Trading Habitat Patches for the Red Cockaded Woodpecker: Incorporating the Role of Landscape Structure and Uncertainty in Decision Making

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14. ABSTRACT

Our SEED project derived a method to trade habitat that incorporates the role of landscape connectivity for population viability, and level of scientific uncertainty regarding landscape-scale processes. Our project focuses on the development and application of spatially-explicit population models (SEPMs) to inform habitat trading decisions. Military readiness will often require changing the spatial allocation of endangered species habitat prior to reaching a scientific consensus regarding the dispersal behaviors of listed species. Therefore, we used Pattern Oriented Modeling to reduce uncertainty in SEPMs regarding dispersal of red-cockaded woodpeckers (RCW) for Camp Lejeune. We used the subset of SEPMs capable of reproducing observed patterns to evaluate six alternative habitat trades. Landscape Equivalency Analysis was used to estimate if the patches traded make equivalent contributions to rates of population growth and migration at a regional scale. Decision analysis indicated that despite the remaining uncertainty in dispersal behaviors, a further reduction in uncertainty will likely not change the estimate of the most cost-effective trade.

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EXECUTIVE SUMMARY **1**

1. PHASE I. REDUCING UNCERTAINTY IN THE RED-COCKADED WOODPECKER SPATIALLY-EXPLICIT POPULATION MODEL WITH PATTERN-ORIENTED MODELING **6**

1.1 OBJECTIVE 6
1.2 BACKGROUND 6
1.3 METHODS 8
1.3.1 Landscape Map *8*
1.3.2 Initial Conditions *10*
1.3.3 Parameters Used in the Simulation *10*
1.3.4 Simulation Conditions *15*
1.3.5 Filtering: Model Calibration by Comparing Observed and Expected Patterns *15*
1.4 RESULTS AND DISCUSSION 19
1.5 CONCLUSIONS 26

2. PHASE 2. HABITAT TRADING FOR THE RED-COCKADED WOODPECKER UNDER UNCERTAINTY REGARDING DISPERSAL BEHAVIORS **27**

2.1 OBJECTIVE 27
2.2 BACKGROUND 27
2.2.1 Habitat Trading *27*
2.2.2 Considering Landscape Processes when Trading *29*
2.2.3 Landscape Equivalency Analysis (LEA) *30*
2.3 METHOD FOR EVALUATING HYPOTHETICAL TRADES WITH LEA UNDER ALTERNATIVE DISPERSAL MODELS 31
2.3.1 Step 1. Constructing Alternative Landscapes *31*
2.3.2 Step 2. Projecting Ecological Services under Uncertainty *37*
2.3.3 Step 3. Estimate Spatially-explicit Debits and Credits with LEA *38*
2.4 RESULTS AND DISCUSSION 40
2.4.1 Mitigation Choice 1: Restore Only Beck and Allen Tracts *40*
2.4.2 Mitigation Choice 2: Restore only Lanier *46*
2.4.3 Mitigation Choice 3: Restore Beck, Allen, Lanier and GSRA *47*
2.4.4 Making Cost-effective Decisions under Uncertainty *49*
2.5 CONCLUSIONS 52

3. PHASE 3: EXPLORING HABITAT-FITNESS RELATIONSHIPS WITH PRE-EXISTING DATA **53**

3.1 OBJECTIVE 53
3.2 BACKGROUND 53
3.3 METHODS 54
3.3.1 Foraging Habitat Data for MCBCL *54*
3.3.2 Spatially Integrating Foraging Habitat Data *54*
3.3.3 Regression Approach *55*
3.4 RESULTS 57
3.5 DISCUSSION 59
3.6 CONCLUSION 61

4. OVERALL CONCLUSIONS AND RECOMMENDATIONS **62**

4.1 SUMMARY OF SIGNIFICANT RESULTS 62
4.2 PRIORITIES FOR FUTURE RESEARCH 63
4.2.1 Habitat Trading for RCWs in Onslow Bight (Bruggeman, JR Walters et al.) *63*
4.2.2 Development of SEPMs for other Species (Bruggeman, T Wiegand et al.) *65*

5. LITERATURE CITED **71**

APPENDIX A **77**

APPORTIONING GENETIC VARIANCE OVER SPACE 77

APPENDIX B **79**
PRESENTATIONS 79

Acronyms

AIC	Akaike Information Criterion
dbh	diameter at breast height
GIS	Geographic Information Systems
GSRA	Greater Sandy Run Area
HCRW	Habitat-based Correlated Random Walk
LEA	Landscape Equivalency Analysis
LSY	Landscape Service Year
MARSOC	Marines Special Operations Center
MU	Management Unit
MCBCL	Marine Corps Base Camp Lejeune
PBG	Potential Breeding Groups
POM	Pattern-Oriented Modeling
RCW	Red-cockaded woodpecker
SEPM	Spatially-explicit population model
USFS	United States Forest Service
USFWS	United States Fish and Wildlife Service
VPI&SU	Virginia Polytechnic Institute and State Univ. (Virginia Tech)

Figures

Figure 1.1. Breeding group structure and demographic transitions for the Red-Cockaded Woodpecker. 7
Figure 1.2. Camp Lejeune land cover map used in the spatially-explicit population model. 9
Figure 1.3. Observed temporal patterns on MCBCL used to establish pattern fulfillment indices for Potential Breeding Groups and Floaters. 16
Figure 1.4. Scatter plot of parameter values for female floater perceptual distance and corresponding pattern fulfillment criteria (N=719). 21
Figure 1.5. Change in parameter estimates for the uncertain dispersal parameters owing to filter optimization. 25
Figure 2.1. The Onslow Bight Landscape in southern coastal North Carolina. 28
Figure 2.2. Silhouette of Camp Lejeune used to highlight proposed changes in allocation of RCW habitat. 34
Figure 2.3. Trajectories of Potential Breeding Groups used to estimate LEA credits derived from the original Letcher SEPM and one parameterization of the Habitat-correlated Random Walk SEPM. 43
Figure 2.4. Trajectories of average expected heterozygosity within breeding groups (Hs) used to estimate LEA credits derived from the original Letcher SEPM and one parameterization of the Habitat-correlated Random Walk SEPM. 44
Figure 2.5. Trajectories of average genetic divergence among breeding groups (D_{ST}) used to estimate LEA credits derived from the original Letcher SEPM and one parameterization of the Habitat-correlated Random Walk SEPM. 45
Figure 2.6. LEA credits remaining after trading on-base clusters for those on the Beck and Allen tracts or for those on the Lanier tract. 46
Figure 2.7. LEA credits remaining after trading on-base clusters for those on the Beck, Allen, Lanier, and Greater Sandy Run Area (GSRA), for all SEPMs used to evaluate changes in RCW population dynamics. 48
Figure 3.1. Frequency distribution of fledglings per group (fitness) observed from 1998 to 2000 on MCBCL. 55
Figure 3.2. A) Frequency distribution of fledglings per group (fitness) predicted by Model C. B) Frequency distribution of residuals from Model C. 59
Figure 4.1. Predicted census population size (N) using the RCW SEPM assuming a HCRW, and N predicted by the null and full linear regression models. 67
Figure 4.2. Prediction of inbreeding coefficient (F) by the RCW SEPM assuming a HCRW, and by the null and full linear regression models. 68
Figure 4.3. Prediction of average coancestry due to population subdivision (F_{ST}) by the RCW SEPM assuming straight dispersal, and by the null and full linear regression models. 69

Tables

Table 1.1.	Modified classification of Camp Lejeune Land Cover Map used to estimate friction of land cover types for dispersal.	8
Table 1.2.	Recruitment and survival parameter values used in Red-Cockaded Woodpecker spatially-explicit population model.	13
Table 1.3.	Dispersal and competition parameter values used in Red-Cockaded Woodpecker spatially-explicit population model.	14
Table 1.4.	Results of filtering for the 21 uncertain parameters using the five pattern fulfillment criteria.	20
Table 1.5.	Spearman Rank correlation coefficient (rho) describing the strength of the relationship between uncertain parameter values and statistical indices of model fit to observed patterns on MCBCL.	22
Table 1.6.	Filter combinations used to reduce parameter uncertainty.	24
Table 2.1.	Description of proposed takes examined with Landscape Equivalency Analysis.	35
Table 2.2.	Forest attributes describing stands in Greater Sandy Run Area that may be suitable locations for RCW nesting cavities.	37
Table 2.3.	Landscape Service Years (LSYs) that evaluate the ability of restoring 9 clusters on the Beck and Allen tracts to offset habitat loss and fragmentation effects resulting from the loss of 4 clusters (best case) or 12 clusters (worst case) on the Main Base.	42
Table 2.4.	Results of Decision Analysis applied to habitat trading using Landscape Equivalency Analysis under uncertainty regarding dispersal.	50
Table 2.5.	Projected management costs for the three mitigation choices (Beck and Allen Only, Lanier Only, and Restore All Possible outside Main Base).	50
Table 2.6.	Cost effectiveness of alternative mitigation choices using the Letcher SEPM and the expected value of the trade given uncertainty in the HCRW SEPM (EV[Trade|M]).	51
Table 3.1.	Derivation of independent variables for use in habitat-fitness relationships.	56
Table 3.2.	Habitat-fitness relationships predicted by linear regression and AIC model selection. Data analyzed represent 154 Potential Breeding Groups observed from 1998 to 2000.	58

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Executive Summary

The objective of our SEED project was to derive a method to trade habitat that incorporates the role of landscape connectivity for population viability, and level of scientific uncertainty regarding landscape-scale processes. Habitat trading provides an opportunity to change the spatial allocation of protected habitat to relieve training restrictions, but may also threaten the long-term viability of some populations. Some species are able to achieve regional persistence through the exchange of individuals among local breeding groups while maintaining a certain level of independence in productivity at local scales, thereby avoiding spatial correlation in demographic cycles that could lead to regional extinction (Hanski and Gaggiotti 2004). Therefore, landscape connectivity, or the extent to which landscape patterns facilitate movement of individuals, may contribute substantially to population viability for many species found on DoD installations.

