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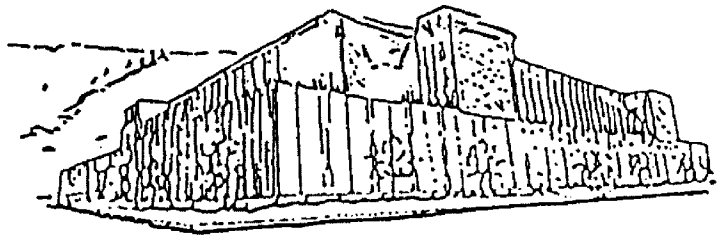
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THE LONG-TERM EFFECTS OF HABITAT CLUSTERING ON
SPOTTED OWL POPULATIONS

by

Matthew R. Seeley

B.A. Cornell University: Ithaca, NY 1993

presented in partial fulfillment of the requirements

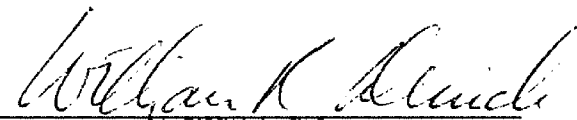
for the degree of

Master of Arts

The University of Montana

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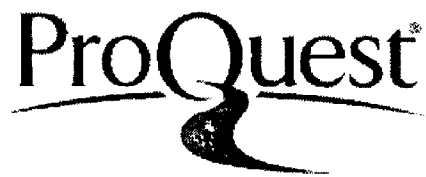


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The Long-Term Effects of Habitat Clustering on Spotted Owl Populations (64 pp.)

Thesis Advisor: Bill Derrick *WLD*

We wish to explore the relationship between the northern spotted owl and its preferred old-growth forest habitat through a series of computer simulations. The persistence of the species depends heavily on the success of juvenile owls searching for new homesites in a fragmented landscape. The investigation emphasizes the relationship between long-term owl population levels and the clustering of the suitable old-growth owl homesites in the forest. We perform repeated 100-year simulation trials, varying the size and spacing of habitable sites.

The resulting population curves show a significant increase when habitable clusters are spaced randomly as opposed to uniformly, suggesting a dispersal advantage due to additional large-scale clustering for the random arrangement. For each habitat pattern, we measure the total deviation for a large sample of local habitat densities. This technique provides a metric with which we can quantify the overall clustering of a given forest arrangement. We compare the deviation metric to other predictors of long-term spotted owl population levels in the context of our model and the simulation results.

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CHAPTER 1

Introduction

1.1 Statement of the Problem

In the last two decades, the problem of maintaining species diversity in the face of rapid harvesting of old-growth forests has come to the forefront of wildlife conservation concerns and caused considerable controversy. On one side, the timber companies would like to continue cutting these valuable trees to maintain local economies and provide high-paying forestry jobs. They promise to replant the cleared lands and create a maintainable cycle of tree growing and harvesting so that the resource is continually renewed. At first, this seems like a reasonable strategy, but it has become apparent that certain species of wildlife require the presence of old-growth trees for their survival. If timber harvesting is allowed to continue unchecked, very few old trees will remain and a variety of wildlife species would likely fade to extinction. A solution to this problem requires that those involved decide and agree upon exactly how much old-growth forest should be left untouched as well as determine the optimal distribution of this valuable habitat. These considerations depend on both a qualitative and quantitative understanding of the threatened species and their dependence on habitat and its distribution. Without this, the process of compromise and negotiation is far more difficult and less productive.

The battle lines have been drawn especially deep in the evergreen forests of the Pacific Northwest and at the center of the controversy lies a small bird. Claimed to

exhibit disastrous sensitivity to loss of old-growth habitat, the northern spotted owl (*Strix occidentalis caurina*) has become the poster species for the growing movement for harvesting reform. It is also one of the United States Forest Service Pacific Northwest Region *management indicator species* (Doak (1989)). For these reasons, the results of studies into the habitat dependence and predicted fate of the spotted owl could play a crucial role in the future of the timber industry.

Experts generally accept the fact that the northern spotted owl prefers the dense canopy and sparse undergrowth of the old-growth forests (100 - 200 years and older). In addition, field data seem to support the claim that the owl population is declining significantly (Forsman (1984), Marcot and Holthausen (1987)). The difficulty comes in accurately quantifying this decline and its dependence on logging practices. This is especially true because the northern spotted owl's scarcity and behavioral secrecy present nearly insurmountable obstacles to attempts at precise observation. However, the current levels of understanding of demographic and behavioral characteristics of the species provide enough of a basis to begin the modelling process necessary to predict future population and design management strategies. We can then update already existing models as more accurate field data become available.

1.2 Previous Investigations

Biologists, ecologists, and mathematicians have created a variety of models to investigate the spotted owl dilemma and predict future population levels. The process began with field studies which attempted to observe and understand the owl's behavioral characteristics and population levels. Forsman (1985) observed and described the

attributes of the species in Oregon and suggested potential management strategies. Others used the available data to quantify behavioral characteristics, demographic parameters, and dependence on old-growth habitat. Owl pairs were shown to be virtually absent in forests of trees younger than 80 years with only a few single adults temporarily residing in very young stands, but the claim that spotted owls can survive only in old-growth forest remains controversial (Bart (1992)). Marcot and Holthausen (1987) summarized radio telemetry data and were able to estimate the rates of fecundity, mortality, adult survival and dispersal success. Other data lead to significantly different values (Lande (1988), Lamberson et. al. (1994)). These authors seemed to agree, however, that the limited number of studies and difficulty in observing spotted owls prevented them achieving any real reliable precision in their parameter values.

Using the somewhat incomplete behavioral knowledge, scientists have endeavored to create models to replicate trends in spotted owl populations and predict future values. Some of these models were strictly probabilistic in nature and incorporated a number of specific characteristics of spotted owl populations. They emphasized the demographic considerations for spotted owl persistence. R. Lande (1987 and 1988) used statistical models to predict the effects of habitat depletion on owl numbers. He used much of the available data to compute extinction thresholds in terms of percentage of suitable habitat. A discussion of edge effects, Allee effects, and stochastic variation in parameters was included. In 1994, Lamberson, McKelvey, and Noon performed a similar analysis, but took a more dynamic approach by incorporating juvenile dispersal and the search for mates. They devised equations to approximate these behavioral movements of

the spotted owls numerically and computed dispersal success probability as a function of the number of sites each juvenile could search before death. This model was only partially spatial as they incorporated owl movements into their probabilities, but did not actually track individual juveniles through a specific habitat grid. The simulations consisted of 250-year trials whose results gave further evidence for the existence of threshold old-growth levels required for spotted owl persistence. Carroll et. al. (1995) generalized the idea of a threshold density by treating the owl habitat as a source-sink model, where the entire region was divided into high quality (sources) and low quality (sinks) habitat. This formulation allowed them to generalize the results of earlier simulations in terms of analytic propositions and theorems. They divided the owl life stages into discrete birth and continuous dispersal and mortality and considered two types of owls: resident (settled) and non-resident (searching). An investigation of the stability of their systems trivial fixed point led them to another version of the minimum habitat density requirement.

To focus on the relationship between owls and their diminishing habitat, other researchers devised models which included simulated forest grids and tracked the locations of each owl. In particular, they were interested in the effects of clustered patches of suitable owl sites as opposed to randomly distributed old-growth habitat. Doak (1989) performed 100 year simulations in a forest of clustered habitat. They were partially spatial in that they recorded the number of owls in each cluster at each time step, but not the exact site location and movements of each individual owl. He assumed that juvenile owls would disperse more successfully inside a cluster than between clusters.

Using a random walk dispersal process with an exponentially decreasing success function, Lamberson et. al. (1994) showed that larger cluster sizes would support considerably higher owl populations. Their model did not, however, explore variations in the spatial arrangement of the clusters themselves. In a somewhat different context, Pulliam et. al. (1991) formulated a model to study the habitat dependence of Bachman's sparrow in southeastern pine forests. They created a hexagonal grid of potential sites and then assigned each a numerical level of suitability according to characteristics of specific forests. Pulliam's simulations began with an assignment of individual birds to sites and then followed each individual bird throughout its lifetime. The sparrows dispersed in straight lines until they either found suitable habitat or died trying. Holthausen et. al. (1995) used a similar, completely spatial approach to conduct one of the most comprehensive spotted owl simulations to date. They fit a hexagonal grid to the forests of the Olympic Peninsula in Washington State and assigned habitat suitability and adult owl pairs according to field study data. In 200-year simulations, both male and female owls were tracked and sites were rated in terms of the frequency with which they supported owl pairs. They were also able to recreate the effects of the preservation or harvesting of specific old-growth regions.

1.3 Another Approach

In 1993, Carroll and Lamberson suggested the idea of using a system of *metered equations* to model the population of northern spotted owls in a diminishing habitat. Their equations were metered in the sense that they combined a system of ordinary differential equations to describe the continuous dispersal of young (*juvenile*) owls

searching for new homesites throughout the season, with a discrete difference equation to describe the annual birth of new juveniles and death of adult owls. The authors considered only female owls, ignoring the mate-search process, and assumed that all habitat was equally accessible. The forest was divided into sites, a certain fraction of which were considered suitable habitat for the owls.

The authors described the forest-owl system in terms of the following parameters and variables.

h = fraction of sites which are habitable

p = constant mortality rate for dispersing juveniles

where $N(t)$ = fraction of adult females per site at time t

$J(t)$ = fraction of juvenile females per site at time t

$T(t) = N(t) + J(t)$ = total fraction of spotted owls per site at time t

Time was scaled so that one unit would represent the length of time it takes one juvenile owl to search one site. Carroll and Lamberson then modelled the dispersal process with the following pair of differential equations:

$$\frac{dN}{dt} = J(h - N), \quad (1.1a)$$

$$\frac{dT}{dt} = -pJ. \quad (1.1b)$$

Notice that the first equation in system 1.1 states that the rate of increase of the spotted owl population is equal to the product of the fractional juvenile population and the fraction of sites which are suitable but uninhabited, $h - N$. This formulation represents a mass action process where the rate of successful dispersals is dependent on the probability that a searching juvenile comes into contact with a vacant habitable site. The first equation has been rescaled to eliminate any constant of proportionality. The authors

do not provide either the original set of equations or the details of the non-dimensionalization process. We assume that the characteristic times can still be represented as the time it takes one owl to search one site.

According to their model, the existing adult owls would give birth to a certain number of juveniles, J_0 , each year. These newborn owls would then flow continuously into any sites which were both suitable and uninhabited, or die in the dispersal process. During the dispersal process, the total owl population would only decrease through juvenile death according to 1.1b, and the adult owl population would only increase by successfully dispersing juveniles according to 1.1a. In other words, the differential equations do not include any adult mortality or reproduction. In the paper, Carroll and Lamberson established that given the length of an entire season, the juveniles would all either successfully disperse or die, so that the adult population would essentially achieve a final value determined by the initial conditions and parameters of the system. This post-dispersal adult population, N_∞ , was shown to satisfy the implicit equation

$$p \left(\ln \left(\frac{h - N_\infty}{h - N_0} \right) \right) = N_\infty - T_0 \quad (1.2)$$

where N_0 and T_0 are the adult and total population fractions at the beginning of the season, respectively. Equation 1.2 could then be solved for N_∞ using Newton's method.

Having analyzed the continuous dispersal equation, the authors added the annual discrete processes of death and rebirth with a system of difference equations to give starting populations for the next generation or season. These equations had the form

$$N_0^{k+1} = sN_\infty^k \quad (1.3a)$$

$$J_0^{k+1} = bN_0^{k+1} \quad (1.3b)$$

where s is the annual adult survival rate and b is the birth rate for the surviving population of adult owls. The superscripts in system 1.3 have been added to between fractional owl populations for the new season, $k + 1$, and those of previous year, k . Thus we have new initial N and J values for the next iteration of the continuous dispersal process.

Next, it was verified that the combined system would have a non-zero stable equilibrium if the proportion of habitable sites was above a certain threshold value,

$$h > \frac{p(1-s)}{s(1+b)-1} = h^* . \quad (1.4)$$

However, since the dispersal phase of each generation cannot be formulated explicitly for a given set of parameters, the combined system of equations 1.1 and 1.3 is difficult to simulate. The implicit, non-linear equation for N_∞ , 1.2, requires repeated application of Newton's method. This turns out to be an unnecessary complication.

In an effort to simplify the Carroll and Lamberson model into something which could be used to generate 100 year owl population simulations and test the validity of their findings, we made the following adjustments. First, we examine the dispersal equation 1.2 more closely. As we will discuss later, field studies and surveys estimate population and habitat values at $h \cong 0.38$ and $N_0 \cong 0.17$, respectively. In addition, a dispersing juvenile mortality rate of $p \cong 0.95$ is necessary so that the fraction of dispersing juveniles who are successful agrees with the experimental value of 18%

(Marcot and Holthausen (1987)). Substituting these values into the equation and solving for the final adult population, we get $N_\infty \cong 0.177139$. Now we can simplify the dispersal equation significantly by making the following observation. For the above values,

$$\frac{(h - N_\infty)}{(h - N_0)} = 0.966 \cong 1, \quad (1.5)$$

so we can replace the natural logarithm with its linearization,

$$\ln x \cong x - 1 \quad \text{when } x \cong 1. \quad (1.6)$$

Substituting our expression 1.5 into 1.6, we get

$$\ln\left(\frac{(h - N_\infty)}{(h - N_0)}\right) \cong \frac{(h - N_\infty)}{(h - N_0)} - 1. \quad (1.7)$$

After making this substitution, we can solve the dispersal equation 1.2 explicitly for N_L , a linear approximation for N_∞ . The result is the following equation which approximates the continuous dispersal process in one discrete step:

$$N_\infty \cong N_L = \frac{hT_0 + N_0(p - T_0)}{h - N_0 + p}. \quad (1.8)$$

Using equation 1.8, we compute $N_L = 0.177192$ which is quite close to our N_∞ value from before, especially considering the lack of precision in the determination of the parameter values themselves.

Having replaced the continuous differential dispersal system with a discrete difference equation, we can combine it with the annual birth and death processes. Since $J_k = bN_k$ from 1.3b, we have $T_k = N_k + bN_k = N_k(1 + b)$. Then we approximate equation 1.3a with

$$N_{k+1} \cong sN_k = s \left(\frac{hN_k(1+b) + N_k(p - N_k(1+b))}{h + p - N_k} \right). \quad (1.9)$$

Simplifying 1.9, we arrive at a single difference equation to describe the entire process.

The equation becomes:

$$N_{k+1} = sN_k \left(\frac{N_k(b+1) - bh - h - p}{N_k - h - p} \right). \quad (1.10)$$

Notice that equation 1.10 has a non-trivial equilibrium at

$$N^* = \frac{(1-s)(h+p) - bhs}{1-s(b+1)}.$$

More importantly, we can take the derivative of the right-hand side of the difference equation 1.10 with respect to N_k and replace N_k in the derivative expression with its equilibrium value N^* . Comparing the resulting value with 1, we see that the equilibrium

is both positive and stable when $h > \frac{p(1-s)}{s(b+1)-1}$. This is exactly the same suitable

habitat density threshold, h^* , that Carroll and Lamberson found for the continuous model, providing further evidence for the validity of our linearized approximation. The advantage of the simplified model is the ease with which it can be manipulated into a simulation of owl populations over many generations. In chapter four, we will use this derived difference equation to compare and evaluate the results of our spatial population simulations.

CHAPTER 2 Approach

2.1 Assumptions

Nearly all of the investigations discussed in the first chapter were motivated by the desire, either in the minds of the authors themselves or that of the scientific community, to prevent the extinction of the northern spotted owl. While studying the complicated behavioral and demographic characteristics of the species is essential for a complete understanding of the problem, the destruction of habitat and formation of wildlife refuge areas are really the only determining factors under human control. In addition, much of the forest has already been harvested and the timber industry will continue to depend on the valuable trees. If the spotted owl is to survive, it has no choice but to exist in a fragmented habitat. For this reason, we will assume that there is a certain limited amount of old-growth forest available and focus on the spatial arrangement of this habitat which optimizes the owl's chance for survival.

