



Modeling the restoration of a metapopulation : implications for resource management
by James Meyer Berkson

A thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in
Biological Sciences
Montana State University
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Abstract:

A simulation model was developed to test the effects of alternative management actions on the restoration of a metapopulation. The probability of extinction was modeled as a function of population growth, environmental stochasticity, and dispersal. Population growth rates varied between patches so source-sink dynamics could be modeled. Environmental stochasticity had two components, one shared by all patches and one unique to each patch. Dispersal rates varied between pairs of patches.

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Results of simulations showed that management intervention, such as moving animals between fragmented populations, recolonizing a “source” patch, or moving animals to ensure dispersal increased metapopulation viability. Improving patches with high growth rates increased viability more than improving low growth rate patches.

Using these results, a strategy to restore metapopulations was developed. The goal was to maximize the overall population growth rate, using a subdivided population to provide buffering. The strategy suggests selecting a number of strong patches possessing buffering capabilities, recolonizing any that are vacant, ensuring dispersal and focusing improvements on them.

The simplicity of the simulations and resulting strategy improves one’s understanding of metapopulation restoration, but also limits its application to any specific case. The ability to apply these results would be strengthened by using spatially structured population viability analysis, simulations of added complexity, and/or an adaptive management strategy.

Endangered Snake River spring/summer chinook salmon, a metapopulation, provided an illustration of the study’s application. Applying the suggested strategy requires greater levels of management intervention than is common in salmon management and is likely to be the subject of great debate. Adaptive management experiments are required to test the benefits of suggested methods.

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**MONTANA STATE UNIVERSITY-BOZEMAN
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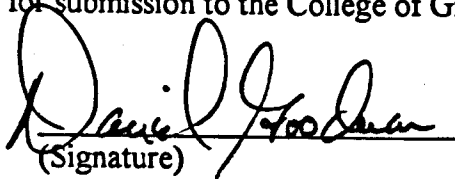
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This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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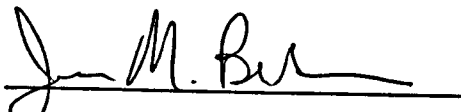

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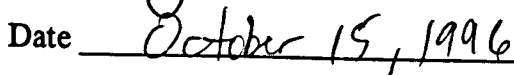
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To Angelo Cortopassi, Mentor and Friend

VITA

James Meyer Berkson was born in Hagerstown, Maryland on December 15, 1962 to Ann Goldstein Berkson (Ann B. Abrams) and Jacob Benjamin Berkson. James graduated Palo Alto Senior High School in Palo Alto, California in 1980. He received his Bachelor of Arts degree from the University of California at San Diego in Ecology, Behavior, and Evolution in 1984 with a minor in Statistics. James received his Master of Science degree in Zoology from the University of British Columbia in Vancouver, Canada in 1987. His thesis was titled "Opportunities for management created by spatial structure: A case study of Finnish Reindeer."

Professionally James has held positions as a Resource Modeler and as a Biometrician. James's work in Resource Management has involved a number of applications including harvest management, fisheries management, wildlife management, marine mammal management, and applying the principles of conservation biology to the restoration of a variety of species. James has been a contractor for the National Marine Fisheries Service and the Canadian Department of Fisheries and Oceans, and was the Lead Biometrician for the California Department of Fish and Game in Southern California. For the past seven years James has been a Fisheries Scientist for the Columbia River Inter-Tribal Fish Commission where his duties involve both conservation biology and harvest management. As part of these duties James serves on the Chinook Technical Committee of the Pacific Salmon Commission providing technical assistance for the International Negotiations.

James, his wife Ginger, and his daughter Torrey Caitlin, live in Aurora, Oregon with their two smooth coated collies, Maggie and Callie.

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ABSTRACT

A simulation model was developed to test the effects of alternative management actions on the restoration of a metapopulation. The probability of extinction was modeled as a function of population growth, environmental stochasticity, and dispersal. Population growth rates varied between patches so source-sink dynamics could be modeled. Environmental stochasticity had two components, one shared by all patches and one unique to each patch. Dispersal rates varied between pairs of patches.

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Results of simulations showed that management intervention, such as moving animals between fragmented populations, recolonizing a "source" patch, or moving animals to ensure dispersal increased metapopulation viability. Improving patches with high growth rates increased viability more than improving low growth rate patches.

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Endangered Snake River spring/summer chinook salmon, a metapopulation, provided an illustration of the study's application. Applying the suggested strategy requires greater levels of management intervention than is common in salmon management and is likely to be the subject of great debate. Adaptive management experiments are required to test the benefits of suggested methods.

CHAPTER 1

INTRODUCTION

Conservation biology is the science of conserving ecological diversity. The task of scientists in the conservation biology field is to provide “the intellectual tools that will anticipate, prevent, minimize, and/or repair ecological damage” (Soulé and Kohm 1989). Although a relatively young field, conservation biology has advanced in the past 20 years from both theory and experience (Soulé and Wilcox 1980a, Soulé 1986).

The goals of restoration can be broad, focusing variously on species diversity, community structure, ecosystem productivity, and ecosystem function. This study concerns single species restoration, also referred to as recovery.

Given the continually increasing risk to species, habitats and entire ecosystems (Soulé and Wilcox 1980b), the need for additional research in conservation biology is greater than ever (Soulé and Kohm 1989).

Spatial Structure and Metapopulations

Spatial structure is a key component in the dynamics of extinction and recovery in populations. The study of island biogeography developed theoretical relationships involving extinction and recolonization rates, distance, and area (MacArthur and Wilson 1963, 1967). Experimental studies reinforced the relationship of spatial

structure to recolonization and extinction processes developed by MacArthur and Wilson (Patrick 1967, Simberloff 1969, Simberloff and Wilson 1969).

An example of a spatial structure common to many species is called a metapopulation (Hanski and Gilpin 1991, Gilpin and Hanski 1991). In a metapopulation, there are a number of populations distributed among patches. Each population has its own internal dynamics, but the populations are connected through the dispersal of animals (Gilpin and Hanski 1991). The concept of metapopulations have been studied for years (Andrewartha and Birch 1954, den Boer 1968) with some of the earliest models developed by Levins (1969, 1970).

The movement of animals among patches is an essential component of the dynamics of the metapopulation. Dispersal provides the metapopulation with a buffer against regional extinction (Levin 1976, Caswell 1978). When a local population goes extinct, its patch can be recolonized by the dispersal of neighboring animals (Shaffer 1981, 1985, Gilpin 1987). When a population experiences a year of poor survival, it can quickly rebound through the dispersal of neighboring animals. The distribution of animals to patches is the basis for the buffering effects (Brown and Kodric-Brown 1977). When one patch is experiencing poor survival, another may be experiencing good survival.

Knowledge of island biogeography and metapopulation dynamics underscores the need to incorporate spatial structure into the development and assessment of management actions for species conservation and recovery. Understanding the

dynamics of metapopulations is essential to effective conservation efforts for many species (Shaffer 1987). The inherent spatial structure of a population may, in fact, dictate some of the most effective management tools to achieve its recovery.

The study of spatial structure has not been limited to population dynamics. A species divided into geographic races, called a Rassenkreis (Futuyma 1986), is an example of a subdivided population that has been the subject of considerable attention in population genetics as well (Falconer 1981, Futuyma 1986, Chakraborty and Leimar 1987). Studies such as Wright's island model (1943), the distance model (Wright 1943, 1951), the migration model (Malecot 1948), and the stepping stone model (Kimura 1953, Kimura and Weiss 1964) have attempted to simulate and better understand the population genetics of subdivided populations. Most of the population genetics work on subdivided populations does not account for colonization and extinction processes, and therefore, does not specifically apply to metapopulations, with limited exceptions (Gilpin 1991).

The work presented in this dissertation is designed to increase our understanding of the population dynamics of metapopulations.

Managing for Recovery

For an individual population, recovery could be associated with the population size needed to provide an acceptable probability of persistence over a reasonable time frame. An example might be the population size where the population has a 95%

probability of persistence over 100 years. The choice of probability and time frame are policy decisions.

For the recovery of a metapopulation, persistence of an individual subpopulation would likely not be sufficient. Defining metapopulation recovery requires policy decisions regarding an acceptable probability of persistence, an acceptable time frame, and an acceptable percentage of patches that must be occupied. As an example, a metapopulation might be considered recovered when there is a 95% probability of persistence of at least 50% of the patches over 100 years.

Strategies to achieve recovery almost always involve management intervention. A policy involving no management intervention might be used, but this would be unlikely to reverse or remove the factors causing the population decline. While the ultimate goal of management is the recovery of the population, managers must work towards more proximate goals such as: halting the decline of the population; minimizing the population's probability of extinction; rejecting measures that place the population in "jeopardy"; extending the population's range; reducing fragmentation; minimizing the loss of genetic diversity; returning the population to its historic range, population size, or density.

In order for managers to make informed decisions in selecting management actions, managers must have information about the likelihood of success using alternative actions. In most cases, managers lack data needed to gain knowledge from past experience (Ballou et al. 1995). For many declining populations, little data of any

kind exists, which often limits management's potential responses to a population's decline. If appropriate data did exist, it is possible that the conditions leading to the population decline could have been actively reversed earlier. Where data on population dynamics does exist, it can not provide information on the effects of alternative management actions that have not been tried in the past, nor for population sizes that have not been observed in the past (Walters 1986).

For this reason managers require a more conceptual tool to assess alternative management actions. Resource modeling provides such tools. Models have been an important foundation of conservation biology, providing many of its most basic principles.

Resource Modeling as a Management Tool

Resource modeling constructs a caricature of the population using the dynamics of the population such as survival rates, birth rates, and the key factors affecting these rates (Walters 1986). Using this tool, managers can study the effects of harvest on survival rates and population growth as an example. In the majority of these general models, all individuals within the population are aggregated into a single group, which is subject to the dynamics, not individuals or subgroups. An example is shown below:

$$N_{t+1} = \lambda \cdot N_t \tag{1.1}$$

where:

N_t = the total population size at time t .

λ = the population growth rate.

It is always an objective to make a model as simple as possible, yet capable of producing realistic results (Walters 1986). Clearly, modeling the day to day existence of each individual within a population is likely to be excessive for studying the basic dynamics of populations. The use of extremely complicated models has been discouraged because dramatic increases in complexity often do not produce dramatic improvements in model performance (Ludwig et al. 1978, Deriso 1980, Goodman 1981, Burgoyne 1981, Walters 1986). This explains, in part, the prominence of models which act on groups of individuals.

But does the fact that modeling at the level of the individual produces unwarranted complexity mean that modeling at any level, other than the entire group, is unwarranted? Are there cases where modeling the entire group as a whole misses some important and necessary complexity of the system? What if the population is subdivided into a complex spatial structure? Does spatial structure need to be considered in developing and assessing management options for recovery?

Modeling Spatial Structure

For a subdivided population, distributed into patches, the rate of turnover (extinction and recolonization) determines whether one should analyze and manage single populations (either as individual patches or the entire population as a whole) or

whether one is dealing with a dynamic structure in which the individual patches come and go in ecological time (Soulé 1987b). In the latter case, the population's spatial structure is called a "metapopulation" (Gilpin 1987, Soulé 1987b, Gilpin and Hanski 1991).

Soulé (1987b) writes:

"In the latter (turnover) case, however, it would be folly to bet heavily on the viability of individual patch populations, because each of these has a high probability of extinction. Rather, one's focus shifts upward in the spatial-temporal hierarchy to the metapopulation - the paramount concern is the persistence of the unit or set of populations, which depends on the rates of extinction and colonization of patches."

An understanding of metapopulation dynamics is essential to effective conservation efforts (Shaffer 1987, E.S.A. 1996).

Models used by managers to assess alternative recovery actions should include spatial dynamics when the population is patchily distributed as in a metapopulation. Models without spatial structure are missing the extinction and recolonization dynamics through dispersal that are essential to metapopulation persistence. If the spatial structure is not included, then recovery actions such as reopening dispersal corridors, likely to be the most beneficial, would not be assessed.

Population Viability Analyses

Understanding the dynamics of single species populations, often as indicators of an ecosystem, is a central premise of conservation biology (Soulé and Kohm 1989, Foose et al. 1995). Studies have increasingly focused on the "viability" of a population

(Soulé 1987a), meaning the probability of the long term persistence of a population (Soulé 1987b). Analyses that study the effects of various factors on a population's viability using resource modeling are called "population viability analyses" (PVA) (Gilpin and Soulé 1986, Soulé 1987a, 1987b, Boyce 1992). Soulé (1987b) writes that the following factors have been introduced in viability analysis: population dynamics, environmental variation, genetics, catastrophe, and metapopulation structure and fragmentation.

Population viability analyses have been developed to link the manager's need to assess the probable effects of alternative management actions with the manager's goals, such as reducing the probability of extinction of a population (Gilpin and Soulé 1986, Soulé 1987a, Shaffer 1990, Boyce 1992, Foose et al. 1995). A PVA typically combines data from field studies with simulation modeling of the potential impacts of various extinction factors (Menges 1990, Murphy et al. 1990, Stacey and Taper 1992, Doak et al. 1994). Practical management strategies can be developed directly from PVA (Conway 1995, ESA 1996), if the PVA is competent.

Choosing between alternative management actions always involves tradeoffs. With limited and declining budgets and staffing, management agencies must make decisions based on the most effective use of their resources. Should a management agency improve habitat in several patches or increase survival and fecundity through captive breeding, or should a mixed strategy be used? In which patches should habitat be improved? When should dispersal be augmented, and between which patches?

By using a PVA, it is possible to provide managers with probable results in terms of tradeoffs by which to evaluate alternative strategies. Ideally, models could provide the crisp kind of functional tradeoff surface shown in Figure 1.1, where strategy number one is the ideal strategy, regardless of the expenditure.

In other cases, the ideal strategy may depend on the amount of expenditure possible such as in Figure 1.2. For simplification Figures 1.1 and 1.2 show the expected value or mean of the distribution of results for each strategy at each expenditure level.

Benefits and expenses can both be measured in many ways. For example, benefits can represent probability of persistence, population size in year 100, or percentage of patches occupied. Expenses can represent cost of management, loss of genetic variation, or foregone opportunity costs.

Because random events are such an important factor in the process of extinction (Shaffer 1981, Foose et al. 1995), models used to assess management actions include stochasticity (Soulé 1987a, Shaffer 1987). Output from these models reflects the influence of random events and uncertainty by producing a distribution of results.

Figure 1.3 shows a result typical of a PVA where the combination of each strategy and each expense produces a probability distribution of outcomes as the result. The distributions of two or more strategies can be compared to see if either produces an acceptable result for an acceptable probability.

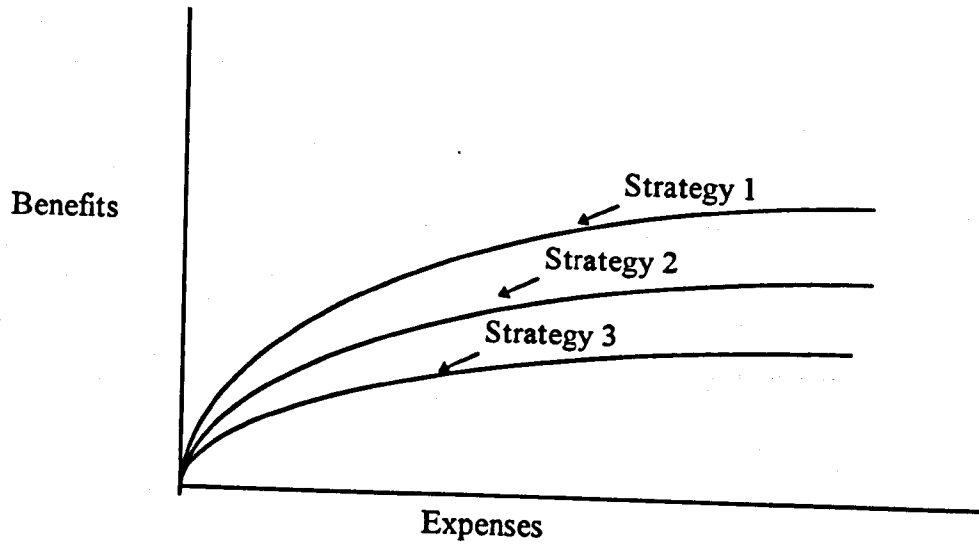


Figure 1.1: Illustration of Expenses to Benefits Relationship of Three Hypothetical Strategies.

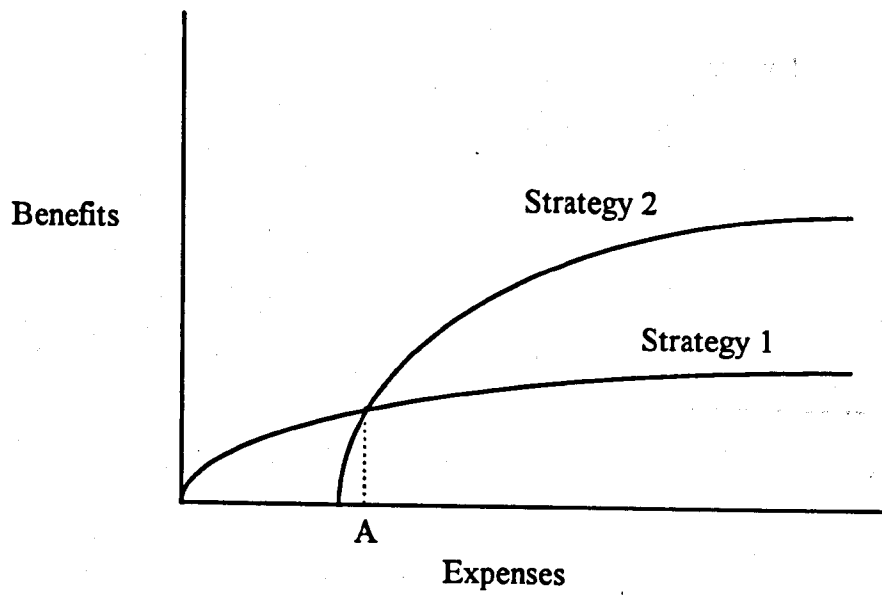


Figure 1.2: Illustration of Expenses to Benefits for Two Overlapping Policies.

Point A represents expense level where the best policy switches from strategy 1 to strategy 2.

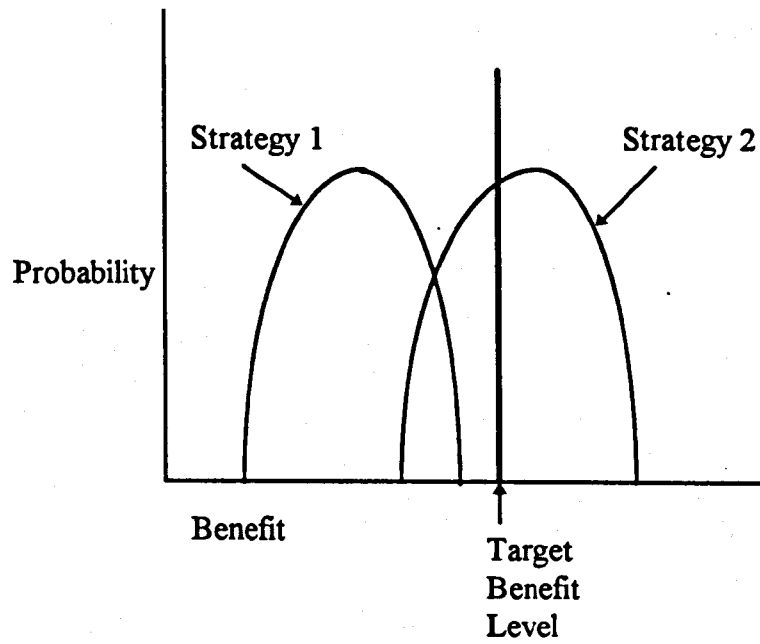


Figure 1.3: Sample Output of a PVA Comparing the Distribution of Results of Two Strategies at a Single Expense Level.

In this case for a certain expense level, strategy one never reaches the target, and strategy two has a 65% probability of exceeding the target. Strategy two would be preferred as it has a greater probability of exceeding the success threshold.

Metapopulations and Viability Analyses

In its review of the Endangered Species Act, the Ecological Society of America (1996) wrote:

“Population viability can seldom be assessed by focusing on a single patch of suitable habitat and the organisms living in it. Most organisms live in islands of suitable habitat, among which there is an exchange of individuals, embedded in a larger landscape. Because the populations in the various patches are linked by the movement of dispersing individuals, the fate of the populations is interconnected. Studies of population viability of many organisms will therefore need to consider the importance of factors that link subpopulations.”

Gilpin (1987) demonstrates the necessity to integrate spatial structure into PVA for populations distributed into patches and provides a template for the integration. There has been a reluctance to address questions of spatial structure in ecological analyses because the data on location and movement of animals is difficult to gather, data demands are intensive, and incorporating the data into systems models has been complex (Gilpin 1987).

The need for understanding the relationship between spatial structure and viability continues. In the book, Research Priorities for Conservation Biology, Soulé and Kohm (1989) write:

“Even more important is the development of such a model that is geographically structured (i.e., a metapopulation model). It may, in

fact, prove true that a certain magnitude of geographical structure is essential for a reasonable prospect of survival. But this question cannot be adequately addressed with current population dynamics models.”

This dissertation attempts to add to our understanding of the relationship of spatial structure to population viability. What management actions will help restore a metapopulation and what actions won't? If resources are limited, what is the best way to use the resources to speed restoration? This dissertation will provide general conclusions on the utility of various management actions and it will demonstrate modeling tools that can be used for more case specific questions.

CHAPTER 2

A SIMULATION MODEL TO STUDY THE DYNAMICS
OF METAPOPOPULATION VIABILITYIntroduction

The spatial structure of a population affects its probability of extinction (den Boer 1968, Gilpin 1987, Chapter 1). An example of a spatial structure common to many species is called a metapopulation, where animals are distributed among patches (Hanski and Gilpin 1991, Gilpin and Hanski 1991, Chapter 1). Each patch contains a subpopulation that has its own internal dynamics, and the subpopulations are connected through dispersal (Gilpin and Hanski 1991, Chapter 1).

Before one can predict the response of a metapopulation to various recovery actions, the general population dynamics of a metapopulation must first be understood. Viability, measured as the probability of the metapopulation persisting, is affected by a number of critical factors. The relationship between viability and dispersal is critical, as dispersal is an essential component of metapopulation dynamics (Levin 1976, Brown and Kodric-Brown 1977). Viability is also dependent on the level of environmental stochasticity experienced by the metapopulation. Patches within the metapopulation will not all share identical environmental affects, providing opportunities for patches to buffer each other (Shaffer 1981, 1985, Gilpin 1987). The distribution of population growth rates among patches affects viability, as growth rates establish the

metapopulation's abilities to resist extremes in environmental conditions and buffer one another (Brown and Kodric-Brown 1977, Pulliam 1988).

In this chapter, a model is described to study the relationship between a metapopulation spatial structure and population viability. The model tests a range of metapopulation dynamics in order to provide results that could be applied to the full range of species and cases distributed as metapopulations.

There are several features unique to this model. In this model, extinction is a function of the population dynamics of the metapopulation. Each year three processes take place: population growth, environmental stochasticity, and dispersal. Population growth rates vary between patches, allowing source-sink dynamics (Pulliam 1988). Environmental stochasticity is divided into two components, a component shared by each patch and a component unique to each patch. Dispersal rates are variable between pairs of patches, allowing some corridors to be open while others are closed.

In the equations which follow, the population size variable has three subscripts which correspond to the specific patch, the specific year, and the specific process, or step, that was last completed (growth, environmental stochasticity, or dispersal)

Model Design

The simulation model was designed to demonstrate the basic dynamics of the metapopulation structure. The simulation followed the population sizes of five patches

over time, keeping track of their probability of persisting through a wide range of conditions.

The population size in each of the patches was the state variable of the system. During each year the population in each patch was subject to population growth, random environmental effects, and dispersal. The three processes were divided into three steps. Steps one and two, growth and environmental effects, occur simultaneously but are broken into separate steps for ease of explanation. Step three, dispersal, follows the completion of growth and environmental effects. The model contained no age structure and no dynamics at the level of the individual.

The system was designed as one metapopulation with five patches. The five patches were arranged in the manner shown in Figure 2.1.

Each patch contained a single population. For each simulation, each population was started with 100 animals.

$$n_{i,0,3} = 100 \quad (2.1)$$

where:

$n_{i,0,3}$ = the population size in patch i , at year 0, following completion of the third step,

for $i = 1, \dots, 5$.

Step One: Population Growth

Each population grew by a constant growth rate unique to its patch, each year.

$$n_{i,t+1,1} = \lambda_i \cdot n_{i,t,3} \quad (2.2)$$

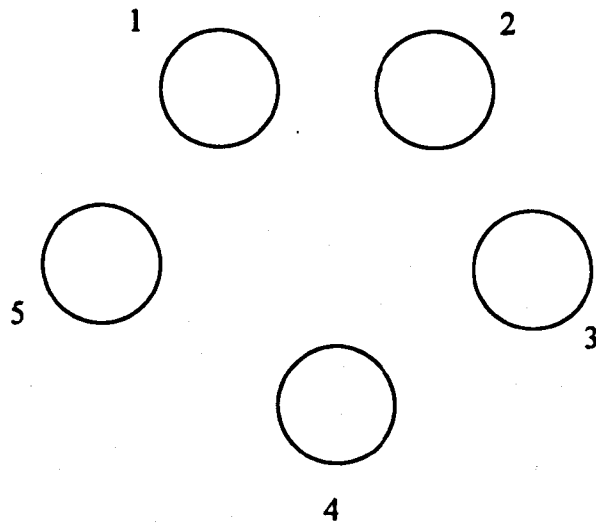


Figure 2.1: Arrangement of Patches in Basic Metapopulation System Modeled.

The patches are arranged in a ring structure. All patches are of equal size. The distance between neighboring patches is constant across all patches.

where:

$n_{i,t+1,1}$ the population size in patch i in year $t+1$ upon completion of step 1.

$n_{i,t,3}$ = the population size in patch i , in year t , upon completion of step 3.

and

λ_i = the discrete growth rate for patch i

The growth rate within a patch did not change within a simulation run, reflecting the average growth of the population in each patch. Patch specific growth rates reflected differences in habitat conditions affecting average growth rates and assumed that all animals were equally capable of reproducing.

The structure permitted a wide array of growth rates to be utilized across patches in the simulations. When all patches had a growth rate of 1.0, growth had no effect, and changes in population size were due entirely to other factors. When a subset of the five patches were given a growth rate greater than 1.0, and the remaining patches were given growth rates less than 1.0, a source-sink system (Pulliam 1988) was modeled. In this case the patches with growth rates greater than 1.0 had continual growth on average, and the patches with growth rates less than 1.0 declined on average.

In order to avoid infinite growth, a ceiling level of 10,000 was placed on each population. If any population size was greater than 10,000 at the completion of the growth step, the population size was set equal to 10,000.

Step Two: Environmental Stochasticity

After growth, each patch was subject to random environmental effects, also known as environmental variation or environmental stochasticity. This represented year to year variation in external circumstances affecting population size. Weather conditions, droughts, floods, availability of prey, density of predators, etc. are all meant to be represented with the inclusion of environmental stochasticity.

Some environmental effects were common to all patches in the metapopulation, such as extreme weather conditions affecting a large area. Other environmental effects were more localized or independent to individual patches such as changes in local predator densities. Environmental stochasticity was modeled to incorporate both common and independent components as illustrated in Figure 2.2.

Environmental effects were modeled in the following way: Each year one value was randomly drawn from a normal distribution to represent environmental stochasticity common to *all* five patches.

$$\alpha_{t+1} \sim N(0, \sigma_{\text{common}}^2) \quad (2.3)$$

where:

α_{t+1} = the common environmental stochasticity in year $t + 1$

and

$N(0, \sigma_{\text{common}}^2)$ = a normal distribution with mean = 0 and

variance = σ^2 common across patches.

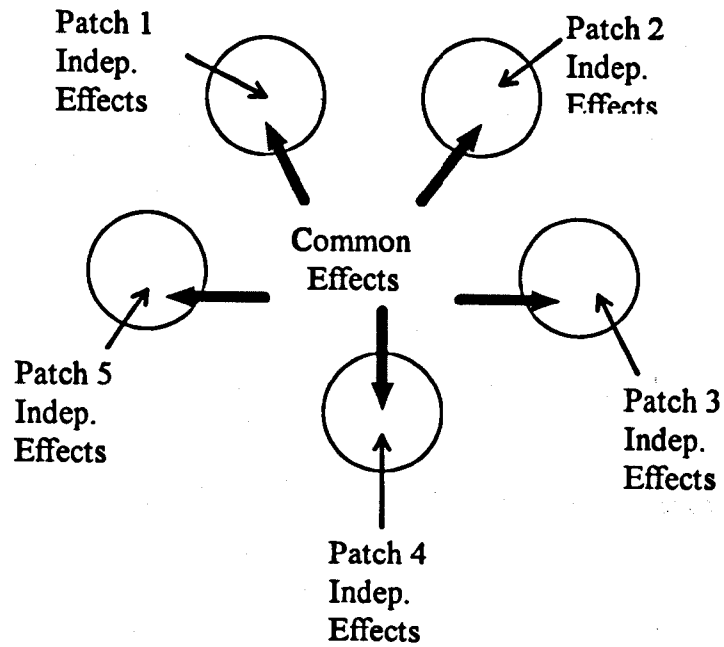


Figure 2.2: Illustration of Effects of Common versus Independent Environmental Stochasticity on Individual Patches.

Each year one value was drawn for *each* patch from a normal distribution to represent environmental stochasticity independent to *each* of the five patches.

$$\beta_{i,t+1} \sim N(0, \sigma_{independent}^2) \quad (2.4)$$

where:

$\beta_{i,t+1}$ = the independent environmental stochasticity for patch *i* in year *t*+1.

and

$N(0, \sigma_{independent}^2)$ = a normal distribution with mean = 0

and variance = σ^2 independent across patches.

For each patch, total environmental stochasticity for each patch was calculated as:

$$\gamma_{i,t+1} = \alpha_{t+1} + \beta_{i,t+1} \quad (2.5)$$

where:

$\gamma_{i,t+1}$ = the total environmental stochasticity for patch *i* in year *t*+1.