Our study focused on the Red-Cockaded Woodpecker (RCW) because its presence on many DoD facilities in the southeastern US has led to training restrictions. Further, there is a scientific consensus that habitat connectivity is critical for population persistence (Cox et al. 2001; Schiegg et al. 2002). RCWs are well studied due to their cooperative mating system and tendency to pass breeding territories to the next generation. A breeding pair inhabits a territory and often shares the habitat with adult helpers who contribute to the defense of the territory and recruitment of offspring (Conner et al. 2001).

We chose to work on U.S. Marine Corps Base Camp Lejeune (MCBCL) because the natural resource managers expressed an interest in helping to restore RCW habitat off-base to relieve training restrictions and prevent urban encroachment. MCBCL is home to the Marine's 2nd Expeditionary Force and is located on the southern coast of North Carolina in Onslow County. MCBCL has already completed cooperative purchases of five off-site parcels through partnerships with North Carolina Wildlife Resources Commission (NCWRC) and North Carolina Coastal Land Trust (NCCLT), in accordance with the U.S. Army's Compatible Use Buffer Program and recommendations of Onslow County's Joint Landuse Study. The cooperative purchase of off-base properties to prevent residential or commercial development is often referred to as Encroachment Partnering.

Determining how Encroachment Partnering will lead to regulatory relief on-base is an important area of research because habitat trading programs will change how habitats are allocated for small and sometimes declining populations. Uncertainty regarding critical biological processes required to maintain persistent subdivided populations should be the focus of any scientifically defensible habitat trading program. We addressed two critical uncertainties. First, we were uncertain how differences in vegetative composition of territories affect reproductive success (James et al. 2001; Walters et al. 2002). Second, we were uncertain how land use patterns between RCW territories affect the probability of successful dispersal (J. Walters, personal communication).

This project derived an approach to integrate uncertainty analysis of critical biological processes with a landscape-scale tradable credit system designed to minimize habitat fragmentation effects

on population viability. Our project focuses on the development and application of spatially-explicit population models (SEPMs) to inform habitat trading decisions. SEPMs represent a hypothesis regarding how a population may respond to changing land use patterns. Our project can be divided into three phases. The first was to use Pattern-Oriented Modeling to calibrate the RCW SEPM for MCBCL while testing a new submodel to describe dispersal behaviors. The second was to use all SEPMs capable of reproducing multiple patterns to evaluate habitat trades on and near MCBCL using the generalized landscape-scale accounting system Landscape Equivalency Analysis. The third phase was to develop a new recruitment submodel that may be used to extend the RCW SEPM to areas that lack historical demographic data available on MCBCL but would still like to participate in habitat trading with DoD.

Phase 1: Uncertainty Regarding Dispersal

Despite a tremendous amount of knowledge regarding the mating system of RCWs, we are still uncertain how RCWs move through a heterogeneous landscape. We tested a new dispersal submodel using Pattern-Oriented Modeling (POM). POM is a structured approach for understanding the underlying processes that generate the patterns we observe in nature (Grimm et al. 2005). POM tests the ability of several thousand SEPMs, each with a different parameterization, to reproduce patterns observed in nature. Often just a few SEPMs satisfy all pattern fulfillment criteria. POM provides an objective and quantitative approach for including multiple models and consequently uncertainty into model-based environmental decision making.

We compiled pre-existing data on land cover patterns and patterns describing the RCW population on MCBCL. Next, the results of 100,000 different SEPMs, each describing different dispersal behaviors, were compared with RCW patterns observed on MCBCL. Only 8 models were capable of reproducing all the patterns—a significant reduction in uncertainty. For parameters relating to floater survival and distance at which a breeding vacancy can be detected, we were able to reduce parameter uncertainty by 54–92%. However, for parameters relating to the attractiveness of different land cover types for dispersal, or conversely landscape friction, we were unable to reduce parameter uncertainty. This may have resulted because existing territory locations are highly clumped on MCBCL and floaters do not have to interact with much of the landscape in order to find a breeding vacancy. POM provides a method of improving SEPMs without spending more money on field data collection and can be used to prioritize which patterns in nature are most useful for reducing prediction uncertainty (Wiegand et al. 2004).

Phase 2: Habitat Trading

Habitat patches often differ in conservation value due to their size, shape, vegetative composition, and location relative to other land cover types in the landscape. We devised the Landscape Equivalency Analysis (LEA) to determine if habitat patches traded make equivalent contributions to rates of recruitment within breeding groups and rates of dispersal among breeding groups (Bruggeman et al. 2005). LEA assigns conservation value to habitat at the local scale based on its contribution to abundance and genetic variance estimated at the regional scale. The uniqueness of this approach lies in the ability of LEA to incorporate the unequal contribution of habitat patches and areas between patches into the estimate of conservation value. A tradable credit system that accounts for differences in conservation value among habitat patches is more likely to achieve sustainable populations at the least cost.

In Phase 2 we used Decision Analysis which provides a structured approach for comparing alternative choices in the face of scientific uncertainty. Alternative mitigation choices were evaluated using the eight SEPMs derived from POM and the Letcher SEPM, the model currently used by DoD and DOI to inform RCW management decisions. For all habitat trades and models considered, restoring RCW habitat outside the Main Base to compensate for the loss of clusters inside the Main Base increased habitat fragmentation effects. The Letcher model predicted the smallest increase in fragmentation effects. Valuing credits based on habitat occupancy, or the number of Potential Breeding Groups (PBGs), indicated that restoring habitat on all parcels outside of the Main Base, including Lanier, Beck, Allen and the Greater Sandy Run Area, is the best decision. In contrast, valuing credits based on changes in rates of recruitment within clusters and rates of migration among clusters indicated that restoring only the Lanier tract is the best habitat trade. The Lanier tract was the smallest parcel considered, but provided the greatest connectivity with RCW clusters on the Main Base. Decision analysis indicated that despite the remaining uncertainty in dispersal behaviors, a further reduction in uncertainty will likely not change the decision to restore only the Lanier tract instead of all possible locations.

LEA estimates the financial value of tradable credits based on the in-kind replacement costs of ecological services that differ in sensitivity to changes in habitat area and connectivity. Therefore, LEA provides a nexus for ecological-economic analysis of management decisions at a landscape scale. Even though no trade considered prevented habitat fragmentation effects, each trade did increase habitat occupancy. For discussion purposes we calculated the value of a LEA credit for Potential Breeding Groups and discussed how DoD could determine when it is more cost-effective to forego a trade to collect more data and update model assumptions to re-evaluate trading choices.

Phase 3: Habitat-Fitness Relationships

In an effort to increase the spatial scale of our model, we investigated statistical relationships between pre-existing data describing foraging habitat on MCBCL and the number of fledglings produced per cluster. Early in the project we determined that data describing RCW demography required by the current SEPM is not available across the Onslow Bight Landscape. The SEPM has been constructed to work with the RCW monitoring programs implemented on MCBCL and Fort Bragg, which have contributed much to management objectives at smaller scales and the field of landscape ecology. We argue that DoD's goal of using Encroachment Partnering to contribute to regulatory relief requires updating model structure to work at broader spatial scales.

The current model estimates the number of fledglings per group (group fitness) based on the ages of parents and number of helpers. While this approach is based on a statistically significant regression equation ($p<0.0001$, $R^2 = 0.08$), it requires knowing the age structure of the breeding population, which may be determined using long-term bird banding studies. Replicating this effort across the Onslow Bight Landscape would be difficult.

Previous researchers have attempted to relate group fitness to vegetative characteristics near cavity trees (James et al. 2001; Convery 2002; Walters et al. 2002). While these efforts have observed that the number of adults in a group is related to vegetative characteristics, statistically significant relationships with fitness were often not observed. However, Convery (2002) did successfully relate group fitness to habitat attributes in 23 territories on MCBCL. Convery

(2002) supplemented pre-existing data on forest structure with surveys of ground cover within a group's home range. Defining a group's home range and characterizing ground cover is labor intensive and these efforts have not yet been replicated for other groups on MCBCL.

In this phase, we explored habitat-fitness relationships using a moving window approach and incorporating yearly variation in recruitment. The moving window approach was used because we will often lack the resources to define home ranges. Instead we characterized the forest structure within 500 m, 1,000 m, and 3,500 m of the cavity tress. The RCW Foraging Habitat Survey conducted on MCBCL from 1998 to 2000 was used to estimate the density of pines and hardwoods within these windows. Further, field observations suggested that variation in rainfall may affect recruitment. To conduct an initial screen of this hypothesis, we included a year effect to determine if year to year variation in environmental factors may be an explanatory variable for fitness. Selection among alternative models was performed using the Akaike Information Criterion (AIC) to determine the most parsimonious model capable of predicting recruitment (Burnham and Anderson 2002).