First, reserve designers must be concerned with the size of the *clusters* of protected habitat surrounded by young harvested forests. A number of researchers have created models which supported the claim that arrangement of old-growth forests into a few large clusters would increase owl numbers (Carroll and Lamberson (1993), Doak (1989), Hanski (1994), Lamberson et. al. (1994), Wilcox and Murphy (1985)). This conclusion is not universal, however. Quinn and Hastings (1987) argued that increased fragmentation might actually prevent extinction for very rare species. Once their size has been established, a second consideration is the spacing of the habitable clusters. Lande

(1987) proposed the idea that if juvenile dispersal distances were much larger than the average distance between clusters, the owls would be equally successful in either random or evenly distributed habitat. Our model will attempt to quantify both of these factors in terms of their influence on spotted owl persistence. In doing so, we will establish some specific grounds for either supporting or refuting the statements of previous investigators.

Before we describe the model which will be used for our simulations, the assumptions need to be clearly stated and justified. Many of these ideas mimic those of the models discussed in chapter 1, while some are unique to this particular investigation. First, we will simplify the population dynamics considerably by tracking only female owls with the assumption that all owls live in pairs and female owls have no difficulty in finding a mate. Of course this is not the case. Holthausen et. al. (1995) tracked both sexes in their model and included the mate search process. Such complications are beyond the scope of our model. We will assume that for current population levels, the difficulty in finding a mate is insignificant compared to that of the search for suitable habitat. Next, the forest habitat will be sharply divided between suitable (old-growth) and unsuitable (young trees or clear-cuts) sites. Eliminating intermediate levels of habitability simplifies the model considerably and is supported by the findings of Bart (1992). The habitable sites will be homogeneous in that each such site, regardless of location, will contribute equally to the probability of success for dispersing juveniles.

The behavioral processes of the spotted owls will be simplified according to the following constraints. Dispersing juveniles will only be allowed to settle in habitable sites which are not currently occupied by adult owls. Young owls who have successfully

settled in a new site will become adult owls in the next generation, capable of reproduction and subject to the normal adult mortality rate. This assumption ignores the observed minimum fecundity age and increased mortality of young adults, so may make the model's predictions somewhat optimistic. Considering the high average lifespan of the adult owls, this effect should be relatively small. Birth and death rates will be assumed constant for all generations and all site locations. Since adult owls are much more adept at finding old-growth sites (Holthausen et. al. (1995)), adult dispersal will be ignored. We will assume that adult owls remain in the same homesite throughout their lives. Adult death will be determined by a constant annual mortality rate so that there will be an average, but not maximum, age of death.

2.2 Understanding Dispersal

The single largest cause of death for northern spotted owls is unsuccessful juvenile dispersal. Mature adult owls are able to protect themselves and their newborn young quite well. It is when the inexperienced juveniles leave the homesite to search for their own territory that they are most vulnerable. More than 80% of young owls die while trying to find suitable habitat (Marcot and Holthausen (1987)). For this reason, any reasonable owl model must take great pains to accurately simulate the dispersal process. The problem is that field studies have had minimal success observing the dispersal behavior in the wild. Search patterns, rates, and orientations to habitat vary between studies and are poorly understood (Marcot and Holthausen (1987)). Radio transmitter studies start out with only a few owls because pre-dispersal juveniles are scarce and

difficult to locate. Once they have been tagged, their movements don't seem to follow any recognizable pattern and the vast majority die before they find suitable territory and settle. Thus far the results have been studies with very small sample sizes and a general failure to accurately explain the dispersal process.

Previous models have avoided the difficulty in simulating juvenile dispersal by foregoing any explicit spatial considerations. They give the young owls a certain probability of success which is based on a specified number of search steps or other habitat parameters. Since they do not actually follow each owl in its search through the forest, there is no need for a detailed understanding of the dispersal process. It would seem, however, that the complex interaction between explicit dispersal behavior and the fragmented landscape is exactly what we need to understand. Over-simplification of the process could artificially reduce the significance of its impact on spotted owl persistence.

Two of the cited models have included explicit dispersal in their investigations. Holthausen et. al. (1995) used a completely deterministic and spatial dispersal simulation to recreate the owl movements in a specific region of the Pacific Northwest. Juveniles moved from their homesites and made decisions based on geographic barriers, old-growth densities, and the presence of other owls. Unfortunately, the details of their dispersal scheme are not presented in the report. In their case study of the Bachman's Sparrow (*Aimophila aestivalis*), Pulliam et. al. (1992) used a site grid similar to ours and had juvenile sparrow's move one site at a time in a straight line until they found a habitable site or died. While this study provided an excellent framework for the present model, it could not really be generalized to the spotted owl. Bachman sparrows have a very

different relationship to their habitat and their dispersal behavior is more clearly understood. The limited observational data available shows spotted owl juveniles making large dispersal moves across many sites and not necessarily following a straight line. Our aim then is to design a model with spatially explicit dispersal process and describe this process in detail. With a limited knowledge of avian behavior, we will not claim to have accurately modeled the real process. By making a reasonable attempt, however, we hope that our simulations will illustrate some important features of the owl's dependence on old growth forest.

2.3 Choosing Parameters

Before a computer simulation model can be implemented, parameter values must be chosen. In the case of the spotted owl, this is a difficult and somewhat subjective process. As described in the previous section, owl field studies have been limited, with little success in generating enough data to reliably quantify the owl's demographic characteristics and behavior. Previous models have relied on a variety of different numerical values for fecundity, mortality, homesite dimensions and dispersal success rates. Due to the disparity between the results of different field studies, most of the authors chose to explore a range of values for each of the pertinent parameters.

For our model, we will be concerned primarily with general population dynamics in relation to habitat patterns, and not accurate numerical predictions. While other models have focused on the sensitivity of the species to changes in forest composition, searching efficiency, and life history parameters, we will instead compare different

patterns of old-growth homesites. Fixing the parameters and manipulating only the habitat arrangement will emphasize the spatial component that has been missing from many of the other models. The disadvantage of this approach is that we must choose one set of parameter values to use for all of the simulations. As biologists make more thorough and accurate observations, the model can be updated to reflect these improvements.

To be as consistent as possible with the majority of previous investigations, we will use the parameter values described by Franklin et. al. (1986), Marcot and Holthausen (1987), Lande (1988), and listed concisely in Doak (1989). They are shown in table 2-1 below.

<u>Parameter</u>	<u>Description</u>	<u>Estimate</u>	<u>Source</u>
<i>h</i>	current percentage of landscape which is habitable	0.38	Lande (1988)
<i>a</i>	fraction of habitable territories which are occupied by adults	0.44	Lande (1988)
<i>u</i>	average female fecundity	0.24	Marcot and Holthausen (1987)
<i>v</i>	fledgling survival	0.60	Marcot and Holthausen (1987)
<i>b</i>	average annual production of juveniles ($= u \cdot v$)	0.144	
<i>s</i>	adult annual survival	0.942	Franklin et. al. (1986)
<i>psd</i>	probability of successful dispersal	0.18 (0.36)*	Marcot and Holthausen (1987)

Table 2.1: Parameter values and sources from Doak (1989)

These are also the numbers which Carroll and Lamberson (1993) used to validate their model and interpret its conclusions. Choosing these values allows us to easily compare

the results of the computer simulations to those of the difference equation system developed in section 1.3. The juvenile birth rate, b , is just the product of the actual birth rate, u , with the probability that each newborn owl will survive until it is ready to begin dispersal, v . Our model will use this composite birth rate and thus eliminate any detailed simulation of fledgling survival. Notice that we have added a second dispersal success probability which is twice as big as the value 0.18 used in Marcot and Holthausen (1987). We will complete a separate set of simulations for each of these two psd values. Our hope is that an increase in the number of young owls dispersing and surviving the process will accentuate the effects of habitat clustering on owl populations. In support of this optimistic success rate, Bart (1995), Holthausen et. al. (1995), and Lamberson (1994) all used dispersal success probabilities above 0.30 in some of their simulations.

2.4 Simple Probability Model

Using the parameters we have chosen, we can develop a simplistic probability model to predict the future levels of the owl population. This will be useful for comparison, both to our linear modification of the Carroll and Lamberson (1993) model as well as the results of our simulations.

Multiplying the values for annual fecundity (0.24) and fledgling survival (0.60), we arrive at a total annual proportion of new juveniles produced by the owl population (0.144). Since we are not modeling the survival of fledgling owls, we will use this last value for our effective birth rate, b . Next, we can multiply this reproduction fraction by each of our two probability of successful dispersal (psd) values to get the total proportion

of new adult owls, ΔN^i , produced each year for the two dispersal success rates. Thus we arrive at the following values:

$$\Delta N^1 = 0.144 \cdot 0.18 = 0.0259 \quad \text{and} \quad \Delta N^2 = 0.144 \cdot 0.36 = 0.0518.$$

At the end of the year, 94.2% of both old and new adult owls will survive to the next reproductive period. Adding this to our model, we produce a simple difference equation which will approximate next year's owl population size as a function of this year's number:

$$\begin{aligned} N_{n+1} &= s \cdot (N_n + \Delta N) \quad \text{or, for each dispersal success rate} \\ N_{n+1}^1 &= 0.942 \cdot (N_n^1 + 0.0259 \cdot N_n^1) = 0.966 N_n^1 \quad \text{and} \\ N_{n+1}^2 &= 0.942 \cdot (N_n^2 + 0.0518 \cdot N_n^2) = 0.991 N_n^2. \end{aligned}$$

These equations exhibit simple exponential decay. We can compare these results to those we observe from the more complicated difference equations of the modified Carroll and Lamberson (1993) model. In the Figure 2-2 we have iterated both of the exponential functions for 100 years and plotted the population level each year as a proportion of the starting population $N_0 = 150$.

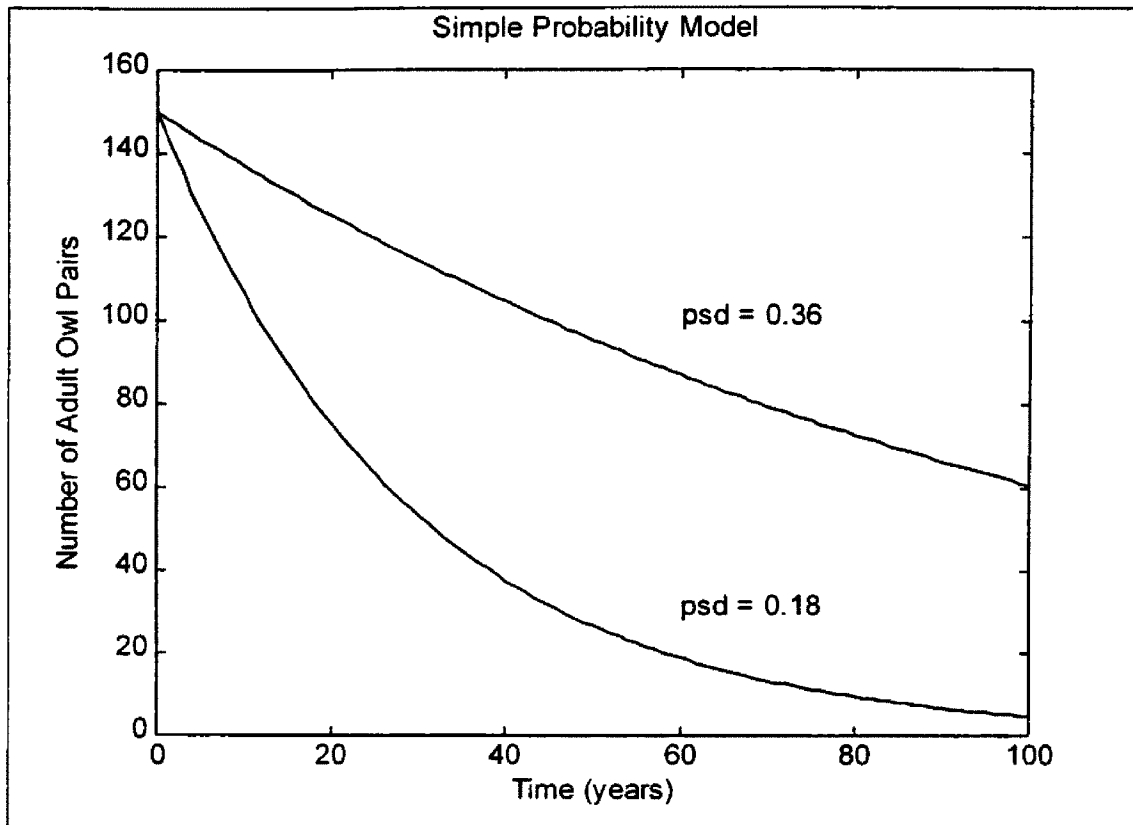


Figure 2.2: Population trajectories for simple probability model

To simplify comparison with the simulation results in chapter 4, we have initialized these functions with 150 adult owl pairs in a forest with 900 total sites, 342 of them habitable. In this way, the probabilities match the landscape habitability percentage $h = 0.38$ and fraction occupied by adults $a = 0.44$ from the table above. The line corresponding to the higher dispersal success rate maintains a much higher population, with 60 of the adult pairs surviving to the 100th year as compared to only 5 for the $psd = 0.18$ line.

Despite its attractive simplicity, there are obvious limitations to this model. In reality, the owl population is very unlikely to exhibit such uniform behavior over a long period of time. Conditions will surely change. The forest habitat will continually evolve through harvest, natural disasters, and species variation. Owl demographics will vary

from one year to the next and small fluctuations might lead to considerable shifts in population numbers. Conclusions drawn from this completely deterministic and homogeneous approach might give the spotted owl populations a false appearance of stability when in fact they could be on the verge of extinction. Even if all conditions were to remain exactly the same, the parameters of the system and other factors would change solely because of the decrease in the number of spotted owls. On one hand, fewer adult owls means more available habitat for dispersing juveniles. Given a very small total population, young owls would experience a significantly higher chance of finding a site in which to settle. However, they would also have more trouble finding a mate and maintaining genetic variation. The first of these small population effects was incorporated into the Carroll-Lamberson equations of section 1.3 and will play a key role in our simulations. The latter two are beyond the scope of this investigation.

2.5 The Carroll-Lamberson Results

To gain additional perspective before exploring the spatial simulations themselves, we will use the parameters listed above to iterate the difference equations for the modified Carroll-Lamberson model described in section 1.3. Substituting the demographic values into equation 1.10, starting the population fraction at $0.167 = 0.44 \cdot 0.38$, and iterating 100 times yields the population trajectories in Figure 2-3.