The total environmental stochasticity was normally distributed with a mean equal to 0, and a variance equal to the combined common plus independent variances.

$$\gamma_{i,t+1} \sim N(0, \sigma_{common}^2 + \sigma_{independent}^2) \quad (2.6)$$

The total environmental stochasticity was incorporated in the following way:

$$n_{i,t+1,2} = n_{i,t+1,1} \cdot e^{\gamma_{i,t+1}} \quad (2.7)$$

where:

$n_{i,t+1,2}$ = the population size in patch i , in year $t+1$,
upon completion of step 2.

Note that taking the exponential of the total stochasticity term transforms the distribution of stochasticity into a lognormal distribution.

$$e^{\gamma_{i,t+1}} = \text{lognormal}(0, \gamma_{i,t+1}) \quad (2.8)$$

This is appropriate for a number of reasons. First the term can not be negative, unlike deviates of the normal distribution. Second, the geometric mean of this distribution is equal to 1.0. Over time the cumulative effects of environmental stochasticity would be equal to the geometric mean of the yearly values, rather than the arithmetic mean. A geometric mean of 1.0 indicates that the effects of environmental stochasticity over time had an expectation of no overall effect or trend. Studying viability over a realistic time frame required the use of a finite time frame, which resulted in a wide distribution of actual effects.

By changing the values of the variances of common and independent variation, without changing the variance of the total, it was possible to examine the effects of independent versus common variation without changing the overall distribution of total environmental stochasticity. In order to do this, the total variance was set constant

across runs, while the proportion of the total variance made up of common stochasticity varied across runs.

$$\sigma_{\text{common}}^2 + \sigma_{\text{independent}}^2 = \sigma_{\text{total}}^2 = k \quad (2.9)$$

where:

$\sigma_{\text{total}}^2 =$ total variance of environmental stochasticity

and

$k =$ a constant

Step Three: Dispersal

Dispersal was structured to be identical for all patches, as expected from the ring structure of the patches (Figure 2.1). The dispersal was structured so that the population size in a patch was equal to its prior value minus its emigrants and plus its immigrants.

$$n_{i,t+1,3} = n_{i,t+1,2} - m_{i,t+1} + r_{i,t+1} \quad (2.10)$$

where:

$m_{i,t+1} =$ the number of animals dispersing *from* patch i in year $t+1$.

and

$r_{i,t+1} =$ the number of animals dispersing *to* patch i in year $t+1$.

It was assumed that the population in each patch regularly dispersed a constant percentage of its occupants. This assumed a density independent rate. For large populations (set at > 300 for this study) this can be written as the following:

$$m_{i,t+1} = d \cdot n_{i,t+1,2} \quad (\text{for } n_{i,t+1,2} > 300) \quad (2.11)$$

where:

$d =$ the dispersal rate from each patch.

In theory, calculating the dispersal component of the model involved two steps. First the number of animals dispersing from a patch was calculated using the dispersal rate. Next a distribution was needed to assign the dispersing animals to their new patches. The dispersing animals were assumed to spread out in a distribution that did not change over time. Each nearest neighbor patch, in terms of geography, received 35% of the animals dispersing from a donor patch. The remaining two patches received 15% of the donor patch's dispersers each. An example of this using patch one as the donor is illustrated in Figure 2.3. In actuality the number of animals dispersing between pairs of patches was calculated by combining the two steps above into a single step, which is shown below.

In the case where all populations were large (> 300), the number of dispersing animals received can be calculated as:

$$r_{j,t+1} = \sum_{i \neq j} n_{i,t+1,2} \cdot d \cdot x_{i,j} \quad (\text{for } n_{i,t+1,2} > 300, i \neq j) \quad (2.12)$$

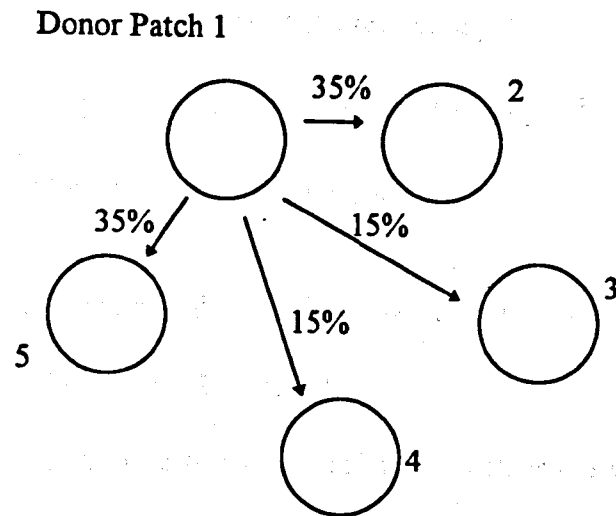


Figure 2.3: Illustration of Distribution of Dispersers from a Donor Patch.

where:

- $i =$ the patch number of the donating patch.
 $j =$ the patch number of the receiving patch.
 $x_{i,j} =$ the percentage of the dispersers from patch i going to patch j
 (35% for nearest neighbors, 15% for others).

The pattern of dispersal described, allowed dispersal between all possible pairings of patches, as illustrated in Figure 2.4.

The number of dispersers to be donated from each patch was calculated first, then the dispersers were distributed between receiving patches. When all patches had substantial population sizes (>300), the dynamics of both donating and receiving dispersing animals were calculated as shown below using patch three as an example:

$$n_{3,t+1,3} = (1-d) \cdot n_{3,t+1,2} + d \cdot (n_{1,t+1,2} \cdot 0.15 + n_{2,t+1,2} \cdot 0.35 + n_{4,t+1,2} \cdot 0.35 + n_{5,t+1,2} \cdot 0.15)$$

(for $n_{i,t+1,2} > 300, i = 1,2,\dots,5$) (2.13)

Modeling realistic metapopulation dynamics of small populations was essential to this study, and for this reason the dispersal equations above were not used to model the dispersal of small populations (≤ 300). If the previous equations had been used, the model could send a fractional number of animals for dispersal, particularly in the case of small population sizes combined with low dispersal rates. This could leave patches apparently occupied with population sizes greater than 0, but less than 1.

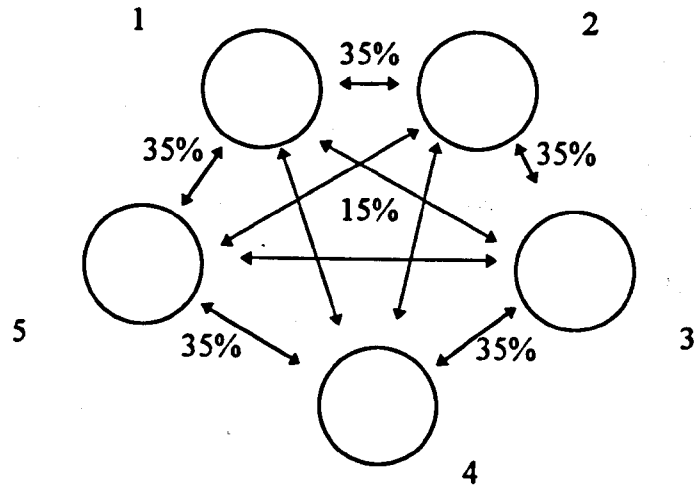


Figure 2.4: Illustration of Dispersal Routes between Metapopulation Patches.

Percentages indicate the percentages of dispersers moving between pairs of patches ($x_{i,j}$ from Equation 2.12).

For large donor populations (> 300), the number of dispersers was truncated to the nearest integer.

In order to avoid fractional dispersers for small donor populations of 300 or less, random numbers were drawn from a binomial distribution to provide an integer numbers of dispersers. The parameters of the binomial distribution used were the number of animals in the donor population and the dispersal rate to an individual receiver patch as shown below:

$$b_{i,j,t+1} = \text{binom}(n_{i,t+1,2}, d \cdot x_{i,j}) \quad (2.14)$$

where:

$b_{i,j,t+1}$ = the number of animals dispersing from donor patch i
(which has ≤ 300 animals), to patch j in year $t+1$.

For small populations the number of dispersers donated would be:

$$m_{i,t+1} = \sum_{j \neq i} b_{i,j,t+1} \quad (\text{for } n_{i,t+1,2} \leq 300) \quad (2.15)$$

The number of dispersers received by a patch remained a summation of the dispersing animals donated to that patch, but was now dependent on the sizes of the donor populations.

$$r_{j,t+1} = \sum_{i \neq j} \begin{cases} n_{i,t+1,2} \cdot d \cdot x_{i,j} & (\text{for } n_{i,t+1,2} > 300) \\ \text{binom}(n_{i,t+1,2}, d \cdot x_{i,j}) & (\text{for } n_{i,t+1,2} \leq 300) \end{cases} \quad (2.16)$$

Summary of Basic Dynamics

Growth, random environmental effects, and dispersal are the dynamics involved in the basic model. Together they operate in the following way:

Step 1 - Population Growth: $n_{i,t+1,1} = n_{i,t,3} \cdot \lambda_i \quad (2.2)$

Step 2 - Environmental Stochasticity $n_{i,t+1,2} = n_{i,t+1,1} \cdot e^{\gamma_{i,t+1}} \quad (2.7)$

Step 3 - Dispersal $n_{i,t+1,3} = n_{i,t+1,2} - m_{i,t+1} + r_{i,t+1} \quad (2.10)$

The three steps can be combined as:

$$n_{i,t+1,3} = n_{i,t,3} \cdot \lambda_i \cdot e^{\gamma_{i,t+1}} - m_{i,t+1} + r_{i,t+1} \quad (2.17)$$

Time Frame

Studies on restoration and viability require the use of longer time frames than are commonly used in most resource modeling exercises (Soulé 1987a, ESA 1996). In order to see the effects on viability in a restoration time frame, 100 years of population dynamics were simulated for each model run.

Output

Population viability is traditionally measured in terms of the probability of extinction of the population, or its complement, the probability of persistence of the population. The model kept track of the presence or absence of a population in each patch in the final year of the simulation, year 100. If one or more individuals were present in a patch in year 100, the patch was considered occupied. When the model was run repeatedly under the same conditions, the model kept track of the percentage of the time that each patch was occupied in year 100. These results can be presented as the probability of persistence of the individual populations.

As a metapopulation, the probability of persistence of populations in the individual patches is not the only way to judge the condition of the overall system. It is also possible to calculate the probability of persistence for any number of the populations. For instance, the probability that all five patches were occupied in year 100 could be calculated, or the probability that three or more patches were occupied in year 100. These examples are summary statistics that provide information on the health of the overall metapopulation, as compared to the health of individual patches. Most of the results in this study report the probability that all five patches were occupied in year 100.

Methods to Test Model Behavior and Sensitivity

The model was tested under a range of dispersal, growth rate, and environmental stochasticity parameter values.

Effects of Dispersal on Viability

The model was tested using a range of values for the dispersal rate from 0.00 to 0.75, encompassing both conditions of no dispersal, as well as, high rates of dispersal.

Effects of Growth Rate Regimes on Viability

Three growth rate regimes were initially tested (Table 2.1). The three cases were not meant to reflect an exhaustive search of possibilities, but rather, to provide an initial, basic test of the behavior of the model. Modeling source - sink conditions, options 2 and 3, tested a metapopulation under conditions where one or more patches supported others.

Table 2.1: Growth Rate Options by Patch for Initial Model Runs.

Option	Patch 1	Patch 2	Patch 3	Patch 4	Patch 5
Base	1.00	1.00	1.00	1.00	1.00
1	1.05	1.05	0.80	1.05	1.05
2	0.75	0.75	2.00	0.75	0.75

The base case, used in many of the model runs in this chapter, reflected conditions when the growth rate had no effect on any of the patches over time, causing all population changes to be a result of environmental stochasticity and dispersal. Option 1 reflected an extreme case, where four patches had positive growth and only

one patch had negative growth. Option 2 reflected an alternate extreme, where one patch had positive growth and the remaining four patches had negative growth. In each case the average growth rate across patches was equal to 1.0.

Effects of the Total Variance of Environmental Stochasticity on Viability

Two values for the total variance of environmental stochasticity were used, 0.025 and 0.500. The proportion of common variation in both cases was set to 50%. Growth rates for all patches were set to 1.0. The model ran over a range of dispersal rates.

Effects of the Proportion of Common to Independent Variance on Viability

A range of values for the proportion of common environmental stochasticity, or common variation, were tested ranging from 20% to 80%. In all cases the total variance equaled 0.50.

All of the model runs previously described ran for 100 years in each iteration and for 1000 iterations.

The Relationship Between Standard Error and Number of Iterations. The standard error of an estimate of the probability of persistence should get smaller as the number of model iterations increases for any particular set of parameters (Pagano 1986). In order to see how the standard error decreased as iterations increased, one particular set of parameter values was tested. Assuming a 60% proportion of common

variation and a 5% dispersal rate, the model was run for 10,000 iterations. The number of patches persisting in year 100 was calculated at the end of each iteration.

Results of the 10,000 iterations were grouped five ways: into 2 groups of 5,000, 10 groups of 1,000, 20 groups of 500, 100 groups of 100, and 1,000 groups of 10. The average probability of persistence of all 5 patches was calculated for each grouping. The standard deviation of the estimates across each group size was calculated as the standard error (Pagano 1986). For example, the average probability of persistence of all 5 patches was calculated for each of the 10 groups of 1,000. Then the standard deviation of the 10 estimates of the average was calculated as an estimate of the standard error. These methods were used for each grouping size.

Effects of Fragmentation on Viability

One way to test the influence of spatial structure on metapopulation viability is to lower the dispersal rate, as described above, which reduces the connectivity equally across all dispersal paths. An alternative approach is to eliminate a number of the dispersal pathways entirely, without changing those remaining.

Fragmentation was modeled as a barrier to dispersal as shown in Figure 2.5. In this example of fragmentation, patches one and five were separated from patches two, three, and four, removing several of the previously available corridors for dispersal.

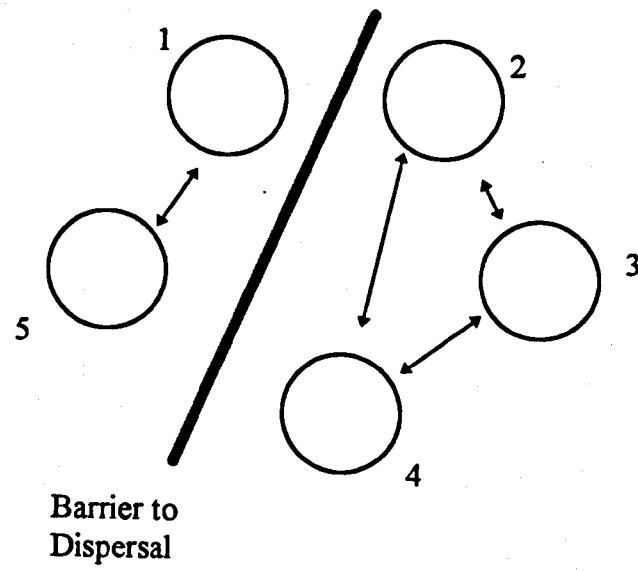


Figure 2.5: Modeled Effects of Fragmentation on Connectivity of the Metapopulation.

Alternative Reactions to Fragmentation. When dispersing animals get blocked, they may react in a number of possible ways. Three alternatives were modeled and are illustrated in Figure 2.6:

1) Animals attempting to travel through blocked corridors are removed from the metapopulation. For short, this option is called “dispersers disappear.”

2) Animals attempting to travel through blocked corridors return to the patch they were dispersing from. This option is nicknamed “dispersers go home.”

3) Animals attempting to travel through blocked corridors disperse to a connected patch, other than their own. For example, an animal trying to reach patch five from patch four, will go to either patch two or patch three. This option is nicknamed “dispersers go elsewhere.”

In order to understand the effects of fragmentation, it was necessary to compare model runs with fragmentation to model runs without fragmentation under similar conditions. In order to accomplish this, the model ran using four metapopulations, the original unfragmented population and a metapopulation for each of the three responses to fragmentation described above (Table 2.2).

Table 2.2: Description of the Four Metapopulations Used to Test the Effects of Fragmentation.

Option Number	Is the Metapopulation Fragmented?	How Do Animals React to Fragmentation
Base	No	-
1	Yes	Dispersers Disappear
2	Yes	Dispersers Go Home
3	Yes	Dispersers Go Elsewhere

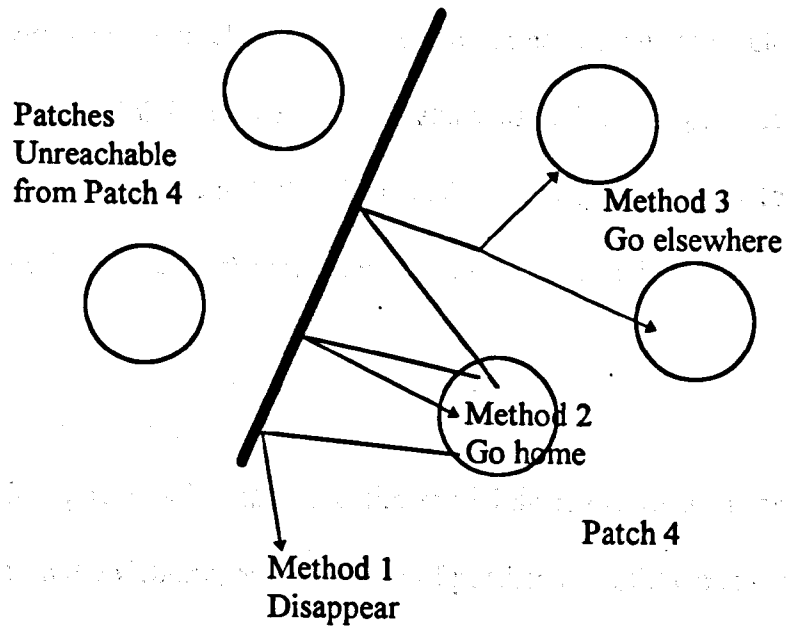


Figure 2.6: Illustration of Three Possible Reactions to Blocked Corridors Using Patch 4 as an Example of the Donor Patch.

The four metapopulations were subject to identical growth rate regimes and identical environmental stochasticity values within each time step. Growth rates were modeled equal to 1.0 in all patches. Values used for the proportion of common variation ranged from 20% to 80%. Dispersal rates ranged from 1% to 21%. For each combination of parameters, the model was run for 250 iterations.

Results

Modeling results indicate that the spatial structure of a metapopulation has a large impact on the viability, or probability of persistence, of the metapopulation.

Effects of Dispersal on Viability

Dispersal had a pronounced effect on the persistence of a patch within the metapopulation (Figure 2.7). With all dispersal rates set to 0% (with 40% common variation) the probability of any given patch persisting for 100 years was 34.9%. Increasing the dispersal rate to 1% per patch raised the probability of persistence of a patch to 78.3%. Raising the dispersal rate to 5% increased the persistence probability to 89.2%. The probability of persistence leveled off as dispersal rates increased.

Effects of Growth Rate Regimes on Viability

The viability of the growth rate regimes modeled was highly dependent on the level of dispersal within the system. Dispersal played a particularly crucial role for the dynamics of source - sink metapopulations (Pulliam 1988).

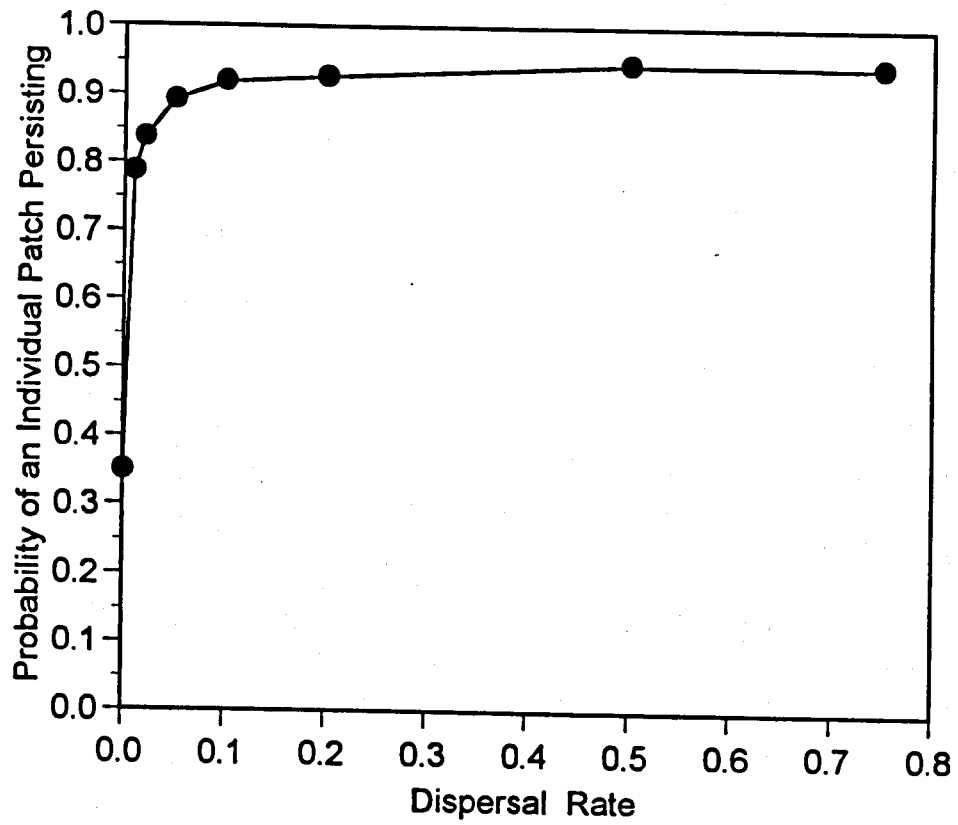


Figure 2.7: Probability of Persistence of an Individual Patch as the Dispersal Rate Increases.
(Growth rate = base option,
Proportion of common variation = 40%)

In these cases, at least one patch had a growth rate greater than 1.0 while at least one had a growth rate less than 1.0. Using option 1 from Table 2.1, four patches had a growth rate of 1.05 and the remaining patch had a growth rate of 0.80. With a dispersal rate of 0%, the one patch with a growth rate below one, persisted 100 years, 0.0% of the time (Figure 2.8). With a dispersal rate of 2%, the probability of persistence of the “sink” patch increased to 99.0% (Figure 2.8). The persistence of the source patches also increased with the addition of dispersal.

In option 2 of Table 2.1, four of the patches had growth rates of 0.75 and one patch had a growth rate of 2.00. Increasing the dispersal rate from 0% to 2% increased the probability of persistence of the four “sink” populations from 0.0% to 100.0% (Figure 2.9). The increased viability of the sink populations as well as the overall metapopulation was due to dispersal from neighboring patches.

Effects of the Total Variance of Environmental Stochasticity on Viability

Decreasing the variance of environmental stochasticity increased the probability of persistence for metapopulations at low dispersal rates (Figure 2.10).

The greatest difference was observed at the 0% dispersal rate where the metapopulation with a low variance of environmental stochasticity had a 40% probability of persistence and the metapopulation with the high variance had a 5% probability of persistence. As the dispersal rate increased, the effect on persistence probability decreased (Figure 2.10).

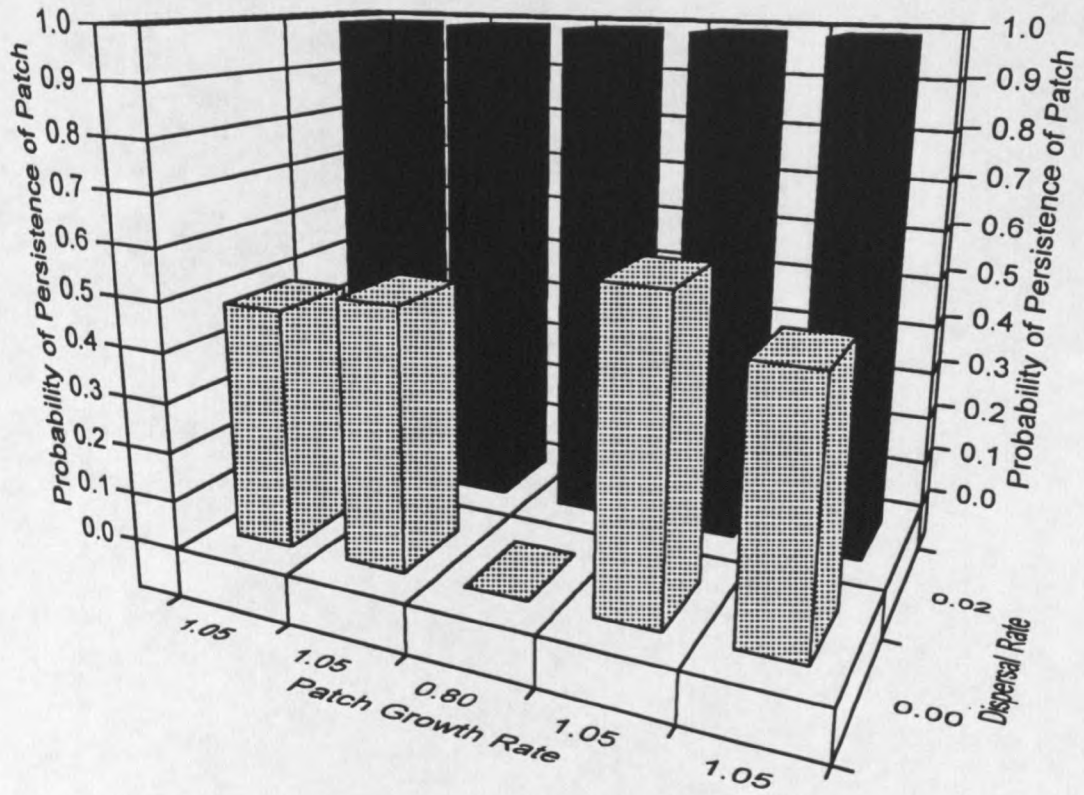


Figure 2.8: Effect of Dispersal on a Source - Sink Metapopulation.
(Proportion of common variation = 20%.)

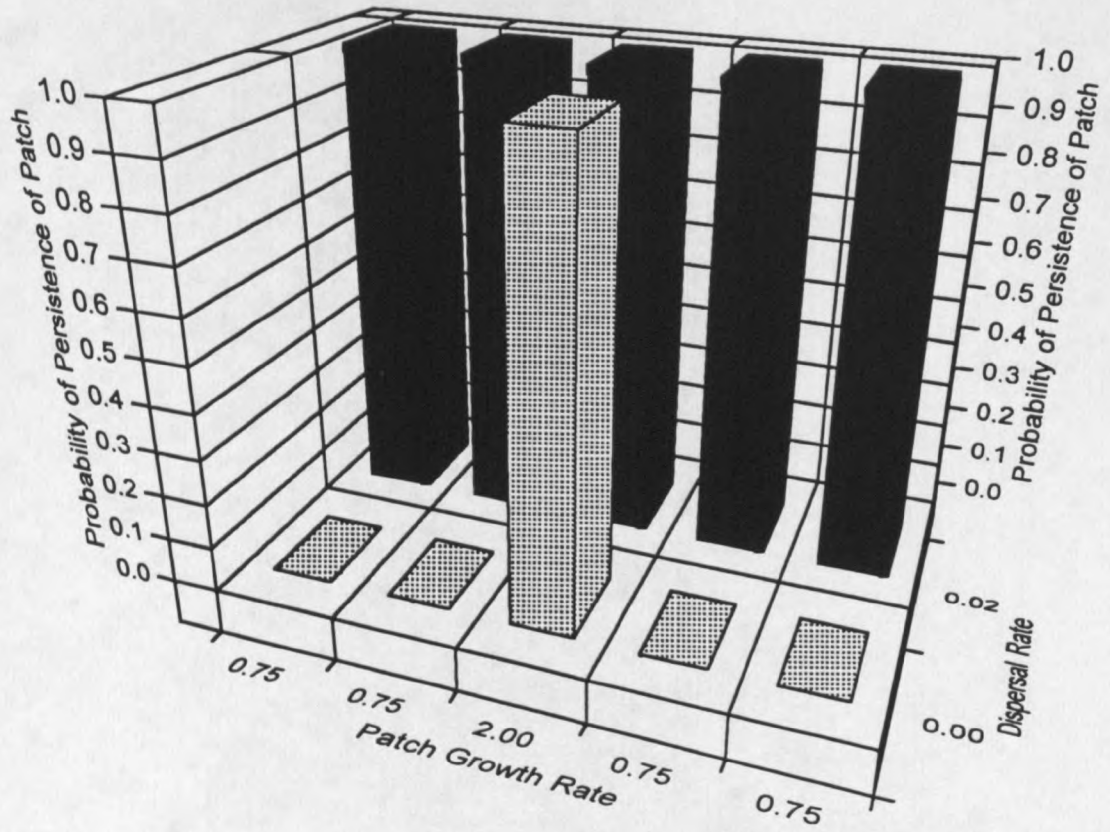


Figure 2.9: Effect of Dispersal on a Metapopulation with Four Sink Patches.
(Proportion of Common Variation = 20%)

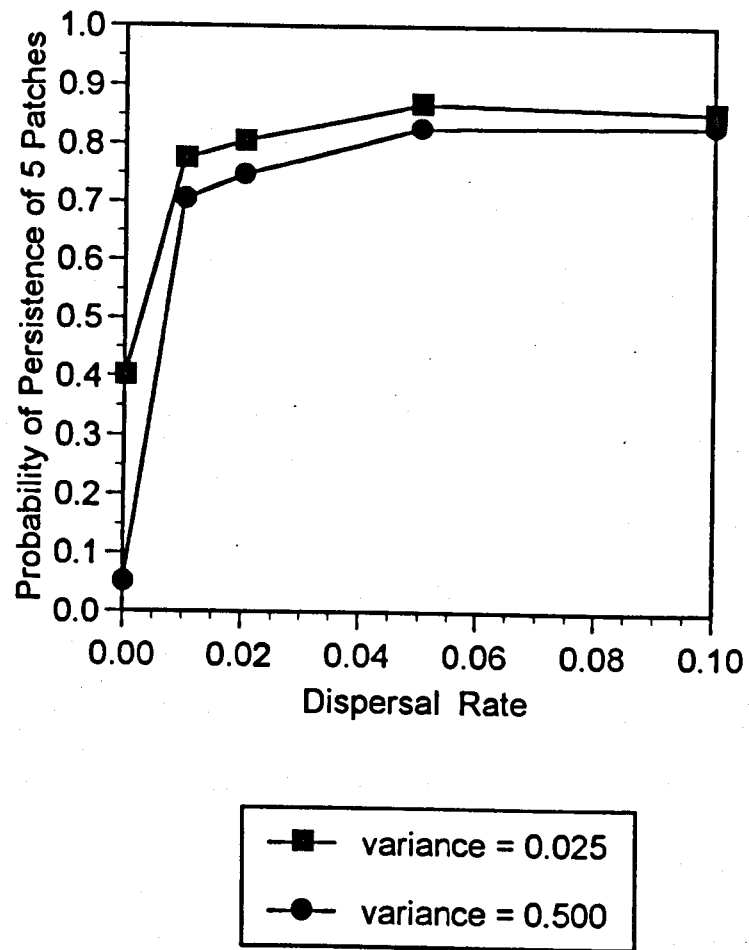


Figure 2.10: Effect of Reducing the Variance of Environmental Stochasticity on Viability. (Growth rates = 1.0, proportion of common variation = 50% in both cases).