We were unable to derive a statistically significant regression predicting group fitness when only habitat variables were included ($p=0.063$, $R^2=0.03$), but these results did suggest that forest structure at the 1,000 m and 3,500 m might affect recruitment. Next, we included the influence of helpers, which improved model fit ($p=0.0014$, $R^2=0.09$). Variables describing forest structure within 3,500 m were still retained in this regression equation. Inclusion of a year effect further improved model fit ($p=0.0001$, $R^2=0.12$), and increased the significance of the habitat variables. We found that the year effect was more important than habitat features but less important than the number of helpers. Researchers have argued that models with AIC scores within 2 units should be treated as equivalent (Richards 2005). Therefore, we further simplified the models until they were within 2 AIC units of the model with the lowest AIC score. This approach indicated that the number of fledglings could be predicted based on the number of helpers and year effect alone ($p=0.0002$, $R^2=0.09$).

We have derived an approach to predict recruitment using data that are more easily collected at broader spatial scales than age structure of breeders. The significance of the year effect and habitat attributes well outside of home ranges was surprising. More research is required to determine if rainfall and/or temperature patterns might contribute to recruitment. These results could lead to a better SEPM and more effective habitat trading program. For example, some parcels may not be very valuable for RCWs if surrounded by non-forested areas within 3,500 m of cavity trees. Ignoring climatic variability could lead to an under- or over-estimate of tradable credits.

Overall Conclusions and Recommendations

The use of Encroachment Partnering to relieve training restrictions due to the presence of endangered species highlights the importance of understanding how changing landscape patterns may affect recruitment and migration. Individually-based, spatially-explicit population models can be used to determine how changing habitat area and / or connectivity will affect population viability. These models allow interaction between rates of recruitment within patches with rates of migration among patches. We applied new techniques to improve how SEPMs can be used for Encroachment Partnering. By integrating LEA and POM we found that existing monitoring

data reduced enough uncertainty regarding dispersal to prioritize trading decisions. However, we also observed that examining habitat trades at this spatial extent always resulted in increasing habitat fragmentation effects.

The current study estimated habitat fragmentation effects relative to the spatial distribution of clusters on the Main Base that have been planned to meet MCBCL's contribution to recovery of the Coastal North Carolina population. The Coastal North Carolina population also includes RCW clusters in Croatan National Forest and Holly Shelter State Game Lands, which are located within the Onslow Bight Landscape. Determining how habitat trading would change levels of habitat fragmentation across the entire Onslow Bight landscape is beyond the scope of a one year SEED grant. However, habitat trades that increase habitat fragmentation relative to the current population on MCBCL may actually decrease fragmentation across the entire Coastal North Carolina recovery population. In order to determine if DoD can spread RCW liability across the Onslow Bight landscape without jeopardizing recovery, we need to understand how landscape patterns affect recruitment and migration at a broad geographic extent.

In order to capture habitat fragmentation effects, LEA assigns a conservation value to trades at a local scale based on marginal changes in ecological services at the landscape (regional) scale, relative to service levels expected in an unfragmented or baseline landscape. We defined baseline for MCBCL as the apportionment of genetic variance within and among breeding groups afforded by their recovery plan. By applying the concept to the entire Onslow Bight, we might define baseline as the apportionment of genetic variance within and among breeding groups, averaged across all three management units (MUs), afforded by reaching property-specific recovery goals (USFWS 2003a). **In contrast to the baseline defined for MCBCL, the baseline for the Onslow Bight does not provide the most clumped distribution of habitat possible, merely the most clumped distribution possible on public lands.** We propose a landscape genetics study in the Onslow Bight to determine if the spatial distribution of RCW clusters specified by the Recovery Plan provides adequate rates of migration or if restoration of private land would increase population viability, justifying the use of Encroachment Partnering to provide regulatory relief.

We propose a second study to develop an SEPM for a different threatened or endangered species. Prior to beginning research on our SEED grant, the Helmholtz Centre for Environmental Research funded collaboration between Douglas Bruggeman and Thorsten Wiegand to establish relationships between structural and biological descriptors of habitat fragmentation (Bruggeman et al. submitted). The research used the RCW SEPM and equilibrium landscape conditions to establish relationships between landscape indices founded in the fundamental theory of point pattern phenomenon and population genetic theory. Results indicated that the second order spatial structure of habitat is well correlated to behavioral- and demographic-rules coded into the RCW SEPM. We propose applying the approach "in reverse" for a new species. In other words, using data describing the second moment approximation of alternative land cover types and population genetic data to begin constructing an SEPM for new species. We stress that relationships between landscape indices and population genetic structure probably do not provide an adequate surrogate for SEPMs when evaluating management decisions that change habitat spatial structure over time.

1. Phase I. Reducing Uncertainty in the Red-Cockaded Woodpecker Spatially-Explicit Population Model with Pattern-Oriented Modeling

1.1 Objective

Uncertainty regarding critical biological processes required to maintain persistent subdivided populations should be the focus of any scientifically defensible habitat trading program. Habitat trading programs will change how habitats are allocated for small and sometimes declining populations. Further, landscape patterns that may facilitate or restrict movement of individuals critical for population persistence will be changing over time. Individually-based and spatially-explicit population models (SEPMs) are one approach to test the response of populations to non-equilibrium conditions, created by habitat trading programs. The objective of this phase was to develop an uncertainty analysis for the Red-Cockaded Woodpecker (RCW) SEPM currently used at Marine Corps Base Camp Lejeune (MCBCL).

1.2 Background

A SEPM is comprised of linked submodels that simulate how different biological processes are affected by land cover patterns. Initially, SEPMs were heavily criticized for their complexity, large data requirements, and reliance on uncertain parameters (Beissinger and Westphal 1998). However, Pattern-Oriented Modeling (POM) has been derived to construct and validate these models with less data than previously imagined (Grimm et al. 2005; Wiegand et al. 2004). POM accomplishes this by using additional information encoded in observed population-level patterns for indirect parameter estimation. A pattern is defined as anything beyond random variation, or any signal beyond noise, and is used as an indicator of the system's internal behavior (Grimm et al. 1996). Pattern-Oriented Modeling also is a method of comparing the ability of different SEPMs to reproduce biological patterns observed in nature (Grimm et al. 2005).

While POM can be used to derive the structure of SEPMs, or the types of submodels included and how they interrelate (Grimm et al. 1996), we focused on using POM to reduce parameter error (Wiegand et al. 2004). Parameter error is the uncertainty associated with the parameter values used in a submodel. POM can be used to reduce parameter error by comparing the ability of alternative parameterizations of a model to reproduce patterns observed in nature. First, one must determine the range of possible parameter values based on expert knowledge or parameters derived in landscapes where data are more abundant. Second, the range of possible parameter values is subdivided into equidistant values. Third, stratified sampling of possible parameter sets without replacement is used to combine all possible parameter values that are treated as uncertain. Fourth, the SEPM is run with several thousand different parameterizations to ensure exhaustive sampling of possible parameter combinations. Fifth, parameterizations unable to reproduce RCW patterns observed on MCBCL are removed from consideration through statistical comparisons between patterns produced by the simulation (i.e., expected patterns) and patterns observed on MCBCL (i.e., observed patterns). This process will be referred to as "filtering" parameterizations.

We applied POM to the RCW SEPM originally described by Letcher et al. (1998). The Letcher model assumes the population consists of breeders, helpers, floaters, and fledglings (Fig. 1.1). The probability of an individual transitioning among these classes depends on demographic,

behavioral, and landscape factors. Our study focuses on uncertainty regarding how dispersal behaviors affect population processes. The Letcher SEPM assumed that when birds leave their natal territory they choose a direction of travel at random and then travel in a straight line. However, field biologists have observed that many fledglings embark on forays, seemingly investigating nearby breeding habitat (Jeffrey Walters, personal communication). Therefore, it may be best to assume that birds use knowledge of forest structure when deciding which direction to travel. Others have observed that birds often avoid crossing non-forested areas during foraging (Connor and Rudolph, 1991; Belisle and Desrochers 2002), seemingly to increase the chance of finding breeding and foraging habitat or refuge from predation. Therefore, birds may chose not to travel straight in order to avoid crossing non-forested areas.

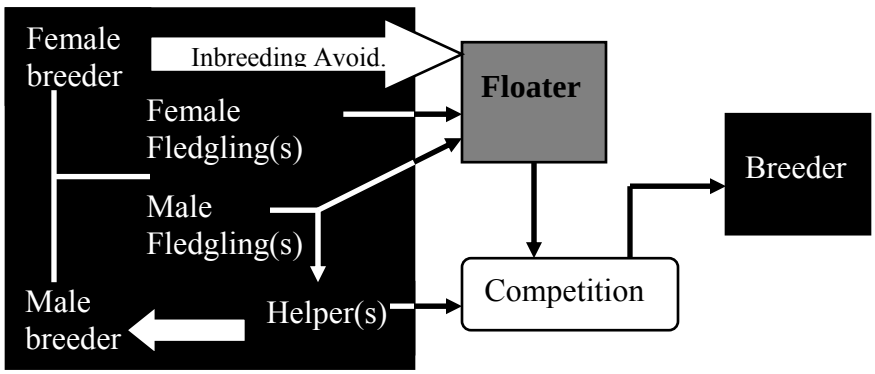

Figure 1.1. Breeding group structure and demographic transitions for the Red-Cockaded Woodpecker. Black boxes denote breeding territories and the grey box denotes the matrix crossed during floating behaviors.