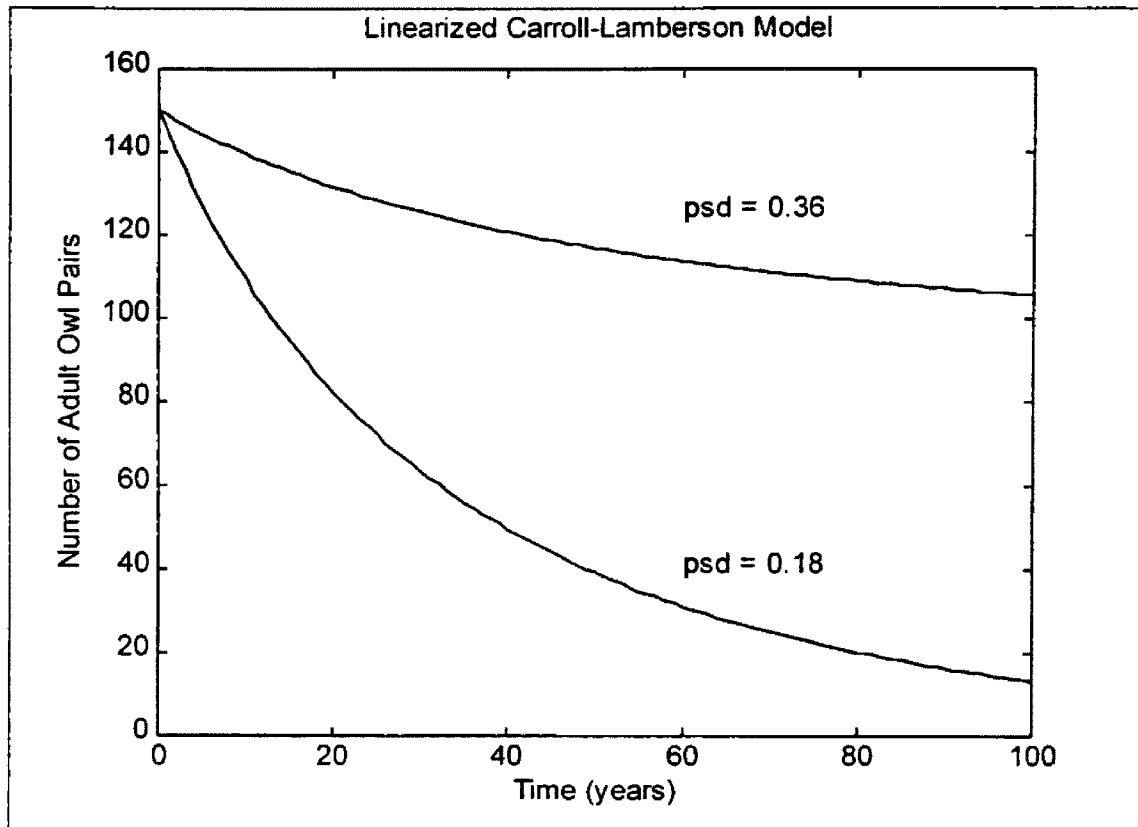


Figure 2.3: Population trajectories for linearized Carroll-Lamberson model

The vertical axis is converted from the population fraction used in the difference equation to an actual number of owls by multiplying by 900, the total number of sites. Notice that while these owl population levels exhibit roughly the same exponentially decreasing behavior as that of figure 2-2, they result in significantly better 100-year population values for both dispersal success probabilities. The $psd = 0.18$ curve finishes more than twice as high and there are approximately 75% more owl pairs for the high success dispersal scheme. As the adult owls become scarce, the fraction of sites which are both available and habitable, $h - N$, increases. This means young owls will have less difficulty finding a new homesite. A greater percentage of the owl population is maintained each year and the population curves veer upward from those of the simple

exponential model. Both of these deterministic models will be useful for comparison with our simulation results.

CHAPTER 3 Description of the Model

3.1 Forest Matrices

Each of the simulations take place on a 30 by 30 matrix which represents the entire forest, or region. The entries in this *forest matrix* represent tracts of land, or *sites*, equal in size to the amount of land required for survival of one adult owl pair. The exact size of such a site is the subject of considerable controversy between environmental organizations and the timber industry. Fortunately, our model can function without specifying this size. We will just assume that the sites are large enough to allow two owl pairs to coexist successfully in adjacent sites, and small enough so that juvenile owls can realistically cover distances corresponding to the width of four or more sites during dispersal. Each of the cells has four *neighbor* cells: those that are immediately adjacent to that cell. Notice that diagonal cells are not considered adjacent. In addition, the forest matrix exhibits wrap-around boundary conditions. This means that cells on the top edge are considered neighbors of those on the bottom, cells on the far right edge have right-hand neighbors on the far left edge, etc. In this way, the matrix of sites will represent an idealized forest of infinite extent without edge effects. If we treat the matrix as representing just a patch of forest, this is equivalent to the assumption that every time an owl flies off one side of the grid, it is replaced by another owl which flies on the other side.

At the beginning of each simulation, $h = 38\%$ of the sites are chosen to be habitable. This assignment may be random, have built-in clustering, or follow a specified

evenly-spaced pattern. The various arrangements of the habitable sites will be discussed in section 3.2. Only habitable sites can support owl residence. Once the habitable sites have been designated, adult owls are assigned randomly to approximately $a = 44\%$ of them. This means that after the initialization process, roughly 17% of the forest sites will contain adult spotted owl pairs. For the purposes of the simulation, the matrix entries were given either the value 0 for unsuitable, 1 for suitable and unoccupied, or 2 for a habitable site, occupied by an adult pair.

3.2 Habitat Patterns

The focus of our investigation was to explore different habitat arrangements and quantify their relationship to long-term owl population levels and the danger of extinction. We chose eight different patterns and these are described and pictured in Figures 3-1 to 3.8. Some of them contain *clusters* which are just groups of adjacent habitable sites. Half are randomly spaced while the other half are evenly spaced. The name *trees* refers to randomly spaced patterns of habitable sites, while *woods* is used for evenly spaced forests.

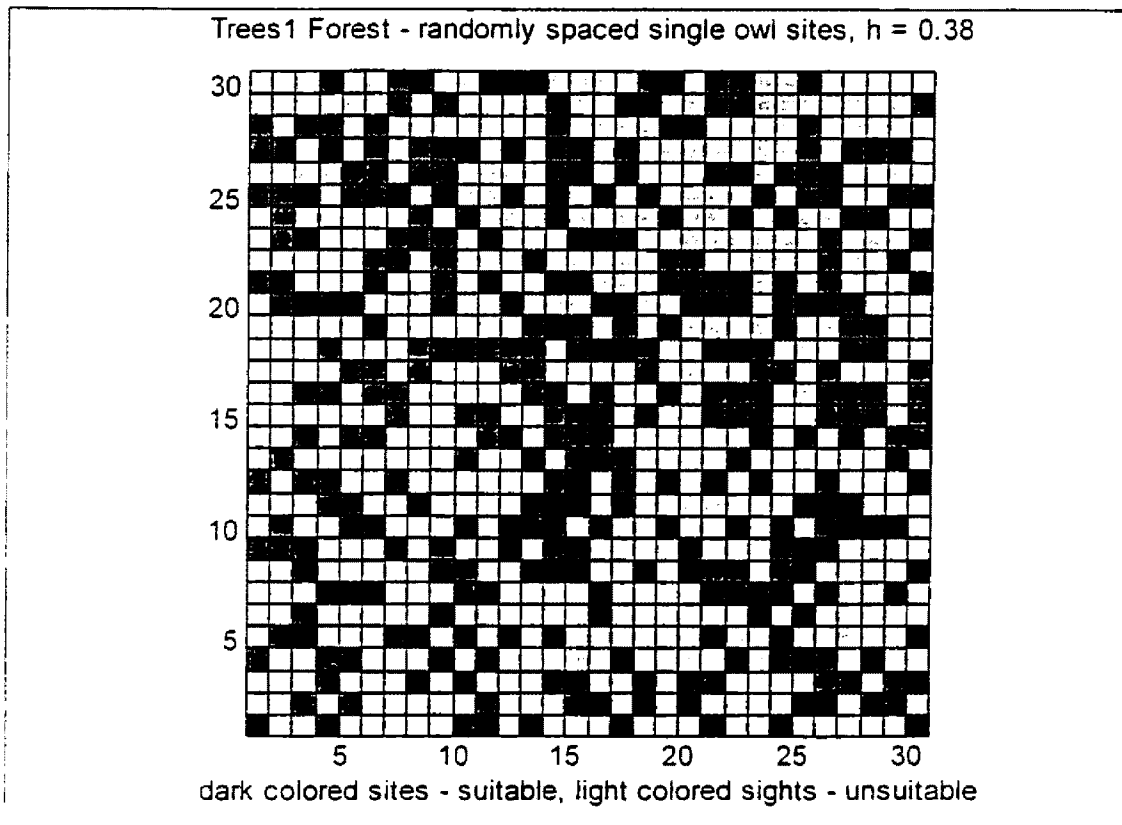


Figure 3.1: *Trees1* forest pattern.

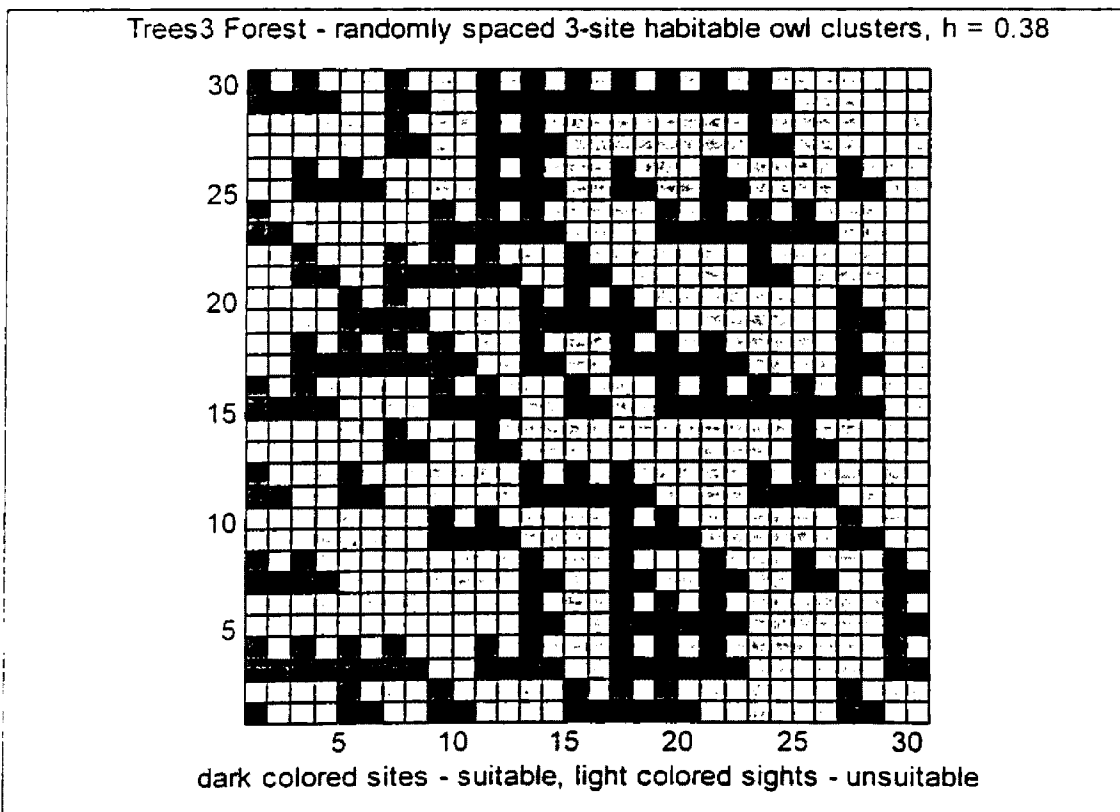


Figure 3.2: *Trees3* forest pattern.

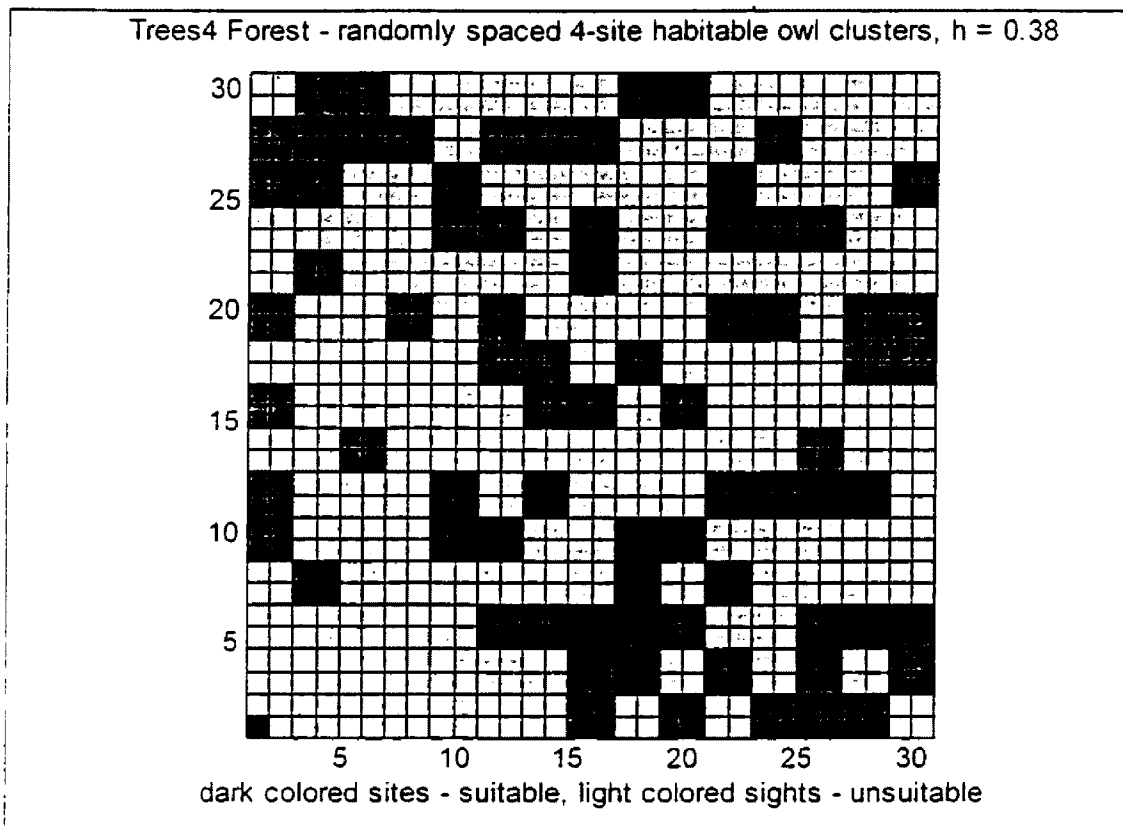


Figure 3.4: *Trees4* forest pattern.

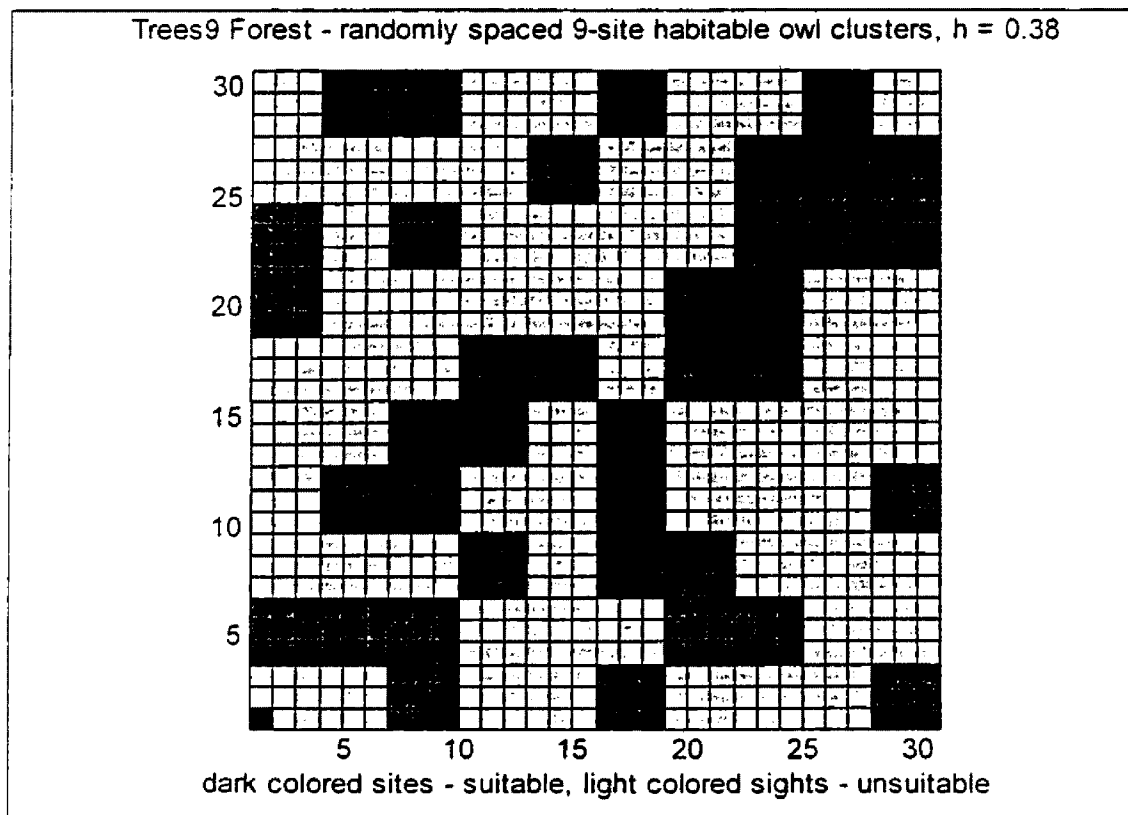


Figure 3.4: *Trees9* forest pattern.