Effects of the Proportion of Common to Independent Variance on Viability

The probability of persistence of the metapopulation was highly dependent on the proportion of the total environmental stochasticity that was common between patches. As the proportion of common stochasticity increased, the probability of persistence decreased, which was measured as the probability of all five patches persisting (Figure 2.11).

Patches with high levels of common variation shared good years and bad years. Independence provided buffer patches against bad years, providing refuge and providing dispersers to aide in the recovery of affected patches.

The Relationship Between Standard Error and Number of Iterations. The standard error of the estimate of the probability of persistence of all 5 patches decreased as the number of iterations increased (Table 2.3). With a small number of iterations, such as 10, the standard error was high relative to the estimate of the mean. By the time the number of iterations reached 1,000 or more, the standard error had decreased substantially relative to the mean. In the model runs studying effects of the proportion of common to independent variance on persistence, 1,000 iterations were used for each combination of parameters.

Table 2.3: Relationship between the Standard Error and Number of Iterations.

Number of Iterations	Mean	Standard Error
10	0.725	0.137
100	0.725	0.042
500	0.725	0.016
1,000	0.725	0.012
5,000	0.725	0.004

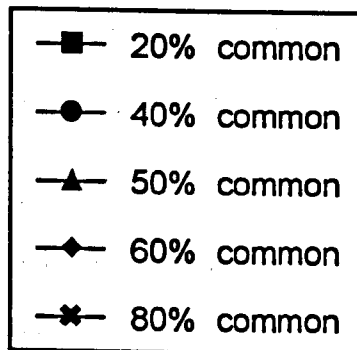
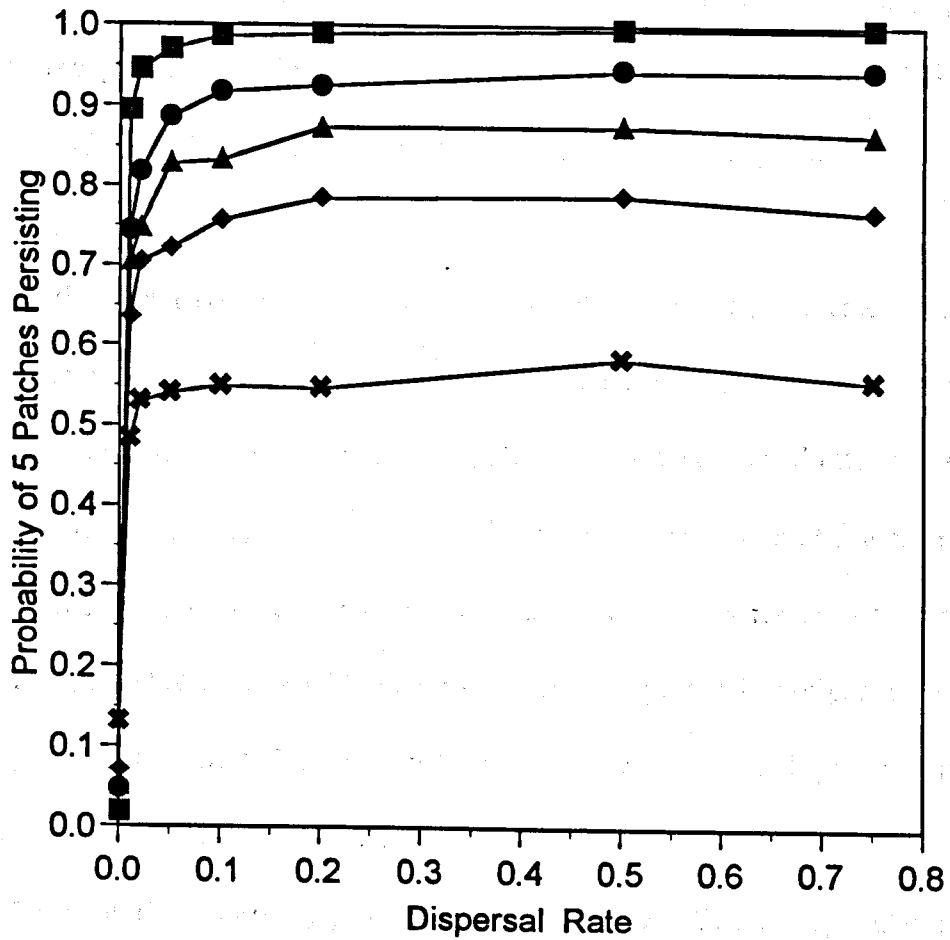


Figure 2.11: Probability of Persistence of 5 Patches as the Proportion of Common Variation and Dispersal Rate Changes. (Growth rate = base option)

Effects of Fragmentation on Viability

Fragmentation, as modeled, removed connectivity within the metapopulation, reducing the probability of persistence of the metapopulation (Figure 2.12). Three responses of individuals attempting to disperse between fragments were modeled (Table 2.2).

In the first case, individuals that could not successfully disperse, disappeared from the metapopulation. This case provided the greatest decrease in persistence probability from the unfragmented metapopulation. As the dispersal rate increased, the probability of persistence decreased, reflecting the increasing drain of dispersers.

In the other two cases, where unsuccessful dispersers returned to their home patch or dispersed elsewhere within their fragment, the probability of persistence of the metapopulation followed the same pattern as the unfragmented population as the dispersal rate increased (Figure 2.12).

Both of these options produced similar results. The metapopulation where unsuccessful dispersers went elsewhere had a slightly higher persistence probability because it had a higher within fragment dispersal rate.

This model run used a smaller number of iterations, 250 due to increased processing time. This produced lines that are less smooth, reflecting the increased standard error found with decreased iteration numbers.

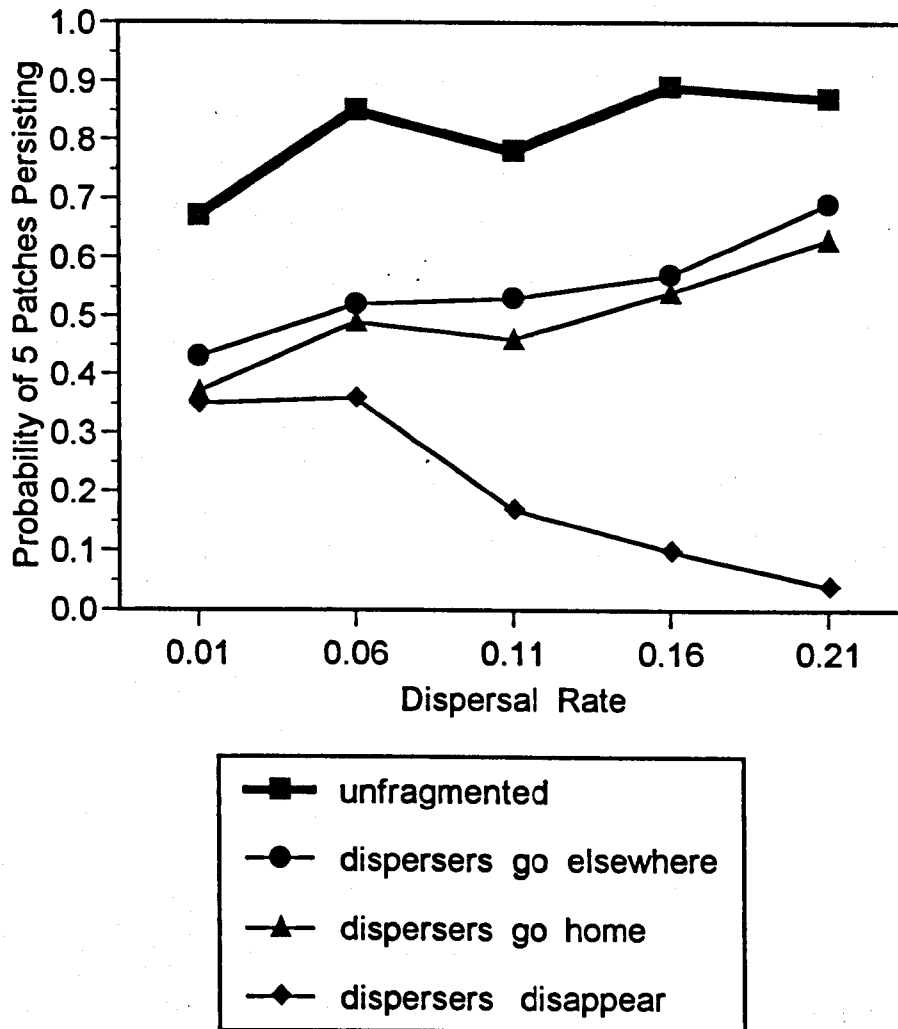


Figure 2.12: Effects of Fragmentation on Metapopulation Persistence.

(Growth rate = base option.

Proportion of common variation = 50%.)

In results from the unfragmented metapopulation, at year 100 the metapopulation usually had either 0 patches occupied, reflecting an extinct metapopulation, or 5 patches occupied (Figure 2.13). The survival of all five patches is largely due to the structure of dispersal in the metapopulation, where any surviving patch in year 100 was likely to disperse to each of the remaining four populations. It was very unlikely to see only 2 or 3 patches occupied in year 100 in the unfragmented population (Figure 2.13).

In the case of the fragmented population, there were cases where only 2 or 3 patches remained, reflecting the survival of only one of the two fragments of the original metapopulation (Figure 2.13).

Discussion

Model Structure

Many of the complexities of the real world have been purposely left out of the model structure developed in this chapter. These complexities include density dependence, age structure, non-constant dispersal rates, effective rates of dispersal, proportions of common to independent variation values that vary between patches, etc. It is not that these complexities are unneeded to better understand metapopulation dynamics, but rather, this study is viewed as an initial step in the understanding of viability in metapopulations, requiring simplicity. Walters (1986) states:

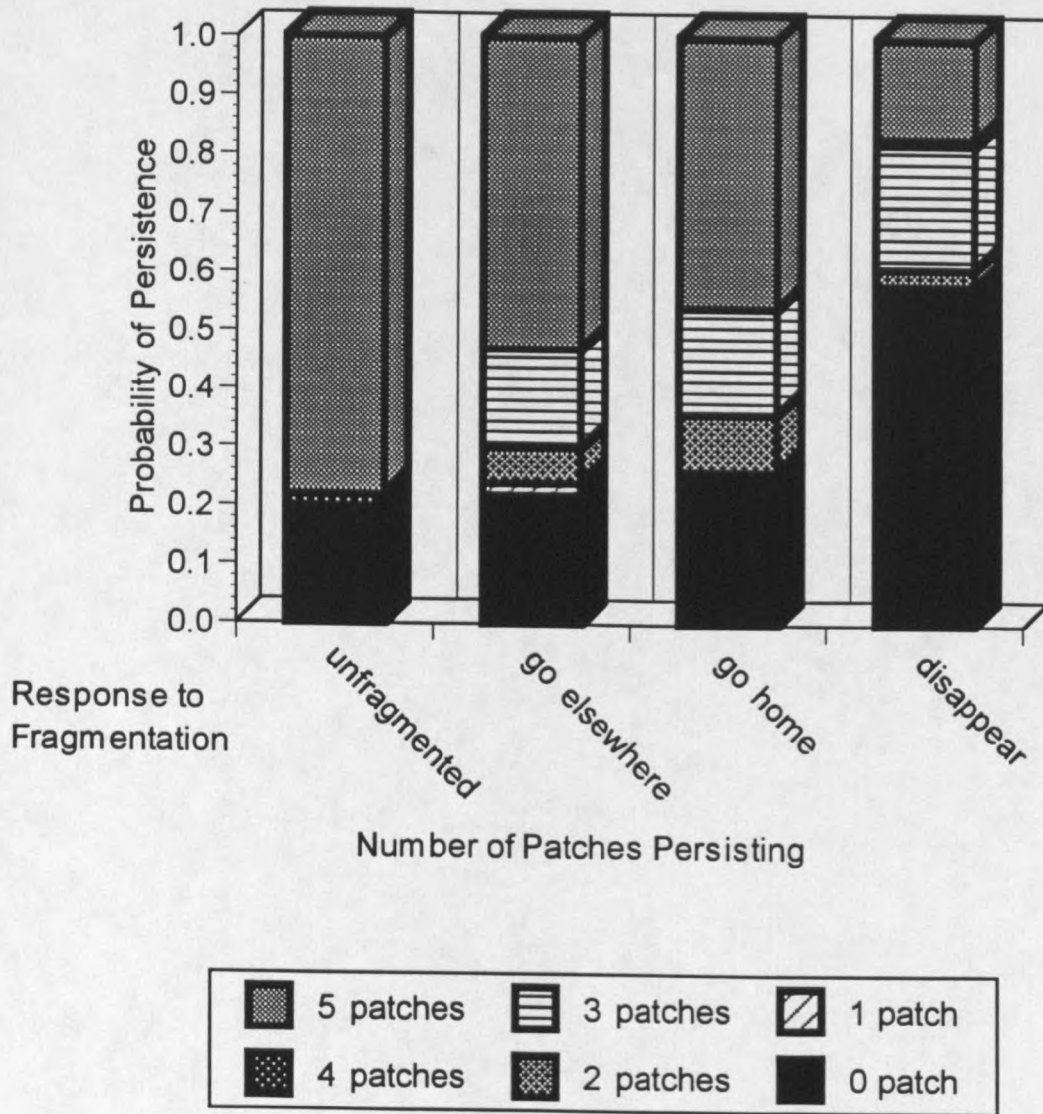


Figure 2.13: Distribution of the Number of Patches Persisting Under Different Responses to Fragmentation. (Growth rate = base option, Proportion of common variation = 50%).

“Indeed, the search for sound but simple models is a basic objective of science, as important in its own right as the search for detailed understanding. ... We can go a step beyond just saying that simple models are easier to understand and evaluate: it appears that simplicity is essential to adaptive learning. ... With experience, we seem to become better logicians, but that is precisely the point: this experience represents adaptive learning through a set of quite modest steps, and we must become psychologically comfortable with each step before proceeding.”

Developing a simple model to study metapopulation viability is an appropriate step in this process. Beginning with five patches, connected as a ring, with constant dispersal rates and proportions of common to independent variation equal between all patches fosters our ability to learn the basic relationships involved in metapopulation viability. At the same time it is important to keep track of the missing complexities that are most likely to affect the results of the simple models, in order to know how to begin the next model building iteration. Missing factors that could be important include density dependent survival and dispersal rates.

Density dependent survival rates affect population growth rates, but for this study there is particular concern for its effects at small population sizes. Traditional relationships used in population dynamics and demography such as the logistic (Verhulst 1838, Pearl and Reed 1920) or the Ricker curve (Ricker 1954, 1958) assume the per capita growth rate increases as population size declines. These models assume limitations to population growth are removed at small population sizes.

Other studies have theorized that per capita growth rates actually decline at extremely small population sizes, known as the Allee effect (Allee 1949, Nelson and

Soulé 1987). One proposed reason assumes animals at extremely small numbers will not be able to find each other to reproduce.

Dispersal rates may also be density dependent reflecting a response to increasing competition for space within each patch.

Adding additional layers of complexity, such as the examples above, could be incorporated to the modeled metapopulation structure in order to continue the learning process started in this Chapter.

Model Results

The results reported in this chapter strongly support a conclusion previously reported (Levins 1969, 1970, Brown and Kodric-Brown 1977) that spatial structure is a key component in the dynamics of extinction. This study has also confirmed that the viability of a metapopulation is highly dependent on its specific spatial structure (Gilpin 1987, Soulé and Kohm 1989, ESA 1996).

Three of the most important components of the spatial structure are the dispersal, the population growth rates, and the proportion of common to independent environmental variation between patches. Dispersal is the central component of metapopulation dynamics (Levin 1976, Caswell 1978, Shaffer 1981 and 1985, Gilpin 1987). Viability increases as dispersal increases. Metapopulations are also characterized by the individual dynamics of their component patches (Pulliam 1988). With dispersal, source patches are capable of continuing the existence of sink patches.

Another key component of metapopulation dynamics is the ability of patches to act as buffers for each other against unfavorable environmental conditions (Levin 1976, Caswell 1978, Brown and Kodric-Brown 1977). The effectiveness of buffering is dependent on the proportion of environmental conditions common across patches (Goodman 1987a, 1987b). While this result was confirmed, there remained a dramatic increase in viability, regardless of the proportion of common variation, when comparing metapopulations with no dispersal to metapopulations with any dispersal.

These results confirm that studies on the viability of metapopulations must include spatial dynamics. At the very least, information on dispersal, productivity and the levels of common and independent variation should be included. The convenience of ignoring spatial structure, a strategy likely to be considered for metapopulations with low levels of dispersal or high proportions of common variation, ignores one of the most critical factors affecting the dynamics of viability based on the results of this study. Even low levels of dispersal had a major influence on viability due to the longer time frames involved. The presence of low levels of independent variation provided opportunities, although limited, for buffering within the 100 year time frame.

This strongly supports earlier conclusions (Gilpin 1987, ESA 1996) that PVAs should incorporate spatial structure in the case of metapopulations due to its importance to extinction dynamics.

CHAPTER 3

MODELING THE EFFECTS OF ALTERNATIVE MANAGEMENT

ACTIONS ON METAPOPOPULATION RECOVERY

Introduction

The impact of metapopulation spatial structure on extinction dynamics has been previously examined (Levins 1969, 1970, Brown and Kodric-Brown 1977, Shaffer 1981, 1985, Gilpin 1987, Gilpin and Hanski 1991, Chapter 2). But metapopulation spatial structure also impacts the relative success of alternative restoration strategies, which has not been examined to the same degree. Resource managers are required to select from alternative management actions in order to recover an endangered or depleted population. With little data available on most endangered species (Ballou et al. 1995), managers use resource modeling to assess alternative management actions (ESA 1996).

Population viability analysis (PVA) estimates the probable effects of alternative management actions in reaching recovery (Soulé 1987a, Gilpin and Soulé 1986, Shaffer 1990, Boyce 1992, Foose et al. 1995). A PVA typically combines data from field studies with simulation modeling of the possible impacts of various extinction factors (Menges 1990, Murphy et al. 1990, Stacey and Taper 1992, Doak et al. 1994). Pragmatic management actions can be developed directly from PVA (Conway 1995, ESA 1996).

Chapter 2 demonstrated the important influence of spatial structure on the viability of a metapopulation. It is essential that spatial structure be incorporated into a PVA for a metapopulation (Gilpin 1987, ESA 1996, Chapter 2). This has been a difficult task because data on animal movement is difficult to gather, and many complex, computational problems have been unresolvable (Gilpin 1987). The development of metapopulation models that combine PVA and spatial structure have been a high priority in conservation biology (Soulé and Kohm 1989).

Using the general model developed in Chapter 2, a number of alternative management actions were tested in terms of their effect on metapopulation viability. This analysis was designed to provide the following:

- 1) Evidence that the assessment of alternative recovery actions requires the incorporation of metapopulation spatial structure in the analysis.
- 2) An example of a PVA which incorporates spatial structure to assess the impacts of alternative management actions on the recovery of a metapopulation.
- 3) General principles or conclusions regarding alternative strategies for recovering a metapopulation.

Selection of Alternative Management Actions to Test

Within the framework of a general model, there are an infinite variety of management actions that could be tested for their effect on metapopulation recovery. A small subset was chosen to accomplish the goals described above. All of the actions

tested involved a spatial component, where proper modeling of the action required the incorporation of spatial structure into the model. The following actions were tested:

- 1) Transferring animals between patches to counter fragmentation.
- 2) Recolonizing additional patches to provide buffers against extinction.
- 3) Increasing the growth rates within specified patches to increase population size.
- 4) Increasing ceiling capacity within specified patches to increase population size.

Actions 1 and 2 take place between patches, whereas actions 3 and 4 take place within patches.

Methods

The general metapopulation simulation model developed in Chapter 2 was the basis for all modeling exercises.

Transferring Animals Between Patches to Counter Fragmentation

Often, fragmentation is a consequence of permanent habitat fragmentation and can not be reversed. In these cases it is possible to mimic dispersal or the reopening of corridors between patches by transferring animals through management intervention. If it is possible to move animals between patches and have this result in successful reproduction, then corridors can, in effect, be reopened.

In order to understand the effects of transferring animals on the viability of the metapopulation, model runs which included the transfer of animals between fragments were compared to runs without transfers, as well as to the original unfragmented metapopulation. All other conditions were identical. The goal was to examine how much of the metapopulation's original viability that was lost to fragmentation, could be restored by transferring animals.

In Chapter 2, fragmentation was modeled three ways, reflecting three possible responses of the animals to the fragmentation (Figure 2.6). For this exercise, each of the three responses was simulated with and without the transfer of animals. Including the unfragmented metapopulation, seven metapopulations were simulated under identical conditions (Table 3.1).

Table 3.1: Description of the Seven Metapopulations Used to Test the Effects of Transferring Animals to Counter Fragmentation.

Metapopulation Number	Is the Metapopulation Fragmented?	How Do Animals Respond?	Are Animals Transferred?
1	No	-	-
2	Yes	Disappear	No
3	Yes	Go Home	No
4	Yes	Go Elsewhere	No
5	Yes	Disappear	Yes
6	Yes	Go Home	Yes
7	Yes	Go Elsewhere	Yes

The population was fragmented as in Chapter 2 (Figure 2.5). Management intervention was set up to move animals across barriers between the two fragments.

Animals could be moved between patches one and two, and between patches four and five (Figure 3.1). The management intervention occurred after the completion of natural dispersal each year.

The transfer of animals between fragments used the following rules: First, it was assumed that a donor patch with an extremely small population would not have to donate animals to another patch.

If $N_{i,t+1} \geq \text{Min_for_donating}$

then $N_{j,t+1} = N_{j,t+1} + \text{transfer}$

and $N_{i,t+1} = N_{i,t+1} - \text{transfer}$ (3.1)

for the following combinations of (i,j): {(1,2), (2,1), (4,5), (5,4)}

where:

$\text{Min_for_donating} =$ minimum number of animals in donor patch i for a transfer to occur. This was arbitrarily set equal to 30 animals.

and

$\text{transfer} =$ number of animals transferred.

This was arbitrarily set equal to 5 animals.

The management intervention was unlike natural dispersal in an unfragmented population in the following ways:

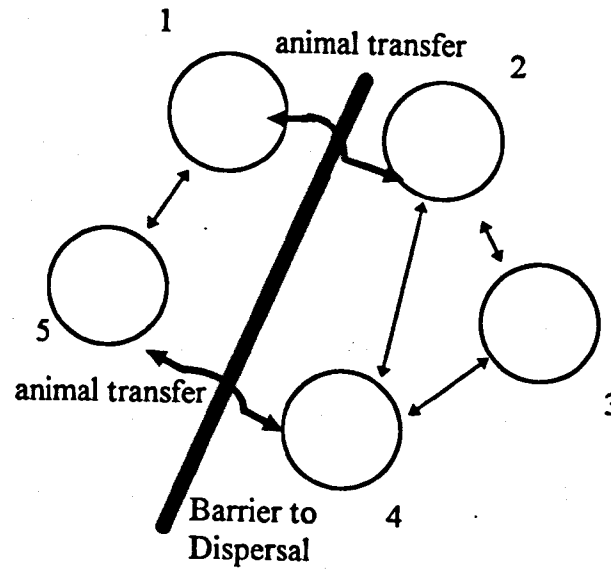


Figure 3.1: Illustration of Pathways for Animal Transfer Modeled to Counter Fragmentation.

Natural dispersal corridors are shown as thin arrows.

Management intervention corridors are shown as thick arrows.

- 1) If the donor population was below a minimum, there was no probability of moving animals.
- 2) When animals were moved, the number moved remained constant, not the movement rate.
- 3) When animals were moved from a donor patch, they were moved to only one recipient patch, rather than four recipient patches.

All patches within the seven metapopulations were given a growth rate of 1.0. The seven metapopulations were subject to identical values of environmental stochasticity at each time step, so the only differences that existed between metapopulations were due to differences in dispersal and transfers. A range of dispersal rates and a range of values for the proportion of common variation were used in the simulations. Each scenario ran for 100 iterations.

Recolonizing Additional Patches to Provide Buffers Against Extinction

The distribution of animals within patches provides a buffer against extinction for a metapopulation (Levin 1976, Brown and Kodric-Brown 1977, Caswell 1978). For many metapopulations, past habitat fragmentation blocked dispersal between patches, resulting in the extinction of a fragmented patch. Recolonizing formerly occupied patches would conceivably provide additional buffers against extinction. A model was designed to test whether the recolonization of additional patches provided additional buffers within a metapopulation, thereby increasing its viability.

The five patch scenario used throughout Chapter 2 is used in this scenario with the addition of a sixth patch (Figure 3.2). Dispersal involving the new patch, six, was limited to its two nearest neighbors, patches four and five, and used lower dispersal rates to simulate greater distance from the existing metapopulation.

In scenarios using five patches alone, nearest neighbors each received 35% of a donor patch's dispersers (Figure 2.3). In this scenario, patches four and five donated 33% of their dispersers to each of their original nearest neighbors and 4% of their dispersers to the newly reachable patch six. Patch six split its dispersers between patches four and five.

To provide additional information, two additional factors were incorporated in this model. One involved the quality of the newly added patch, and one involved the rate of recolonization.

The additional patch to be recolonized could realistically contain habitat of any quality, from low to high suitability. In order to see if the value of recolonization depended on the quality of the patch to be recolonized, the patch was modeled in two ways: While patches one through five were given a neutral growth rate of 1.0, patch six was set up as either a "sink" patch (Pulliam 1988) with a growth rate of 0.90 or a "source" patch (Pulliam 1988) with a growth rate of 1.10. Patch six used the same level of common to independent stochasticity as the original five patches.

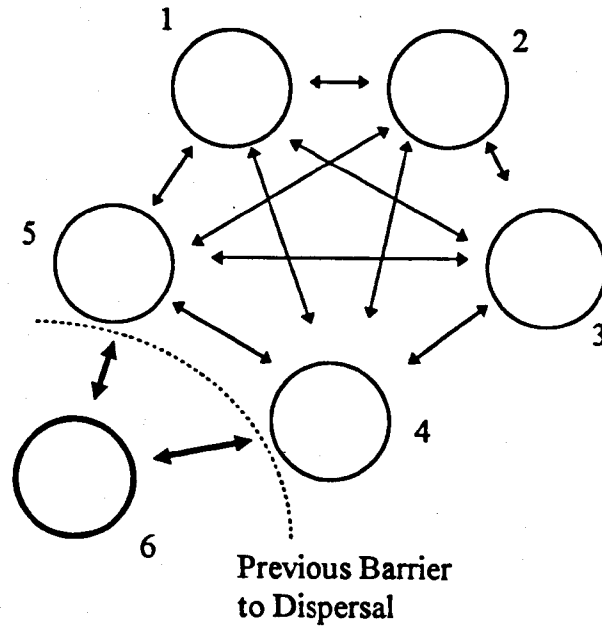


Figure 3.2: Illustration of Dispersal Corridors After Recolonizing a Sixth Patch.

This scenario also investigated the difference between a natural recolonization process, using the dispersal rates discussed above, and a more abbreviated recolonization process using management intervention. Both cases started with patch six unoccupied. In the first option, patch six became occupied by dispersal from patches four and five as described above. In the second case, natural dispersal was artificially aided through management intervention. For each of the first ten years of the scenario, upon the completion of natural dispersal, 10% of the populations of patches four and five were moved to patch six. This had the effect of speeding up the recolonization process.

In order to compare the various options, each model run included five metapopulations (Table 3.2) subject in all other ways to identical conditions:

Table 3.2: Description of the Five Metapopulations Used to Test the Effects of Recolonizing Additional Patches to Provide Buffers Against Extinction.

Metapopulation Number	Five or Six Patch Metapopulation?	Is Sixth Patch a Source or Sink?	Is Recolonization Aided Through Intervention?
1	Five	-	-
2	Six	Source	No
3	Six	Sink	No
4	Six	Source	Yes
5	Six	Sink	Yes

All five metapopulations were subject to the same environmental stochasticity values. Simulations used a range of values for the proportion of common variation and the dispersal rate. Each combination was run through 250 iterations.

Because the simulation was designed to test the effects of recolonizing a sixth patch on the viability of the original five patch metapopulation, output from this simulation focused on the probability of persistence of the original five patch metapopulation.

Increasing the Growth Rates Within Specified Patches to Increase Population Size

Population growth rates are increased by either increasing survival rates at one or more stages of the animal's life history or by increasing the reproduction of the animal. Increasing the survival or reproduction of a depleted population within a patch must, by definition, improve the viability of the population within that patch. With limited resources available to managers, which patches should be the focus of improvements? Should an emphasis be placed on helping the weakest patches or further strengthening the strongest patches? Should all patches be helped a little or should one patch alone be helped more substantially? For the purposes of these simulations, changes in survival rate and reproduction were both assumed to be represented by changes in the growth rate term.

Simulations were conducted to answer a number of questions about the relationship of population growth rates and viability. These questions included:

- 1) Is it worthwhile to improve a patch's growth rate regardless of its current value? For instance, are there noticeable changes in the viability of the overall metapopulation by slightly improving the weakest "sink" patch? Do

incremental increases in growth rates at any level provide constant improvements in viability?

In the simulation designed to test this, the base option used growth rates of 0.97 for patches one through four, and patch five had a growth rate of 0.90 (Table 3.3). In the next five options, the growth rate of patch five gradually increased to 1.20, while all other patches remained constant. In each of final two options, an additional patch was given a growth rate of 1.20.

Table 3.3: Growth Rate Values Used in First Growth Rate Simulation.

