}(1).$$

This shows that

$$\vec{N}_{t+1}(2) = J_{21}\vec{N}_t(1) + J_{22}\vec{N}_t(2)$$

for large enough t. It again follows from the discrete-time variation of parameters formula that

$$\lim_{t\to\infty} \vec{N}_t(2) = (I - J_{22})^{-1}J_{21}\vec{K}(1),$$

finishing the proof.