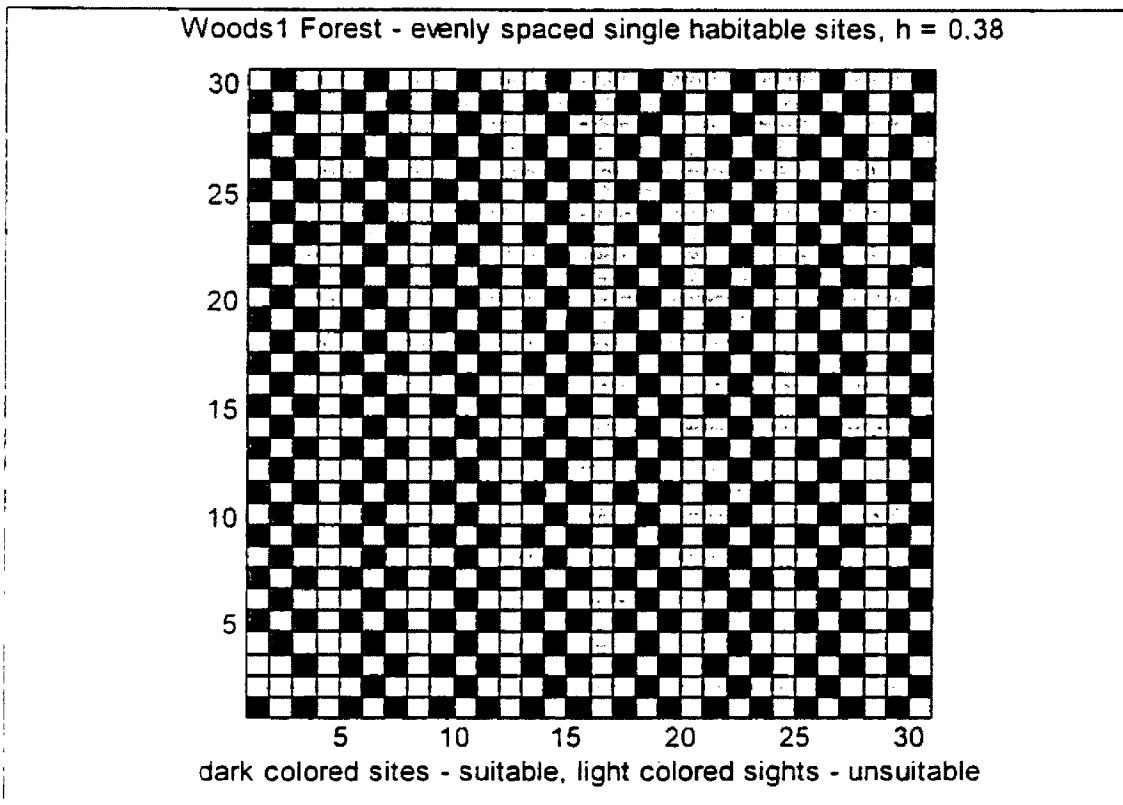


Figure 3.5: *Woods1* forest pattern.

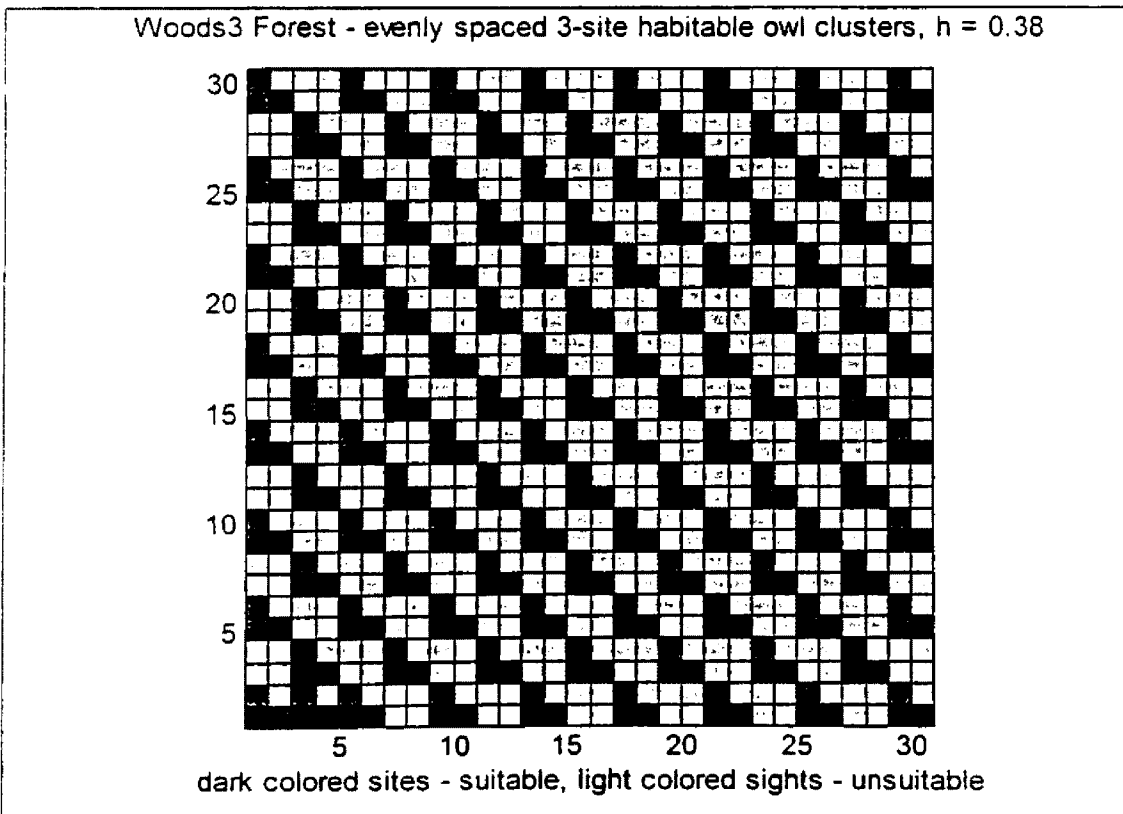


Figure 3.6: *Woods3* forest pattern.

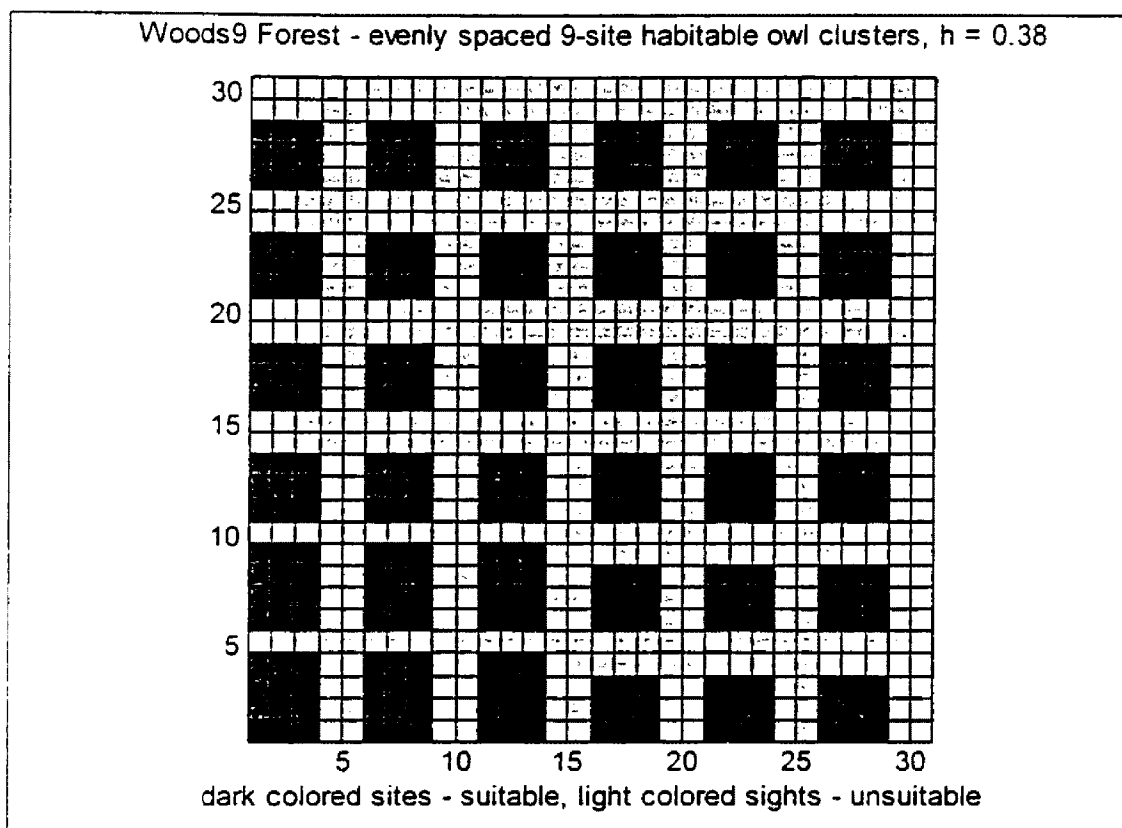


Figure 3.7: *Woods9* forest pattern.

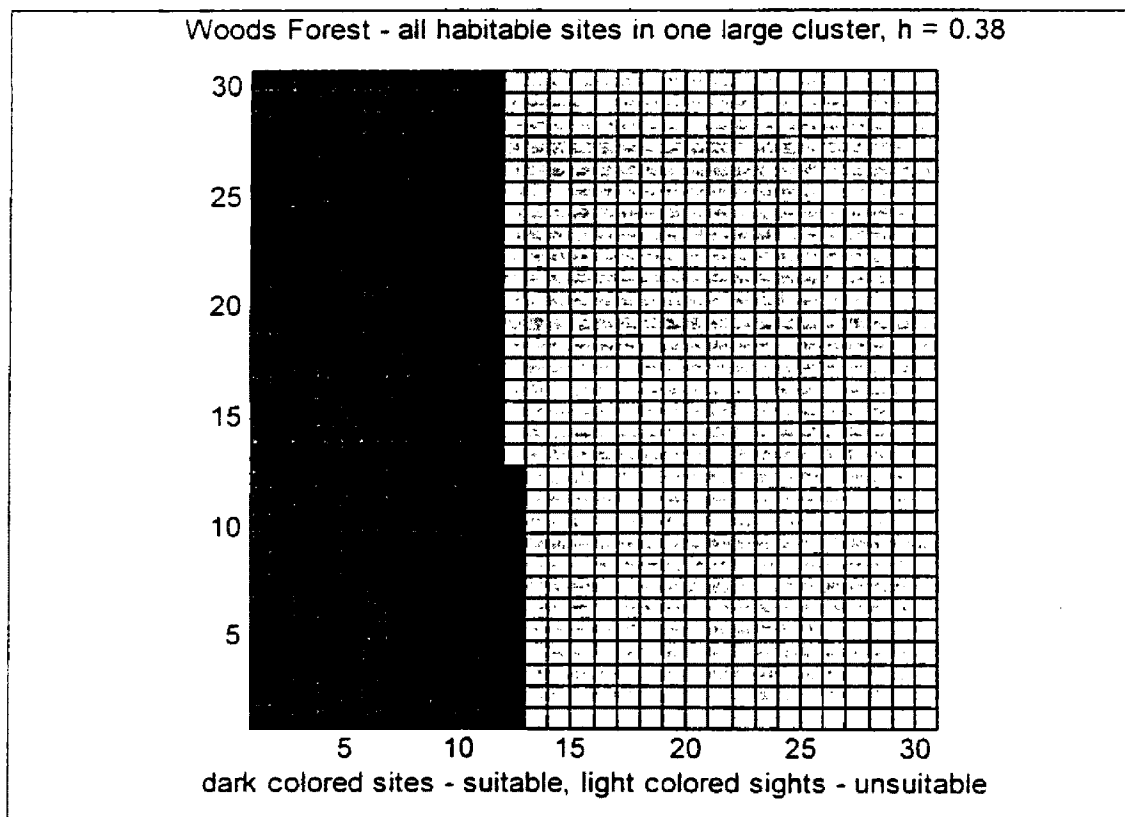


Figure 3.8: *Woods* forest pattern.

3.3 Simulation Phases

After the pattern of suitable habitat is chosen and the initial population of adults is assigned, the simulation proceeds in a three-step annual cycle. First, each of the existing adult owl pairs give birth to a young owl with probability $b = 0.144$. The matrix elements representing sites containing newborn owls are temporarily assigned the number 3. Once all of the births have occurred, the young owls begin to disperse. When each juvenile owl vacates its homesite, the corresponding matrix element is returned to a value of 2, representing the remaining parent adult pair. Dispersing juveniles complete the search process described in section 3.4. There are two possible outcomes of this undertaking. First, the young owl might fail to settle in a habitable site and die. This is by far the most likely occurrence and does not alter the forest matrix. The second possibility is that the juvenile spotted owl disperses successfully. It finds a site which contains suitable habitat and is not occupied by an adult pair. The matrix element representing the newly discovered site is temporarily given the value 4. Once all of the season's young owls have had a chance to disperse, the successful searchers find mates and become adult owls (4's become 2's). Finally, the new and old adult pairs must face the threat of seasonal mortality. Each adult pair survives to the next year with probability $s = 0.942$. Habitable sites which were home to adults that did not survive become vacant and are labelled 1 because they are capable of supporting new adults the following year. The matrix again contains only 0's, 1's, and 2's and is ready to start the next season with the birth process. The adult owl population is recorded at the beginning of each year.

3.4 Habitat Quality

Before dispersal can be executed, each of the sites in the forest matrix is assigned a *site index*. For each cell, this value is an integer equal to the number of habitable cells in its five cell *neighborhood*. This neighborhood consists of the cell itself plus the four adjacent cells. In this way, the site index z for a given cell must be an integer between one and five. Notice that these cells might wrap around to the opposite edge of the grid when we assign the site index to a border cell. The site index value roughly quantifies the density of old-growth forest in the vicinity of a site and will later be used to determine whether a dispersing juvenile is likely to stop and search, fly past, or die in a particular site. Despite the limited amount of observational evidence, it seems reasonable that a dispersing juvenile would be more likely to choose to search and survive the search process in regions dominated by old growth forest. Here we are assuming that some juveniles will not waste their energy carefully searching a mostly uninhabitable region while others will probably die attempting such a search due to limited food sources and increased predation in these areas. This idea is central to our dispersal model.