Option Number	Patch 1	Patch 2	Patch 3	Patch 4	Patch 5
Base	0.97	0.97	0.97	0.97	0.90
1	0.97	0.97	0.97	0.97	0.95 *
2	0.97	0.97	0.97	0.97	1.00 *
3	0.97	0.97	0.97	0.97	1.05 *
4	0.97	0.97	0.97	0.97	1.10 *
5	0.97	0.97	0.97	0.97	1.20 *
6	0.97	0.97	0.97	1.20 *	1.20
7	0.97	0.97	1.20 *	1.20	1.20

* indicates value changed from previous option.

- 2) If improvements could be made to only one patch in a metapopulation, should the improvements be made to a patch with a low growth rate or to a patch with a high growth rate?

For this simulation, growth rates in the base option climbed from 0.85 in patch one to 1.05 in patch five (Table 3.4). In each of the following five options, one patch was increased by 0.05 over its base value. The average

growth rate in the base run was 0.95. The average in each of the other five options was 0.96.

Table 3.4: Growth Rates Used in Second Growth Rate Simulation.

Option Number	Patch 1	Patch 2	Patch 3	Patch 4	Patch 5
Base	0.85	0.90	0.95	1.00	1.05
1	0.90 *	0.90	0.95	1.00	1.05
2	0.85 *	0.95 *	0.95	1.00	1.05
3	0.85	0.90 *	1.00 *	1.00	1.05
4	0.85	0.90	0.95 *	1.05 *	1.05
5	0.85	0.90	0.95	1.00 *	1.10 *

* indicates value changed from previous option.

- 3) Should changes be made to reduce or increase the variance in growth rates between patches? Is it better to have moderate growth rates in all patches, or large growth rates in some patches and small growth rates in others?

In the base option of this simulation, all patches had a growth rate of 1.00 (Table 3.5). In the following four options, patches one and two further lowered their growth rates by an additional 0.05 for each option and patches four and five further increased their growth rates by an additional 0.05 for each option. This increased the variance in growth rates without changing the average growth rate across patches.

Table 3.5: Growth Rates Used in Third Growth Rate Simulation.

Option Number	Patch 1	Patch 2	Patch 3	Patch 4	Patch 5
Base	1.00	1.00	1.00	1.00	1.00
1	0.95	0.95	1.00	1.05	1.05
2	0.90	0.90	1.00	1.10	1.10
3	0.85	0.85	1.00	1.15	1.15
4	0.80	0.80	1.00	1.20	1.20

In each of the three growth rate simulations, all options were run under identical values of environmental stochasticity and dispersal rates so that differences between the options were due to solely to differences in growth rates. Each simulation was run under a range of values for dispersal rates and proportions of common variation. Each combination of dispersal rate, proportion of common variation, and growth rates ran for 250 iterations.

The Relationship Between Standard Error and Number of Iterations. Many of the conclusions in this study involve comparing the results between two model runs, to see if the probability of persistence in one run is larger or smaller than in another. The ability to conclude whether an actual difference is likely to exist involves the standard error of the resulting difference in the probabilities of persistence calculated in the two model runs. If the standard error is large relative to the estimated difference, then one has less confidence in concluding that a difference actually exists.

The standard error should get smaller as the number of model iterations increases for any particular set of parameters (Pagano 1986, Chapter 2). In order to see how the number of iterations affected the ability to detect differences between runs, three model runs were used to conduct a test. The second growth rate simulation described above provided the three model runs. Two pairings were used for the comparison. Option 1 (Table 3.4), reflecting an increase in the growth rate of the weakest patch was compared to the Base option (Table 3.4). Option 5 (Table 3.4), reflecting an increase in the growth rate of the strongest patch was also compared to

the Base option (Table 3.4). Each option ran for 10,000 iterations. The number of patches persisting in year 100 was calculated at the end of each iteration. The goal was to measure the standard error of the difference in the probability of persistence of 5 patches.

Results of the 10,000 iterations were grouped six ways: into 2 groups of 5,000, 10 groups of 1,000, 20 groups of 500, 100 groups of 100, 200 groups of 50, and 1,000 groups of 10. The difference in the average probability of persistence of all 5 patches between the two options and the base run was calculated for each grouping. The standard deviation of the estimated difference across each group size was calculated as the standard error (Pagano 1986). For example, the average probability of persistence of all 5 patches was calculated for each of the 10 groups of 1,000 for the base run and the two options. The difference between the base run and each of the options was calculated. Then the standard deviation of the 10 estimates of the difference was calculated as an estimate of the standard error. These methods were used for each grouping size.

Increasing Ceiling Capacity within Specified Patches to Increase Population Size

In the previous simulations, the effect of increasing growth rates was examined. This reflected the speed at which the population could build, but had no effect on the maximum population size allowed within a patch. As described in Chapter 2, this simple model does not include density dependence, but a ceiling level is imposed on

each patch, beyond which a population can not grow. For all model runs to this point, the ceiling level was set to 10,000 per patch.

In this model the ceiling level was changed to study its effect on viability. Patch five was used as the test patch. Its ceiling could be set at 100, 500, 1000, or 10,000. Patches one through four always shared the same ceiling value which could be set at 10,000 per patch or at 100 per patch. The growth rates of patches one through four were set at 1.00 and patch five was set at either 1.00 or 1.05. The model ran a range of values for dispersal rates and proportion of common variation. Each combination of parameters ran for 250 iterations.

Results

Results indicate that a wide variety of alternative management actions can be assessed using a spatially structured model to predict their affect on metapopulation recovery.

Transferring Animals Between Patches to Counter Fragmentation

Results from Chapter 2 indicate that dispersal is critical to the viability of a metapopulation, and that breaking up the connectivity of the modeled metapopulation decreases its overall viability. Results from these models show that restoring the connectivity of a metapopulation can minimize the effects of fragmentation, and that if natural dispersal cannot be reestablished, restoring connectivity through management intervention dramatically improves the viability of the population.

Regardless of how dispersing animals react to fragmentation, the probability of persistence of the modeled metapopulation dramatically improves when individuals are moved between patches (Figure 3.3). In the cases where the unsuccessful dispersers go home or go elsewhere, moving individuals produced persistence probabilities nearly identical to the unfragmented metapopulation.

In the case where unsuccessful dispersers disappear, the persistence probability of the modeled metapopulation improved when individuals were moved across all dispersal rates. With or without movement, persistence probabilities decreased as dispersal rates increased, reflecting the increased loss of individuals attempting to disperse.

Results of this model suggest that restoring connectivity through management intervention restores much, if not all, of the viability lost through fragmentation. In the case where unsuccessful dispersers disappear, including management intervention to prevent their disappearance, together with moving animals, would restore the viability to pre-fragmentation levels.

Recolonizing Additional Patches to Provide Buffers Against Extinction

Reopening a historically occupied patch can either increase or decrease the viability of the existing metapopulation depending on the quality of the reopened patch. When the patch has a growth rate greater than 1.0, it becomes a “source” population, creating dispersers for neighboring patches (Figure 3.4).

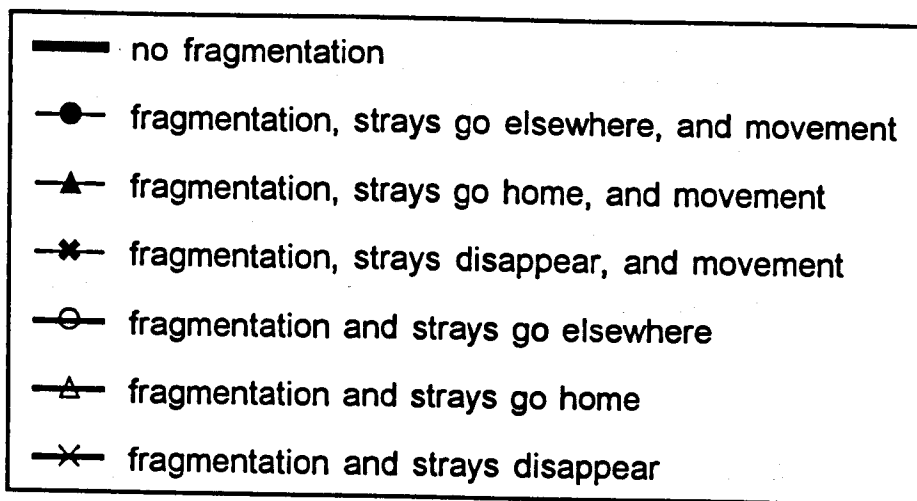
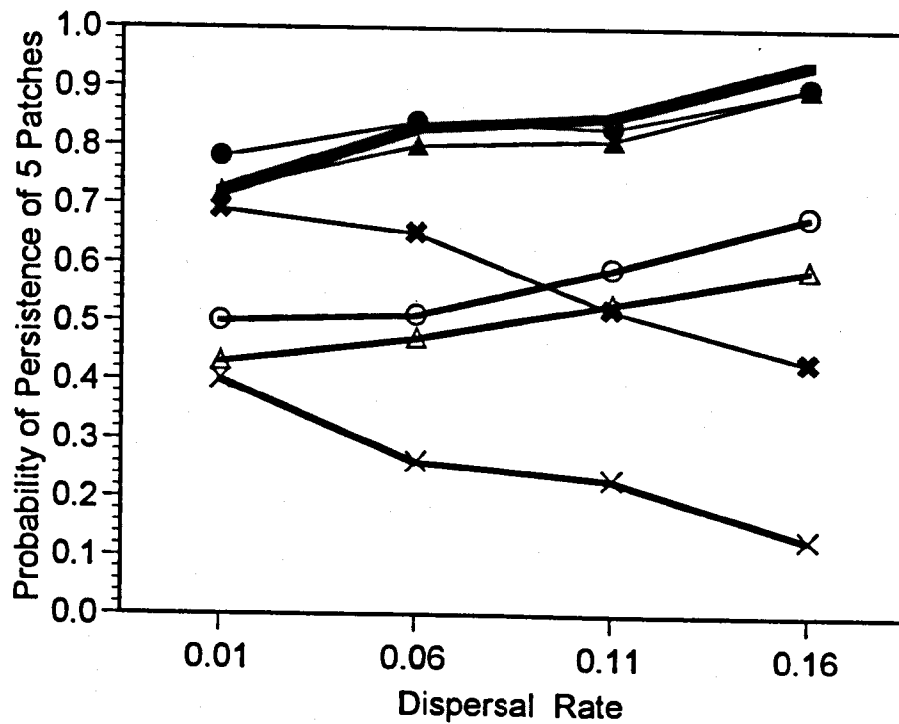


Figure 3.3: Effects of Moving Animals to Counter Fragmentation.
 (Growth rate = base option.
 Proportion of common variation = 50%.)

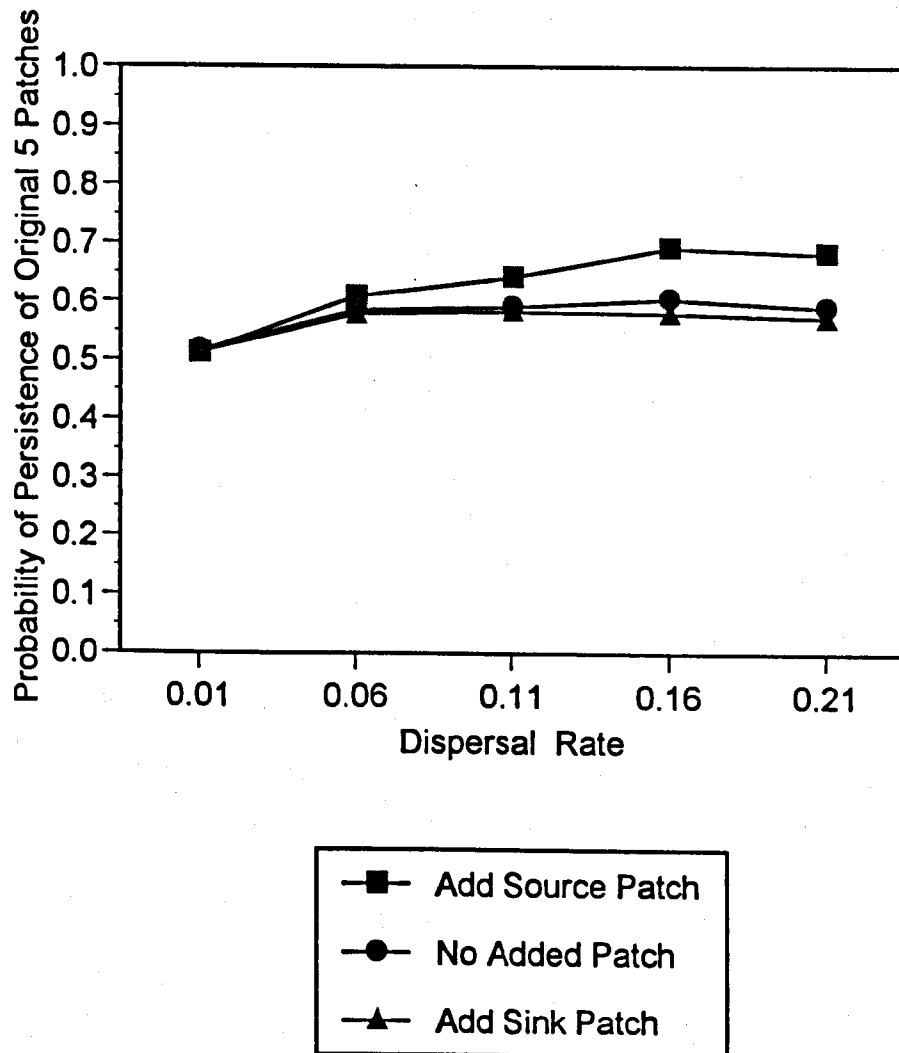


Figure 3.4: Impact of Adding a New Patch on the Persistence of the Original Metapopulation. (Proportion of common variation = 80%.)

When the patch has a growth rate less than 1.0, animals from neighboring patches that disperse to the new patch reduce their productivity, lowering the viability of the metapopulation (Figure 3.4).

Management intervention to hasten the recolonization effort speeds up the consequences of the recolonization. When reopening a “source” patch, speeding up dispersal improves the viability of the existing metapopulation (Figure 3.5).

When reopening a “sink” patch, management intervention removes animals from patches of stable growth on average and places them in a less productive patch, more quickly than would occur naturally (Figure 3.5).

Increasing the Growth Rates Within Specified Patches to Increase Population Size

These simulations were designed to answer three sets of questions about improving growth rates. The results provide guidance on prioritizing patches for improvements.

Simulation One. The first simulation addressed the questions: Is it worthwhile to improve a patch’s growth rate regardless of its current value? For instance, are there noticeable changes in the viability of the overall metapopulation by slightly improving the weakest “sink” patch? Do incremental increases in growth rates at any level provide constant improvements in viability? Growth rates were set up as shown in Table 3.3.

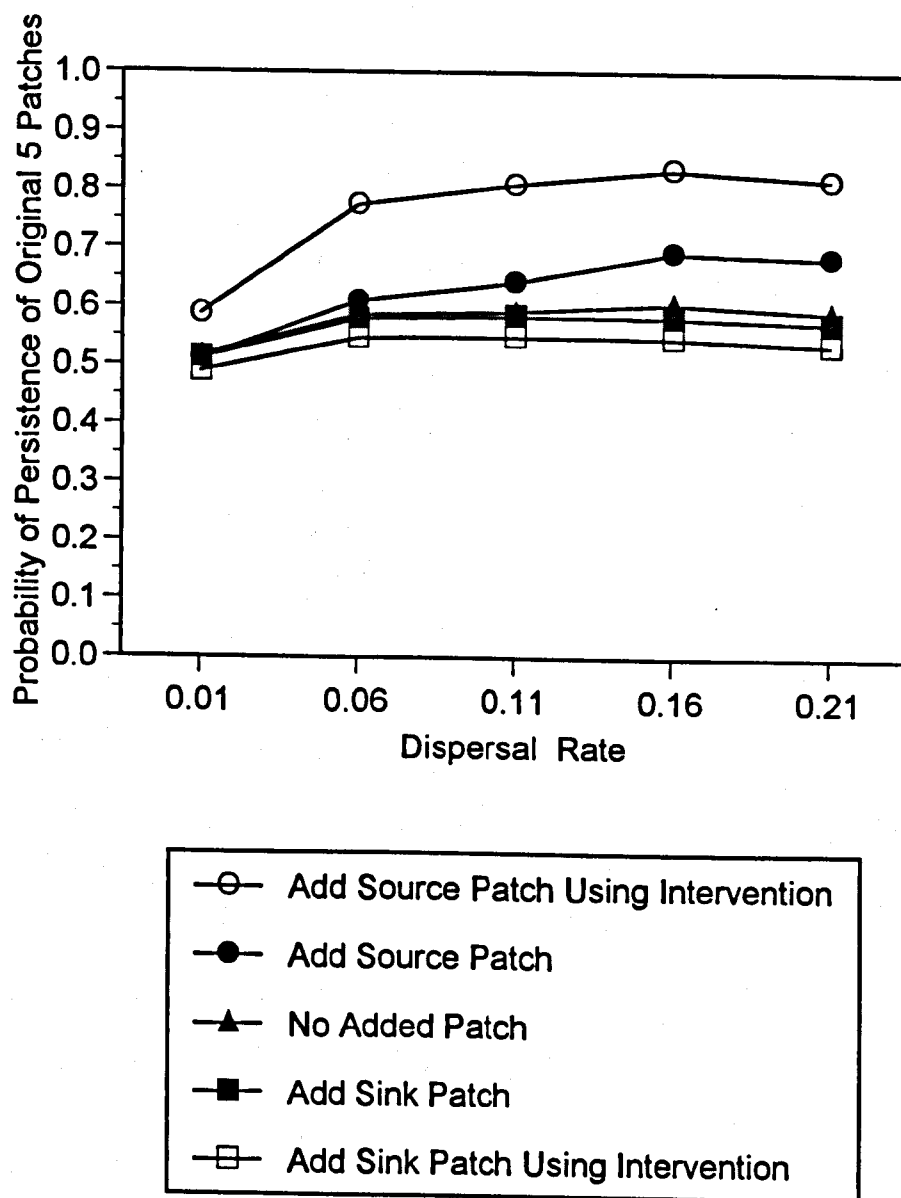


Figure 3.5: Comparison of Adding a New Patch with and without Intervention.
(Proportion of common variation = 80%.)

Results indicate that an increase in the growth rate of a single patch increases the viability of the metapopulation (Figure 3.6), regardless of whether the patch's prior value was low or high relative to the other patches. This was true regardless of the dispersal rate.

Increasing the growth rate had the greatest incremental gain in viability for the metapopulation with the lowest dispersal rate (Figure 3.6). This allowed the metapopulation with the lowest dispersal rate to nearly converge in terms of viability with metapopulations with higher dispersal rates (Figure 3.6). This indicates that metapopulations can make up for low levels of dispersal through increases in patch population growth rates. It also demonstrates that often there is more than one way to increase viability.

As the number of patches with a growth rate of 1.20 increased, the viability continued to increase (Figure 3.7). Since viability, expressed as a probability, can not exceed 1.0, eventually viability must asymptote the 1.0 level as growth rates continue to improve. For a patch with 20% common variation, increasing the number of patches with a growth rate of 1.20 from 2 to 3 provides little benefit, as viability was already extremely high (Figure 3.7). With higher proportions of common variation, increasing the number of patches with high growth rates provided larger gains in viability (Figure 3.7).

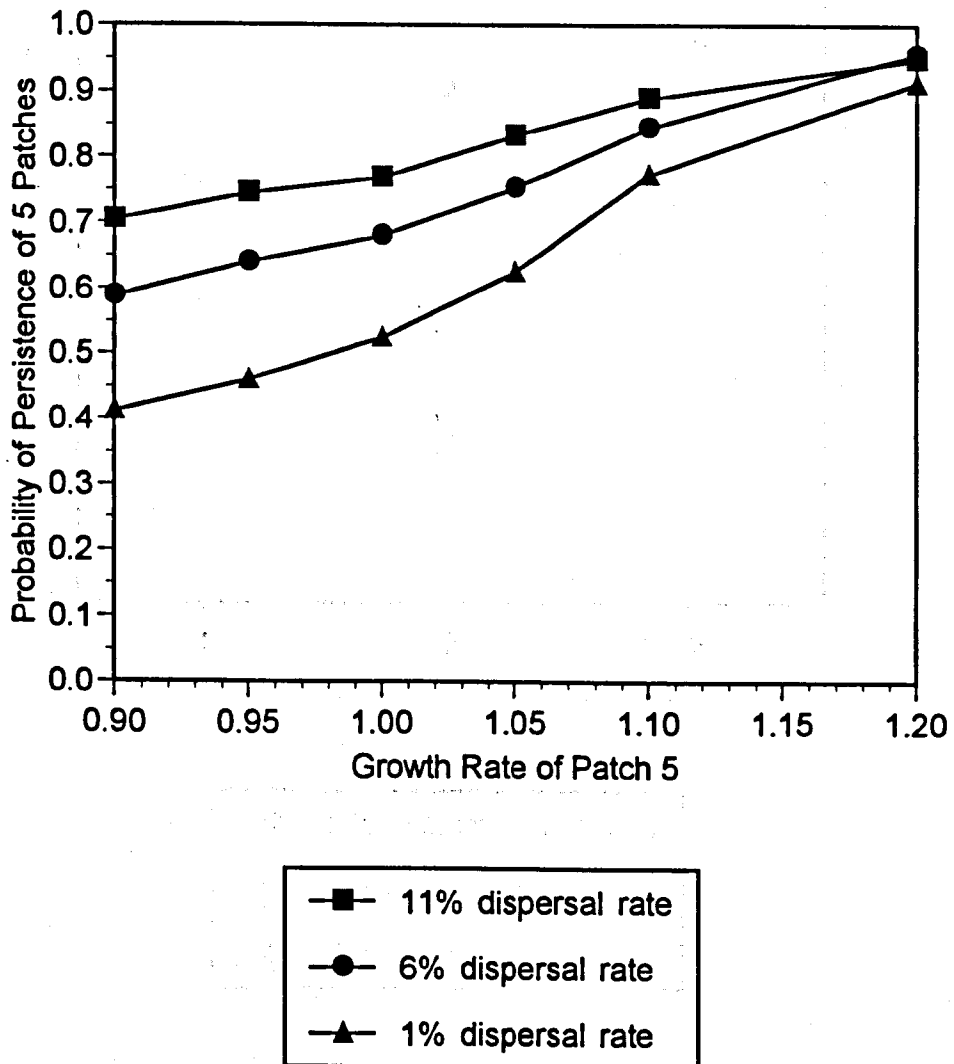


Figure 3.6: The Effect of an Individual Growth Rate on Persistence Probability.

(Growth rates in patches 1 - 4 = 0.97

Proportion of common variation = 50%)

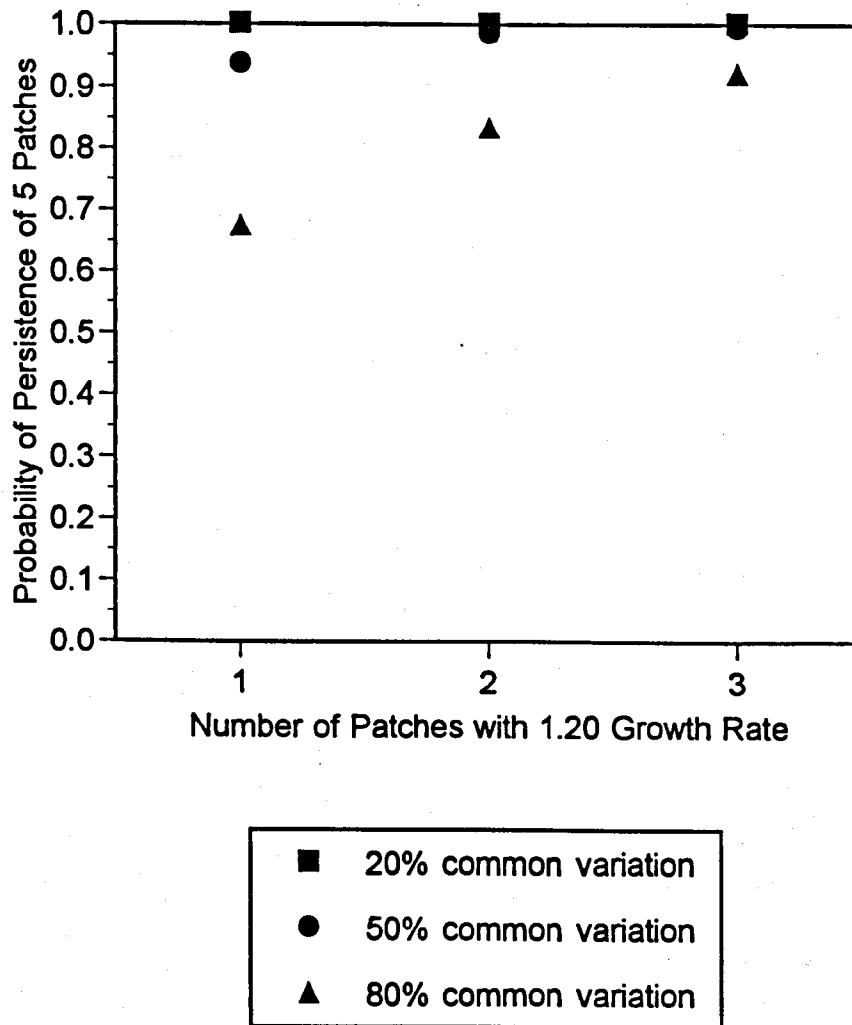


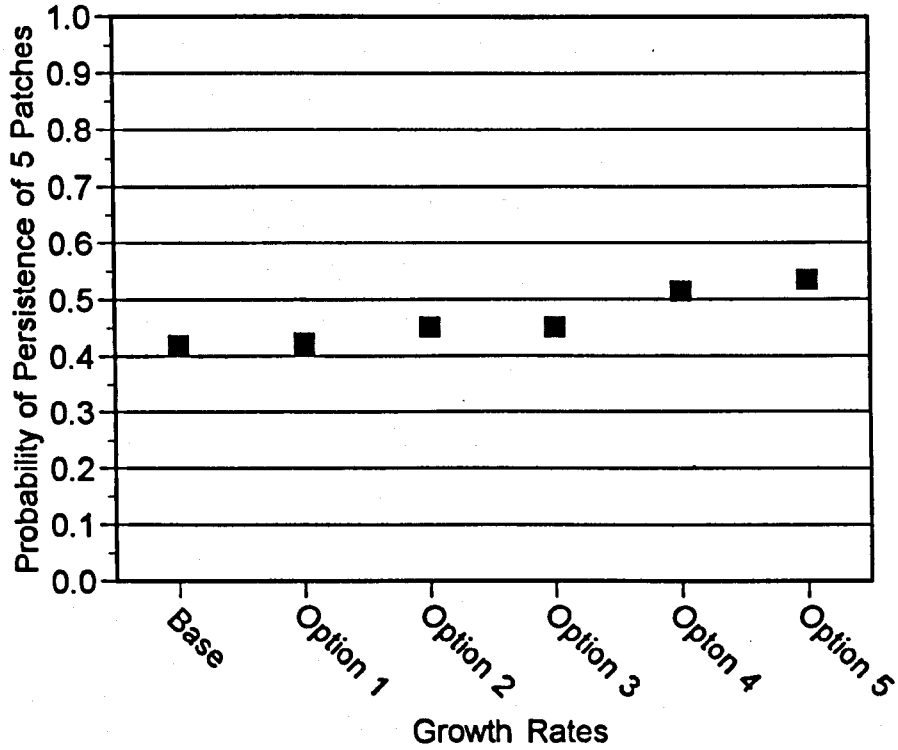
Figure 3.7: The Effect on Persistence of Substituting High Growth Rate Patches.
(Dispersal rate =21%)

When 3 patches were given growth rates of 1.2, the viability of the metapopulations under different proportions of common variation began to converge (Figure 3.7). High growth rates were able to compensate for the effects of high proportions of common variation.

Simulation Two. The second simulation was designed to answer the following question: If improvements could be made to only one patch in a metapopulation, should the improvements be made to a patch with a low growth rate or to a patch with a high growth rate? Growth rates were set up as shown in Table 3.4.

Results indicate that viability increases the most when the growth rate of the strongest patch in the metapopulation is improved (Figure 3.8). Improving the growth rate of patch five from 1.05 to 1.10 (Option 5) increased metapopulation viability more than improving the growth rate of patch one from 0.85 to 0.90 (Option 1) (Figure 3.8). Viability steadily increased from Option 1 to Option 5, from improving the weakest patch to improving the strongest patch (Figure 3.8).

Simulation Three. The third simulation addressed the following questions: Should changes be made to reduce the variance in growth rates between patches or to increase the variance in growth rates between patches? Is it better to have moderate growth rates in all patches, or large growth rates in some patches and small growth rates in others? Growth rates were set up as shown in Table 3.5.



	Patch 1	Patch 2	Patch 3	Patch 4	Patch 5
Base	0.85	0.90	0.95	1.00	1.05
Option 1	0.90	0.90	0.95	1.00	1.05
Option 2	0.85	0.95	0.95	1.00	1.05
Option 3	0.85	0.90	1.00	1.00	1.05
Option 4	0.85	0.90	0.95	1.05	1.05
Option 5	0.85	0.90	0.95	1.00	1.10

Figure 3.8: A Comparison of Increasing the Growth Rate of a Weak Patch versus a Strong Patch.
 (Dispersal rate = 6%,
 Proportion of common variation = 80%.)

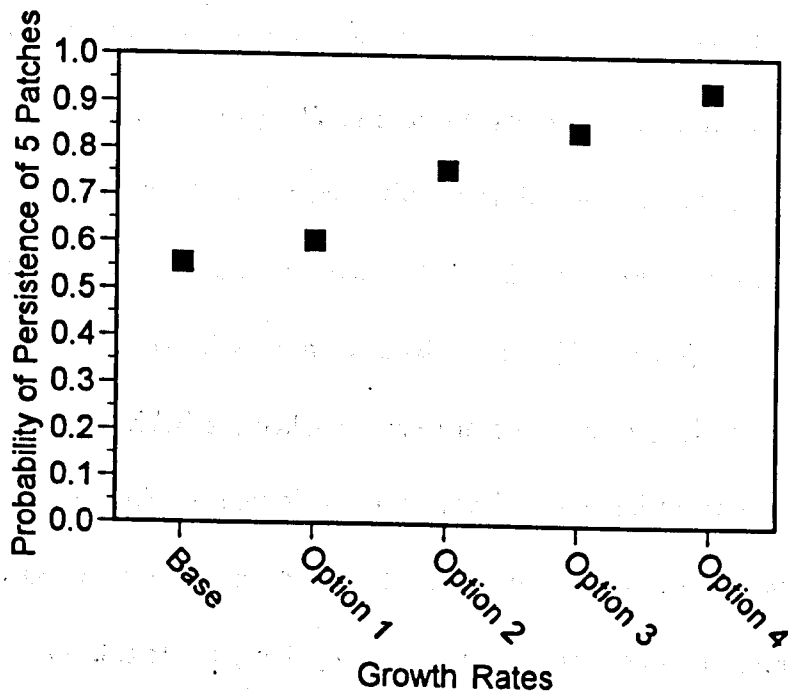
The simulations show that the viability of a metapopulation is highly dependent on the growth rates in the strongest patches, regardless of the growth rates in the weakest patches (Figure 3.9). The metapopulation with 2 patches at a growth rate of 0.80 and two patches with a growth rate of 1.20 (Option 4) had a higher viability than the metapopulation where all patches had a growth rate of 1.00 (Base Option) (Figure 3.9).