Ecologists have derived many ways of simulating dispersal behaviors. The most simple is a random walk in which individuals choose each step at random. Under a correlated random walk, the turning angles between successive moves are not statistically independent (Zollner and Lima 1999). A random component remains in this model because the direction of travel selected is based on comparing probabilities of turning ($d_{0°}$, $d_{45°}$, etc…) to a random number, often creating a zigzag pattern of dispersal even if the probability of not turning ($d_{0°}$) is large. To incorporate the influence of forest cover, we will derive a Habitat-based Correlated Random Walk (HCRW) similar to that used by Kramer-Schadt et al. (2004). HCRW combines the probabilities of turning different angles with the probability that a bird will select different land cover types for dispersal (Ricketts et al. 2001). Some land cover types may limit or facilitate dispersal among habitat patches, thus varying in levels of "landscape friction", modeled as parameter "m". By introducing a third parameter "B" that weighs the level of importance birds place in directional or habitat rules, the HCRW can be represented as:

$$P[C^i{}_{t+1} \mid C^j{}_t] = (1-B)d^i + B\left(m^i / \sum m\right). \qquad (1.1)$$

Where $P[C^i_{t+1}|C^j_t]$ is the probability the bird will be in cell i at time t+1 given that it is currently in cell j now, d^i is the probability of turning toward cell i relative to the direction of travel in the previous time step, and m^i is the landscape friction assigned to cell i, which is normalized by the sum of the friction values for all 8 cells in the floaters immediate neighborhood.

We are uncertain what the appropriate parameter values for d, m, and B in the HCRW should be. The objective of Phase 1 was to use POM to estimate parameter values for the HCRW using RCW patterns observed on MCBCL. The Letcher model was derived from monitoring data from Fort Bragg not Camp Lejeune. So we examined uncertainty in other parameters associated with dispersal, including the number of steps taken, survival of floaters, and distance at which a bird can detect a breeding vacancy. A total of 21 parameters are treated as uncertain. The uncertain parameter values were filtered through multiple RCW patterns observed on MCBCL. Examples of patterns include temporal patterns of population dynamics and spatial patterns of territory connectivity and pairwise genetic distances among groups. To the best of our knowledge this study represents the first application of population genetic patterns to POM. Below we describe POM in the context of calibrating the RCW SEPM to the patterns observed on Camp Lejeune.

1.3 Methods

1.3.1 Landscape Map

The Camp Lejeune Land Cover Map was used for the simulation. The Land Cover Map provided a general description of forest cover updated every ten years, and information on the characteristics of non-forested areas thought to create landscape friction. The Land Cover Map classifies areas on MCBCL into 13 types; we condensed this list down to 7 types by combining similar areas (Table 1.1). Land Cover maps for offsite areas were not available so we assumed that these areas are homogeneous with regard to RCW dispersal behaviors and designated them as an eighth type.

Table 1.1. Modified classification of Camp Lejeune Land Cover Map used to estimate friction of land cover types for dispersal.

Code	Camp Lejeune Land Cover Classes
1	Predominantly Pine Forest
2	Mixed Pine and Hardwood Forest
3	Bottomland Hardwood / Upland Hardwood Forest
4	Forest plantation under 10 years
5	Bare ground / cropland / grasses / marshland / scrub, shrub
6	River, Stream, Lake
7	Business or Commercial area / Residential Area
8	Off site areas

Combined classes designated by "/".

The Land Cover shape file was converted into a raster file in ArcView 3.3 using Spatial Analyst, for use in dynamic simulation modeling. A 100 x 100 m cell size (1 ha) was chosen as the grain for the simulation study. This value represents a tradeoff between a need to limit computer simulation time to test many uncertain parameters (i.e., summarizing more area with fewer cells) and level geographic complexity perceived by RCWs when making dispersal choices. The Letcher model assumes that birds can detect breeding vacancies within 3 km, so we felt a 1 ha cell size was sufficiently conservative. MCBCL also provided a shape file with approximate cluster centers for all existing RCW territories. After creating the land cover raster file, we used ArcView 3.3 Spatial Analyst to generate a raster file of cluster centers, each consisting of a 1-ha cell.

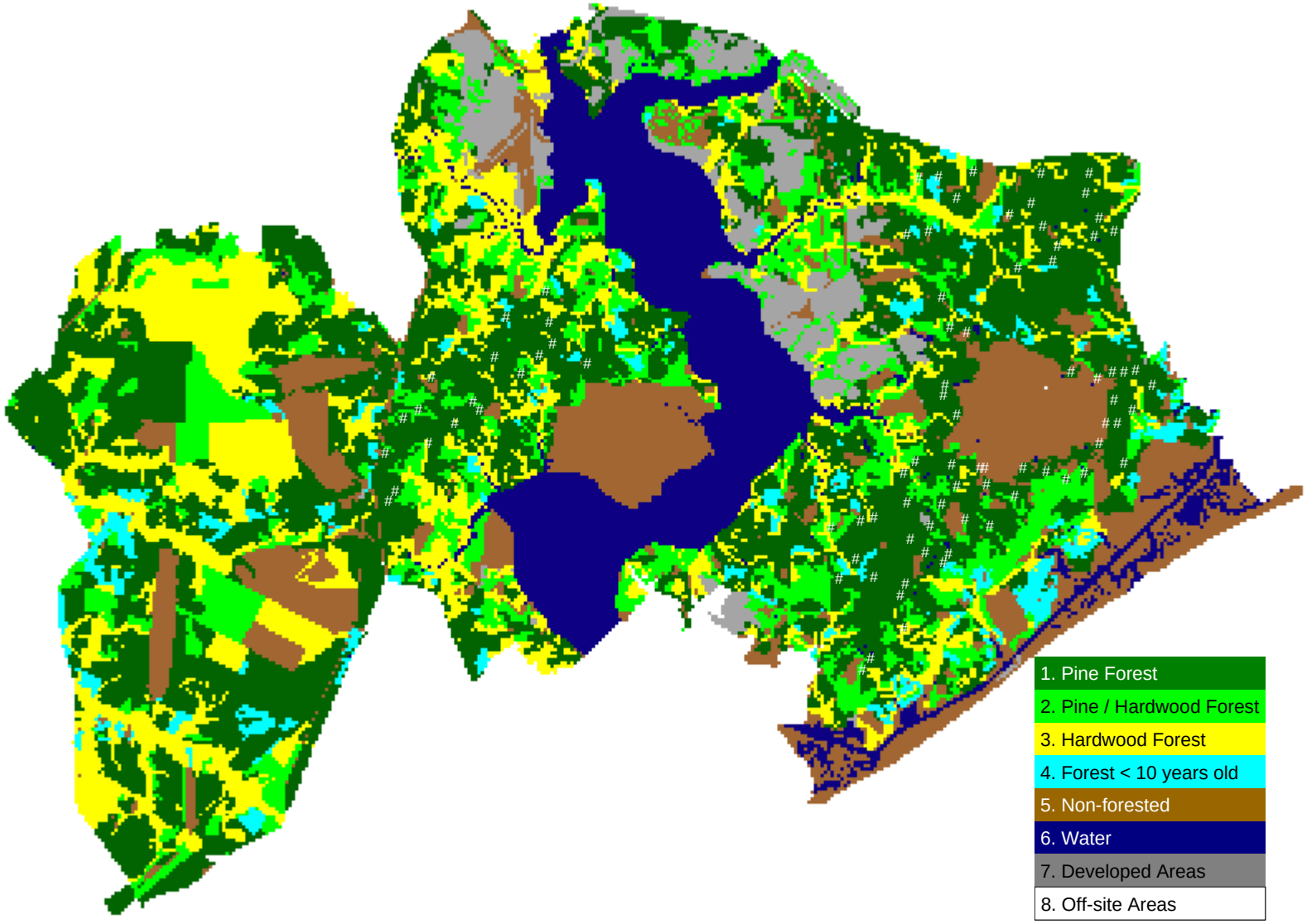

Figure 1.2. Camp Lejeune land cover map used in the spatially-explicit population model. Cell size is 100 m x 100 m, or 1-hectare. White dots designate approximate cluster centers. All clusters plotted were available for RCWs as of 2005.

1.3.2 Initial Conditions

Landscape pattern data are updated at least every 10 years in MCBCL's GIS system. Therefore, we calibrated the RCW SEPM to landscape patterns for the years 1995-2005. We used the RCW monitoring data, provided thanks to Dr. Jeffrey Walters, VPI&SU, to determine the population structure present at year 1995. We identified each bird's natal territory, past and current breeding territory, present location, age, status (fledgling, helper, floater or breeder), and sex. There were 192 birds in the initial population. All immigrants to Lejeune between 1995 and 2005 were also identified – 65 in total. The location, age, and sex were unknown for some floaters and immigrants, so we assigned these at random before the start of each simulation, which was replicated 50 times. We felt this is an effective way to remove any bias caused by randomly assigning unknown characteristics to birds because we summarize the results of one SEPM with an average of 50 replicate simulations.