3.5 Modeling Dispersal

Since our aim is to explore the effects of various habitat configurations, both the dispersal process and its probability of success are dependent on the type of habitat in a small neighborhood of the dispersing owl. We would also like to reiterate the idea that this model does not claim to recreate real spotted owl dispersal. It is merely an estimation of the process which, we hope, is reasonable and probable enough to illustrate

some important aspects of the relationship between spotted owl population levels and the arrangement of the old growth habitat.

When a young owl is ready to leave its homesite, we assume it begins with some knowledge of the habitat suitability in its immediate vicinity. In other words, it will be generally aware of the site quality of its place of birth. If the site index of the homesite is greater than or equal to three, the juvenile will conduct a thorough search of the four adjacent sites. In this process the juvenile either finds and settles in a vacant habitable cell or continues its search. Conversely, low quality habitat in the immediate neighborhood of the homesite ($z \leq 2$) results in the owl either dying or moving on to search in a different area. Notice that due to the fact that the homesite itself must be habitable, the site index condition imposed for the homesite search is really equivalent to at least two of the homesite's four neighbors being habitable. The sequence of events and possible outcomes is represented in Figure 3-9.

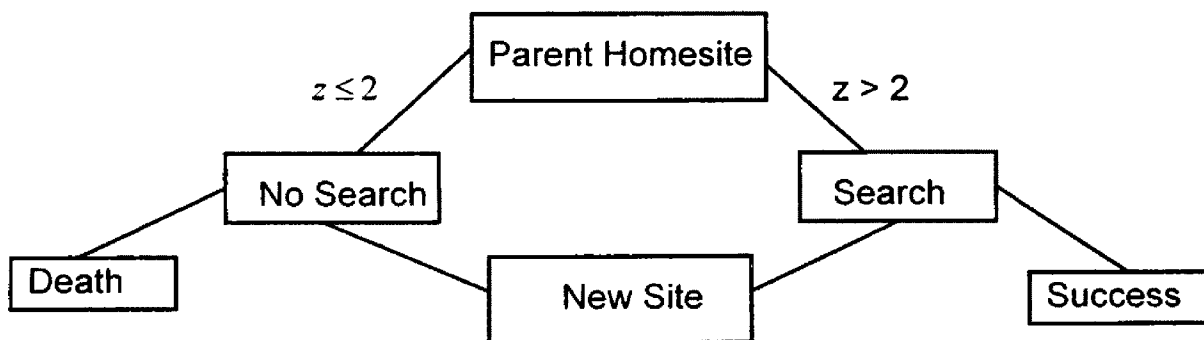


Figure 3.9: Flow diagram for homesite search

Later in this section, and the next, we will describe the probabilities associated with each one of these paths, the details of the site search process, and the means by which a young owl moves to a new search site.

Upon arrival in a new potential search site, the owl's fate will again depend on the quality of the habitat in that region. This time, the owl will conduct a careful search of the site and its four neighbors if at least two of these sites are habitable. We write this condition as $z \geq k$, where $k = 2$. Otherwise, the owl will either die or fly to another site. At each stage of the dispersal process, the owl is faced with the same habitat dependent search option and the associated outcomes. The owl has a limited amount of energy, we assume that the probability of completing a search successfully will decrease each time the owl flies to a new site. To incorporate this idea in the model, we increase the minimum site index value, k , by one for each additional dispersal step. Detailed searching requires $z \geq 3$ for the second site, $z \geq 4$ for the third, etc. Of course this limits the dispersal to a maximum of five steps. Given the step size used (see below), this maximum search distance seems roughly consistent with those observed in radio telemetry studies (Marcot and Holthausen (1987)).

When the juvenile finds a site with the requisite site index value, it searches the site itself and then each of the four adjacent sites, one at a time. If one of these sites is both habitable and available, the owl is given a probability $q = 0.28$ of recognizing the habitability of the site, avoiding predators, and successfully settling. Otherwise it flies away to continue the search process. We are assuming here that the owl will not die during this stage of the dispersal, but may be forced to leave and might perish in the attempt to move to and search another site.

If the young owl searches without success or survives for a time in an undesirable location without searching, it must choose a direction in which to move and continue the

search for a homesite. In our model, this direction is selected randomly from four choices: NE, NW, SE, SW. This means that the young owls do not make intelligent direction choices when they disperse outward from their homesites. In other words, though they will die or choose not to search carefully in very poor habitat, they are just as likely to fly into a clear-cut or mountainous area as they are to fly to a large section of suitable forest. Once a direction has been chosen, the owl is assigned a corresponding direction vector, d , which just represents one diagonal step in that direction. This means, for example, that if a dispersing juvenile was assigned the direction SE, it would have a direction vector $d = (1, -1)$. The owl will continue to fly in this general direction for the rest of its dispersal flights.

Given this vector, search flights will be made according to the following guidelines. A universal step size is chosen as an average largest flight distance before an owl begins searching. For our model, we set the maximum step size in each direction at 3 (the distance across 3 owl sites). For each dispersal step, we chose the vector representing the actual search flight randomly from the set of all possible vectors generated by multiplying each of the components of the direction vector by an integer between 1 and the step size. For the particular example introduced above, the search flight vector would be selected randomly from

$$\{(1, -1), (1, -2), (1, -3), (2, -1), (2, -2), (2, -3), (3, -1), (3, -2), (3, -3)\}.$$

Each time this particular juvenile finishes with one site, it is randomly assigned one of these vectors and follows it to a new potential search location. In this way, the owl

maintains the same general flight direction but displays some variability in the exact choice of path. Figure 3-10 shows a starting site for an owl with the direction vector in our example along with the nine potential destination sites for the next step in its dispersal.

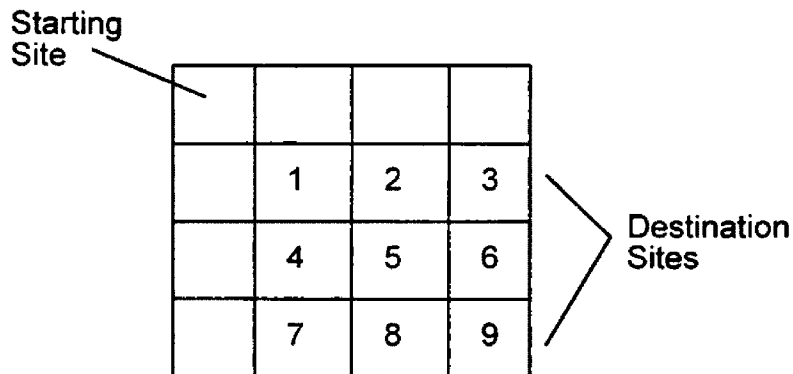


Figure 3.10: Potential destination sites for an individual dispersal flight

To maintain simplicity and avoid overlapping paths, we have eliminated the possibility of an owl flying directly North, East, South, or West. However, since the owl's search will include the sites adjacent to its destination site, this particular owl maintains the possibility of settling in one of the sites directly to the right or below its starting site. These edge cells are also potential settling sites for dispersal in one of the other three possible compass directions. In this way, the dispersal probability density for the entire 48-site neighborhood of the starting site (7×7 square minus the initial site itself) is not significantly different from uniform.

3.6 Theoretical Success Probabilities

The next task is to determine the probabilities associated with each of the stages in the dispersal process. There are two types of probabilities present: those that are

dependent on suitable habitat density and those that are not. Both the decision to search and the chance of being successful on a given search are habitat dependent. Assuming that the habitable sites are randomly distributed, as is the case for the *trees1* pattern, we can perform simple computations to get the probability that an owl will conduct a careful search in the neighborhood of an arbitrary site. Searching occurs when the site index meets the minimum requirement for the current dispersal step. The searching probability values for each site index requirement are listed in table 3-11.

<u>Site type</u>	<u>Search requirement</u>	<u>Prob(searching)</u>	<u>Prob(success)</u>
Homesite	$s > 2$	0.49	0.37
Other site	$s > 1$ (step 1)	0.63	0.41
	$s > 2$ (step 2)	0.29	0.47
	$s > 3$ (step 3)	0.08	0.52
	$s > 4$ (step 4)	$\cong 0$	0.57
	$s > 5$ (step 5)	0	-

Table 3.11: Theoretical search and success probabilities

The last column of table 3-11 gives the cumulative probability that a young owl will successfully find and settle in a vacant habitable site, given the minimum value of the site index for the center cell. These probability values are computed using the parameters for the habitable site fraction ($h = 0.38$), the adult occupancy fraction ($a = 0.44$), and the chance of recognition and settling ($q = 0.28$). In each of the k sites known to be habitable, the juvenile will settle with a probability of $(1 - a) \cdot q = 0.1568$, whereas the chance for success in one of the remaining $5 - k$ sites will be only $h \cdot (1 - a) \cdot q = 0.0586$. Notice that while the probability of successful search increases with increasing k ,

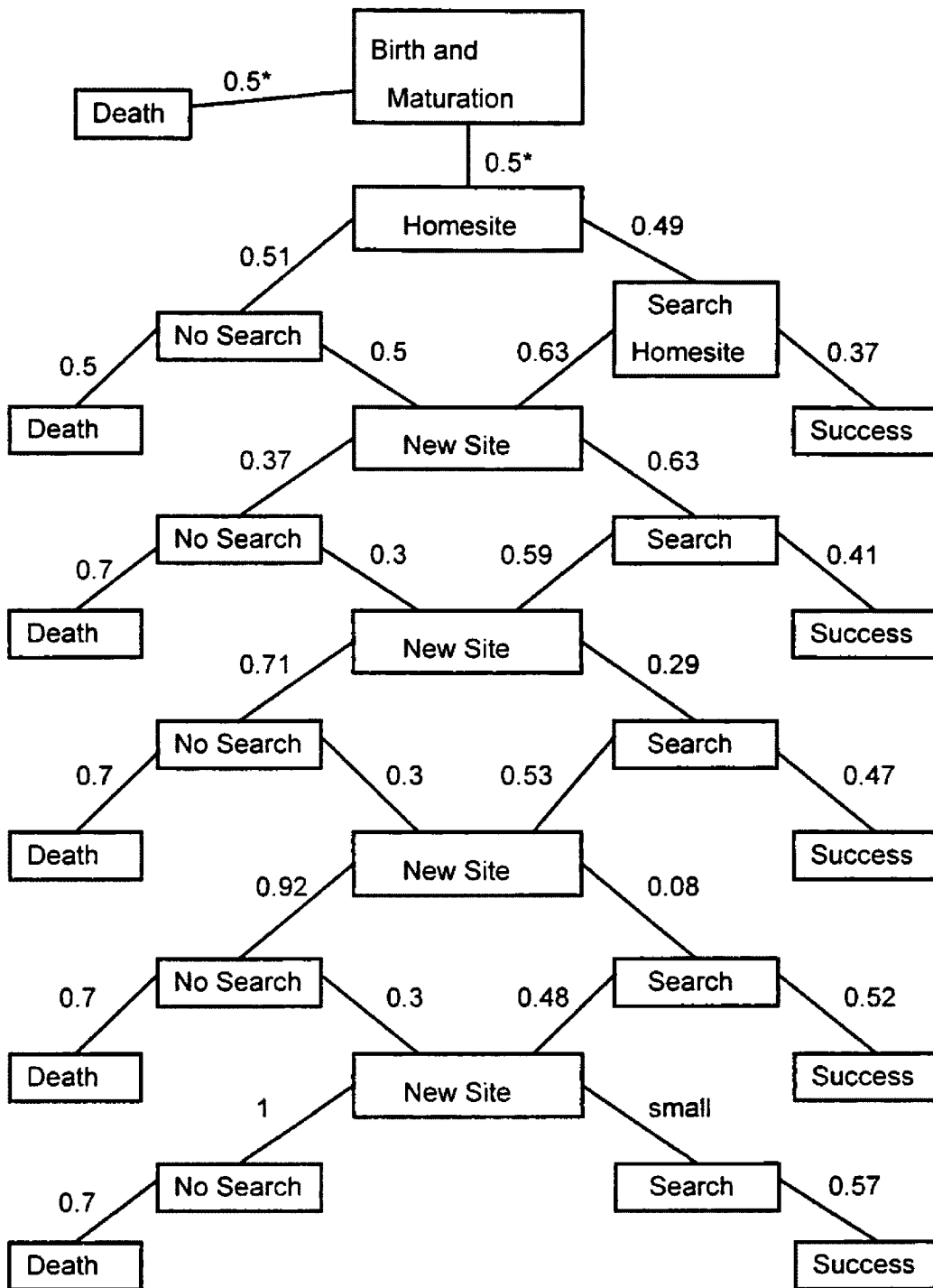
searches are conducted with much less frequency. As a result, a young owl's chances of successfully find a new home decrease significantly with each additional dispersal step away from the homesite. Since no cell can have a site index greater than five, it is impossible for any dispersal to have more than four moves. We would also like to emphasize the fact that these probabilities are dependent on the arrangement of the habitable sites and the percentage of these sites which are occupied by adults. They were computed assuming that the sites were distributed in a completely random manner. During our simulations the dispersing owls might encounter higher or lower rates depending on the habitat pattern involved as well as the current size of the owl population.

To complete the dispersal model, we need to assign mortality probabilities to owls that do not undertake site-neighborhood searches. Since dispersal mortality is largely due to predators and energy depletion, the associated probabilities will not be directly dependent on local habitat configuration. An indirect dependence, however, is inherent in the system because lack of suitable habitat is the necessary condition for an owl to take the "no search" path. Only in this case is death possible. We assume that a young owl whose homesite index is not high enough will have a 50-50 chance of surviving to move on to another site. We have chosen this number arbitrarily as there was very little observational data to suggest any specific value. Again, we are merely trying to generate a reasonable dispersal process which reproduces the dispersal success probabilities used in the literature. Once the juvenile has moved to a new search site, energy levels and protection from predators will have diminished. Surviving temporarily in poor habitat

will be significantly more difficult. For this reason, we increase the mortality rate to 70% for juveniles who find themselves in poor habitat after they have left their homesite. While this non-homesite mortality rate remains constant, the chance of death increases for each step of the dispersal because the owls are far less likely to be able to conduct a careful search.

A flow diagram for the entire dispersal process is shown in figure 3-12. Each connecting line represents a possible step in the process and is labeled with the corresponding probability from the above discussion. If we sum the total probability of successful dispersal along all paths, we get a value of $psd \cong 0.36$. To achieve the $psd \cong 0.18$ determined by Marcot and Holthausen (1987), we have added an initial dispersal death probability of 0.5. This might correspond to some danger which the owl faces upon first leaving the nest. Inclusion or removal of this initial mortality condition allows us to switch between the two proposed probability of successful dispersal values, 0.18 and 0.36.

Juvenile Dispersal - Flow Diagram



* Predispersal death probability only for psd = 0.18.

Figure 3.12: Full dispersal flow diagram with probabilities

3.7 Limitations of the Model

Our model has many limitations. Most importantly, we have based our dispersal process on little more than a semi-educated guess. It seems reasonable that juvenile owls might search in a manner similar to ours. The successful dispersal distances and final destinations do not appear to contradict any of the available field data, and the successful dispersal probabilities and population curves agree with contemporary models. The difficulty, however, is that the specific details of the search behavior of each juvenile spotted owl are beyond the scope of current scientific knowledge. Tagging young owls with radio transmitters has only given researchers a very limited amount of field data. A clear understanding of how each juvenile makes searching decisions will require considerably more observational effort. As more knowledge is gathered, our dispersal process should be updated and new simulations conducted. In order to provide specific numerical results, we conducted trials with certain commonly accepted parameter values. Further field investigation might also change and improve these values. Finally, we have decreased the accuracy of our model through a number of simplifying assumptions. We followed only female owls in our simulations, ignoring mate search difficulties, inbreeding risks, and other problems associated with small populations. We did not impose a fecundity age or maximum life span on the adult females. Mortality and reproduction rates did not depend on the owl's age. Our square-grid habitat structure was extremely simple and did not distinguish between more than two levels of site suitability. Each of these assumptions could be eliminated in favor of a more complicated, yet more accurate model. For example, the effects of specific habitat arrangements might be

considerably different if our simulations were run on a hexagonal grid. Many of our neglected considerations are explored in some of the models discussed in Chapter 1.