Results from all three simulations show that patches with the highest growth rates have the greatest influence on the viability of the metapopulation.

The Relationship Between Standard Error and Number of Iterations. The ability to conclude that differences existed between models runs was highly dependent on the number of model iterations run. Using the second growth rate simulation (Table 3.4), options 1 and 5 were compared to the Base option. The increases in the probability of persistence achieved by increasing growth rates in options 1 and 5 compared to the Base option were calculated along with the standard error of the calculated increases (Table 3.6).

Table 3.6: Effect of Number of Iterations on Estimating Differences Between Options.

Number of Iterations	Option 1 - Base Option		Option 5 - Base Option	
	Mean	Standard Error	Mean	Standard Error
10	0.014	0.058	0.142	0.109
50	0.014	0.027	0.142	0.049
100	0.014	0.019	0.142	0.036
500	0.014	0.010	0.142	0.018
1000	0.014	0.007	0.142	0.011
5000	0.014	0.002	0.142	0.006



	Patch 1	Patch 2	Patch 3	Patch 4	Patch 5
Base	1.00	1.00	1.00	1.00	1.00
Option 1	0.95	0.95	1.00	1.05	1.05
Option 2	0.90	0.90	1.00	1.10	1.10
Option 3	0.85	0.85	1.00	1.15	1.15
Option 4	0.80	0.80	1.00	1.20	1.20

Figure 3.9: The Effect of Variance in Growth Rates on Persistence.

(Dispersal rate=6%,

Proportion of common variation = 80%.)

The standard error of the estimated mean difference decreased as the number of iterations increased (Table 3.6). With a small number of iterations, such as 10, the standard error was high relative to the estimate of the mean difference (Table 3.6). By the time the number of iterations reached 1,000 or more, the standard error had decreased substantially relative to the mean difference (Table 3.6).

Option 1 provided a smaller increase in persistence probability than option 5 (Figure 3.8, Table 3.6). Although the increase in the persistence probability sharply climbed between options 1 and 5, the standard error did not climb at the same rate (Table 3.6). For this reason, a larger number of iterations of option 1 is required, relative to option 5, to identify differences from the base run. For example, it could require 5,000 or more iterations to provide reasonable confidence that a difference exists between option 1 and the base option (Table 3.6). In contrast, 100 iterations may be sufficient to conclude differences exist between option 5 and the base run (Table 3.6).

Increasing Ceiling Capacity within Specified Patches to Increase Population Size

Changes to the ceiling level of one patch affected the viability of the metapopulation (Figure 3.10). This was particularly true as the ceiling increased from small population sizes. Changing the ceiling from 100 to 1,000 had a greater effect than changing the ceiling from 1,000 to 10,000. The benefits were greatest at low dispersal rates (Figure 3.10).

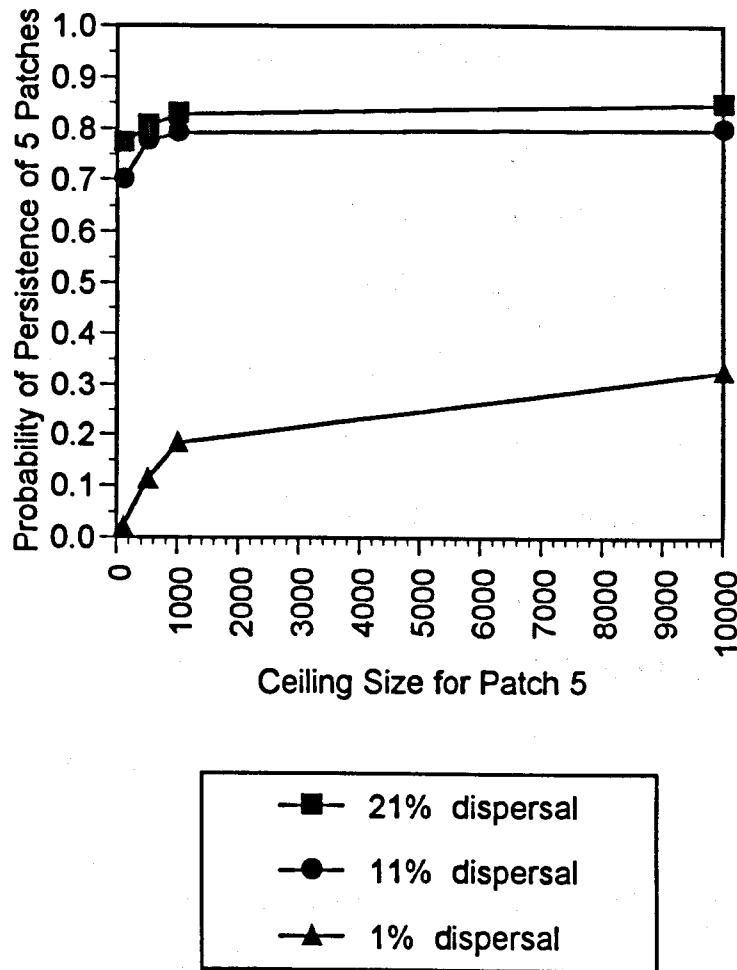


Figure 3.10: The Effects of Increasing the Ceiling of Patch 5 on the Probability of Persistence. (Patch 1 - 4 ceiling = 100, Growth rate = 1.0, Proportion of common variation = 80%.)

The existing ceiling levels of the unchanged patches had a substantial impact on the effect of changing a ceiling level (Figure 3.11). When the ceilings for patches one through four were set to 10,000, changing the ceiling of patch five from 100 to 10,000 had little effect. When patches one through four had ceilings equal to 100, increasing the ceiling of patch five from 100 to 10,000 caused large increases in the probability of persistence of the metapopulation (Figure 3.11).

The growth rate of patch five was also an important factor. Increases in viability, caused by increasing the ceiling of patch five, were even greater when patch five had a growth rate of 1.05 (Figure 3.12). The higher growth rate produced a greater rate of gain in viability as the ceiling increased (Figure 3.12).

Discussion

Restoring an endangered species is complicated by a lack of data on endangered species (Ballou et al. 1995) and a lack of first hand knowledge of the effects of alternative management actions (Walters 1986). Given the difficulties of restoration, managers rely on resource modeling to assess the effects of alternative management options. The scientific method used to estimate the viability of a population given a set of management actions is called Population Viability Analysis (PVA) (Gilpin and Soulé 1986, Shaffer 1990, ESA 1996). This study strongly supports the need to incorporate spatial structure into PVA, particularly for species distributed as a metapopulation (Chapter 2, Gilpin 1987, ESA 1996).

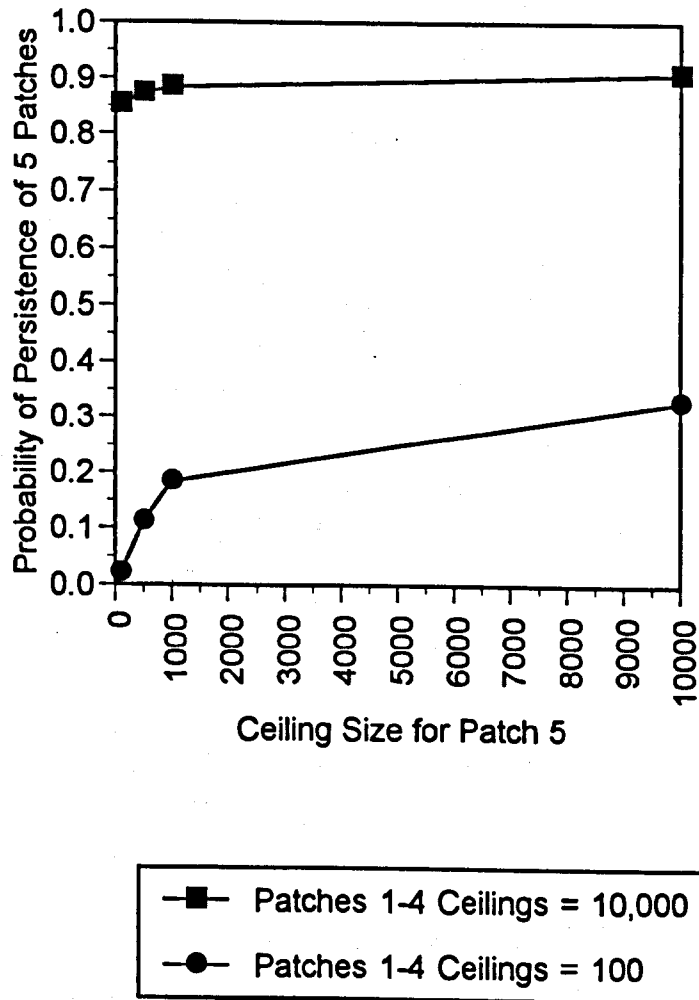


Figure 3.11: Impact of Ceiling Changes Against Existing Ceiling Sizes.
(Growth rate = 1.0, Dispersal rate = 1%,
Proportion of common variation = 80%.)

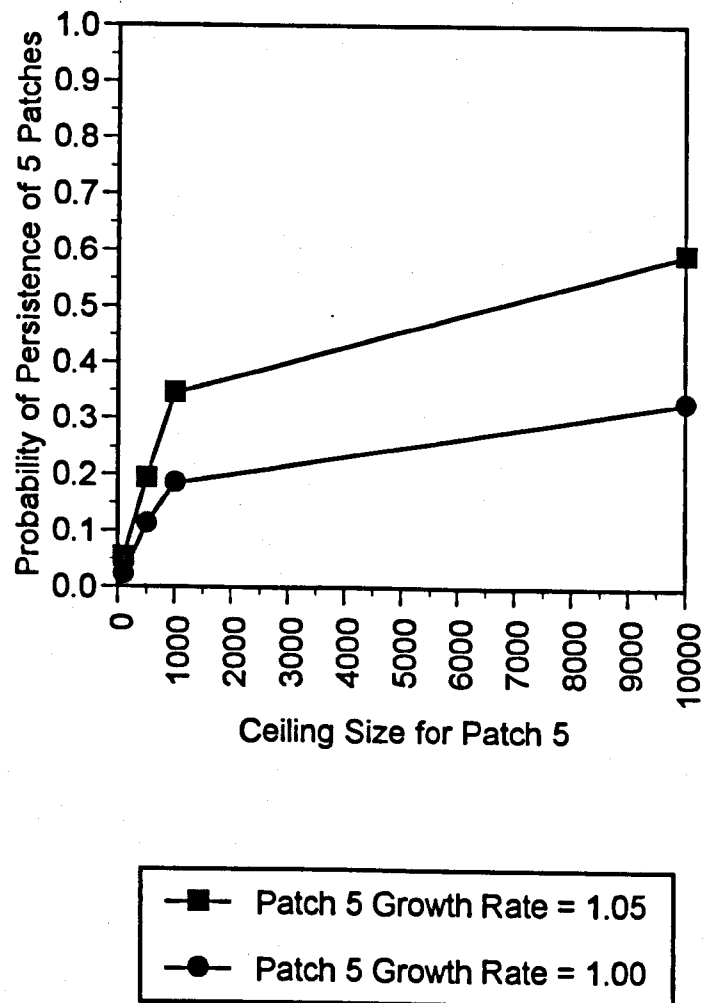


Figure 3.12: Impact of Ceiling Changes Against Patch Growth Rates.
(Patch 1 - 4 ceiling = 100, Dispersal rate = 1%, Proportion of common variation = 80%).

Managers who ignore spatial structure in attempts to restore a metapopulation will likely ignore many of the policies most likely to contribute to restoration. Policies such as transferring animals to counter fragmentation or recolonizing a source patch would not be considered without incorporating spatial structure into the policy analysis.

Modelers who ignore spatial structure when developing a PVA for a metapopulation will ignore one of the most important factors affecting viability, and will not have the capability to model many of the most beneficial policies. None of the four recovery actions examined in this chapter could be adequately assessed without incorporating spatial structure into the framework of an analysis.

Model Structure

The simple structure of the model limits its effectiveness in developing broad sweeping recommendations likely to hold for all species. This study uses a simple model as a means to improve our understanding of the processes likely to improve the viability of a metapopulation.

Although similar to other recent efforts to model viability with spatial structure for an individual species (Lamberson et al. 1992, Doak 1995), the structure of this model is more general allowing comparisons across wide ranges of dispersal rates, proportions of common variation, and growth rates. The structure of the current model allows the study of a wide range of potential management actions.

Some of the complexities not included in the model will affect results to varying degrees. The inclusion of density dependence in the model will, by definition, cause the

population growth rate and/or dispersal rate to change as population size changes. Additional simulations could be developed to test the effects of additional complexities such as density dependence, age structure and/or sex ratios.

Results of the current simulations do, however, point to a number of general principles regarding management actions and metapopulation recovery. Additional work is needed to test the appropriateness of the principles by conducting the following types of studies: adding layers of complexity to the simulation model structure currently presented, building species and case specific Population Viability Analyses (PVA), and conducting experiments in the field.

Results also indicate that iterations on the order of 1,000 or more are often needed to identify differences between the outcomes of various model runs. High standard errors, associated with fewer iterations, suggest that differences in outcomes may be the result of using too limited a drawing of random numbers rather than the result of any true difference between model runs. Running large numbers of iterations requires a tremendous amount of computer processor time and may be a factor limiting the utility of applying these methods.

Principles for Recovery

Results of the study apply most appropriately to metapopulations where the lack of sufficient viability is due to a decline in total population size. The basic strategy resulting from this study relies on maximizing population growth, using a divided population to provide protection against environmental stochasticity.

Increasing Population Growth Rates and Patch Ceiling Capacities. Increasing population growth rates and patch ceiling capacities increases the viability of a metapopulation (MacArthur 1972, Goodman 1987b). But results indicate that the magnitude of the increase is dependent on which patch within the metapopulation is being improved. The probability of extinction of an individual patch is highly dependent on the population size in the patch. Increasing the population size decreases the impacts of the three major causes of extinction: environmental stochasticity (Goodman 1987a, Shaffer 1987), demographic stochasticity (MacArthur and Wilson 1967), and genetic effects (Soulé 1980).

The patch least likely to go extinct is the patch with the highest population size, all else being equal. Results of model runs from Chapter 2 showed that with dispersal, a strong "source" population could support multiple "sink" populations (Pulliam 1988) (Figure 2.9). If dispersal is adequate, the existence of animals in one or more patches, will ensure the existence or potential existence of animals in all other patches. Therefore, the best way to reduce the probability of extinction of a metapopulation is to reduce the probability of extinction of its strongest patches, by increasing growth rates and ceiling capacities, while ensuring adequate dispersal.

Increasing ceiling capacity can be accomplished by increasing the amount of available habitat. The relationship between area and extinction rates is an integral part of the theory of island biogeography (MacArthur and Wilson 1963, 1967). More

recently, empirical work on bull trout has shown an increasing probability of occurrence as patch size increases (Rieman and McIntyre 1995).

Results of this study also show that improving growth rates and ceiling capacities can compensate for low dispersal rates and/or high proportions of common variation. Where costs of improving dispersal corridors or moving animals are too high, and the proportion of common variation can not be decreased, improving the population growth rates of one or more of the strongest patches may have an even greater benefit.

Maintaining Buffer Patches. The results from the growth rate simulations may suggest that managers should rely on the strength of their one strongest patch, however this is not the case. Results of model runs from Chapter 2 demonstrated the value of buffer patches, where independence in environmental stochasticity provided buffers against unusually bad, common environmental effects. The inclusion of catastrophes in this analysis would have added emphasis on the need for buffers (Shaffer 1981, Ewens et al. 1987). Other analyses have pointed out the need to rely on multiple reserves rather than only one (Goodman 1987a, 1987b) to protect against multiple bad years or catastrophes.

When considering which patches to focus improvements on, buffering abilities must be considered with growth rates. As an example, suppose the patches with the highest growth rates within a metapopulation had high levels of common variation, with little buffering capability. And suppose that there was another patch located

further away, which was subject to different weather conditions than the other patches. Focusing improvements on the more distant patch combined with the high growth rate patches provides additional buffering against catastrophes or bad years. The gains due to independent variation may be so great as to support making improvements to a moderate “sink” patch. Selecting the patches to focus on, considering both growth rates and independence, is an example of where a species specific, case specific PVA is required.

Recolonizing Patches. The recolonization of a historic patch or the colonization of a new patch can either help or hurt the recovery of a metapopulation. If the patch is in excellent condition, it could become a “source” patch, increasing the viability of the metapopulation by producing surplus animals available to the metapopulation through dispersal. If the patch is in poor habitat, it could become a “sink” population, removing animals through dispersal from more productive habitats to its less productive habitat (Donovan et al. 1995). Management intervention to speed up the recolonization process by moving animals can either speed up the benefits of the recolonization, or the harm, depending on the condition of the patch.

Managers may feel a need to restore the historical range of a species early in the recovery process. Simulations show that recolonizing patches can be beneficial to the metapopulation only if the patches are likely to become contributors to its recovery. While a viable, healthy metapopulation may be able to regularly provide dispersers to recolonize and maintain a “sink” population, a weak, declining metapopulation will

likely not have the same productivity. Opening an additional "sink" patch causes an additional drain on the metapopulation.

Consideration must also be given to an unoccupied patch's ability to buffer the existing patches. If environmental effects are largely independent from existing patches, it may be worthwhile to recolonize the patch, despite a modest growth rate.

Ensuring Adequate Dispersal. Dispersal is essential to the survival of a metapopulation (Levin 1976, Caswell 1978). Connectivity between patches, particularly the patches with the highest growth rates and independence, must be reestablished, enhanced, or maintained depending on its current condition (Gilpin 1987, Goodman 1987a, 1987b, Foose et al. 1995).

Reversing Fragmentation and Connectivity Loss. Fragmentation breaks connectivity between patches, reducing viability. To restore viability, connectivity must be restored. When this is not possible under natural conditions, management intervention should be incorporated to move animals between patches (Goodman 1987a, Soulé and Simberloff 1986). Results demonstrate that a relatively small intervention program can restore most, if not all, of the reduced viability, as defined by all five patches having a population of at least one animal in year 100.

If achieving an adequate level of viability required each patch to be occupied by a much higher number of animals, such as 100 animals, moving only 5 animals between

patches each year would be insufficient. The magnitude of the intervention required would be considerably larger.

Reducing Unsuccessful Dispersal. Results recommend that animals that are likely to disperse without finding suitable patches, should be actively prevented from dispersing. For a species with a low probability of successful dispersal, managers may wish to reduce natural dispersal, if possible, and replace it with management intervention to transfer animals between patches (Foose et al. 1995). This could enhance connectivity, while removing a constant drain of animals from the metapopulation.

The Role of Management Intervention. For many managers of “natural” or “wild” metapopulations, management intervention has been minimized. Many of these managers are unlikely to have pursued management strategies such as redistributing animals or moving animals between patches. This study concludes that managers who accept a more active role in managing their metapopulations will more quickly increase their overall population size and, therefore, reduce the probability of extinction more quickly, than managers that refuse a more active role (Foose et al. 1995).

The simulations, results, and conclusions in this Chapter are based on the assumption that the various kinds of management intervention presented are conceivable, testable, usable, and most importantly, successful. In cases where management intervention to transplant and/or crossbreed between patches is not

possible, or is only partially successful, results would differ. The goals of maximizing population growth and maintaining dispersal are both central to metapopulation recovery. A case specific PVA or a more complicated simulation model could test the effects of partially successful management intervention. In cases where the probabilities of success are unknown or the probabilities of success could potentially be improved, adaptive management (Holling 1978, Walter 1986) can be used to conduct management experiments.

Incorporating Relative Costs. This study did not consider the relative costs of alternative management actions. It may be for a particular metapopulation that weak patches can be improved greatly for a fraction of the cost required to make improvements of a similar magnitude to a strong patch. In this case, the best way to increase the viability of the metapopulation may be to improve the weak patches. In order to assess the effects of alternate management actions for any particular case, a case specific PVA must be used that incorporates both the costs and benefits of alternative actions.

CHAPTER 4

A SUGGESTED STRATEGY TO RECOVER A METAPOPOPULATION

Introduction

Based on the simulations in Chapters 2 and 3, a number of principles regarding metapopulation recovery were presented (Chapter 3). Using these principles, a strategy for metapopulation recovery is presented.

As discussed in Chapters 2 and 3, the simulation models developed in this study were designed to provide a better understanding of the recovery process. Simple simulation models work well in this task (Walters 1986, Chapter 2). However, the simplicity which leads to greater understanding also limits the utility of implementing the resulting strategy in any particular case (Chapter 2, Chapter 3).

Development of a metapopulation recovery strategy serves a number of purposes, however, including:

- 1) Emphasizing the importance of spatial structure in the selection of recovery actions.
- 2) Increasing the understanding of the potential outcomes of alternative recovery actions.
- 3) Providing a starting point, an initial strategy, for use in a metapopulation PVA.

- 4) Introducing a strategy which takes into account spatial structure when an appropriate PVA is not available.
- 5) Emphasizing the importance of including spatial structure in the development of a PVA for a metapopulation.

The Suggested Strategy

The suggested strategy for recovering a metapopulation is presented in eight steps. A series of conceptual figures accompanies the description. The basic strategy resulting from this study relies on maximizing population growth, using a subdivided population to provide protection against environmental stochasticity.

Step 1. Define the Structure

Using historic data, define the structure of the metapopulation (Figure 4.1) including:

- a) All patches that comprise the metapopulation, including unoccupied patches.
- b) Individual patch growth rates, survival rates, or indicators of patch specific growth rates such as habitat quality.
- c) All dispersal corridors and dispersal rates.
- d) The proportion of common variation between pairs of patches.

Before the most appropriate recovery methods can be assessed and selected, the metapopulation system being recovered must be identified as fully as possible.

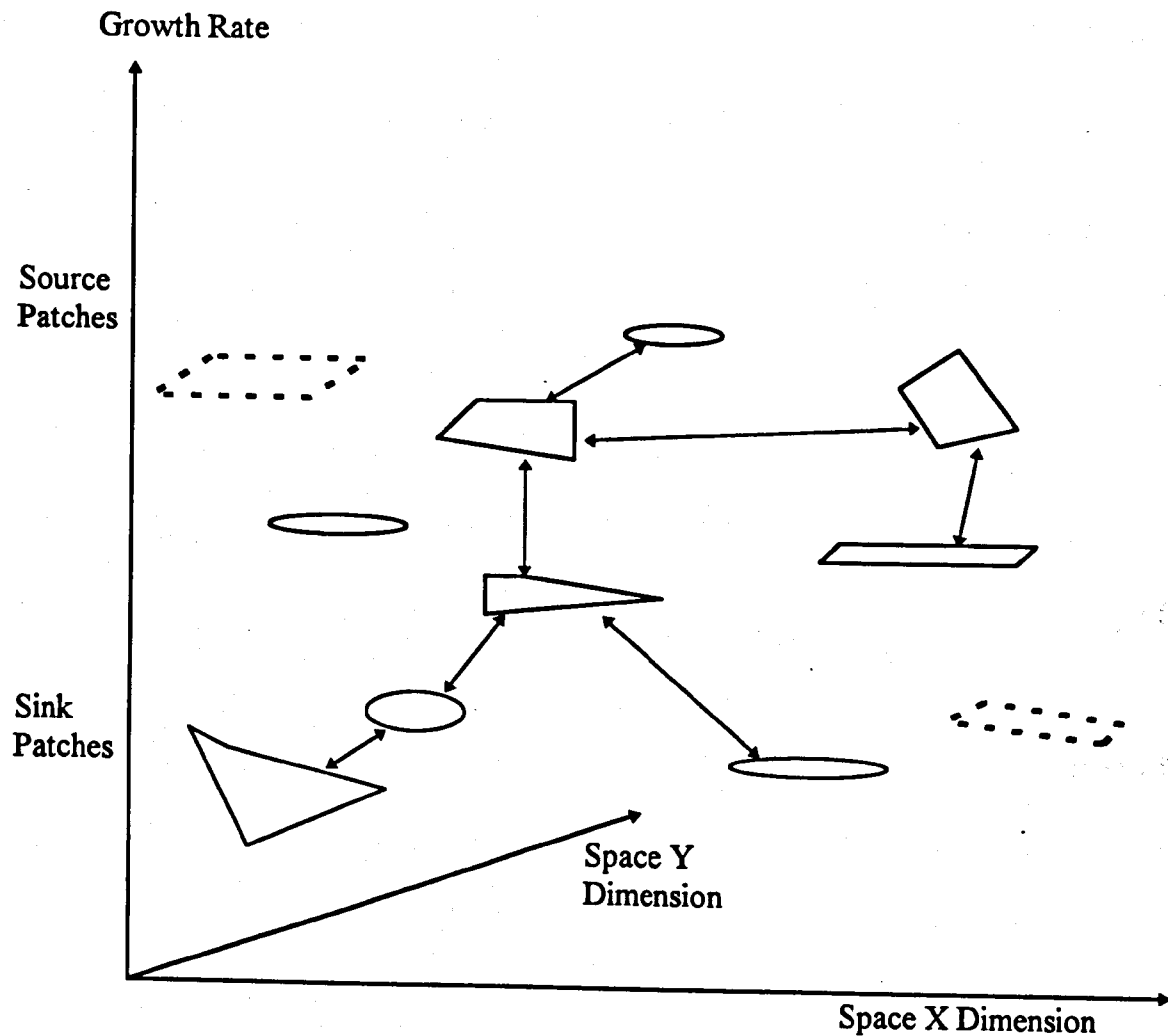


Figure 4.1: Step 1 of Recovery Strategy: Define the Structure. Identify metapopulation patches, associated growth rates, and dispersal corridors and rates.

Step 1 also includes identifying the proportion of common variation between pairs of patches, which is not illustrated here.

Patches with solid outlines are occupied. Patches with dashed outlines are vacant. Arrows represent open dispersal corridors.

Few data sets will provide all of the information requested in step (1). Where information is lacking, a range of values incorporating uncertainty should be developed.

Background on the Series of Figures. Figure 4.1 is the first in a series of figures to conceptually illustrate the general strategy being presented. In the three dimensional plots, the x and y axes represent two spatial dimensions. The z axis represents the growth rate of individual patches. The patches in a conceptual metapopulation are distributed along the two spatial dimensions and in terms of their patch specific growth rates. The variety of shapes representing the patches is meant to reflect the variety of shapes of the patches.

Due to limits in dimensionality, a key factor is not presented in the series of figures beginning with Figure 4.1. Simulations from Chapter 2 and 3 demonstrated that the proportion of common variation is extremely important in metapopulation dynamics and the recovery of metapopulations. Although it is not shown in the conceptual figures, there are many steps dependent on identifying patches with high levels of independent variation, to provide buffering to the overall metapopulation. This remains an essential part of the strategy despite its exclusion from the figures.

Step 2. Secure the Metapopulation

Secure all of the defined components of the metapopulation (Figure 4.2).

- a) Insure that all metapopulation patches remain available to the metapopulation and do not deteriorate in quality.

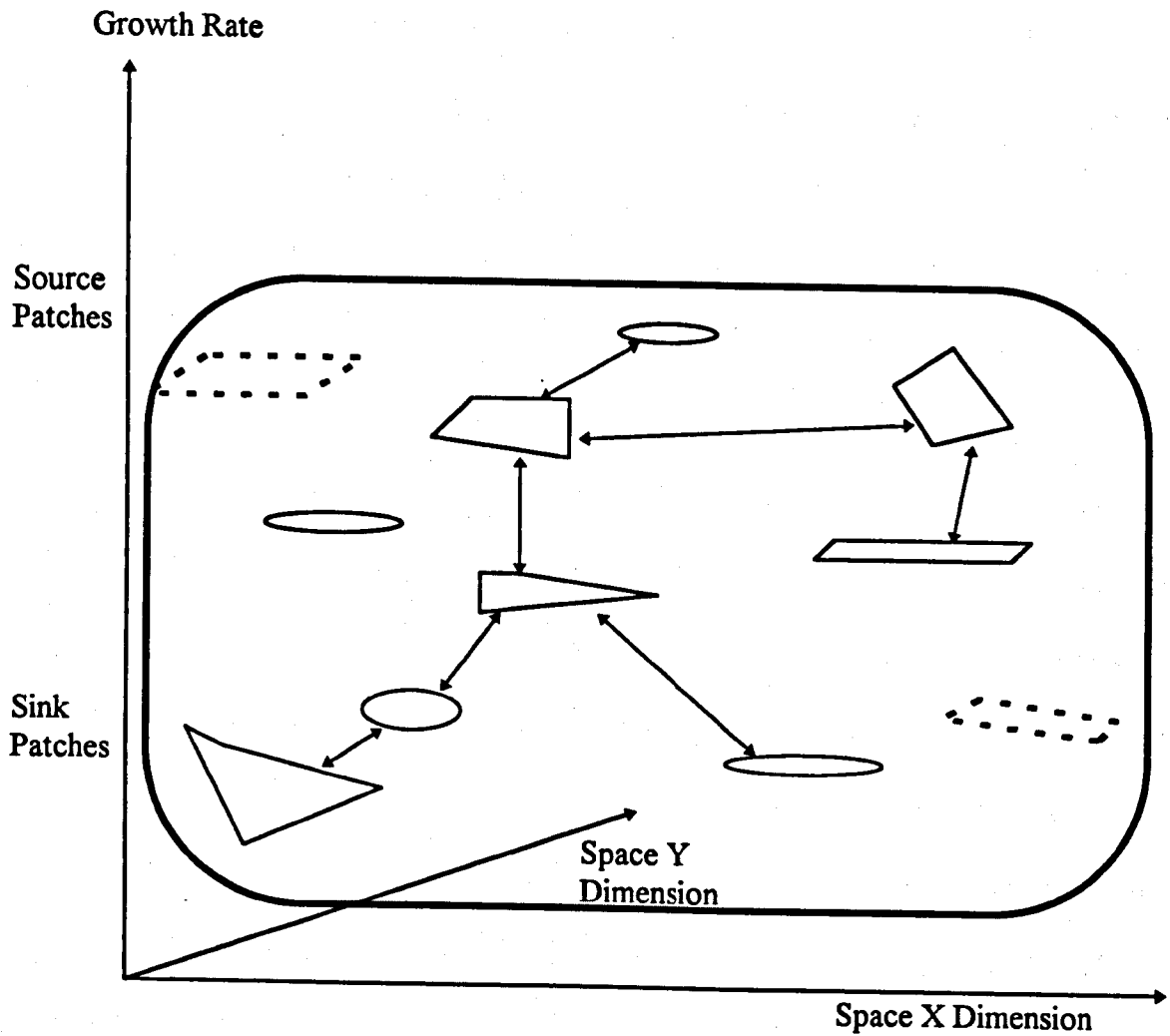


Figure 4.2: Step 2 of Recovery Strategy: Secure the Metapopulation. Maintain the quality of all metapopulation patches and dispersal corridors and stop any dispersal likely to be unsuccessful.