In order to estimate the population genetic structure of RCWs on MCBCL we used an infinite alleles model (Lacy and Lindenmayer, 1995). The infinite alleles model assumes that every founding individual is heterozygous and contains two unique alleles (i.e., total alleles = 2 x number of breeders in the founding population). By making this assumption we can examine how the processes of inbreeding, genetic drift and gene flow interact in a spatially subdivided population. To apply the infinite alleles model, we identified all founding individuals or individuals observed between 1986 and 1995 that reproduced but for which their parentage is unknown. Each was assigned 2 unique alleles at a locus, therefore, founders were assumed to be unrelated. Next, we applied a gene drop which simulates the transmission of alleles from parents to offspring assuming Mendelian inheritance (i.e., their offspring had an equal probability of inheriting each of the two alleles). This stochastic process was repeated for the years 1986 to 1995 at the start of each simulation.

The internal structure of the model must closely approximate conditions and processes observed in nature to apply POM (Wiegand et al. 2004). Therefore, all immigrants to MCBCL between 1995 and 2005 were also assigned 2 unique alleles at a locus. In other words, we treated all observed immigrants as "founders" as it is possible that they may successfully reproduce some time during the simulation. Further, when recruitment clusters were made available under the MCBCL RCW Management Plan or when budding or pioneering behaviors led to new groups, the territories were included in the simulation at the appropriate time.

1.3.3 Parameters Used in the Simulation

1.3.3.1 Recruitment and Survival. The Letcher model uses an age-based recruitment submodel in which the probability that birds attempt to nest, probability of nest success, and number of fledglings produced is a function of the age of the male and female breeder and the number of helpers present. We did not have data regarding which groups attempted to nest and of those how many were successful. Therefore, we used the point estimates for probability that birds attempt to nest and probability of nest success from the Sandhills population used previously in the Letcher model. However, we did directly estimate the number of fledglings produced from the Camp Lejeune population using the regression equation #3 from Letcher et al. (1998), for the years 1995-2005:

$$FL = b_4 + b_5 e^{-Age_m} + b_6 e^{-Age_f} + b_7 HP. \qquad \text{(eqn 1.2)}$$

The resultant parameter estimates are reported in Table 1.2 ($F(3,458)=14.65$, $p<0.00001$).

Estimates of the probability of individual survival on Camp Lejeune were recently estimated by Walters (2004) for the years 1986-2000 (Table 1.2). We used these estimates for our simulation study. However, estimates for female helpers and floaters of both sexes were not included in the previous study. The presence of female helpers is a recent observation and may be due to population growth rates exceeding rates at which recruitment clusters have been provisioned on MCBCL (Walters 2004). This change in population structure was not the focus of our research so we assumed that female helpers have the same survival probability as male helpers, because floaters of both sexes have also been shown to have equal survival probability (Letcher et al. 1998). Probability of floater survival for both sexes was treated as uncertain because we are concerned about understanding floater behaviors in this landscape. We included a range of values for probability of seasonal survival, 0.8 to 1.0, because the average observed in the Sandhills' population was 0.89 (Letcher et al. 1998).

1.3.3.2 Dispersal Behaviors. The RCW SEPM simulates dispersal behaviors in two steps. The first step is to determine if individuals delay dispersal and stay as helpers. To simulate this step we used point estimates, as was done for the Letcher model, from the years 1995-2005 (Table 1.3) because we were most interested in how land use mediates dispersal. We did make an important structural improvement by allowing females to delay dispersal. Ignoring this structural difference between the model and conditions observed on Camp Lejeune would prevent POM from effectively reducing uncertainty.

The second step is simulating floating or dispersal behaviors in a heterogeneous landscape. We must first determine the number of steps taken each season. The Letcher model assumes that females and first year male floaters can disperse farther than older male floaters. We treated these values as uncertain, allowing dispersal steps to vary from 1-10 km per season for females and first year male floaters, and 1-8 km per season for the older male floaters (Table 1.3).

Next, we need to simulate where each bird moves to with each step, using the HCRW model described above. We are uncertain regarding the preferences RCW have for different land cover types during dispersal, or conversely the level of friction land cover types represent. Therefore, we used a range of values for the degree of landscape friction the eight land cover types (Table 1.1) represent. The values for "m" (eqn 1.1) range from 0.01, meaning that birds have a low probability of entering, to 1.0. Similarly, we are uncertain regarding the turning decisions birds make during dispersal. From a human's perspective on the ground, RCWs are often seen to be dispersing in a straight line (Letcher et al., 1998). However, a human's perceptual distance, without the aide of radio telemetry, is limited, so directional preferences should be treated as uncertain. When assigning values to all possible "d" parameters, we must recognize that these values are not statistically independent, when turning a bird may turn to the left or the right, and they should sum to unity ($d_{0°} + 2(d_{45°}) + 2(d_{90°}) + 2(d_{135°}) = 1$). Therefore, we started by

randomly assigning the value for $d_{0°}$, tendency for straight movement. Then a random number between $d_{0°}$ and 1 was selected and divided by 2 to determine $d_{45°}$. This step was then repeated for the remaining two possible directions.

1.3.3.3 Competition for Breeding Vacancies. Competition for breeding vacancies is an important biological process that ultimately determines if a dispersing bird will contribute to population growth. The competition rules used by the Letcher model were reproduced here. For males, it assumes that the oldest male helpers will always win the breeding vacancy in the territory in which they are helping. If no helpers are present, then helpers and floaters within a specified search radius will compete for the vacancy. The model assumes that the closest individual to the vacant territory will win, but if individuals are equi-distant, the oldest individual wins.

For females, the Letcher model assumes that the oldest individual within a specified search radius will win. However, by adding female helpers we had to examine how competition rules could be extended to a new class of birds. Investigating the RCW monitoring data revealed that unlike male helpers, female helpers rarely inherit their natal territory. This occurred twice, on Cluster 14 in 1990 and on Cluster 28 in 1989. Both females were born in 1987, only the second year of bird banding studies on Camp Lejeune, and their parentage was uncertain. On cluster 14 the female helper inherited the position despite there being a male fledgling present, which stayed as a helper in that territory. In territory 28, only female fledglings were produced prior to the occurrence of a breeding vacancy. In both cases, a new male breeder was observed. In 2003 at Cluster 48, a female fledgling assumed the breeding position after her parents and the helper disappeared from the cluster. These events were rare and may reflect predation events that are not well characterized by the model. Therefore, we assumed that female fledglings, helpers, and floaters could not win a vacancy in their natal cluster. Further, as assumed in Letcher et al. (1998), we assumed that when a male helper takes a breeding position, the female breeder dispersers and can not re-win a vacancy where she successfully bred in the past.

The ability of birds to detect and acquire breeding vacancies will have a large impact on the persistence and population structure in a fragmented landscape. In absence of empirical estimates of a bird's search radius the Letcher model assumes that all fledglings, helpers, and floaters of both sexes can compete for breeding vacancies within 3 km of their current location. Such a large search radius may be plausible for female floaters and helpers because it is believed that solitary males drum on pine trees to attract distant females (Conner et al., 2001). Also, male and female helpers are known to conduct forays. However, male floaters investigating new areas may have a very small search radius. We used POM to test the assumption that floaters and helpers of both sexes have a similar search radius. Therefore, we expanded the model to include 4 search radii (one for each sex for helpers and floaters) and varied the values from 0.1 to 6 km (Table 1.3). We assumed that birds are able to detect vacancies at this distance are willing to cross all land cover types to acquire a breeding vacancy (e.g., Norris and Stutchbury 2001).

Table 1.2. Recruitment and survival parameter values used in Red-Cockaded Woodpecker spatially-explicit population model.

Parameter	**Value**	**Source**
α Female nesting attempt	1.14569	Letcher et al. 1998
b_0 Nest success intercept	2.3404	Letcher et al. 1998
b_1 Nest success male's effect	-2.4295	Letcher et al. 1998
b_2 Nest success female's effect	-1.1527	Letcher et al. 1998
b_3 Nest success helper's effect	-1.1012	Letcher et al. 1998
b_4 Mean fledgling intercept	1.8661	This study
b_5 Mean fledgling male's effect	-1.4351	This study
b_6 Mean fledgling female's effect	-0.3288	This study
b_7 Mean fledgling helper's effect	0.1766	This study
Seasonal probability of survival – Male Fledgling	0.88	Walters 2004
Seasonal probability of survival – Male Helper	0.94	Walters 2004
Seasonal probability of survival – Male Breeder	0.95	Walters 2004
Seasonal probability of survival – Male Floater	0.8 – 1.0	This study
Seasonal probability of survival – Female Fledgling	0.81	Walters 2004
Seasonal probability of survival – Female Helper	0.94	Walters 2004
Seasonal probability of survival – Female Breeder	0.94	Walters 2004
Seasonal probability of survival – Female Floater	0.8 – 1.0	This study
Maximum age	17	Conner et al. 2001

Table 1.3. Dispersal and competition parameter values used in Red-Cockaded Woodpecker spatially-explicit population model.