CHAPTER 4 Simulation Results

4.1 Simulations

A single simulation *trial* of this model consists of selecting a forest habitat pattern, assigning adult pairs randomly to 44% of the habitable sites, and then allowing the birth-dispersal-death process to repeat for 100 cycles or years. Population levels in terms of number of adult owl pairs are recorded at the end of each year. For both values of the probability of successful dispersal (psd) and each of the 8 habitat patterns, we conducted 30 such trials and recorded the average population for each year. By averaging multiple trials, we were able to minimize the stochastic variation due to the initial random assignment of habitat and adult pairs, as well as the generational fluctuation in the actual birth, dispersal, and death fractions. This was especially important for the trials that operated on randomly spaced forests. Such trials varied considerably. We recorded standard deviation data at each time step and found that population values varied as much as 30-40 %. This deviation seems to be inherent in the system. For comparison, we ran trials with different forest matrix dimensions, dispersal step-sizes, and search conditions. As we will discuss in section 4.4, all of these altered trials showed the same general results and none had significantly smaller deviations. For this reason, the simulation populations must be viewed as averages. While the average of 30 trials might stay above zero for the entire 100 years, a particular population of owls could drop to extinction.

4.2 High Dispersal Success

For the first set of trials, we used the high value for dispersal success probability, $psd = 0.36$. The resulting 100-year population curves are shown in Figure 4-1. Each curve is labeled with the forest pattern on which we conducted the simulation.

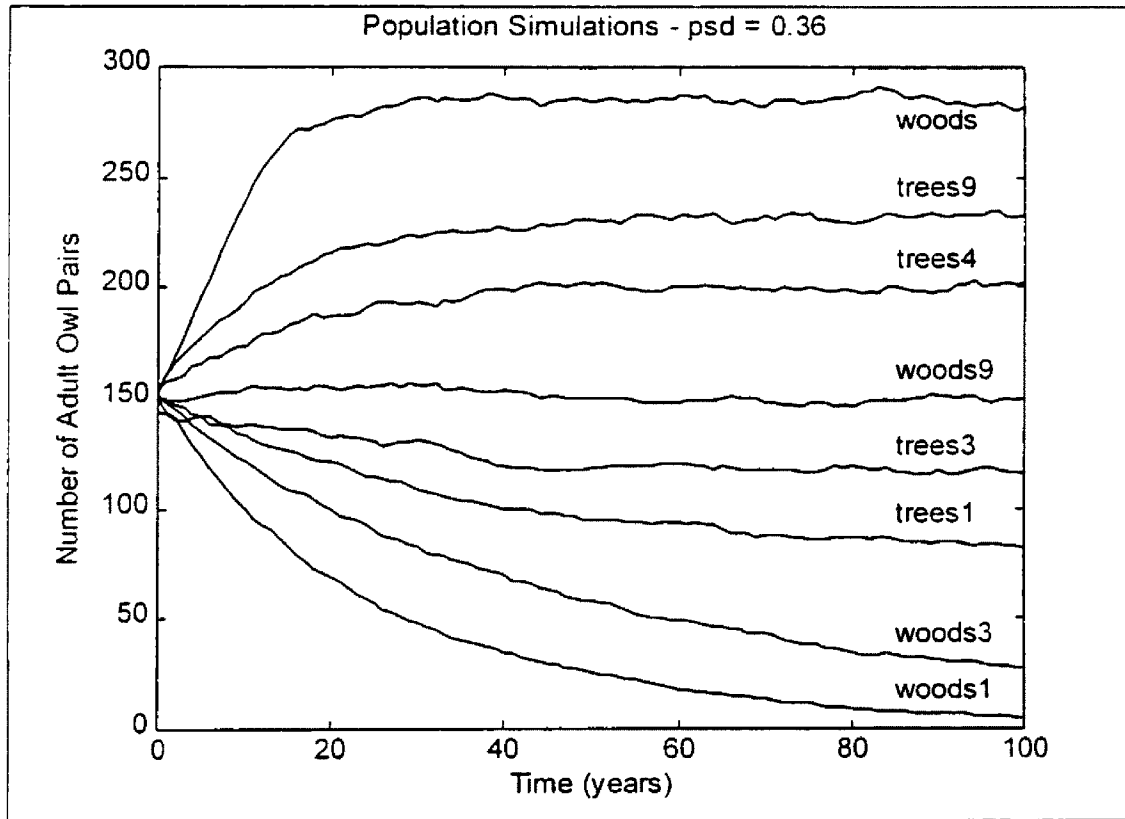


Figure 4.1: Population trajectories for simulations with high dispersal success

Obviously there was considerable variation due to the arrangement of habitat. The *woods* arrangement as well as the forests with large site clusters arranged randomly, *trees4* and *trees9*, showed increasing owl populations. Others stayed relatively stable and only the evenly spaced 3-site and 1-site forests, *woods3* and *woods1*, saw the owl population drop to dangerously low levels. While the other populations seem to have attained some type of equilibrium value, the owl populations for these last two habitat patterns are

continuing to drop, right up to the 100-year mark. To get another representation of the data, we have taken the average of the owl population over the last ten years of the simulation for each of the forest arrangements. Figure 4-2 shows each of these average final populations plotted as a fraction of the starting population. Viewing the results in this manner emphasizes the comparisons between the patterns and minimizes the effects of any initial deviation from 150 owl pairs due to random assignment of habitat and owls.

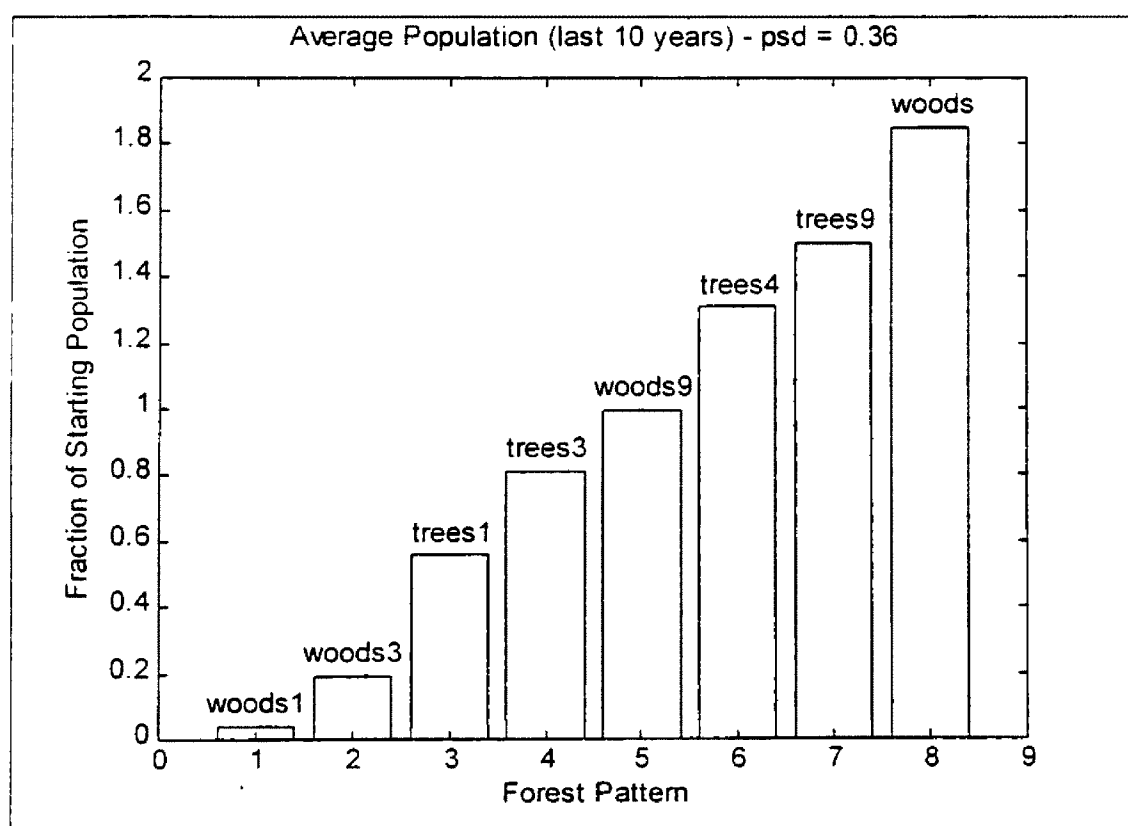


Figure 4.2: Average population for last ten years (high *psd*)

A number of authors have developed models in support of the notion that spotted owl populations will have more success if their old growth habitat is arranged in larger clusters (Carroll and Lamberson (1993), Lamberson et. al. (1994), Lande (1987), Wilcox and Murphy (1985)). The results in Figure 4-2 seem to refute this claim in two specific

places. The *trees1* pattern supports owls significantly better than does the *woods3* and the same observation can be made about the relationship between *trees4* and *woods9*. In each of these cases, a pattern with smaller clusters is supporting the owls better than one with large clusters. The difference appears to be a result of the spatial arrangement of the clusters. Randomly spaced forests are outperforming those that have evenly spaced habitat. Another means of comparison is the fact that randomly spaced 3-site clusters, *trees3*, support four times as many owls as their evenly spaced counterparts, *woods3*. Having made this observation, we turn to the more realistic low dispersal success simulations.

4.3 Low Dispersal Success

Figures 4-3 and 4-4 show the outcome of the same trials as in the previous section, except we have used the low probability of success, $psd = 0.18$, dispersal process. Notice that while the owl populations fare considerably worse for all habitat patterns, we see the same evidence of the superiority of the randomly spaced arrangements.

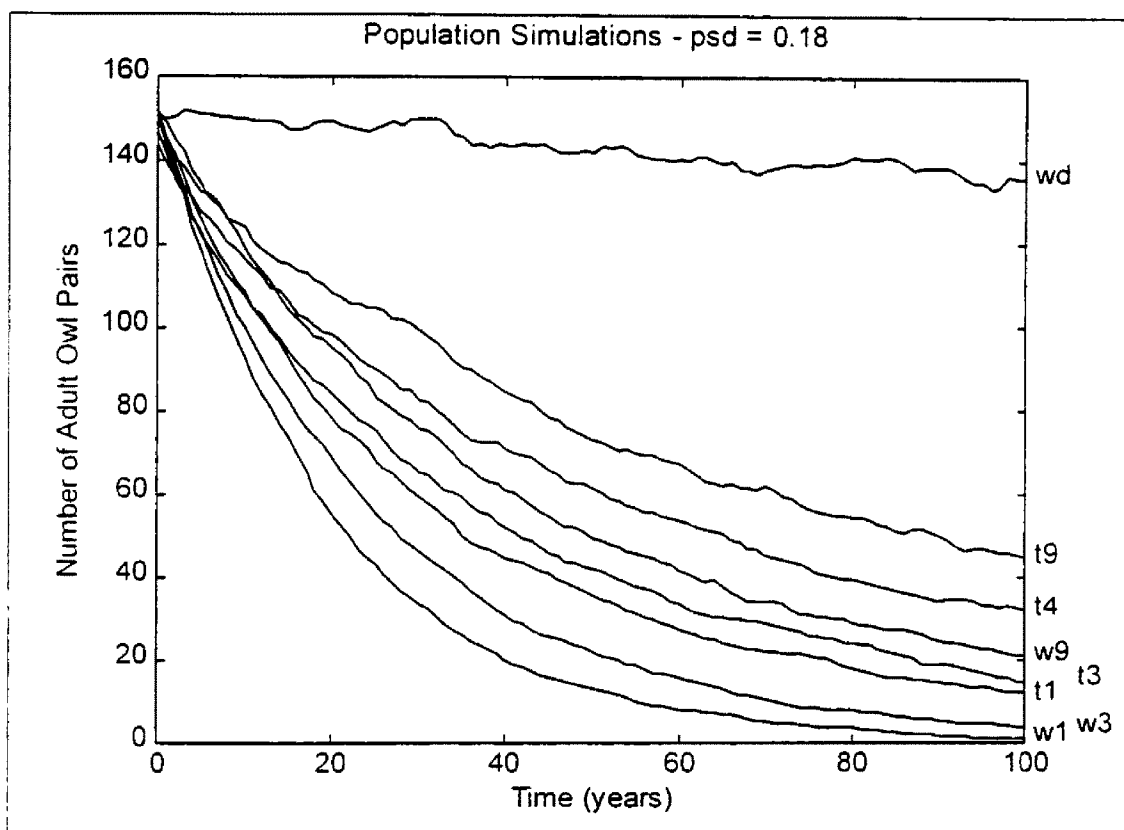


Figure 4.3: Population trajectories for simulations with low dispersal success

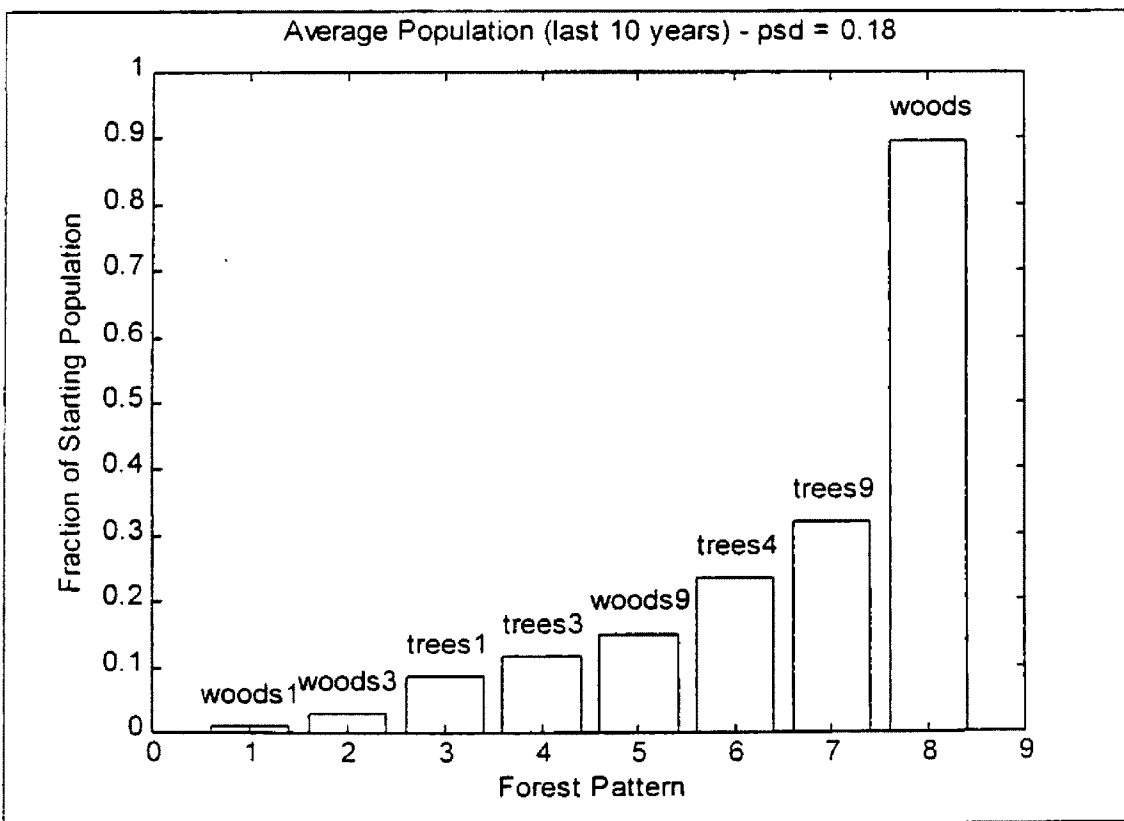


Figure 4.4: Average population for last ten years (low *psd*)

These results show that our dispersal process functions much more effectively on randomly spaced habitat patterns. In the two cases described above, this random influence even overcomes the more obvious advantage of larger site cluster size. It seems that the owls are finding greater success due to some sort of clustering effect on a larger scale. Looking at the habitat pattern diagrams in Section 3.2, we can see that the random arrangements have some larger connected habitat clusters which do not appear in the evenly spaced forests. In Chapter 5, we will quantify this form of clustering and investigate its correlation to the long-term owl population levels for the different forests.