Patches with solid outlines are occupied. Patches with dashed outlines are vacant. Arrows indicate open dispersal corridors.

- b) Maintain the quality of dispersal corridors.
- c) Stop any dispersal likely to be unsuccessful using methods such as placing fences as barriers, transplanting lost animals, etc.

Results from Chapter 3 indicate that removing patches from the metapopulation lowers its potential ability to recover and stabilize. Each patch offers additional buffering capabilities, particularly if growth rates within the patch are greater than replacement levels (Chapters 2 and 3). Metapopulation stability depends on the overall network of patches. Reducing the network through additional fragmentation lowers current and future potential viability (Chapter 2). Patches currently unoccupied may be perceived as being sacrificial, but may, in fact, be key to recovery through either their independence in environmental variation or their potentially higher growth rates.

It is also not desirable to permit further deterioration in patch growth rates and between-patch dispersal rates as this will further decrease metapopulation viability (Chapters 2 and 3). As shown in Chapter 3, decreasing growth rates, whether in the strongest or the weakest patch, causes a decrease in overall viability.

Natural dispersal corridors should be maintained to permit natural dispersal and to discourage the probability of unsuccessful dispersal (Chapter 2). Although Chapter 3 showed that transferring animals using management intervention could replace natural dispersal in many cases, it might be a difficult policy to successfully implement or to maintain in the long term.

Chapter 2 demonstrated that unsuccessful dispersal drained animals away from the metapopulation reducing overall viability. Attempts should be made to stop unsuccessful dispersal through management intervention so that the animals that would be lost from the metapopulation remain reproductively active metapopulation members.

Step 3. Identify Priority Patches

Make a prioritized list of patches for growth rate and ceiling level improvements (Figure 4.3).

- a) Rank all patches based on their growth rates.
- b) Include unoccupied patches using their expected growth rates.
- c) Review combinations of patches that have high proportions of independent variation from step (1d).
- d) Select a number of priority patches where focused improvements will best improve viability based on both growth rates and proportion of independent variation.

Results in Chapters 2 and 3 indicate that improvements should be focused on the patches providing the greatest contributions to metapopulation viability. These include the most productive patches, providing the greatest increases in population growth, and the patches with the greatest independence in environmental variation, providing the greatest buffering capabilities.

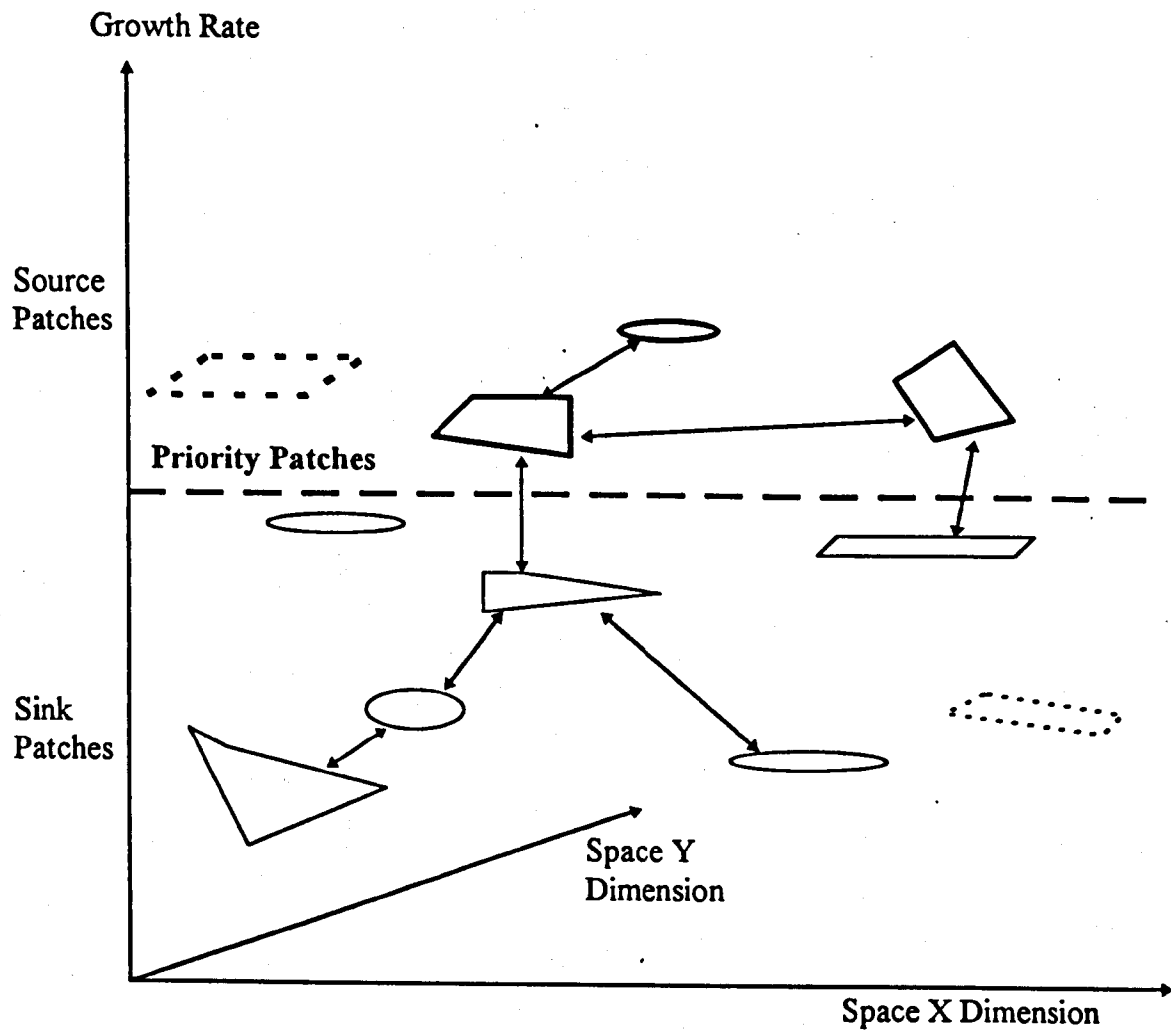


Figure 4.3: Step 3 of Recovery Strategy: Identify Priority Patches. Select a number of patches where focused improvements will be made.

Actual consideration involves both growth rates and levels of independence in environmental effects between patches, which is not illustrated.

Patches with solid outlines are occupied. Patches with dashed outlines are vacant. Arrows indicate open dispersal corridors.

Ideally, the number of patches selected and the actual patches selected would be based on a PVA where a range of alternatives could be compared. Without a PVA, managers should select a workable number of the patches providing the greatest benefits.

Step 4. Recolonize Unoccupied Priority Patches

Recolonize any unoccupied patch selected as a priority patch in step (3d) (Figure 4.4).

- a) Actively recolonize unoccupied patches from (3d) with animals from less productive patches using management intervention if necessary.

Unoccupied priority patches should be recolonized as soon as possible to provide for greater increases in population size and additional buffering opportunities (Chapter 3). The patches should be recolonized using animals from less productive, non-priority patches.

Step 5. Ensure Dispersal among Priority Patches

Ensure sufficient dispersal between priority patches (Figure 4.5).

- a) Review the quality of dispersal corridors and dispersal rates from step (1c) between patches selected in step (3d).
- b) Estimate the dispersal rate needed to maximize viability.

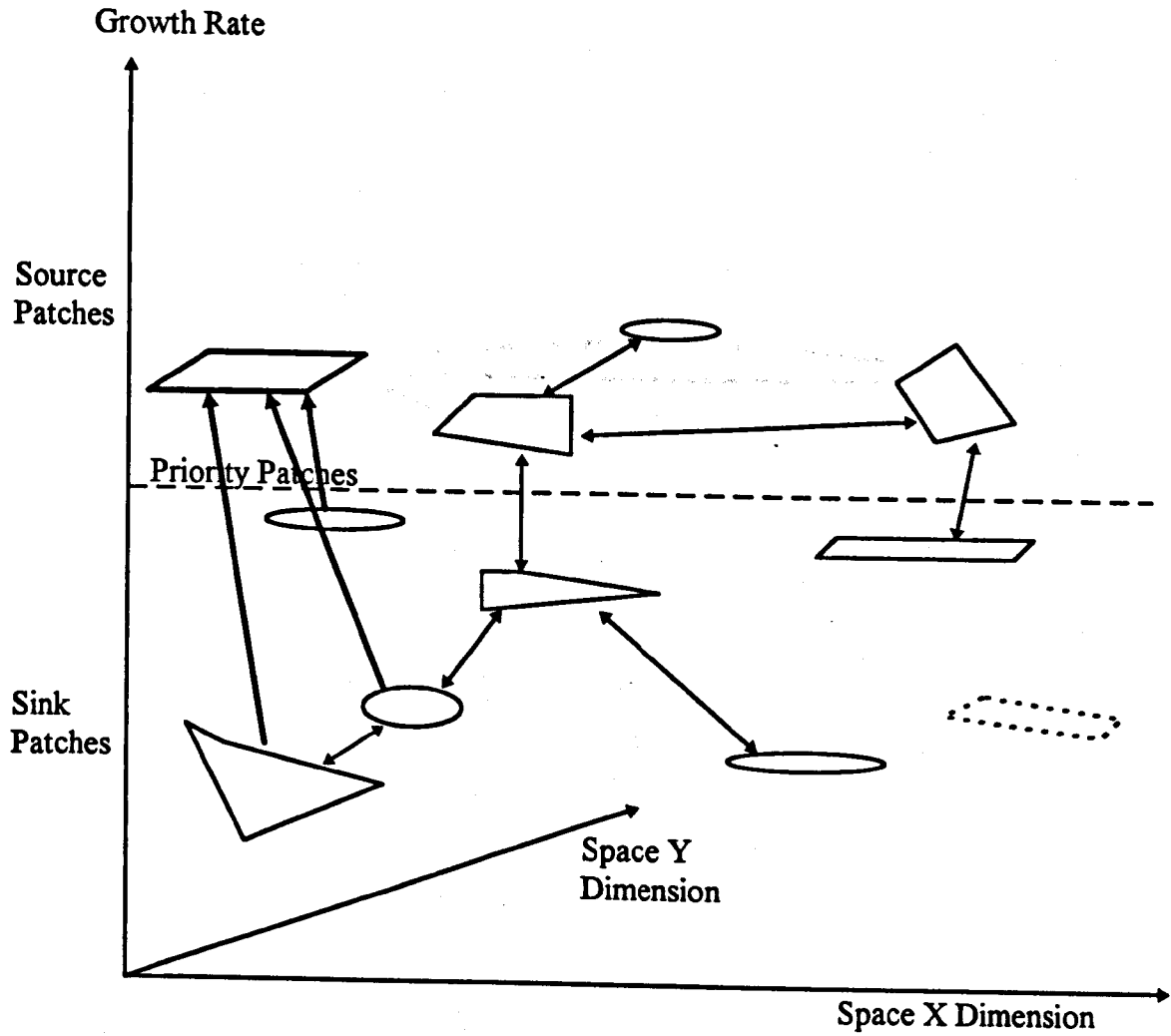


Figure 4.4: Step 4 of Recovery Strategy: Recolonize Unoccupied Priority Patches. Actively recolonize any vacant priority patch using animals from less productive patches.

Patches with solid outlines are occupied. Patches with dashed outlines are vacant. Arrows indicate open dispersal corridors.

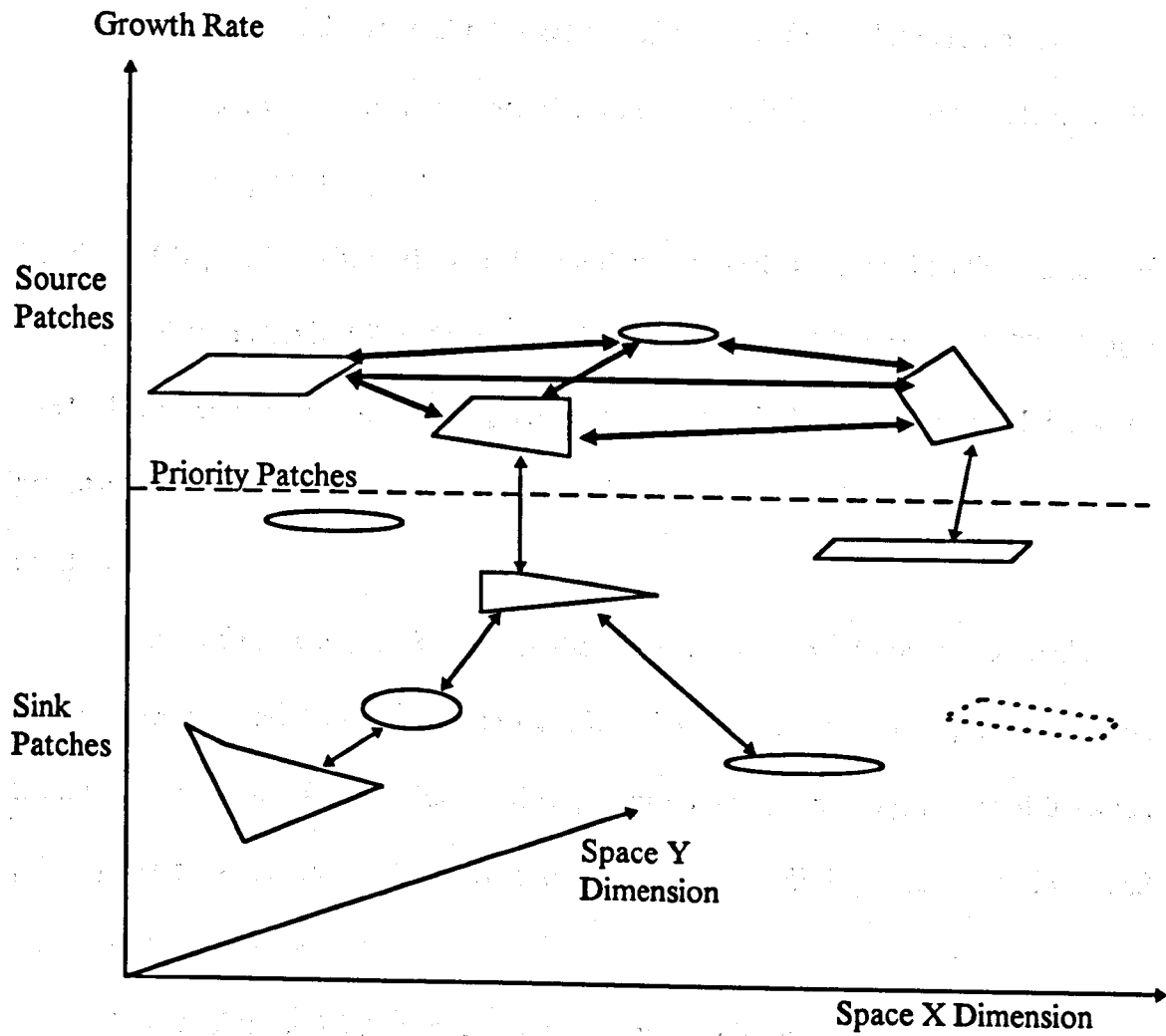


Figure 4.5: Step 5 of Recovery Strategy: Ensure Dispersal Between Priority Patches.

Patches with solid outlines are occupied. Patches with dashed outlines are vacant. Arrows indicate open dispersal corridors.

- c) If natural dispersal rates are insufficient or if corridors are not available, use management intervention to provide sufficient dispersal calculated in step (5b).

Results in Chapter 2 reaffirm the conclusion that dispersal is essential to the viability of a metapopulation (Levin 1976, Brown and Kodric-Brown 1977, Caswell 1978, Shaffer 1981, 1985, Gilpin 1987). During recovery, dispersal should be ensured between priority patches. Within a healthy metapopulation dispersal is expected to connect all patches.

Results from Chapter 3 suggest that during recovery, dispersal to weakened, sink patches is likely to have limited benefits, if any, and may actually drain animals from the population. During the initial stages of recovery, ensuring dispersal between priority patches provides the metapopulation with buffering, augmentation, and recolonization benefits.

If available, a PVA can estimate optimum dispersal rates between priority patches. Results in Chapter 2 indicate that viability is sharply higher in cases with small amounts of dispersal compared to identical cases with no dispersal. As dispersal rates increase, viability levels off, providing diminishing gains in viability. From this it is clear that managers should ensure some level of dispersal between priority patches. If dispersal is already naturally occurring, increasing it may or may not provide substantive benefits.

Where natural dispersal between priority patches is not available, management intervention should be used to provide dispersal between priority patches (Chapter 3). Transplanting a relatively small number of animals can provide benefits equal to natural dispersal in some cases (Chapter 3). The absence of detectable natural dispersal data between patches does not negate the potential increase in viability achieved through this type of management intervention.

Step 6. Improve the Priority Patches

Increase the population growth rates and ceiling levels within the priority patches (Figure 4.6).

- a) Assess the costs and benefits of all available options to increase the population growth rates and ceiling levels within the priority patches selected in step (3d). This would include actions such as habitat improvement, predator removal, captive propagation for vulnerable stages of the life history, etc.
- b) Select and implement the options that provide the greatest increases in viability within allowable costs.

Increasing the productivity of the patches with the highest growth rates provides greater improvements to metapopulation viability than increasing the productivity of weaker patches, assuming equal costs (Chapter 3). There are typically a wide variety of actions that can be taken to increase population growth rates.

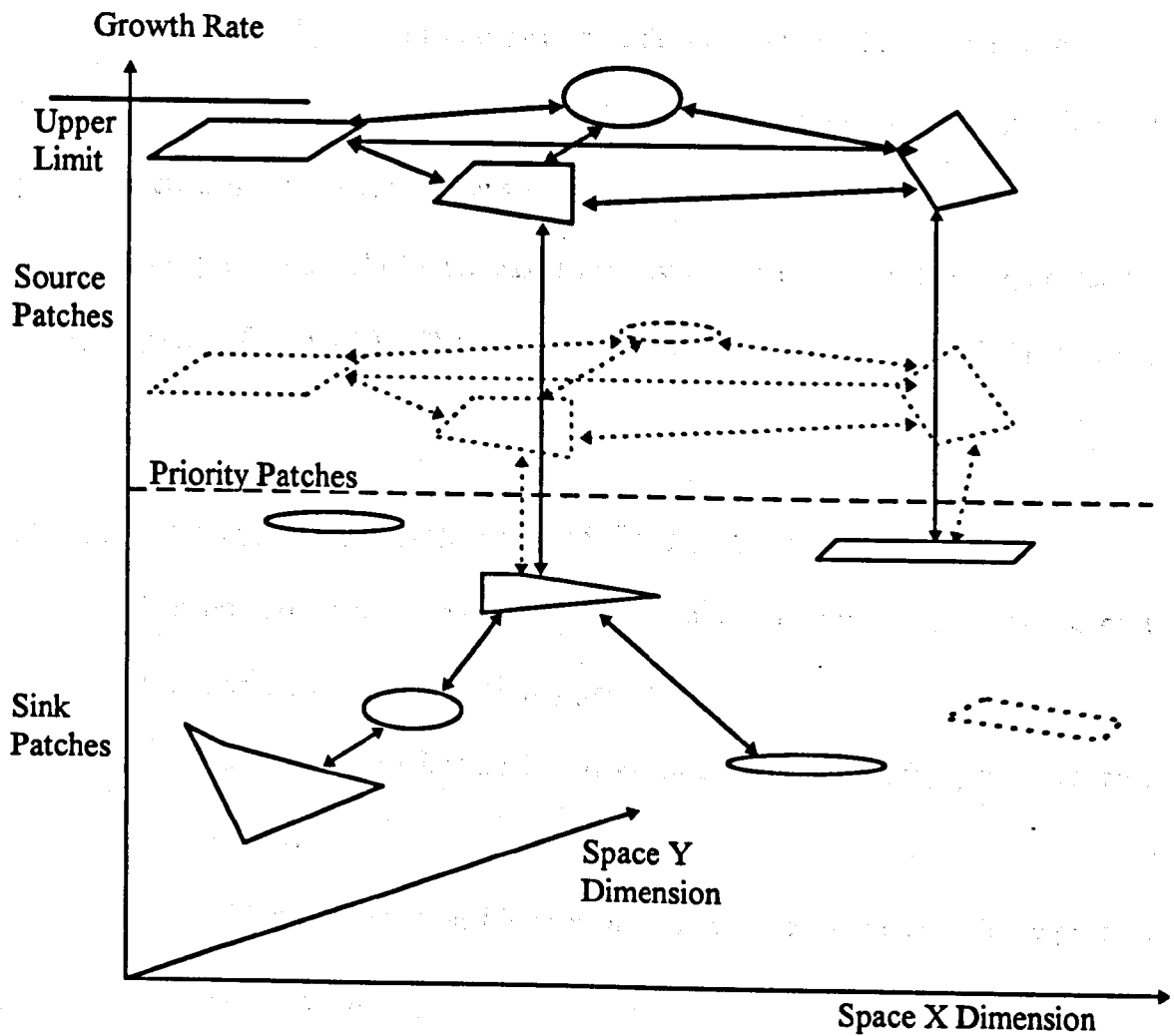


Figure 4.6: Step 6 of Recovery Strategy: Improve the Priority Patches. Increase the population growth rates and ceiling levels within the priority patches.

Dotted priority patches and dispersal corridors represent their original position prior to step 6.

Patches with solid outlines are occupied. Non-priority patches with dashed outlines are vacant. Arrows indicate open dispersal corridors.

A PVA would provide a comparison of the costs to benefits of various options. In the absence of a PVA managers should select actions expected to provide the greatest increases in total population size.

Ceiling levels should be increased for any of the priority patches approaching ceiling capacity (Chapter 3). This can be done by increasing the usable habitat of the species.

Step 7. Continue the Process with a Second Tier of Patches

When no further improvements to the first tier of priority patches are cost effective, focus on a second tier of priority patches.

- a) Identify if any further improvements to each priority patch are cost effective.
- b) If there are additional improvements possible, continue with the process in step (6b).
- c) If not, return to step (3) and select a second tier of priority patches using the highest ranking priority patches remaining (Figure 4.7).
- d) Continue through step (4). Recolonize any of the second tier priority patches which are unoccupied.
- e) Continue through step (5). Ensure sufficient dispersal between the second tier priority patches and between the first and second tier patches (Figure 4.8).

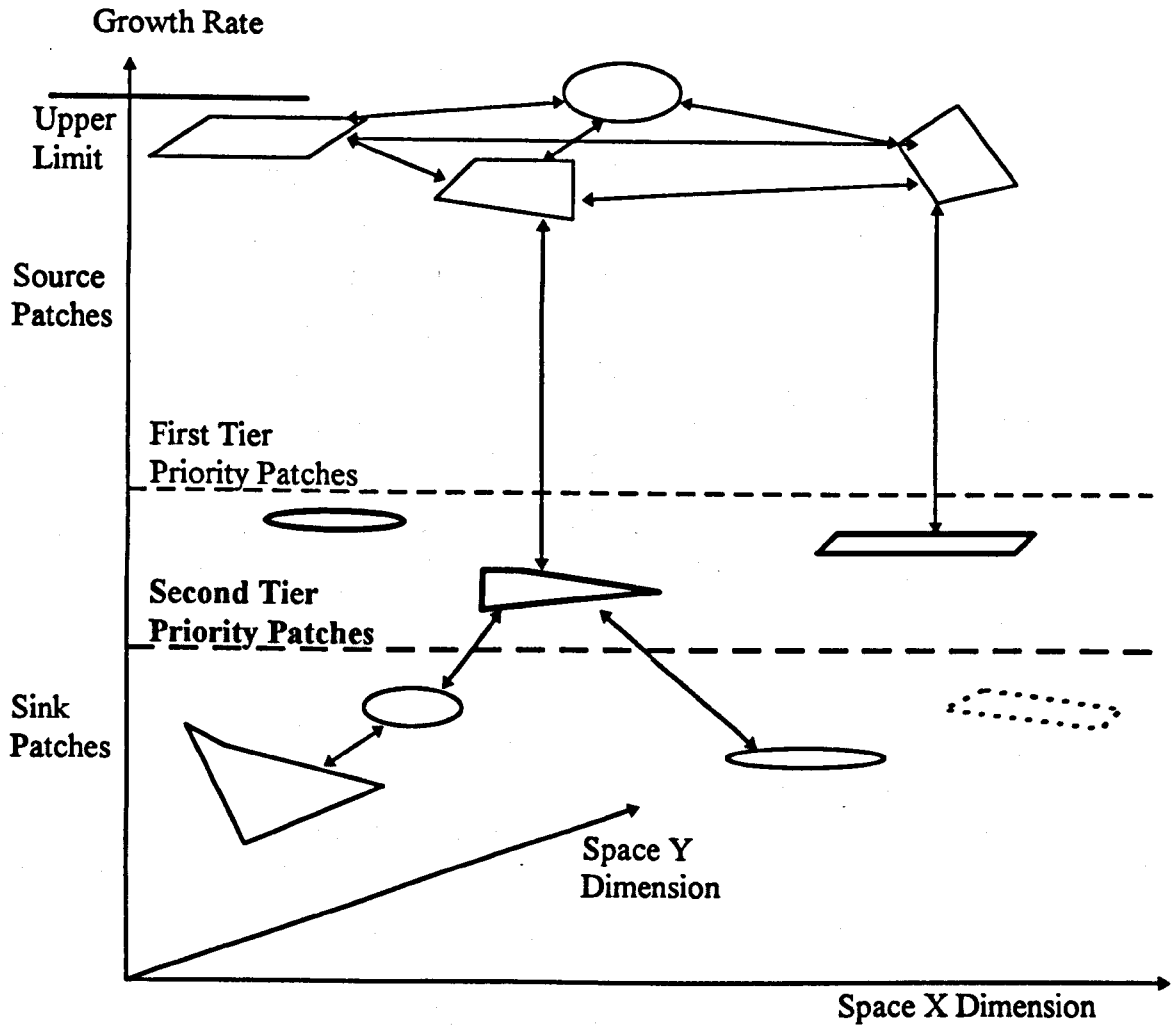


Figure 4.7: Step 7c of Recovery Strategy: Identify a Second Tier of Priority Patches.

Patches with solid outlines are occupied. Patches with dashed outlines are vacant. Arrows indicate open dispersal corridors.

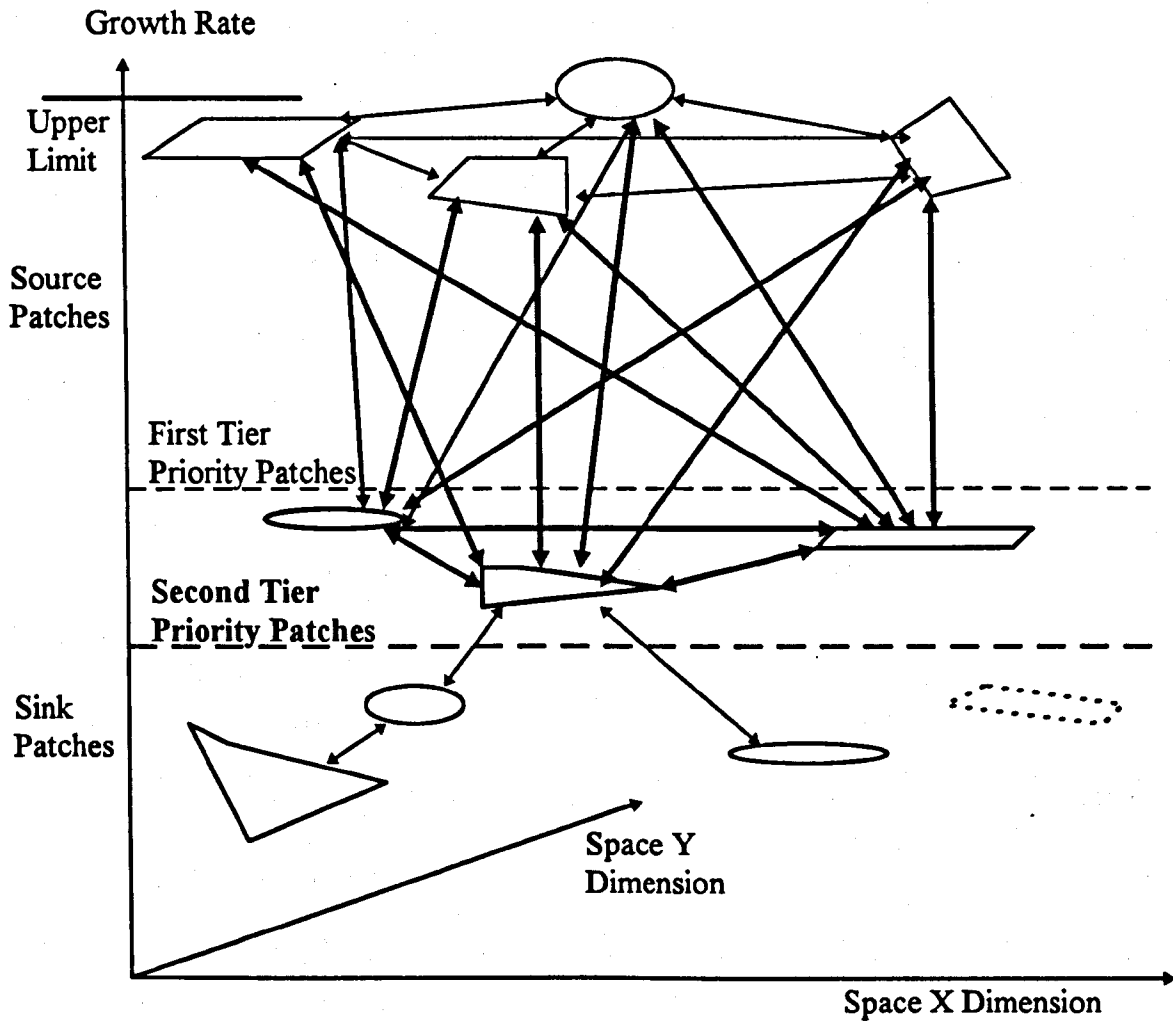


Figure 4.8: Step 7e of Recovery Strategy: Ensure Dispersal Between All Priority Patches.