Parameter	Value	Source
Probability of Male Natal Dispersal	0.568	This study
Probability of Female Natal Dispersal	0.874	This study
Female floater and Male natal dispersal speed (per season)	1 - 10 km	This study
Male floater dispersal speed (per season)	1 - 8 km	This study
m1 Probability of entering predominantly pine forest	0.01 – 1.0	This study
m2 Probability of entering mixed pine and hardwood forest	0.01 – 1.0	This study
m3 Probability of entering bottomland hardwood / upland hardwood forest	0.01 – 1.0	This study
m4 Probability of entering forest plantation under 10 years	0.01 – 1.0	This study
m5 Probability of entering bare ground / cropland / grasses / marshland / scrub, shrub	0.01 – 1.0	This study
m6 Probability of entering river, stream, lake	0.01 – 1.0	This study
m7 Probability of entering business or commercial area / residential area	0.01 – 1.0	This study
m8 Probability of entering off site areas	0.01 – 1.0	This study
$d_{0°}$ Probability of traveling in same direction that was chosen in last time step	0.01 – 1.0	This study
$d_{45°}$ Probability of turning 45° away from direction traveled in previous time step	0.01 – 1.0	This study
$d_{90°}$ Probability of turning 90° away from direction traveled in previous time step	0.01 – 1.0	This study
$d_{135°}$ Probability of turning 135° away from direction traveled in previous time step	0.01 – 1.0	This study
B Strength of preference for habitat-based or directional dispersal rules. B = 1, only land cover type matters B = 0, only directional rules matter	0 – 1	This study
Perceptual distance of Male Helpers	0.1 – 6 km	This study
Perceptual distance of Male Floaters	0.1 – 6 km	This study
Perceptual distance of Female Helpers	0.1 – 6 km	This study
Perceptual distance of Female Floaters	0.1 – 6 km	This study

1.3.4 Simulation Conditions

The SEPM was run with 100,000 different parameterizations, generated by a Latin hypercube, to ensure exhaustive sampling of possible parameter combinations. A Latin hypercube design is used to provide a stratified sampling of possible parameter sets without replacement (McKay et al. 2000). The range of values for each of the 21 uncertain parameters reported above were subdivided into 21 equidistant values. The Latin hypercube was then used to randomly assemble parameter values for the 21 uncertain parameters. This represented one possible parameterization. Each parameterization was then simulated for 11 years (1995-2005) and replicated 50 times.

1.3.5 Filtering: Model Calibration by Comparing Observed and Expected Patterns

The RCW SEPM was calibrated to MCBCL by filtering the 100,000 parameterizations based on their ability to reproduce patterns observed in nature. Pattern fulfillment indices are developed that measure the deviance between observed and simulated patterns. Multiple indices were used because compensatory mechanisms such as low probability of floater survival being offset by high dispersal speed may result in several different parameterizations being able to reproduce the same pattern. Therefore, observed patterns were chosen to reflect multiple biological processes to remove the effects of compensatory mechanisms. Further, we must derive pattern fulfillment criteria that recognize that the patterns observed may not reflect underlying biological process but instead may be due to random chance. Pattern fulfillment criteria are the statistical criteria used to remove parameterizations that simulate patterns that do not differ significantly from patterns resulting from random processes. The pattern fulfillment criteria represent the "porosity" used during filtering. Filtering is then the removal of parameterizations with pattern fulfillment indices not able to satisfy the pattern fulfillment criteria

1.3.5.1 Index 1. Potential Breeding Groups (PBG) serve as the regulatory benchmark for RCW Recovery (USFWS 2003a). We tested the ability of different parameterizations to reproduce the time series of PBG observed on MCMCL from 1995 to 2005 (Fig. 1.3). We measured the deviance between the PBGs present at the start of the breeding season in the simulation ($S[PBG_t]$) and those observed on MCBCL ($O[PBG_t]$) for each of the 11 years. An error measure, E^{PBG}, was derived using the root squared mean deviation between the observed and expected time series (Wiegand et al. 2004):

$$E^{PBG} = \sqrt{\frac{1}{11}\sum_{t=1995}^{2005}\left(O[PBG_t] - S[PBG_t]\right)^2} \quad . \qquad \text{(eqn. 1.3)}$$

Because each parameterization was replicated 50 times, the error value for each replicate was estimated. The average E^{PBG} from these 50 replicates was used to characterize the suitability of the parameterization (Wiegand et al. 2004).

The pattern fulfillment criteria, or filter porosity, for E^{PBG} was determined using a randomization approach. Random time series of PBGs were assembled by randomly assigning a year between 1995 and 2005 to each of the 11 observed PBGs (i.e., random permutation), generating random time series, $R[PBG_t]$. E^{PBG}_{Rand} was then calculated:

$$E^{PBG}_{Rand} = \sqrt{\frac{1}{11}\sum_{t=1995}^{2005}\left(O[PBG_t] - R[PBG_t]\right)^2} \quad . \quad \text{(eqn. 1.4)}$$

To ensure consistency in analysis between the simulated and random time series, random permutation of the time series was repeated 50 times and the final E^{PBG}_{Rand} represents an average of the 50. This procedure was repeated 10,000 times to produce a distribution of E^{PBG}_{Rand}. The pattern fulfillment criteria for PBG specified that E^{PBG} must be less than 95% of all E^{PBG}_{Rand} or a root squared mean deviation of 15.2. This very strict criterion was chosen because PBGs have regulatory significance and sampling of potential breeding habitat for RCWs is conducted thoroughly each year. Therefore, we should expect our SEPM to predict this trend with little error.

1.3.5.2 Index 2. The number of male and female floaters observed each year on MCBCL served as our second index (Fig. 1.3). Index 2 was developed exactly as Index 1 because they are both time series data. Criteria for males, for example, were derived by substituting $O[mFloater_t]$, $S[mFloater_t]$, and $R[mFloater_t]$ in the equations to derive $E^{mFloater}$ and $E^{mFloater}_{Rand}$.

Unlike PBG, we expect a large amount of observational error in O[Floater] on MCBCL, because the monitoring program focuses on individuals located in clusters, not floaters. However, it is important to include this pattern when filtering, because parameterizations including high floater survival may lead to unrealistic rates of immigration and territory occupancy. To account for the large amount of observational error, the pattern fulfillment criteria for Floaters specified that $E^{Floater}$ be within the range of error values generated when the time series was randomized. In other words, $E^{Floater}$ must be no greater than the maximum error observed when the time series were randomized, $\max(E^{mFloater}_{Rand}) = 2.9$ and $\max(E^{fFloater}_{Rand}) = 7.95$.

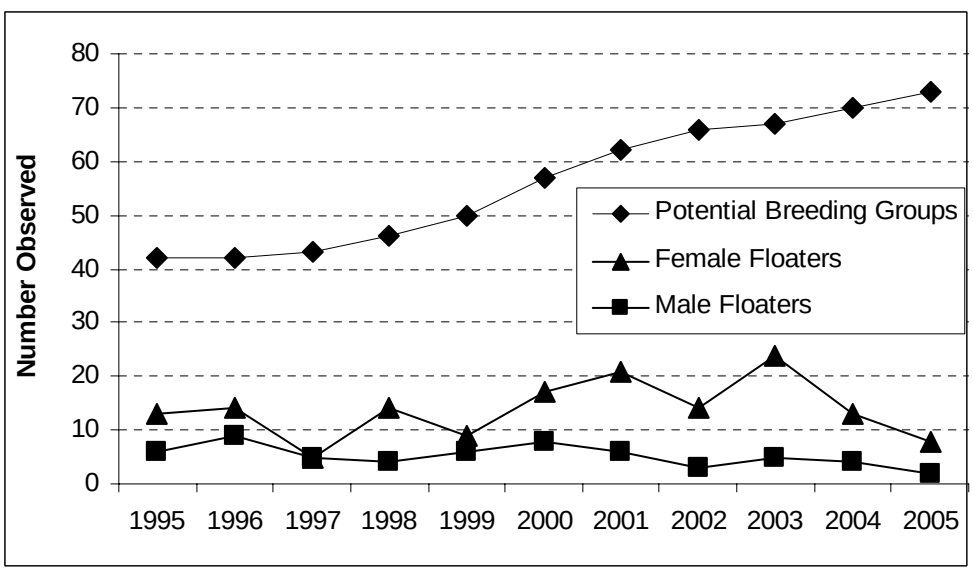

Figure 1.3. Observed temporal patterns on MCBCL used to establish pattern fulfillment indices for Potential Breeding Groups and Floaters.

1.3.5.3 Index 3. Group size observed at each territory and each year was also used as a pattern. We defined group size as the number of breeding adults and helpers in a territory. To test the ability of one parameterization to reproduce the temporal and spatial distribution of breeding adults and helpers observed on MCBCL, a Pearson correlation coefficient was calculated by comparing group size observed at each territory and each year in the simulation with those observed in the field. We will refer to this as our "observed test statistic", r_{Obs}. An average correlation coefficient from the 50 replicates was used to characterize the ability of each parameterization to reproduce patterns observed on MCBCL.