To gain greater perspective on our results, we can compare them with the population curves from the simple probability model and the linearized Carroll-Lamberson model of Section 2.4. We find that for both of the *psd* values, the Carroll-Lamberson population values lie between our *trees1* and *trees3* curves. This seems reasonable since these patterns come closest to a completely random assignment of habitable sites in the forest matrix. Our simulations have come quite close to recreating Carroll and Lamberson's differential equations in a discrete, explicitly spatial environment. For the simple probability model, the population curves give values which are near or just higher than the *woods3* curves. Initially, the simulations drop more quickly than do their exponentially decaying counterparts. This is caused by the fact that the dispersal success probabilities were computed for a *trees1* random habitat and are a bit more optimistic than the actual success rates in a *woods3* environment. In the last 50 years, however, our simulations recover somewhat because the amount of available habitat has increased. As we discussed earlier, this effect is not considered in the simple

probability model. The combination of these two considerations leads to a slightly increased curvature for the *woods3* and *woods1* curves.

4.4 Harvesting

Before we proceed with an in-depth discussion of habitat clustering, we will look at a few variations on our basic simulation model. First we will consider the effect of continued harvesting of the old-growth habitat itself. Lamberson et. al. (1992) looked at projected timber sales and simulated this effect by removing 4% of the old-growth forest until the suitable habitat fraction had been lowered from the current level to 0.20. At this point they assumed that further harvesting of old-growth would cease until some of the replanted stands had matured enough to support spotted owls. For our third set of simulations, we chose to incorporate this same harvesting effect. During each of the first 10-20 years of the trials, we removed 4% of the habitable sites. These sites were chosen randomly and the process continued until less than 20% of the forest sites were habitable. On average, this harvesting process lasted 15 years. If one of the harvested sites contained an adult owl pair, they were assumed to be dead and removed from the population. Both the random harvesting pattern and the inability of displaced adults to disperse are simplifications which might cause our model to differ somewhat from actual populations in harvested forests.

The population curves from our harvesting simulations are shown in Figure 4-5. The number of adult owl pairs for each year is computed as the average of 20 trials. All

other conditions and parameters remain unchanged from the simulations of the last section. The probability of successful dispersal is 0.18 as in section 4.2.

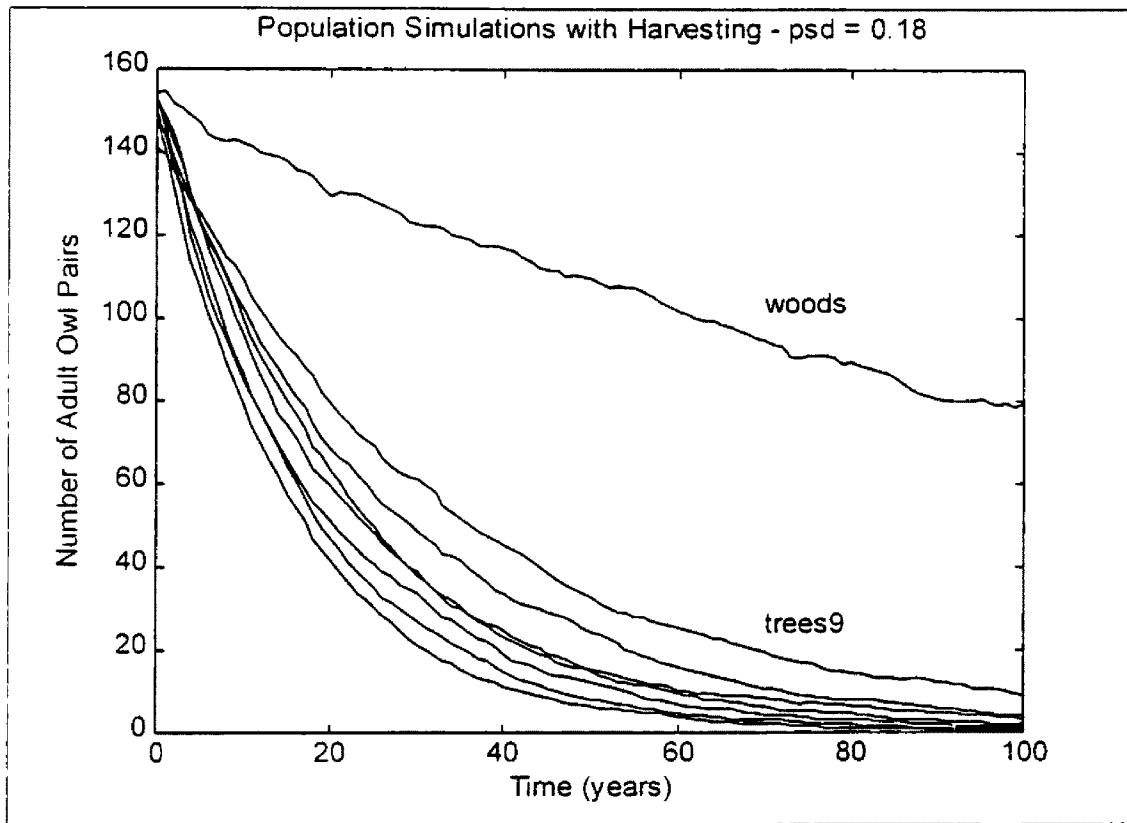


Figure 4.5: Population trajectories for simulations with harvesting

With the exception of the *woods* and *trees9* forests, the simulations yield disastrous population declines for all habitat patterns. While they seem to maintain roughly the same hierarchical order, it is difficult to distinguish between the remaining six arrangements. Faced with continued destruction of their habitat all owl populations in these forests drop below five pairs for the last ten years, a condition that would essentially mean the end of the population. Unlike the results of the Lamberson et. al. (1992) harvesting model, our simulations did not recover to a new equilibrium value after the harvesting ceased, but continued to fall towards zero.

To get a better sense of the relative merits of the different forest patterns in the face of continued harvesting, in each of the simulations we recorded the number of trials which led to complete extinction, or a population of zero in the 100th year. We recorded these values as fractions of the total number of trials (20 for each habitat pattern). These values are represented in Figure 4-6, where they are listed in order of increasing last ten year average populations.

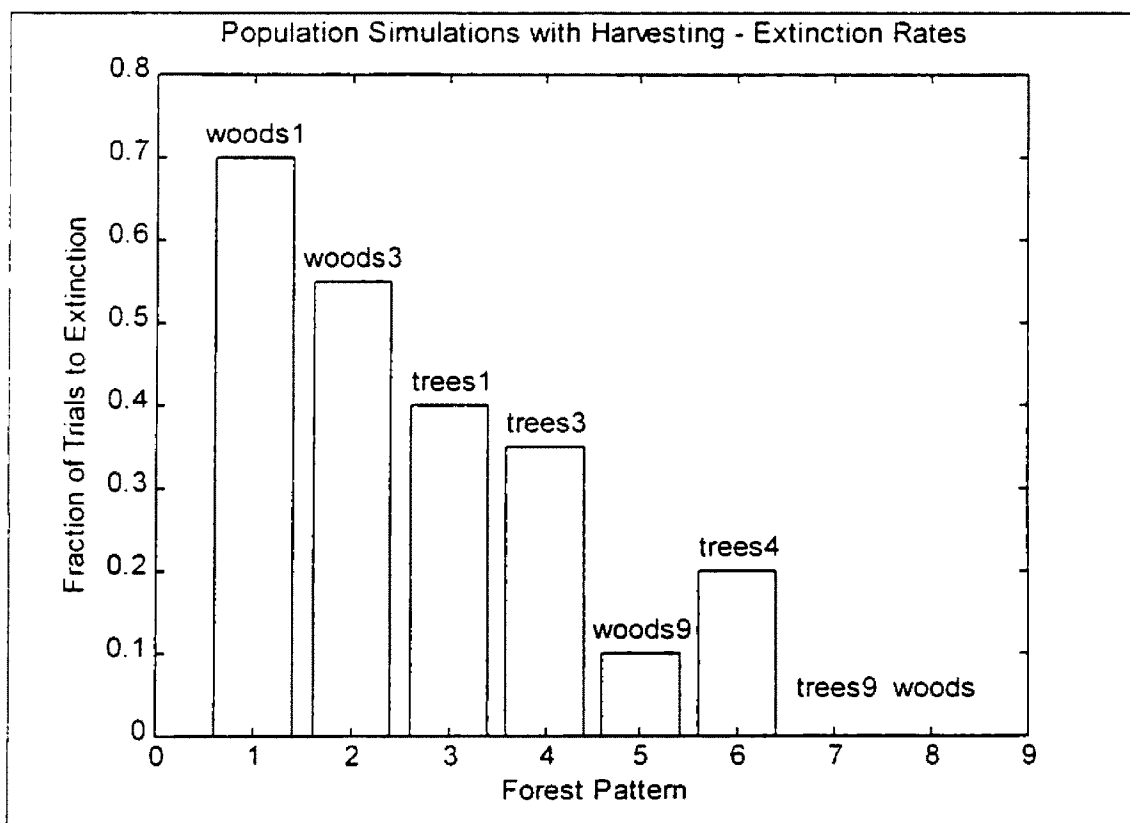


Figure 4.6: Extinction rates for simulations with harvesting

Again, the randomly spaced forests seem to be superior to the evenly spaced forest with the same sized habitat clusters. Unlike the population curves from the last two sections, however, the owls are avoiding extinction better in the *woods9* forest than in the *trees4* arrangement. This may have to do with the fact that extremely small owl populations

might be able to persist in one nine-site cluster better than two or three connected adjacent four-site clusters. Notice that none of the individual trials in the *trees9* and *woods* simulations ended in extinction. Despite a minor variation in the order, these extinction rates provide further evidence that randomly spaced habitat is significantly better at supporting owls.

4.5 Other Variations

Some concern might be raised with regard to the arbitrariness of our choices of forest matrix size, dispersal step-size, and dispersal search probabilities. Each of these could have a considerable effect on the outcome of our simulations. To explore this possibility, we conducted several experimental simulations with different values for each of these model characteristics. First, we looked at two variations on the careful search conditions of our dispersal process. In one case, instead of increasing the search parameter k by one for each dispersal step, we held it constant at $k = 3$ for all steps. For the other search condition, we let k be chosen randomly, for each stage of the dispersal, from the integers 2, 3, and 4. Over the 100 years of our trials, neither of these variations led to significantly different results on any of the habitat patterns.

We also experimented with different dispersal step sizes to see if this parameter was connected to the success of certain old-growth arrangements. For each of the step sizes 2 - 6, we simulated the dispersal of 10,000 juveniles on the *woods3* and *trees3* forests and recorded the number of these dispersals which were successful. Again, for both of these patterns, the step size had little or no effect on these experimental dispersal

success probabilities. The experimental *psd* values are listed in table 4-7. They are determined from dispersal simulations using the high, $psd = 0.36$, dispersal success program.

forest pattern	dispersal step-size				
	$l = 2$	$l = 3$	$l = 4$	$l = 5$	$l = 6$
<i>trees3</i>	0.4290	0.4249	0.4078	0.4199	0.4187
<i>woods3</i>	0.2185	0.2301	0.2506	0.2421	0.2264

Table 4.7: Dispersal success probabilities for different maximum search step-sizes

Finally, we increased first the number of trials averaged for each simulation and then the size of the forest matrix in an effort to decrease the deviations in our owl population curves. For each of the trials per simulation values 20, 30, 40, ..., 100 and forest matrix sizes 30x30, 40x40, ..., 90x90, we recorded the standard deviations of the owl populations for the first five years. While these fluctuations decreased somewhat with more trials and larger matrices, the results were small and did not seem to improve the precision of our results enough to warrant the exponential increase in simulation computer time.

CHAPTER 5 Quantifying Clustering

5.1 Observed Effects of Habitat Clustering

One of the most significant results of our simulations was the disparity between the randomly spaced and evenly spaced habitat patterns. For both of the dispersal schemes, owl populations were substantially and consistently higher for forest which were made up of randomly assigned clusters of habitat. In some cases, a random forest even sustained higher populations than an even forest composed of larger individual habitat clusters. We observed a similar effect when we included the effects of the destruction of owl habitat due to continued harvesting of old-growth timber. In this case, randomly spaced forests proved superior with lower extinction rates. We conclude that for our model, the macroscopic clustering caused by random placement of habitable clusters must increase a juvenile owl's prospects for successful dispersal and thus the likelihood of persistence and success for the entire population. To further explore this effect, we have devised a metric with which we can quantify the amount of clustering for each of the habitat patterns.

5.2 Cluster Deviation

Macroscopic habitat clustering results in a variation of the habitat density for different sections of the forest matrix. A highly clustered forest will have some regions with very high percentages of suitable sites and other areas with little or no old-growth. This characteristic is especially evident in the *trees9* and *trees4* patterns. Conversely, the

evenly spaced patterns like *woods1* and *woods3* have very consistent distributions of habitable sites throughout the matrix. To measure the density variation, we chose an integer $n \in \{2,3,\dots,10\}$ and sampled the habitable density for all possible n by n square subforests in the larger forest. In other words, for every cell in the forest matrix we counted the number of habitable owl sites in the n by n square with the original cell in its lower left corner. We divided each of these values by the number of cells in the square, n^2 . Thus, for each value of n we obtained 900 different local habitat densities. For all of our habitat arrangements, the mean of these values simply restated the fraction of habitable sites for the entire forest, usually near 0.38. However, the standard deviation gave us a measure of the level of macroscopic clustering for each forest. We will call this clustering metric the *cluster deviation*. Due to the variability of the randomly spaced patterns, we computed the cluster deviations of 20 different forests and used the average value. The cluster deviation values for each of the randomly spaced forest patterns are shown in Figure 5-1, plotted against the side length, n , of the sampling squares.