Patches with solid outlines are occupied. Patches with dashed outlines are vacant. Arrows indicate open dispersal corridors.

f) Continue through step (6). Make any cost effective changes to increase the growth rate and ceiling levels of the second tier patches (Figure 4.9). Step (7) comes into play when the process through step (6) has been exhausted. When there are no longer cost effective improvements to be made to the priority patches, and if the actions taken to this point have not recovered the population, then the process should continue using an additional tier of priority patches, selected by ranking the remaining patches.

The second tier of patches should be selected in the same way as the first tier. Once identified, unoccupied second tier patches should be recolonized using animals from less productive patches.

Dispersal should connect all second tier patches to each other and to all first tier patches. If it is not possible to directly connect each possible pairing, connections between intermediate patches should exist allowing the dispersal of animals between all patches.

Improvements should be made to the growth rates and ceiling levels of the second tier patches causing continued improvement to the viability of the overall metapopulation.

Step 8. Continue the Process Until Recovery

Continue the process incorporating additional patches for improvements over time.

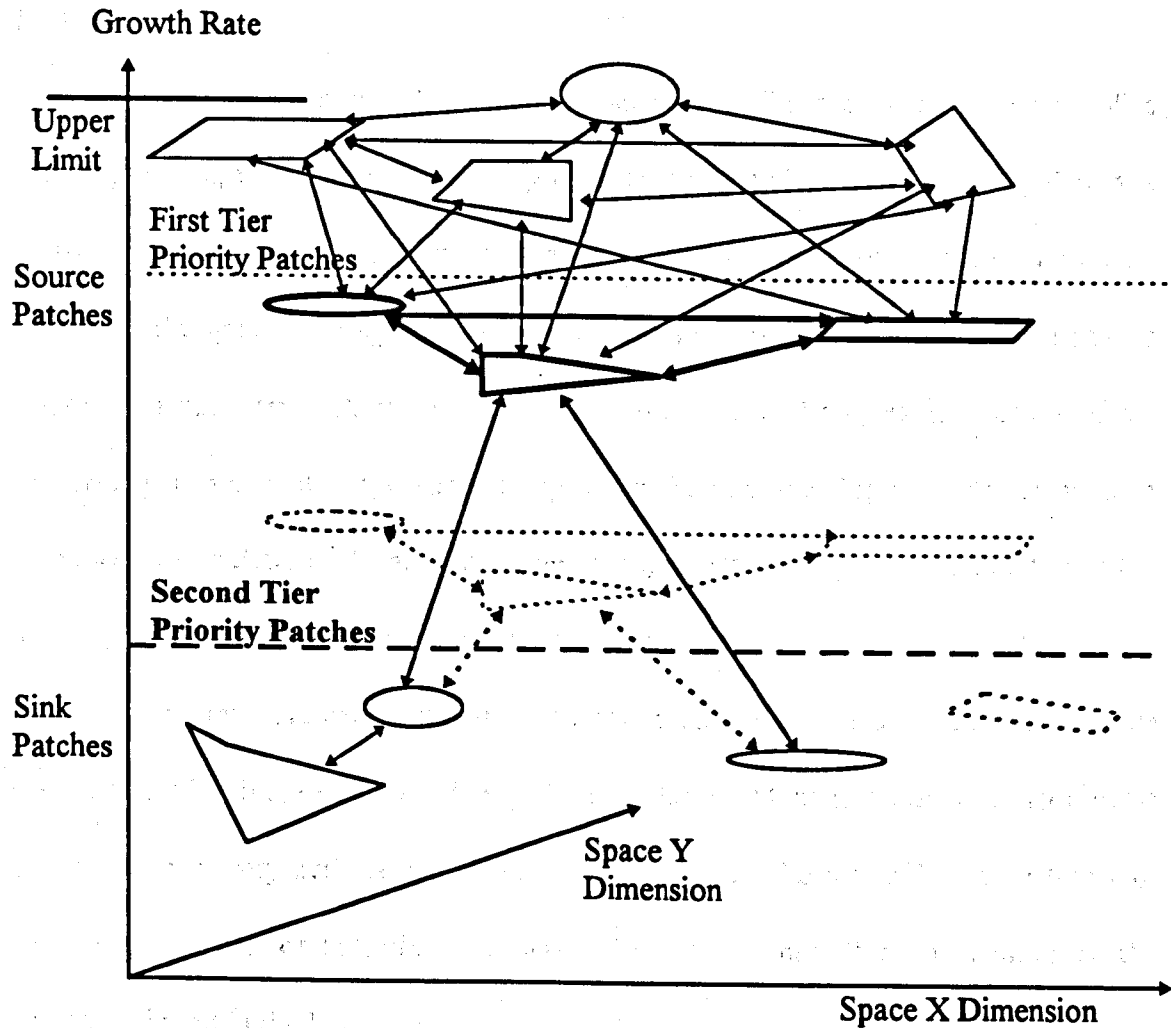


Figure 4.9: Step 7f of Recovery Strategy: Improve the Second Tier of Priority Patches. Make any cost effective changes to increase the growth rate and ceiling levels of the second tier patches.

Dotted priority patches and dispersal corridors represent their original position prior to step 7f.

Patches with solid outlines are occupied. Non-priority patches with dashed outlines are vacant. Arrows indicate open dispersal corridors.

Post Recovery

The process described above was structured for the recovery stage of a metapopulation, to try to maximize improvements in viability. Once the population is recovered, a management strategy based on maximizing increases in viability may no longer be the goal. Management strategies can shift to metapopulation maintenance rather than recovery. A wide variety of management strategies is possible, from preserving a remnant population away from human development to creating a harvestable population. In any case, the management strategy should not lower the viability of the metapopulation below recovery conditions.

Some improvements to patch growth rates or dispersal rates may not be affordable, effective, or manageable in the long term. Managers may wish to replace short term recovery actions with other actions that may be less effective in terms of population growth or buffering, but would be more manageable, in maintaining the metapopulation in the long term.

If managers wish to obtain a sustainable harvest from the metapopulation, maximizing population growth past the point of recovery may remain the highest priority until the population is at harvestable levels. Once a harvest begins, sufficient viability must be maintained with the inclusion of harvest.

Managers may ultimately wish to stabilize some of the weaker patches, left unimproved in the strategy described above. These patches may have special value to the resource users. Management resources can be rearranged at this point to

strengthen weaker patches or their source patches, as long as overall metapopulation viability does not decline.

Discussion

The strategy presented emphasizes the importance of spatial structure in the selection of recovery actions. Most of the actions described above, such as recolonizing open patches and reconnecting dispersal corridors, have a spatial component. Without considering the impacts of spatial structure when developing a recovery strategy, managers are likely to ignore many of the most beneficial management strategies (Gilpin 1987, ESA 1996, Chapter 2, Chapter 3).

The conservation literature provides support for the strategy presented above. Conserving individual species, as discussed throughout this study, often provides the best opportunities for preserving an entire ecosystem, particularly if the species is a keystone or umbrella species (Soulé and Simberloff 1986, Soulé 1987b, Foose et al. 1995).

Maintaining subdivided populations provides protection from uncertainty (Shaffer 1987), environmental stochasticity (Goodman 1987), the loss of genetic variation (Lande and Barrowclough 1987), and catastrophe (Gilpin 1987). For that reason the literature on reserve design recommends maintaining multiple reserves, rather than a single reserve (Soulé and Wilcox 1980b, Goodman 1987a, 1987b, Shaffer 1987). Reserves can also be thought of, in this case, as patches. Goodman (1987b)

points out the beneficial role of multiple reserves that experience at least partially independent environmental variation, which is a key component in the selection of priority patches as recommended above.

Recent literature also supports the conclusion that there is a demographic cost to recolonizing sink patches (Donovan et al. 1995), which is why the recommended strategy advocates recolonizing priority patches only.

Maintaining connectivity, or dispersal, between patches is an essential part of a metapopulation recovery strategy (Gilpin 1987, Goodman 1987a, 1987b, Lande and Barrowclough 1987, Foose et al. 1995) providing both genetic and demographic benefits.

The need for management intervention in restoring a metapopulation has been advocated previously (Goodman 1987a, 1987b, Foose 1989, Foose et al. 1995). Strategies previously mentioned have included "to translocate otherwise doomed dispersing animals to available habitat to which they could not migrate naturally" (Foose et al. 1995). This is stated most directly in Foose et al. (1995):

"Metapopulation strategies will entail interactively managing the subpopulations to maximize the probability of the species' survival ... Managed migration is one example of the kinds of intensive management and protection of viable populations in the wild. ... As wild populations continue to be limited in size and distribution, they will increasingly require the intensive levels of management now commonly applied only to captive populations. Thus, conservation strategies for small populations in nature will become increasingly similar to those in captivity. This reality must be recognized by all those concerned with the continuing survival of the species now facing extinction."

Applying and Building on the Suggested Strategy

The simplicity of the simulation models in this study increases our understanding of metapopulation recovery (Walters 1986, Chapter 2). The very simplicity that helps build intuition, however, limits its applicability in the real world. As Walters (1986) describes it, quoted in Chapter 2, learning is completed in steps, by gradually adding layers of complexity.

The strategy developed from the simulation model similarly builds intuition, while having limited applicability with any particular case due to the lack of complexity included in its development. What are the next steps that can be taken to build on the development of this strategy? Further work can proceed in three directions: developing additional models, applying the strategy to existing PVAs, and conducting experiments in the field.

Additional Model Development. Additional layers of complexity can be added to the simulations developed in this study. The effects of density dependence, age structure, hierarchical straying rates, etc. can all be examined using the model structure developed in this study. By adding additional layers of complexity, improvements to our understanding can continue and the model can be made more applicable to specific cases. Some of the complicating factors, such as density dependence, have the potential to modify the strategy presented above. Additional work is needed to continue this process.

Applying to Existing PVAs. The suggested strategy developed in this paper could be applied to a variety of spatially structured PVAs to compare its effectiveness in restoring viability to alternative strategies. By applying the strategy to PVAs developed for a number of species and conditions, it would be possible to identify the conditions where the suggested strategy is likely to be effective, and the conditions where it is not. By using PVAs it is also possible to fine tune the suggested strategy to improve its effectiveness.

Field Experiments. Information can be gained about the utility of the strategy by conducting experiments in the field. The strategy and the simulations on which it's based assume transferring and crossbreeding is possible and likely to be successful. Experiments could test the plausibility of recolonizing vacant patches, eliminating unsuccessful dispersal, transferring animals between patches, etc. The ability of animals from different patches within the metapopulation to successfully interbreed is important to the success of a metapopulation recovery strategy emphasizing dispersal. Using experiments, the ability to successfully transplant and crossbreed animals between patches could be tested. To test the principal components of the strategy, it may be preferable to experiment on a viable population, rather than conducting experiments on an already weakened population.

Suggestions for Resource Managers

How can managers use the information and recommendations in this study in metapopulation recovery efforts? This depends on the information and tools available to the manager in each case.

Use a Spatially Structured PVA. If available, managers should consult a competent, species and case specific, spatially structured Population Viability Analysis (PVA) (Gilpin and Soulé 1986, Soulé 1987a, 1987b, Boyce 1992, ESA 1996, Chapter 2, Chapter 3) to assess the probable outcomes of alternative management actions before making management decisions regarding metapopulation recovery actions (Conway 1995, ESA 1996).

If a spatially structured PVA does exist, the strategy presented above could be used as a starting point toward finding the optimal policy. While the simulations from Chapters 2 and 3 led to the development of the suggested strategy, it may not be optimal for any particular case (Chapter 2, Chapter 3). By using the strategy as a starting point, metapopulation dynamics and spatial structure are both considered in the process. The suggested strategy could then be compared with alternative strategies and fined tuned, if appropriate, for the particular species and case.

As discussed in Chapter 1, developing a spatially structured PVA is a complicated and difficult task (Gilpin 1987, Soulé and Kohm 1989). Often a competent and functional PVA will not be available at the time when decisions regarding recovery actions are needed.

Build General Rules. While managers can not rely on the existence of perfected PVAs or on generalized simulation models to guide all of their recovery action decisions, neither do they have to develop restoration strategies for each species from scratch. Using theory and experience, decision makers have an increasing amount of information on which to base their decisions. The Ecological Society of America's report on science and the Endangered Species Act (ESA 1996) affirms this by stating:

“In other words, as experience is gained, each new case can build upon the results of previous cases. Rather than treating each new species to be protected as a totally novel situation, more powerful general rules can be applied and the process thereby simplified.”

By combining information from a variety of PVAs, additional simulations, field experiments, and metapopulation recovery experience, managers can create a database on which to build more powerful, general rules as described above by the Ecological Society of America (1996).

Incorporate Adaptive Management. Managers will gain increased information about appropriate recovery actions through the incorporation of adaptive management (Holling 1978, Walters 1986). Adaptive management requires regular and active probing experiments in order to provide information, or feedback, to management (Walters et al. 1988). With a subdivided population, unique opportunities exist for management experiments (Walters 1986, Berkson 1988). New management policies can be tested on a small number of experimental units while other units maintain

control policies. Managers can then assess the benefits and costs of the experimental policy relative to the control baseline (Berkson 1988).

An adaptive management approach for a metapopulation could experiment with transplanting animals between patches and with crossbreeding animals between patches. Experiments could test whether these methods are likely to be successful, or, could test possible improvements to these methods. Testing these policies on a smaller scale, would be preferable in many cases to an initial full scale implementation. Other experiments could include efforts to improve growth rates on both source and sink patches or efforts to recolonize vacant patches. Future management decisions would be based on the results of the various tests.

Adaptive management within a metapopulation provides opportunities to test alternative management policies, without having to implement the policy over the entire population (Berkson 1988). Whether managers have a competent, species and case specific, spatially structured PVA for a particular metapopulation, or managers have little information available, policies based on adaptive management should be instituted, providing management with the opportunity to learn and increase effectiveness over time.

CHAPTER 5

A CASE STUDY: THE SNAKE RIVER SPRING/SUMMER

CHINOOK SALMON

Introduction

Snake River chinook (*Oncorhynchus tshawytscha*) are characterized as “spring”, “summer”, or “fall” runs based on the time adults enter freshwater to begin their return upriver to spawn. Adult chinook passing Bonneville Dam from February through May are classified as spring chinook and adult chinook passing Bonneville Dam from June through July are classified as summer chinook (Burner 1951) with few exceptions (NMFS 1995).

An anadromous and semelparous species, chinook begin in freshwater, migrate to the ocean where they mature, return upriver to spawn, and die after spawning once. Snake River spring and summer chinook are classified as “stream-type” as defined by Gilbert (1913), typical of headwater populations, rearing one year in freshwater, migrating offshore as yearlings, spending several years in the ocean, then returning in spring or summer, several months before spawning (NMFS 1995).

The Snake River Basin encompasses an area of 107,000 square miles in the states of Idaho, Nevada, Oregon, Washington, and Wyoming. Spring and summer chinook historically spawned throughout the Snake River basin, wherever suitable

habitat was accessible (Evermann 1896, Fulton 1968). Spring chinook historically were observed spawning more than 930 miles from the sea, as far upstream as Rock Creek (Evermann 1896).

Historic Distribution and Abundance

Historically, of all the tributaries, the Snake River produced the greatest number of anadromous fish in the Columbia River system (NMFS 1995). Before the turn of the century 10-16 million salmon returned annually to the Columbia River (NPPC 1993), which was acknowledged to be the largest chinook producer in the world (Van Hyning 1968). It is estimated that between 2.5 and 3.0 million spring and summer chinook annually returned to the Columbia River from 1881 to 1895 (Chapman 1986). The total annual production of spring and summer chinook in the Snake River was estimated to be in excess of 1.5 million fish during the late 1800s (NMFS 1995), or about half of the total production.

Snake River salmon declined dramatically from historic levels due to a number of factors. One of the primary factors was the construction of 12 dams on the mainstem Snake River, beginning in 1901. Construction of the Lewiston Dam, for instance, nearly eliminated chinook runs (spring, summer, and fall) in the Clearwater River Basin between 1927 and 1972 (CBFWA 1990, Fulton 1968). Major production areas in the upper Snake River basin for spring and summer chinook were completely eliminated by the Hells Canyon dam complex completed in 1967, consisting of

extremely high dams designed and constructed without fish passage facilities (NMFS 1995).

Population sizes have declined dramatically over the past 30 years (Figure 5.1). Annual returns of Snake River spring and summer chinook were estimated at 125,000 from 1950 through 1960 (Fulton 1968), 59,000 between 1962 and 1970, then dropping to less than 10,000 from 1980 to 1990 (Mathews and Waples 1991). By 1995, when approximately 1500 returned, spring and summer chinook had been reduced to 0.1% of their historical abundance during the late 1800's.

Spring/Summer Chinook and the Endangered Species Act

In June of 1990, a number of organizations including Oregon Trout, the Oregon Natural Resources Council, the Northwest Environmental Defense Center, American Rivers, and the Idaho and Oregon Chapters of the American Fisheries Society submitted petitions to list Snake River spring and summer chinook salmon (along with Snake River fall chinook) on the endangered species list. The National Marine Fisheries Service (NMFS) is the federal agency responsible for implementing the Endangered Species Act (ESA) for anadromous fish.

NMFS issued a finding that Snake River spring and summer chinook should be considered one species as defined legally under the ESA and that the population had experienced such a substantial decline in abundance that it could only be found over a fraction of its former range.

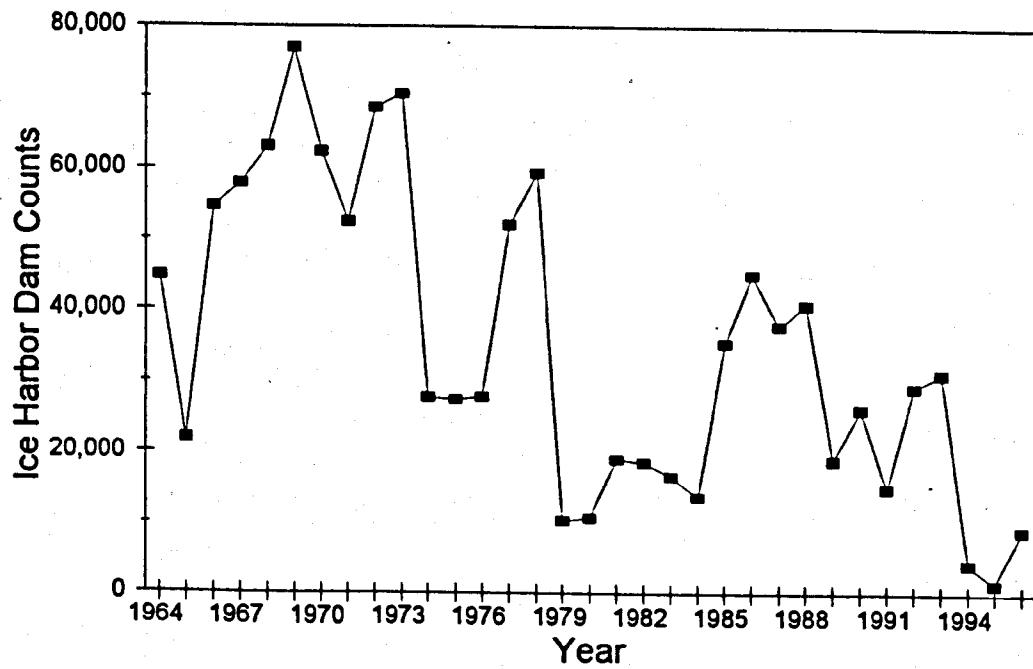


Figure 5.1. Number of Snake River Spring/Summer Chinook Adults Passing Ice Harbor Dam by Year (1964-1996).

This resulted in NMFS listing Snake River spring/summer chinook as threatened on April 22, 1992. Reacting to the continued decline of Snake River spring/summer chinook, the agency reclassified the listed species as endangered on August 18, 1996.

Defining the Spring/Summer Chinook as a Metapopulation

Using the definition of metapopulation in the conservation biology literature (reviewed in Chapter 1, Gilpin and Hanski 1991, Hanski and Gilpin 1991), Snake River spring/summer chinook are spatially distributed as a metapopulation (Figure 5.2, Table 5.1) (SRSRT 1994, Mundy et al. 1995, NMFS 1995, NRC 1996). They are distributed in patches (Healey 1991, SRSRT 1994, NMFS 1995), which are connected by dispersal (Ashworth 1868, Rich and Holmes 1928, Quinn 1984, 1985, Healey 1991). Dispersal, known as "straying" in salmon, is adaptive and results from natural selection (Quinn 1984, 1985). Dispersal in salmon increases the likelihood of eluding unfavorable local conditions (Leider 1989), provides the opportunity to colonize new habitats (Milner and Bailey 1989), and advances genetic heterogeneity at the population level (Utter 1991).

Chinook salmon share other characteristics common to other species structured as metapopulations. Chinook exhibit considerable plasticity and are able to adapt rapidly to new situations (Healey 1991, Quinn et al. 1991, Pascual and Quinn 1994).

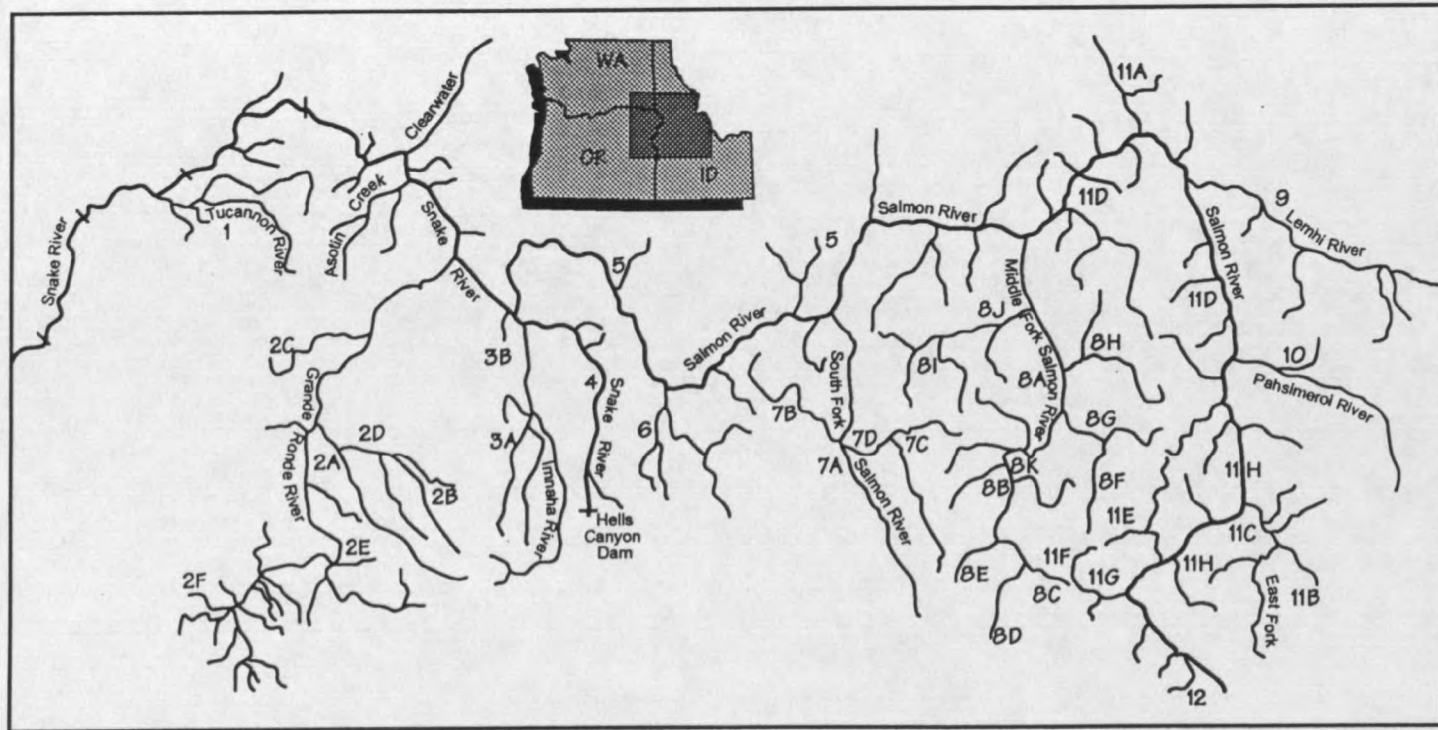


Figure 5.2. Map of Snake River Basin with Snake River Spring/Summer Chinook Stocks Numbered and Subpopulations Lettered (according to SRSRT 1994). Stocks labeled in Table 5.1.

There are also numerous examples of localized extinctions, successful colonizations, and shifting of spawning locations due to adverse conditions in salmon (Kwain and Lawrie 1981, Larkin 1981, Withler 1982, Quinn 1985, Gharrett et al. 1988, Healey 1991, Quinn and Unwin 1993).

Table 5.1: Snake River Spring/Summer Chinook Stocks and Associated Number of Subpopulations (According to SRSRT 1994).

Number on Map	Stock Name	Run Timing	Number of Subpopulations
1	Tucannon	Sp	1
2	Grande Ronde	Sp	6
3	Imnaha River	Sp/Su	2
4	Snake River mainstem	Sp	1
5	Lower Salmon River	Sp	1
6	Little Salmon River	Sp/Su	1
7	South Fork Salmon River	Su	4
8	Middle Fork Salmon River	Sp	8
8	Middle Fork Salmon River	Su	3
9	Lemhi River	Sp	1
10	Pahsimeroi River	Sp	1
11	Upper Salmon River	Sp	5
11	Upper Salmon River	Su	3
12	Salmon River headwaters	Sp	1
TOTAL SUBPOPULATIONS			38

Note: Sp denotes spring chinook, Su denotes summer chinook, Sp/Su denotes spring and summer chinook located in the same area.

While only a few examples of successful introductions to barren rivers exist (Withler 1982), the success of transplants to New Zealand, Chile, and the Great Lakes testify to the adaptability of the species and the ability of the species to colonize (Healey 1991).

Salmon and Common Variation. One important and unique characteristic of salmon metapopulations is the high proportion of common to independent variation they experience in comparison with other species. Unlike most metapopulations where animals from individual patches remain separated for all or most of their life cycles, salmon within a metapopulation spend most of their lives aggregated. Salmon spawning areas can be thought of as traditional metapopulation patches, each having its own dynamics and connected through dispersal. But, from the time the salmon move downstream into the estuary, then the ocean, and back upstream to their patches, the individuals from the separate patches of the metapopulation are aggregated. Particularly during these aggregated stages, the metapopulation is subject to common environmental variation.

Common environmental variation is also expected at the segregated stages of the salmon life history between adjacent patches as has been demonstrated in a number of salmonids (Milner et al. 1993, Rieman and McIntyre 1996). While high proportions of common variation within patches in the Snake River basin is expected, independent variation between patches is expected to provide some level of buffering.

Results in Chapter 2 showed that spatial structure and metapopulation dynamics were important in simulated metapopulations subject to high levels of common variation. Dispersal provided increased viability to the simulated metapopulation when as much as 80% of the variation was common between patches (Chapter 2). However, buffering capability is likely lower than in metapopulations subject to a greater

proportion of independent variation (Chapter 2). For this reason, increasing the total population size as quickly as possible becomes especially critical for salmon recovery, while ensuring dispersal between the individual patches, or tributaries (Chapter 3).

Developing a Recovery Strategy

Chapter 4 suggests a number of ways to apply the results of this study in the design of endangered species management strategies including: using a spatially structured PVA, building and applying general rules, and developing adaptive management approaches.

Spatially Structured PVA

Currently there is no spatially structured Population Viability Analysis for Snake River spring/summer chinook available to test a range of alternative recovery actions. In the Columbia Basin there are two "life cycle" models in various stages of development (Schaller et al. 1992, Lee and Hyman 1992). Neither of the models in current development incorporates spatial structure. Instead, no connectivity and no spatial structure is assumed (Schaller et al. 1992, Lee and Hyman 1992).

Because the viability of a metapopulation is highly dependent on its specific spatial structure (Gilpin 1987, Soule and Kohm 1989, ESA 1996, Chapter 1, Chapter 2, Chapter 3), an appropriate PVA for the spring/summer chinook metapopulation should be spatially structured (Gilpin 1987, ESA 1996, Chapter 1, Chapter 2, Chapter 3). Without incorporating spatial structure, modelers will ignore one of the most

important factors affecting viability, and will not have the capability to assess many of the potentially most beneficial recovery policies (Chapter 3). Because Snake River spring summer chinook salmon are a metapopulation (SRSRT 1994, Mundy et al. 1995, NMFS 1995, NRC 1996), an appropriate PVA must include spatial structure and connectivity.

Building General Rules - Applying the Suggested Strategy

In Chapter 4 it was suggested that managers synthesize information from a variety of sources, including spatially structured PVAs and simulation models, for use in developing recovery strategies. Managers should test and modify the suggested strategy from Chapter 4 with a variety of spatially structured PVAs and with additional simulations that add complexity and realism (Chapter 4).

In the absence of this additional work, managers can apply the suggested strategy to spring/summer chinook as an initial attempt to incorporate spatial structure into the selection of recovery actions, recognizing its limitations (Chapter 3, Chapter 4). In this section the suggested strategy from Chapter 4 will be applied to Snake River spring/summer chinook salmon.

The Initial Steps. The first two steps of the suggested strategy are to define and secure the metapopulation (Chapter 4). Managers of Snake River spring/summer chinook salmon should identify the components of the metapopulation and ensure that conditions don't get worse (Chapter 4).