To derive the pattern fulfillment criterion, we calculated a distribution of test statistics by randomly exchanging group size among years and territories (i.e., random permutation) and correlating this random pattern with the observed pattern, r_{Rand}. Recall that the simulation introduces new territories to the landscape to reflect when recruitment clusters were installed by MCBCL and when new clusters started by RCWs, through budding and pioneering behaviors, were observed. Therefore, to control for this autocorrelation between the simulation and field conditions, values for group size were randomly exchanged only among territories that were available, whether occupied or not. The random permutation was repeated 10,000 times and r_{Rand} was calculated for each permutation. The null hypothesis tested was that the correlation between simulated and observed distribution of group sizes is no different than would be due to random processes. We can calculate the probability that r_{Obs} resulted due to random processes using the following equation (Manly 1986):

$$p = \frac{Nr_{Rand} \geq r_{Obs}}{10{,}000} \quad \text{(eqn 1.5)}$$

Where, $Nr_{Rand} \geq r_{Obs}$ is the number of times r_{Rand} was observed to be greater than or equal to r_{Obs}. The maximum value for r_{Rand} was 0.56. Therefore, the probability of observing r_{Obs} equal to 0.56 resulting from random spatial processes is 1/10,000 or p=0.0001. The pattern fulfillment criterion for group size specified that parameterizations must produce r_{Obs} greater than 0.56 ($p<0.0001$).

1.3.5.4 Index 4. Connectivity of territories was used as the fourth pattern. Connectivity was estimated only for fledglings, helpers, and floaters that transitioned into a breeding position in both the simulation and observed demographic transitions on MCBCL. Connectivity was estimated for males and females separately, simply as the number of individuals exchanged among territories between 1995 and 2005 (e.g., x_{ij}, where x = number of females originating at territory i and achieving breeding status in territory j). MCBCL has numbered each RCW cluster from 1 to 90. Therefore, a square 90x90 matrix of connectivity values was used to summarize pair wise, directional connectivity among territories. A diagonal value in the matrix for males then indicates the number of times a male helper inherited the territory. A Mantel test, which estimates correlation among matrices, was used to test for the degree of similarity between the observed connectivity matrix and expected connectivity matrix generated in the

simulation (Bailey and Gatrell 1995). An average Mantel correlation coefficient from the 50 replicates was used to characterize the ability of each parameterization to reproduce patterns observed on MCBCL, Mr^{C}_{Obs}.

To derive the pattern fulfillment criterion, we calculated a distribution of Mantel test statistics by randomly exchanging connectivity values among territories (i.e., random permutation) and correlating this random pattern with the observed pattern, Mr^{C}_{Rand}. This was performed 10,000 times as explained above for Group Size. The pattern fulfillment criterion for connectivity specified that parameterizations must produce Mr^{C}_{Obs} greater than 0.116 ($p<0.0001$) for males and 0.065 ($p<0.0001$) for females.

1.3.5.5 Index 5. Pair wise minimum genetic distance (D_{ij}) among all territories was also used as a pattern (Nei 1973). A mathematical definition is given in equation A4 in Appendix A. When D_{ij} is close to zero, then alleles are present in territory i and j at very similar frequencies, indicating that gene flow between the groups is high. Recall that an infinite alleles model of genetic variance was included in each simulation, and that a gene drop was used to simulate the transmission of alleles from parents to offspring. Therefore, a 90x90 matrix of the minimum genetic distance among breeding groups was estimated at year 2005 in each simulation, to reflect the accumulated influence gene flow and genetic drift had on the genetic differences among groups.

We used a similar approach to estimate the **observed** minimum genetic distance among territories. The MCBCL monitoring data were used to compile a pedigree of all breeding events from 1986 to 2005. A gene drop was then applied to this pedigree assuming an infinite alleles model. At year 2005 the minimum genetic distance was estimated. This process was repeated 10,000 times and the estimated observed minimum genetic distance represents an average of this process.

A Mantel test was used to test for the degree of similarity between the observed minimum genetic distance and minimum genetic distance generated in the simulation (Bailey and Gatrell 1995). An average Mantel correlation coefficient from the 50 replicates was used to characterize the ability of each parameterization to reproduce genetic patterns observed on MCBCL, Mr^{D}_{Obs}.

To derive the pattern fulfillment criterion, we calculated a distribution of Mantel test statistics by randomly exchanging minimum genetic distance values among territories (i.e., random permutation) and correlating this random pattern with the observed pattern, Mr^{D}_{Rand}. This was performed 10,000 times as explained above for Group Size and Connectivity. The pattern fulfillment criterion for connectivity specified that parameterizations must produce Mr^{D}_{Obs} greater than 0.069 ($p<0.0001$).

1.3.5.6 Filter Optimization. For model parameterizations capable of fulfilling all patterns, we investigated the sensitivity of pattern fulfillment indices to the remaining parameter uncertainty. This was accomplished by performing a Spearman rank correlation between the remaining range of possible parameter values and each of the five filters. Large correlation coefficients indicate that model fit could be improved by further

restricting pattern fulfillment criteria. Filter optimization also indicates which patterns are most useful for reducing prediction uncertainty and can be used to guide further data collection.

1.4 Results and Discussion

Parameterizations generating patterns unable to meet all five pattern fulfillment criteria were excluded from further analysis. We found that zero parameterizations produced patterns meeting all five criteria. Examining the distributions of pattern fulfillment indices indicated that only 8 parameterizations produced $E^{mFloater}$ less than or equal to 2.9. Of these 8 parameterizations, none were able to meet the pattern fulfillment criteria for the remaining filters. Recall that very few male floaters are observed in the landscape (Fig. 1.3) and that we expect a large amount of observational error associated with this monitoring data. We decided to allow for a larger amount of error for this pattern fulfillment criteria by specifying that $E^{mFloater}$ must be less than or equal to 90% of $E^{mFloater}$ observed in the 100,000 parameterizations, $E^{mFloater} <= 7.32$.

After applying the adjusted pattern fulfillment criteria for male floaters, we found that only 719 parameterizations produced patterns meeting all five criteria. Therefore, filtering removed 99.3% of all parameter sets tested—a significant reduction in uncertainty. However, the parameter state space, or range of parameter values, for the 21 uncertain parameters remaining after filtering often equaled the initial parameter state space included in the simulations. Therefore, the percent of parameter state space removed was often zero (Table 1.4). The biggest exception was observed for probability of male floater survival, indicating the 35.9% of the parameter state space has been removed. Table 1.4 also indicates that ~50% of parameter state space for $d_{45°}$, $d_{90°}$, and $d_{135°}$ was removed. This filtering actually reflects the autocorrelation in the probability of turning described above in the Habitat-based Correlated Random Walk model.

These results indicate that the Letcher model is insensitive to the dispersal rules included in the model. In other words, the demographic parameters and behavioral rules that were not treated as uncertain are capable of approximating patterns observed on MCBCL. These results may also reflect the clumped spatial distribution of RCW territories on MCBCL. In other words, individuals do not have to travel far or interact much with landscape structure in order to facilitate the exchange of individuals among groups required to reproduce patterns.

Table 1.4. Results of filtering for the 21 uncertain parameters using the five pattern fulfillment criteria. N=719 (number of parameterizations remaining after filtering).

	Uncertain Parameter	Mean	Standard Deviation	Percent[1] filtered
fFS	Seasonal probability of survival – Female Floater	0.840	0.034	0
mFS	Seasonal probability of survival – Male Floater	0.824	0.023	35.9
mHP	Perceptual distance of Male Helpers	8.51	12.7	0
mFP	Perceptual distance of Male Floaters	38.7	13.5	13.6
fHP	Perceptual distance of Female Helpers	24.1	17.1	0
fFP	Perceptual distance of Female Floaters	25.1	12.4	13.6
mSp	Male floater dispersal speed	43.8	21.0	0
fSp	Female floater and Male natal dispersal speed	56.6	27.2	0
$d_{0°}$	Probability of traveling in same direction that was chosen in last time step	0.532	0.304	0
$d_{45°}$	Probability of turning 45° away from direction traveled in previous time step	0.122	0.114	50.0
$d_{90°}$	Probability of turning 90° away from direction traveled in previous time step	0.058	0.071	55.0
$d_{135°}$	Probability of turning 135° away from direction traveled in previous time step	0.054	0.072	55.8
m1	Probability of entering predominantly pine forest	0.506	0.306	0
m2	Probability of entering mixed pine and hardwood forest	0.501	0.302	0
m3	Probability of entering bottomland hardwood / upland hardwood forest	0.516	0.301	0
m4	Probability of entering forest plantation under 10 years	0.520	0.302	0
m5	Probability of entering bare ground / cropland / grasses / marshland / scrub, shrub	0.488	0.298	0
m6	Probability of entering river, stream, lake	0.526	0.305	0
m7	Probability of entering business or commercial area / residential area	0.505	0.306	0
m8	Probability of entering off site areas	0.497	0.290	0
B	Strength of preference for habitat-based or directional dispersal rules (e.g., B = 1, only land cover type matters)	0.475	0.312	0

[1]Percent filtered = 1 – [range of values from 719 / range of values from 100,000 parameterizations]

Filter Optimization. Spearman rank correlations between parameter values remaining after filtering and pattern fulfillment indices indicated that all filters are sensitive to the remaining uncertainty in parameter values (i.e., Table 1.5, $p<0.05$ observed for at least one parameter in all indices). Therefore, by further restricting the pattern fulfillment criteria we should be able to reduce a considerable amount of uncertainty in these parameters. Spearman rho values indicate that Mantel's r for female and male connectivity, Error PBG, and Pearson's r for Group Size are strong filters, indicating that continuation of the current monitoring program will help reduce uncertainty regarding dispersal behaviors.