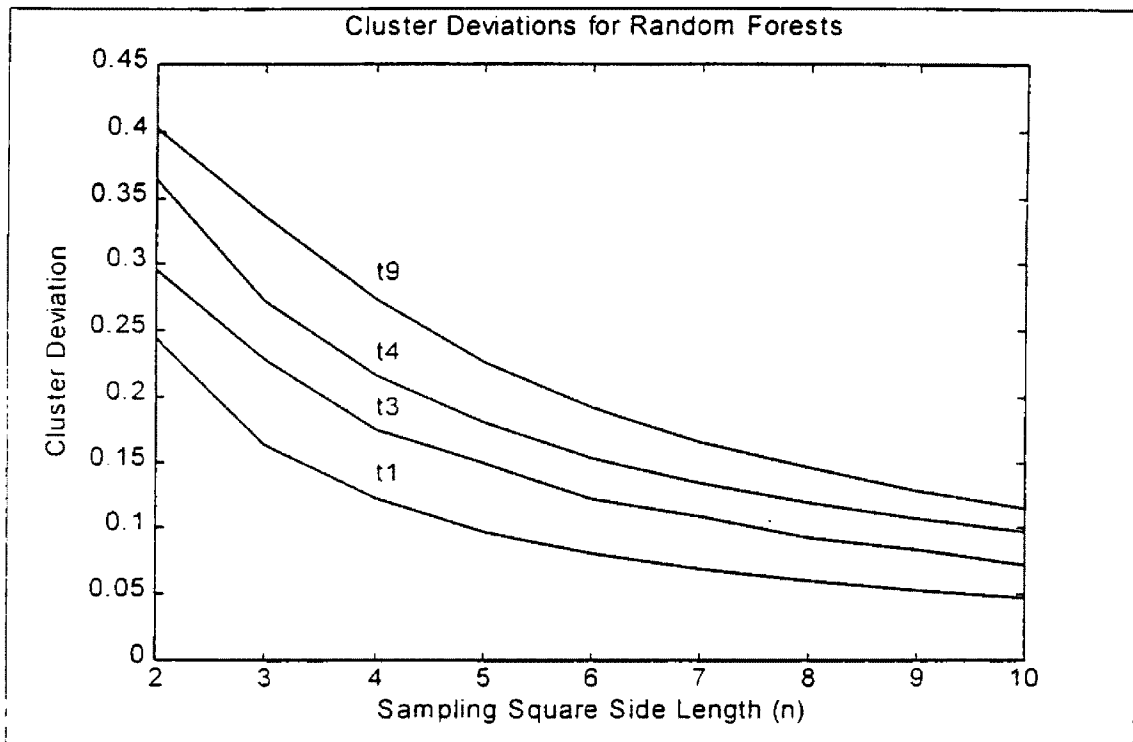


Figure 5.1: Cluster deviation values for the randomly spaced forest patterns

These curves show a hierarchy and relative spacing which is remarkably consistent with the 100-year population levels for our simulations on the random forests. As the value of the sampling square size n gets larger, each curve in Figure 5-1 also seems to tend to an equilibrium value. The apparent consistency of these clustering measures with the simulation results gave us confidence that we had discovered a valid method for measuring the overall habitat clustering of a particular landscape pattern. In contrast, the cluster deviation values for the evenly spaced forests varied considerably with the size of the sampling square. We show the results in Figure 5-2. Considering the fact that exactly the same forest pattern was used for each measurement ($n = 2$ through $n = 10$), it seems unreasonable that such significant variability should exist for the evenly spaced patterns. For certain sampling dimensions, the consecutive squares failed to accurately represent the uniformity of the pattern. This caused an erroneous cluster deviation for

certain values of n . For example, when sampling with squares of side-length $n = 5$, the highly clustered *woods9* forest has an artificially low clustering deviation number. This error is especially apparent because the *wood9* curve actually drops below *woods1* and *woods3* at this point. Upon initial inspection, it appears that the deviation values computed using larger sampling squares ($n \geq 7$) give the most accurate measure of the actual clustering present in these evenly spaced forests.

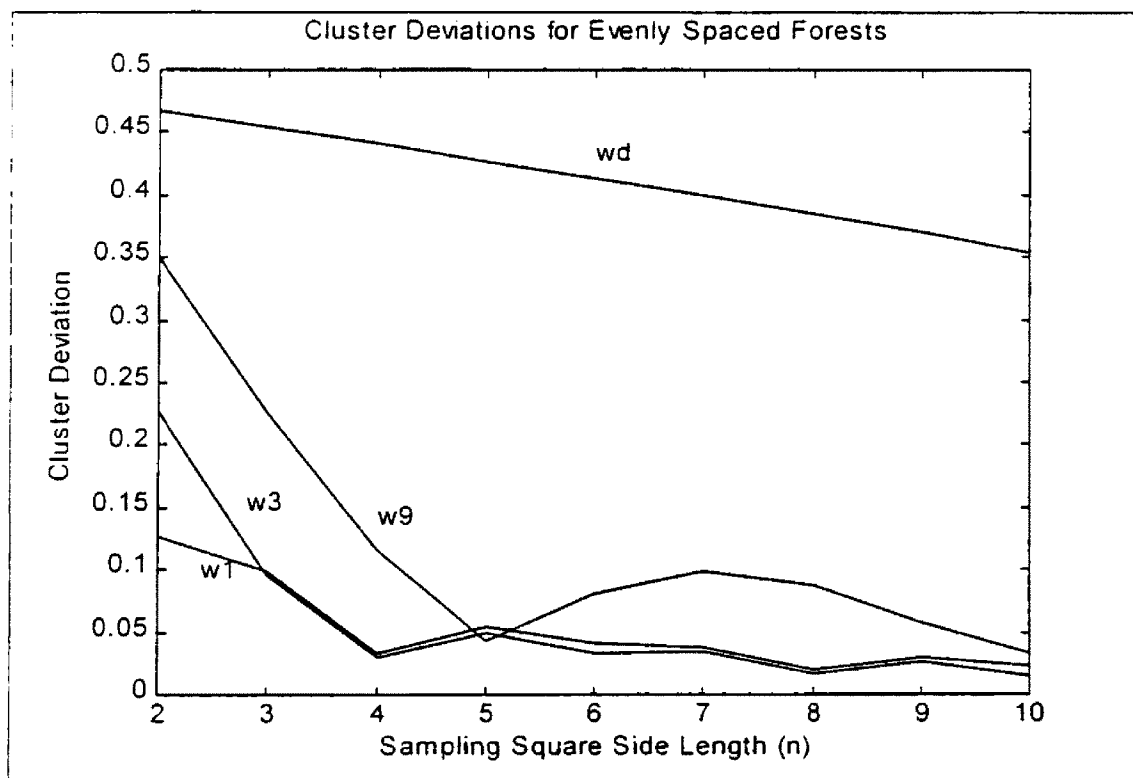


Figure 5.2: Cluster deviation values for evenly spaced forest patterns

In order to confirm the cluster deviation metric as a predictor of spotted owl success in our model, we computed correlation coefficients for the relationship between each habitat pattern's cluster deviation and the number of adult owl pairs it supported through the 100th year of our simulations. The 100-year populations were taken from the more realistic low dispersal success ($psd = 0.18$) version of the model. As Figure 5-3 shows.

the correlation coefficients were significantly high, particularly for the sampling square sizes $n = 7$ and $n = 8$.

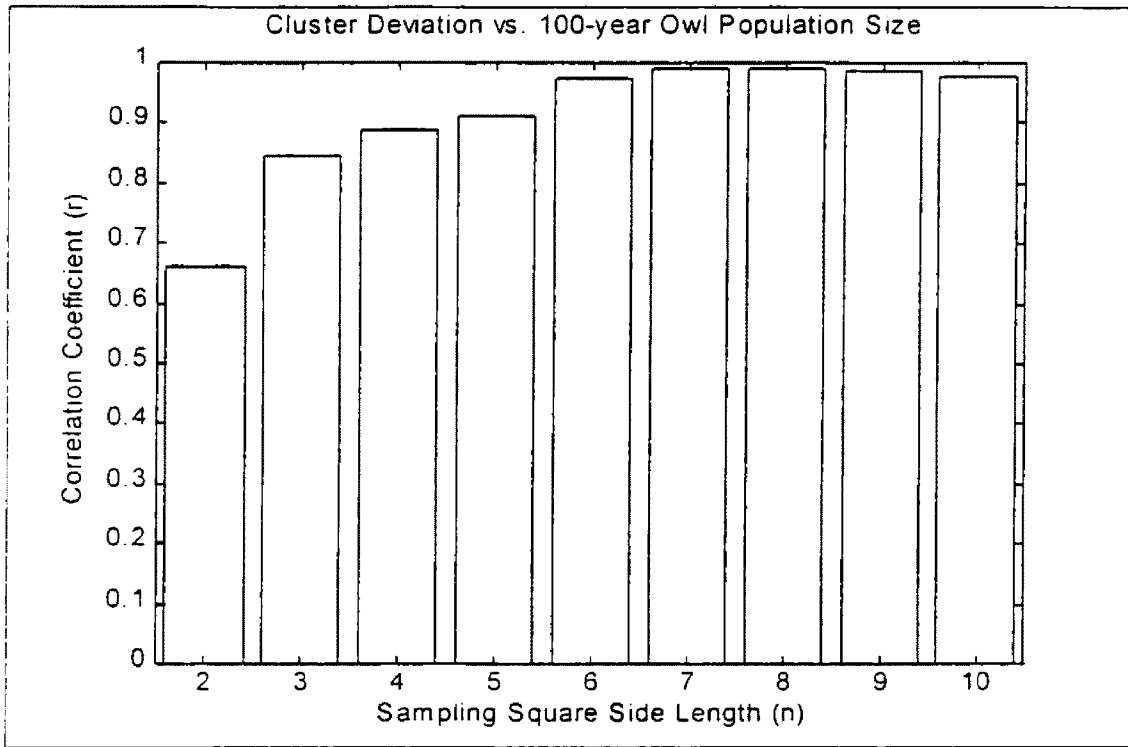


Figure 5.3: Correlation values: cluster deviation vs. final population size

These correlation values support the claim that our cluster deviation metric is an excellent predictor of long-term spotted owl success. Given a particular old-growth habitat configuration, we could compute its cluster deviation and use this number to evaluate its suitability for owl persistence and success. These correlation results, however, are intrinsically connected to the particular dispersal process which we have chosen for the simulations. Therefore, the relevance of this metric to real-world spotted owl populations depends considerably on the accuracy of our model. Of course, determining the accuracy of the simulation procedure is difficult. The metric could also be tested by determining

the old-growth clustering of known forests and comparing the values to observed owl populations.

5.3 Other Metrics

To validate our results internally, we devised two additional means of measuring the suitability of a particular habitat arrangement. First, we can scan through the matrix and compute the average site index value for the habitable owl sites in the forest. Due to the nature of our dispersal search conditions, it would seem reasonable that a forest with high average site index would allow a greater number of dispersing juveniles to successfully settle into habitable sites. The average site index values for each of the habitat patterns are listed in Table 5-4. As before, we averaged 20 different forests for each of the randomly spaced patterns in order to minimize the variability due to random assignment of suitable habitat.

forest pattern	<i>woods1</i>	<i>woods3</i>	<i>trees1</i>	<i>trees3</i>	<i>woods9</i>	<i>trees4</i>	<i>trees9</i>	<i>woods</i>
average site index	1.0	2.44	2.52	3.00	3.70	3.74	4.17	4.82

Table 5.4: Average site index values for all forest patterns

The order and magnitude of these values appear to be consistent with the simulation results. The *woods1* value of 1.0 is quite low and comes from the fact that all of the habitable sites in this forest are neighborless.

The second alternative metric is the experimental probability of successful dispersal. By the nature of our model, it seems reasonable that the probability of each juvenile owl finding a new home would have a significant effect on the propagation rates

and long-term population size. Thus far, we have only discussed the dispersal success rates of our model in terms of the theoretical probabilities associated with dispersal in a completely random forest or *trees1* pattern. The 0.18 and 0.36 *psd* values were computed with the assumption that every cell had an equal chance of being habitable and vacant, regardless of the characteristics of its neighbors. It is clear that this assumption will not be valid in a forest containing habitable sites which are evenly spaced or arranged in clusters of more than one site. For example, the neighbor of a habitable cell would have zero probability of being habitable in a *woods1* pattern and a rather high probability of being habitable in a *trees9* arrangement. The combination of our complex dispersal process and these habitat dependent probabilities makes the computation of dispersal success probabilities on non-random patterns exceedingly difficult.

We chose instead to compute these *psd* values experimentally. For each of the eight forest habitat patterns, we allowed 20,000 juvenile owls to disperse and recorded the number of such dispersals that were successful. Dividing this number by 20,000 gave us the experimental probability of successful dispersal for that particular forest. Forest matrices were not updated after successful dispersals so that habitable territories do not fill up. To avoid skewed results due to the variability of random assignment of habitable sites and initial adult pairs, the trials consisted of 1,000 dispersals on each of 20 different forest/adult configurations. To begin each dispersal attempt, a juvenile owl was assigned randomly to one of the habitable sites in the forest. The resulting values for each of our habitat patterns are listed in Table 5-5.

forest pattern	<i>woods1</i>	<i>woods3</i>	<i>trees1</i>	<i>trees3</i>	<i>woods9</i>	<i>trees4</i>	<i>trees9</i>	<i>woods</i>
experimental	0.0703	0.1286	0.1584	0.2110	0.2639	0.3036	0.3420	0.4362
<i>psd</i>								

Table 5.5: Experimental successful dispersal probabilities

The dispersal success measurements above were computed using the $psd = 0.18$ dispersal process. Again, the increasing sequence of these values agrees with the order of the 100-year population sizes recorded in our simulations. It should be noted that the experimental psd value for the *trees1* is slightly lower than the predicted value of 0.18. Despite the large number of sample dispersal attempts, the owls seem to be having more trouble finding habitable sites than expected. This apparent discrepancy between theoretical and experimental success rates is probably due to the fact that the juveniles always start their search from a habitable site so the actual chance that a neighboring site is habitable is slightly less than 0.38.

5.4 Comparing Correlations

We can now compute correlation coefficients to determine the predictive value of each of these alternative measures of habitat suitability. These values will provide comparison for an internal assessment of our original cluster deviation metric. Compared separately with the 100-year simulation population percentages, the correlation coefficients for each of the three metrics are listed in Table 5-6.

<u>metric</u>	<u>correlation coefficient</u>
cluster deviation ($n = 8$)	0.990
average site index	0.610
experimental psd	0.764

Table 5.6: Correlation values for habitat metrics vs. final population

These results point to the conclusion that the macroscopic clustering of habitat contributes much more significantly to the long-term owl population sizes than do either the quality of individual sites or the actual chance of dispersal success for searching juveniles in the initial forest. Another interesting observation is that the average site index values are highly correlated with experimental *psd*'s ($r = 0.941$), confirming the built-in assumption that our dispersal strategy and process is highly dependent on the site index characteristic.

CHAPTER 6

Conclusion

The northern spotted owl is a species whose continued survival depends on its relationship to and dependence on diminishing old-growth habitat. Unlike the majority of other models, we have taken an explicitly spatial approach to an inherently spatial problem. We set out to increase our understanding of this relationship with a series of computer simulations which recreated the population dynamics of the spotted owl in a variety of specific habitat settings. The forests themselves were varied systematically according to both the size of the clusters of habitable owl sites and the spacing of these clusters throughout the entire region. Cluster size varied from single owl sites to nine adjacent territories of old-growth forest, and these clusters were arranged either randomly or evenly (uniformly) to form each habitat pattern. The simulations themselves consisted of a random assignment of adult owl pairs to a certain percentage of the habitable sites in a given forest pattern, followed by a repeated cycle of birth, juvenile dispersal, and death. Each trial lasted 100 years and we recorded the overall population each year, while keeping track of the location of each owl. Despite their assumptions and simplicity, our simulations give specific numerical results for a declining population which propagates through dispersal in a highly fragmented habitat landscape.

As expected, the population curves supported the commonly accepted notion that, given a limited amount of habitat, larger clusters of suitable sites are capable of supporting a larger population. In addition, we found that with a fixed cluster size, spacing these clusters randomly throughout the forest yielded significantly higher long-

term owl populations compared to a uniform pattern of clusters. It seemed that the random spacing promoted the formation of large-scale clusters of clusters which gave the young owls more extensive regions of connected habitat in which to disperse.

To verify these observations, we devised a metric with which we could quantify the overall clustering of a given forest pattern. For each pattern, we measured the total variation in a large sample of local habitat densities. The resulting *cluster deviation* values correlated very highly with the long-term population levels of the computer simulations. Finally, we compared the cluster deviation metric with two other means of quantifying overall habitat suitability and found that neither of the alternative methods could reproduce the same high correlation with long-term population success.

It is clear from the simulations that random spacing of habitat and the resulting clustering have a profound effect on the success of the owl populations in our model. We hope that the advantages of random versus even spacing discovered here can be explored in more detail and incorporated into future harvest strategies. The cluster deviation metric might also be investigated, tested, and adapted to quantify overall suitability of real owl habitat patterns. If specific spatial models can be designed, tested, and improved to more accurately recreate the population dynamics of endangered species in nature, they will provide an excellent tool for predicting and responding to concerns about complete extinction.

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