Intercept and Transplant Unsuccessful Dispersers. Securing the metapopulation also involves stopping any dispersal likely to be unsuccessful (Chapter 4, Foose et al. 1995). In the examples in Chapters 2 and 3, the unsuccessful dispersing animals did not reach any metapopulation patch. For Snake River spring/summer chinook, there are currently two additional cases that can be considered unsuccessful dispersal. First spring/summer chinook can disperse to poor quality habitat, not capable of providing successful spawning and rearing. Second, spring/summer chinook can disperse to patches where the density of returning adults is too low to assure finding a suitable mate, one of the cases of the Allee effect (Allee 1949).

With the proximate goal for recovery being to maximize population growth, particularly since this metapopulation is subject to high proportions of common variation and therefore limited buffering ability, it is not useful to allow cases of unsuccessful dispersal to continue, if avoidable (Chapter 2, Chapter 3, Foose et al. 1995). Spring/summer chinook managers should consider intercepting salmon bound for habitat and/or densities unlikely to provide successful spawning and rearing, and transplanting them to "priority patches."

Recolonize Unoccupied Priority Patches. Priority patches should be identified considering both potential patch growth rates and proportions of independent variation between patches (Chapter 4). Unoccupied priority patches should be recolonized using fish from less productive patches, using management intervention (Chapter 3, Chapter 4). Intervening to assist with faster recolonization of a high

quality priority patch increases population size faster and thus increases viability more quickly than waiting for a slower non-intervention process (Chapter 3).

Ensure Dispersal Through Management Intervention. Dispersal may not occur naturally between priority patches for a number of reasons. Low dispersal rates may provide dispersers consistently at large population sizes, but might provide few if any at extremely small population sizes. Fragmentation may have disconnected natural dispersal corridors (Chapter 2). Dispersal is essential to metapopulation viability (Levin 1976, Brown and Kodric-Brown 1977, Caswell 1978, Shaffer 1981, 1985, Gilpin 1987, Chapter 2). Results in Chapter 2 indicate that viability is sharply higher in cases with small amounts of dispersal compared to identical cases with no dispersal, even when there is a high proportion of common variation. Where natural dispersal between priority patches is not detected, managers should intervene to transplant returning spawners between priority patches (Chapter 3, Gilpin 1987, Goodman 1987a, 1987b, Foose et al. 1995). Results showed that transferring small numbers of individuals provided large viability gains, in the absence of natural dispersal (Chapter 3).

Improve Survival Rates. In the suggested strategy in Chapter 4, longer term actions would focus on making improvements to the priority patches. The life history of the salmon complicates this by aggregating animals from their natal patches for a majority of their lives. Many of the possible actions, such as downstream and upstream

passage improvements, and mainstem harvest restrictions, occur when the fish are aggregated.

Managers must decide whether to make improvements to life history stages when the fish are aggregated, separated, or a combination of both. For instance, should downstream passage survival be increased 2% for the entire metapopulation, or should habitat improvements increase survival by 5% for an individual priority patch? This type of question is best answered by a spatially structured PVA which could compare the expected results of various management actions in terms of increases in viability.

In terms of effectiveness and cost, the proper combination of actions would likely improve survival at key stages when fish are aggregated, as well as, at key stages when fish are separated into patches.

Rather than focusing improvements on non-priority patches this study recommends halting their further degradation, while focusing improvements on the priority patches (Chapter 3).

The Role of Management Intervention. A strategy aimed at maximizing population growth while maintaining buffering capabilities advocates a strong role for management intervention. In the case of Snake River spring/summer chinook, management intervention could include transplanting unsuccessfully dispersing fish to priority patches, transplanting fish from less productive patches to vacant or underutilized priority patches, and transplanting fish to facilitate dispersal between

priority patches (Chapter 4, Foose et al. 1995). In the first two cases, the strategy attempts to increase the expected reproductive potential of the individual, while in the third case, the strategy attempts to fill the important role dispersal plays in a metapopulation.

The simulation study concludes wild, depleted metapopulations will increasingly require more intensive levels of management (Foose et al. 1995). This implies that managers who accept a more active role in managing their metapopulations will likely increase their overall population size more quickly and therefore reduce the probability of extinction more quickly than managers who refuse to intervene (Chapter 3).

Although successful cases of transplanting salmon do exist (Fedorenko and Shepherd 1986), management intervention to transplant and crossbreed Snake River spring/summer chinook may or may not prove successful. A number of alternative management strategies exist. In the most obvious case, managers could attempt to transplant returning adults between patches. As an alternative, managers may remove returning adults, spawn them in a hatchery, and outplant the eggs or young to a new patch. This method is one type of supplementation (Cuenco et al. 1993). When done correctly, supplementation can aid in natural stock restoration by providing a less variable and more protective environment at early life history stages, resulting in increases in survival rates (Cuenco et al. 1993). Supplementation has been shown to be successful in a number of cases (Miller 1990).

One potential hurdle to transplantation is a consequence of salmon population declines. Returning salmon provide a substantial amount of the nutrients to stream biota (Bilby et al. 1996). Without historic numbers of returning salmon contributing nutrients, the quality of the patch will likely decline. Transplanting fish into what was a high quality patch when previously occupied, may submit the new transplants to a much lower quality patch than expected.

Using adaptive management (Holling 1978, Walters 1986), managers of Snake River spring/summer chinook can potentially test the methods and role for intervention.

The Debate Over Salmon Metapopulations

Although the term metapopulation is frequently used to describe Snake River spring/summer chinook (SRSRT 1994, Mundy et al. 1995, NMFS 1995, NRC 1996), a debate exists over the role of dispersal within the metapopulation. As reviewed in Chapter 1, the conservation biology literature states that dispersal is a critical component for a metapopulation, enabling patches to buffer each other against regional extinction (Levin 1976, Caswell 1978, Brown and Kodric-Brown 1977, Shaffer 1981, 1985, Gilpin 1987).

In 1992, Congress requested advice from the National Research Council (NRC) on the effectiveness of proposed actions to slow, halt, or reverse the Northwest salmon declines with due economic weight taken into account (NRC 1996). In response, the NRC's Board on Environmental Studies and Toxicology assembled the expert Committee on Protection and Management of Pacific Northwest Anadromous

Salmonids (NRC 1996). The resulting book discusses both sides of the dispersal debate. Describing one of the viewpoints, the NRC (1996) writes:

“The individual local breeding populations within a drainage basin or other geographical area are usually connected in a higher level of organization by exchange of animals through “straying”. ... New populations are expected to be established from strays from other local breeding populations within the metapopulation. ... Local breeding populations of salmon are small enough and exist in such variable environments that they are likely to have relatively short persistence times.”

In this case, the role of dispersal in salmon is consistent with the role of dispersal in a metapopulation according to the conservation biology literature (Levin 1976, Caswell 1978, Brown and Kodric-Brown 1977, Shaffer 1981, 1985, Gilpin 1987).

In describing the alternative view, the NRC (1996) writes:

“The homing of salmon to their natal streams produces a branching system of local reproductive populations that are largely demographically and genetically isolated. ... The homing behavior of anadromous salmon results in a complex pattern of genetic differentiation among local populations because individual fish that home to different streams cannot breed with each other. ... In other words, evolution has made a local breeding population better able to survive and reproduce in its home stream than in other streams.”

In this view dispersal may have a role over a longer evolutionary time frame, but the development and maintenance of local adaptation is more important in the short term.

Proponents of the first view believe dispersal should not drop below a minimum level needed to maintain metapopulation viability. Augmenting dispersal over current levels is viewed as beneficial because it restores metapopulation viability.

Proponents of the second view believe dispersal should not increase above a maximum level in order to prevent the loss of local adaptation and genetic differentiation between populations. Augmenting dispersal over current levels is viewed as detrimental because it decreases genetic differentiation between populations.

Individuals supporting the "dispersal hurts local adaptation" view point out that not all dispersing salmon successfully reproduce (Tallman and Healey 1994). Individuals supporting the "dispersal helps the metapopulation" view point out that some dispersing salmon clearly do successfully reproduce (Tallman and Healey 1994).

Although the two views of dispersal are not mutually exclusive, the debate has become extremely polarized. It is beyond the scope of this paper to discuss all of the genetic, demographic, and political aspects of this debate. However its outcome will determine what recovery strategy is ultimately adopted.

Opponents of augmenting dispersal are likely to object to nearly all strategies which include transplanting fish between patches, arguing that the risk to a patch's genetics by introducing fish from another patch is too great and would result in a decrease in genetic fitness.

In order to resolve the debate, data on gene flow between patches would ideally be available. Due to the small numbers of spring/summer chinook remaining, adequate sample sizes for genetic or dispersal studies are difficult, if not impossible, to achieve. Results of genetic studies could possibly estimate genetic differences between

populations, but would not answer whether the genetic differences have any adaptive significance that would prohibit the mixing of stocks.

Adaptive Management

The most promising approach to settle this debate is offered through adaptive management (Holling 1978, Walters 1986). Using adaptive management, a small number of patches can be used as experimental units while others are used as controls (Walters 1986, Berkson 1988) to test the ability of Snake River spring/summer chinook to transplant and crossbreed between patches.

In one study, adults from the Rapid River spring chinook stock spawned in Lookingglass Creek, a tributary of the Grande Ronde watershed of the Snake River Basin (Lofy and McLean 1995). The Rapid River stock originated above the Hells Canyon Hydropower Complex, from a drainage adjacent to the upper Grande Ronde watershed (Lofy and McLean 1995). Based on results from PIT tag studies, comparing a number of endemic stocks in other tributaries to Rapid River transplants in Lookingglass Creek, the juveniles from Lookingglass Creek had survival rates among the highest observed (Lofy and McLean 1995, Walters et al. 1995). While this result looks promising, still more experiments are needed.

If transplantation efforts prove unsuccessful or the offspring of experimental crossbreeding between patches have lower survival rates, it would suggest that the transplanted fish were not adapted to their new patches. In this case, many of the elements of the strategy presented in this study would be reduced or removed. If

transplantation and crossbreeding should prove to be successful, then the strategy presented in this paper could be more fully implemented.

Without experimentation of this type, the debate over the role of dispersal will continue, as will the debate over the effectiveness of alternative recovery strategies.

Unfortunately, this debate may out survive the Snake River spring/summer chinook.

LITERATURE CITED

- Allee, W.C. 1949. Principles of Animal Ecology. Saunders. London.
- Andrewartha, H.G. and L.C. Birch. 1954. The Distribution and Abundance of Animals. Univ. of Chicago Press. Chicago.
- Ashworth, T. 1868. The Salmon Fisheries of England. Longmans, Green and Co. London.
- Ballou, J.D., M.E. Gilpin, and T.J. Foose [eds.] 1995. Population Management for Survival and Recovery. Columbia University Press. New York. 375 pgs.
- Berkson, J.M. 1988. Opportunities for Management Created by Spatial Structure: A Case Study of Finnish Reindeer. Masters Thesis. University of British Columbia. Vancouver, B.C. 126 pgs.
- Bilby, R.E., B.R. Fransen, and P.A. Bisson. 1996. Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of small streams: evidence from stable isotopes. *Can. J. Fish. Aquat. Sci.* 53:164-173.
- Boyce, M.S. 1992. Population viability analysis. *Ann. Rev. Ecol. Syst.* 23:481-506.
- Brown, J.H. and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: Effect of immigration on extinction. *Ecology* 58:445-449.
- Burgoyne, G.E. 1981. Observations on a heavily exploited deer population. Pgs. 403-413 in C.W. Fowler and T.D. Smith [eds.]. *Dynamics of Large Mammal Populations*. Wiley. New York.
- Burner, C.J. 1951. Characteristics of spawning nests of Columbia River salmon. *USFWS Fishery Bulletin* 61.
- CBFWA. (Columbia Basin Fish and Wildlife Authority). 1990. Proposed mainstem flows for Columbia basin anadromous fish. March 1990. Portland, OR
- Caswell, H. 1978. Predator mediated coexistence: a nonequilibrium model. *Amer. Nat.* 112:127-154.

- Chakraborty, R. and O. Leimar. 1987. Genetic variation within a subdivided population. Pgs. 89-120 in N. Ryman and F. Utter [eds.] *Population Genetics and Fishery Management*. University of Washington Press. Seattle.
- Chapman, P.F. 1986. Occurrence of the noninfective stage of *Ceratomyxa shasta* in mature summer chinook in the South Fork Salmon River, Idaho. *The Progressive Fish-Culturist*. 48:304-306.
- Conway, W. 1995. Foreword: Altered states: Population viability analysis, planning and caring for wildlife in parks. Pgs. xiii - xix in J.D. Ballou, M. Gilpin, and T.J. Foose [eds.] *Population Management for Survival and Recovery*. Columbia University Press. New York.
- Cuenco, M.L., T.W.H. Backman, and P.R. Mundy. 1993. The use of supplementation to aid in natural stock restoration. Pgs. 269-293 in J.G. Cloud and G.H. Thorgaard [eds.] *Genetic Conservation of Salmonid Fishes*. Plenum Press. New York.
- den Boer, P.J. 1968. Spreading of risk and stabilization of animal numbers. *Acta Biotheor.* 18:165-194.
- Deriso, R.B. 1980. Harvesting strategies and parameter estimation for an age-structured model. *Can. J. Fish. Aquat. Sci.* 37:268-282.
- Doak, D.F. 1995. Source-sink models and the problem of habitat degradation: General models and applications to the Yellowstone Grizzly. *Cons. Biol.* 9:1370-1379.
- Doak, D., P. Kareiva, and B. Klepetka. 1994. Modeling population viability for the desert tortoise in the Western Mojave desert. *Ecol. Appl.* 4:446-460.
- Donovan, T.R., R.H. Lamberson, A. Kimber, F.R. Thompson III, and J. Faaborg. 1995. Modeling the effects of habitat fragmentation on source and sink demography of neotropical migrant birds. *Cons. Biol.* 9:1396-1407.
- ESA. (Ecological Society of America). 1996. Strengthening the use of science in achieving the goals of the Endangered Species Act: An assessment by the Ecological Society of America. Ecological Society of America Ad Hoc Committee on Endangered Species. *Ecol. Appl.* 6(1):1-11.
- Evermann, B.W. 1896. A report upon salmon investigations in the headwaters of the Columbia River in the state of Idaho in 1895. *Bulletin of the U.S. Fish Commission.* 16:151-202.

- Ewens, W.J., P.J. Brockwell, J.M. Gani, and S.I. Resnick. 1987. Minimum viable population size in the presence of catastrophes. Pgs. 59-68 in M.E. Soulé [ed.] *Viable Populations for Conservation*. Cambridge University Press, Cambridge.
- Falconer, D.S. 1981. *Introduction to Quantitative Genetics*. Longman Scientific and Technical. New York. 340 pgs.
- Federenko, A.Y. and B.G. Shepherd. 1986. Review of salmon transplant procedures and suggested transplant guidelines. *Can. Tech. Rep. Fish. Aquat. Sci. No.* 1479. 144 pgs.
- Foose, T.J. 1989. Globalization of species survival programs: The world as a megazoo. Pgs 383-392 in B.L. Dresser, R.W. Reece, and E.J. Maruska [eds.] *Proceedings: 5th World Conference on Breeding Endangered Species in Captivity*. Cincinnati Zoo and Botanical Garden, Center for Reproduction of Endangered Wildlife. Cincinnati, Ohio.
- Foose, T.J., L. de Boer, U.S. Seal, and R. Lande. 1995. Conservation management strategies based on viable populations. Pgs. 273-294 in J.D. Ballou, M. Gilpin, and T.J. Foose [eds.] *Population Management for Survival and Recovery*. Columbia University Press. New York.
- Fulton, L. 1968. Spawning areas and abundance of chinook salmon *Onchorhynchus tshawytscha* in the Columbia River - past and present. USFWS, Special Scientific Report - Fisheries No. 571.
- Futuyma, D.J. 1986. *Evolutionary Biology*. Sinauer Associates, Inc. Sunderland, MA. 600 pgs.
- Gharet, A.J., C. Smoot, A.J. McGregor, and P.B. Holmes. 1988. Genetic relationships of even-year northwestern Alaskan pink salmon. *Trans. Am. Fish. Soc.* 117(6):536-545.
- Gilbert, C.H. 1913. Age at maturity of the Pacific coast salmon of the genus *Onchorynchus*. *Bull. of Bur. of Fish. (US)* 32:1-22.
- Gilpin, M.E. 1987. Spatial structure and population vulnerability. Pgs. 125-139 in M.E. Soulé [ed.] *Viable Populations for Conservation*. Cambridge University Press. Cambridge.
- Gilpin, M.E. 1991. The genetic effective size of a metapopulation. In: M.E. Gilpin and I. Hanski. [eds]. *Metapopulation Dynamics*. Academic Press. New York.

- Gilpin, M.E. and I. Hanski. 1991. *Metapopulation Dynamics*. Academic Press. New York.
- Gilpin, M.E. and M.E. Soulé. 1986. Minimum viable populations: Processes of species extinction. Pgs. 19-34 in M.E. Soulé [ed.] *Conservation Biology: The Science of Scarcity and Diversity*. Sinauer. Sunderland, Mass.
- Goodman, D. 1981. Life history analysis of large mammals. In C.W. Fowler and T.D. Smith [eds.]. *Dynamics of Large Mammal Populations*. Wiley. New York.
- Goodman, D. 1987a. Considerations of stochastic demography in the design and management of biological reserves. *Natural Resource Modeling* 1:205-234.
- Goodman, D. 1987b. The demography of chance extinction. pgs. 11-34 in M.E. Soulé [ed.] *Viable Populations for Conservation*. Cambridge University Press. Cambridge.
- Hanski, I. and M.E. Gilpin. 1991. Metapopulation dynamics: brief history and conceptual domain. Pgs 3-16 in M.E. Gilpin and I. Hanski [eds.] *Metapopulation Dynamics*. Academic Press. New York.
- Healey, M.C. 1991. Life history of Chinook salmon. Pgs. 311-393 in C. Groot and L. Margolis [eds.] *Pacific Salmon Life Histories*. UBC Press. Vancouver, BC.
- Holling, C.S. [ed.] 1978. *Adaptive Environmental Assessment and Management*. Wiley. Chichester, New York. 377 pgs.
- Kimura, M. 1953. "Stepping stone" model of population. *Annual Report of the National Institute of Genetics. Japan.* 3:62-63
- Kimura, M. and G.H. Weiss. 1964. The stepping stone model of population structure and the decrease of genetic correlation with distance. *Genetics* 49:561-576.
- Kwain, W.H. and A.M. Lawrie. 1981. Pink salmon in the Great Lakes. *Fisheries* 6(2):2-6.
- Lamberson, R.H., R. McKelvey, B.S. Noon, and C. Voss. 1992. A dynamic analysis of Northern Spotted Owl viability in a fragmented forest landscape. *Cons. Biol.* 6:505-512.
- Lande, R. and G.F. Barrowclough. 1987. Effective population size, genetic variation, and their use in population management. Pgs. 87-123 in M.E. Soulé [ed.] *Viable Populations for Conservation*. Cambridge University Press. Cambridge.

- Larkin, P.A. 1981. A perspective on population genetics and salmon management. *Can J. Fish. Aquat. Sci.* 38:1469-1475.
- Lee, D.C. and J.B. Hyman. 1992. The stochastic life cycle model (SLCM): simulating the population dynamics of anadromous salmonids. Research Paper INT-459. Ogden, UT: USDA Forest Service, Intermountain Research Station, 30 pgs.
- Leider, S.A. 1989. Increased straying by adult steelhead trout, *Salmo gairdneri*, following the 1980 eruption of Mount St. Helens. *Environmental Biology of Fishes* 24:219-229.
- Levin, S.A. 1976. Population dynamics in heterogeneous environments. *Ann. Rev. Ecol. Syst.* 7:287-310.
- Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull. Entomol. Soc. Am.* 15:237-240.
- Levins, R. 1970. Extinction. Pgs. 77-107 in M. Gerstenhaber [ed.] *Some Mathematical Problems in Biology*. American Mathematical Society, Providence, R.I.
- Lofy, P.T. and M.L. McLean. 1995. Evaluation of reestablishing natural production of spring chinook salmon in Lookingglass Creek, Oregon, using a non-endemic hatchery stock. CTUIR Project No. 63, Contract No. 14-48-0001-94517. Dept. of Natural Resources, Fisheries Program, Confederated Tribes of the Umatilla Indian Reservation. Pendleton, OR.
- Ludwig D., D. Jones, and C.S. Holling. 1978. Qualitative analysis of insect outbreak systems: The spruce budworm and the forest. *J. Animal Ecology.* 47:315-332.
- MacArthur, R.H. 1972. *Geographical Ecology*. Harper and Row. New York.
- MacArthur, R.H. and E.O. Wilson. 1963. An equilibrium theory of insular zoogeography. *Evolution.* 17:373-387.
- MacArthur, R.H. and E.O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton Univ. Press. Princeton.
- Malecot, G. 1948. *Les Mathematiques de l'Heredité*. Masson, Paris.
- Mathews, G.M. and R.S. Waples. 1991. Status review for Snake River spring and summer chinook salmon. NOAA/NMFS F/NWC-200.

- Menges, E. 1990. Population viability analysis for an endangered plant. *Cons. Biol.* 4:52-62.
- Miller, W.H. 1990. Analysis of salmon and steelhead supplementation. Report for Contract No. DE-A179-88BP92663, Project Number 88-100. Bonneville Power Administration. Division of Fish and Wildlife. Portland, OR.
- Milner, A.M. and R.G. Bailey. 1989. Salmonid colonization of new streams in Glacier Bay National Park, Alaska. *Aquaculture and Fisheries Management* 20:179-192.
- Milner, N.J., R.J. Wyatt, and M.D. Scott. 1993. Variability in the distribution and abundance of stream salmonids, and the associated use of habitat models. *J. Fish Biol. (Supplement 43 A)*:103-119.
- Mundy, P.R., T.W.H. Backman, and J.M. Berkson. 1995. Selection of conservation units for Pacific salmon: Lessons from the Columbia River. *Amer. Fish. Soc. Sym.* 17:28-38.
- Murphy, D.D., K. E. Freas, and S.B. Weiss. 1990. An environmental-metapopulation approach to population viability analysis for a threatened invertebrate. *Cons. Biol.* 4:41-51.
- NMFS. (National Marine Fisheries Service). 1995. Proposed Recovery Plan for Snake River Salmon. U.S. Department of Commerce.
- NPPC. (Northwest Power Planning Council). 1993. Columbia River Basin Fish and Wildlife Program. NPPC 93-6. Portland, OR.
- NRC. (National Research Council). 1996. *Upstream: Salmon and Society in the Pacific Northwest*. National Academy Press. 452 pgs.
- Nelson, K. and M. Soulé. 1987. Genetical conservation of exploited fishes. Pgs 345-368 in N. Ryman and F. Utter [eds.] *Population Genetics and Fishery Management*. Univ. of Wash. Press. Seattle.
- Pagano, R.P. 1986. *Understanding Statistics in the Behavioral Sciences*. West Publishing Co. St. Paul. 486 pgs.
- Pascual, M.A. and T.P. Quinn. 1994. Geographical patterns of straying of fall chinook salmon, *Oncorhynchus tshawytscha*, (Walbaum), from Columbia River (USA) hatcheries. *Aquaculture and Fisheries Management*. 25, Supplement 2, 17-30.

- Patrick, R. 1967. The effect of invasion rate, species pool, and size of area on the structure of the diatom community. *Proc. Natl. Acad. Sci.* 58:1335-1342.
- Pearl, R. and L.J. Reid. 1920. On the rate of growth of the population of the United States since 1790 and its mathematical representation. *Proc. of the Natl. Acad. of Sci.* VI:275-288.
- Pulliam, H.R. 1988. Sources, sinks, and population regulation. *American Naturalist.* 132:652-661.
- Quinn, T.P. 1984. Homing and straying in Pacific salmon. Pgs. 357-362 in J.D. McCleave, G.P. Arnold, J.J. Dodson and W.H. Neill [eds.] *Mechanisms of Migration in Fishes.* Plenum Press. New York.
- Quinn, T.P. 1985. Homing and the evolution of sockeye salmon (*Oncorhynchus nerka*) Pgs. 353-366 in M.A.R. Rankin [ed.] *Migration: Mechanisms and Adaptive Significance.* .
- Quinn, T.P., R.S. Nemeth, and D.O. McIsaac. 1991. Homing and straying patterns of fall chinook salmon in the lower Columbia River. *Trans. Am. Fish. Soc.* 120:150-156.
- Quinn, T.P. and M.J. Unwin. 1993. Variation in life history patterns among New Zealand chinook salmon (*Oncorhynchus tshawytscha*) populations. *Can. J. Fish. Aquat. Sci.* 50:1414-1421.
- Rich, W.H. and H.B. Holmes. 1928. Experiments in marking young chinook salmon on the Columbia River 1916 to 1927. *Bull. Bur. Fish. (U.S.)* 44:215-264.
- Ricker, W.E. 1954. Stock and recruitment. *J. Fish. Res. Board Can.* 11:559-623.
- Ricker, W.E. 1958. Handbook of computations for biological statistics of fish populations. *Bull. Fish. Res. Board Can.* 119:300 pgs.
- Rieman, B.E. and J.D. McIntyre. 1995. Occurrence of Bull trout in naturally fragmented habitat patches of varied size. *Trans. Amer. Fish. Soc.* 124:285-296.
- Rieman, B.E. and J.D. McIntyre. 1996. Spatial and temporal variability in Bull trout redd counts. *N. Amer. J. Fish. Mgmt.* 16:132-141.

- SRSRT. (Snake River Salmon Recovery Team) 1994. Snake River Salmon Recovery Team: Final Recommendations to the National Marine Fisheries Service. May 1994.
- Schaller, H., C. Petrosky, E. Weber, and T. Cooney. 1992. Draft Documentation: Snake River spring/summer chinook life cycle simulation model for recovery and rebuilding plan evaluation. Oregon Dept. of Fish and Wildlife. Portland, OR.
- Shaffer, M.L. 1981. Minimum viable population sizes for conservation. *Bioscience* 31:131-134.
- Shaffer, M.L. 1985. The metapopulation and species conservation: the special case of the northern spotted owl. Pgs. 86-95 in R.J. Gutierrez and A.B. Carey [eds.] Ecology and management of the spotted owl in the Pacific northwest. General Technical Report. USDA Forest Service. Pacific Northwest Forest and Range Equipment Station. Portland, OR.
- Shaffer, M.L. 1987. Minimum viable populations: coping with uncertainty. Pgs 69-86 in M.E. Soulé [ed.] *Viable Populations for Conservation*. Cambridge University Press. Cambridge.
- Shaffer, M.L. 1990. Population viability analysis. *Cons. Biol.* 4:39-40.
- Simberloff, D.S. 1969. Experimental zoogeography of islands: A model for insular colonization. *Ecology* 50:296-314.
- Simberloff, D.S. and E.O. Wilson. 1969. Experimental zoogeography of islands: The colonization of empty islands. *Ecology* 50:278-296.
- Soulé, M.E. 1980. Thresholds for survival: maintaining fitness and evolutionary potential. Pgs 151-169 in M.E. Soulé and B.A. Wilcox [eds.] *Conservation Biology. An Evolutionary - Ecological Perspective*. Sinauer Associates, Inc. Sunderland, MA.
- Soulé, M.E. [ed.] 1986. *Conservation Biology: Science of Scarcity and Diversity*. Sinauer Associates. Sunderland, MA.
- Soulé, M.E. [ed.] 1987a. *Viable Populations for Conservation*. Cambridge University Press. Cambridge. 189 pgs.
- Soulé, M.E. 1987b. Introduction. Pgs 1-10 in M.E. Soulé [ed.] *Viable Populations for Conservation*. Cambridge University Press. Cambridge.

- Soulé, M.E. and K. A. Kohm [eds.] 1989. *Research Priorities for Conservation Biology*. Island Press. Washington, D.C. 98 pgs.
- Soulé, M.E. and D. Simberloff. 1986. What do genetics and ecology tell us about the design of nature preserves? *Biol. Cons.* 35:19-40.
- Soulé, M.E. and B.A. Wilcox [eds.] 1980a. *Conservation Biology. An Evolutionary - Ecological Perspective*. Sinauer Associates, Inc. Sunderland, MA. 395 pgs.
- Soulé, M.E. and B.A. Wilcox. 1980b. *Conservation Biology: Its scope and its challenge*. Pgs. 1-8 in M.E. Soulé and B.A. Wilcox [eds.], *Conservation Biology. An Evolutionary - Ecological Perspective*. Sinauer Associates, Inc. Sunderland, MA.
- Stacey, P.B. and M. Taper. 1992. Environmental variation and the persistence of small populations. *Ecol. Appl.* 2:18-29.
- Tallman, R.F. and M.C. Healey. 1994. Homing, straying and gene flow among seasonally separated populations of chum salmon (*Onchorhynchus keta*). *Can. J. Fish. Aquat. Sci.* 51:577-588
- Utter, F.M. 1991. Biochemical genetics and fishery management: an historical perspective. *Journal of Fish Biology* 39(suppl A.). Pgs. 1-10.
- Van Hying, J. 1968. Factors affecting the abundance of fall chinook in the Columbia River. Oregon State University. Research Reports of the Fish Commission of Oregon. Vol. 4(1). 87 pgs.
- Verhulst, P.F. 1838. Notice sur la loi que la population suit dans son accroissement. Correspondance mathematique et physique publiee par A. Quetelet (Brussels). X:113-121.
- Walters, C.J. 1986. *Adaptive Management of Renewable Resources*. Macmillan. New York. 374 pgs.
- Walters C.J., J.S. Collie, and T. Webb. 1988. Experimental designs for estimating transient responses to management disturbances. *Can J. Fish. Aquat. Sci.* 45:530-538.
- Walters, T.R., E.W. Carmichael, and M.L. Keefe. 1995. Annual Progress Report. Smolt migration characteristics and mainstem Snake and Columbia Rivers detection rates of PIT-tagged Grande Ronde and Imnaha River naturally

produced spring chinook salmon. Project Number 94-36. OR. Dept. of Fish and Wildlife. Portland, OR.

Withler, F.C. 1982. Transplanting Pacific salmon. Can. Tech. Rep. Fish. Aquat. Sci. 1079. 27 pgs.

Wright, S. 1943. Isolation by distance. *Genetics*. 28:114-138.

Wright, S. 1951. The genetical structure of populations. *Annals of Eugentics* (London). 15:323-354.

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