The largest correlations were observed for female floater perceptual distance. Female floater perceptual distance was negatively correlated with E^{PBG} (rho = -0.736). Therefore, the longer a female floater's perceptual distance, the error in predicting PBG will be smaller. Female floater perceptual distance was negatively correlated with Mantel's r for female connectivity (-0.768). Therefore, the longer a female floater's perceptual distance, the correlation between observed and expected female connectivity will be smaller (Fig 1.4). Further, the relationship between female floater perceptual distance and Mantel's r for minimum genetic distance shows a positive relationship (0.549). Therefore, the correlation between observed and expected minimum genetic distance among clusters is greater when female floater perceptual distance is larger. By using multiple filters we will likely find an intermediate value for female floater perceptual distance that would be otherwise missed if only one filter were used.

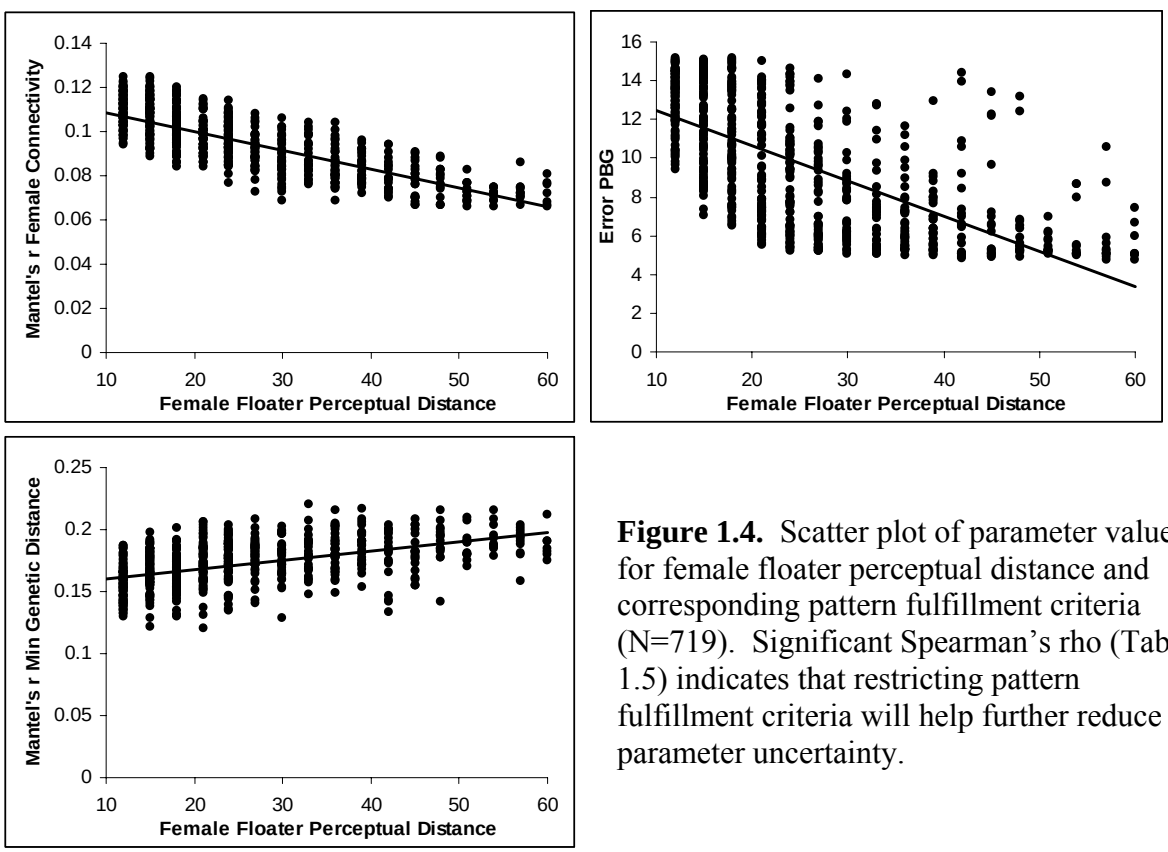

Figure 1.4. Scatter plot of parameter values for female floater perceptual distance and corresponding pattern fulfillment criteria (N=719). Significant Spearman's rho (Table 1.5) indicates that restricting pattern fulfillment criteria will help further reduce parameter uncertainty.

Table 1.5. Spearman Rank correlation coefficient (rho) describing the strength of the relationship between uncertain parameter values and statistical indices of model fit to observed patterns on MCBCL. N=719.

Parameter	Error PBG	p-value	Error mFloat	p-value	Error fFloat	p-value	r Group Size	p-value	Mr Male Conn	p-value	Mr Female Conn	p-value	Mr Dij	p-value
fFS	0.058	0.123	-0.030	0.419	**0.324**	**<0.001**	0.018	0.622	0.070	0.061	-0.070	0.061	0.014	0.710
mFS	**0.155**	**<0.001**	0.065	0.080	**-0.098**	**0.008**	-0.038	0.308	0.026	0.494	**0.246**	**<0.001**	-0.028	0.453
mHP	**0.446**	**<0.001**	**0.292**	**<0.001**	**-0.127**	**0.001**	**-0.145**	**<0.001**	**-0.661**	**<0.001**	**0.381**	**<0.001**	**-0.353**	**<0.001**
mFP	**-0.133**	**<0.001**	**-0.075**	**0.043**	**0.134**	**<0.001**	**0.653**	**<0.001**	**-0.554**	**<0.001**	**0.235**	**<0.001**	**0.135**	**<0.001**
fHP	**-0.232**	**<0.001**	0.033	0.378	-0.073	0.051	-0.001	0.969	0.049	0.193	**-0.143**	**<0.001**	0.003	0.937
fFP	**-0.738**	**<0.001**	**0.167**	**<0.001**	**0.414**	**<0.001**	**0.384**	**<0.001**	**0.609**	**<0.001**	**-0.768**	**<0.001**	**0.549**	**<0.001**
mSp	0.023	0.535	-0.037	0.318	**-0.097**	**0.009**	-0.009	0.818	-0.036	0.339	0.022	0.557	0.002	0.959
fSp	-0.047	0.204	-0.030	0.415	0.000	0.994	0.036	0.338	-0.038	0.310	**-0.174**	**<0.001**	0.065	0.080
$d_{0°}$	-0.058	0.123	-0.048	0.201	-0.002	0.962	0.081	0.031	-0.014	0.700	**-0.127**	**0.001**	**0.090**	**0.016**
m1	0.020	0.597	0.023	0.545	-0.059	0.114	-0.012	0.745	0.008	0.829	0.056	0.137	0.019	0.617
m2	-0.030	0.417	-0.047	0.209	0.026	0.480	0.039	0.292	0.041	0.270	0.018	0.629	0.066	0.078
m3	0.033	0.381	0.027	0.462	0.037	0.327	-0.027	0.465	0.002	0.948	0.024	0.524	-0.068	0.068
m4	0.031	0.406	-0.007	0.847	-0.020	0.593	-0.034	0.359	0.003	0.942	0.050	0.177	0.049	0.189
m5	0.001	0.989	0.005	0.892	0.036	0.339	0.009	0.809	0.015	0.690	-0.004	0.921	0.043	0.253
m6	-0.026	0.489	-0.033	0.373	0.030	0.420	0.064	0.084	**-0.081**	**0.030**	0.066	0.078	-0.010	0.793
m7	0.041	0.277	-0.039	0.295	-0.016	0.665	-0.035	0.355	-0.028	0.448	0.038	0.314	-0.024	0.528
m8	0.004	0.915	0.015	0.684	0.063	0.092	0.051	0.169	-0.055	0.141	-0.001	0.973	0.016	0.667
B	-0.070	0.061	**0.088**	**0.018**	0.062	0.097	0.051	0.169	**0.086**	**0.021**	**0.129**	**0.001**	0.066	0.076

Bold values = $p<0.05$

Spearman rho values indicate that parameter values of the Habitat-based Correlated Random Walk tended to be insensitive to the five pattern fulfillment indices. We did observe negative correlations between the probability of not turning ($d_{0°}$) and model fit for female connectivity (p=0.001). This suggests that flexibility in directional choices is important for approximating connectivity values observed in the landscape. In contrast, a small positive correlation was observed between Mantel's r for minimum genetic distance and the probability of not turning (rho = 0.09, p = 0.016). Therefore, straighter dispersal, which would allow individuals to move farther, does improve the fit between observed and expected genetic distance. Among the preferences for land cover types, only m6, probability of crossing water, shows a correlation with Mantel's r for male connectivity (rho = -0.081, p = 0.03). The strength of preference for habitat-based dispersal rules (B) was positively correlated with model fit for male and female connectivity. In contrast, E^{mFloat} was positively correlated with preference for habitat-based dispersal rules. Therefore, when B is higher we observed a poorer fit between observed and expected number of male floaters in the landscape. This correlation may indicate that habitat based dispersal rules lead to retaining more floaters in the landscape than straight dispersal, which leads to greater emigration away from MCBCL.

We investigated how further constraining pattern fulfillment criteria may reduce parameter uncertainty. We derived 4 filter combinations by increasing strength, or decreasing filter porosity, of the pattern fulfillment criteria. Derivation filter combination A was explained above using random permutation testing and led to the reduced 719 parameterizations (Table 1.6). Using the distribution of pattern fulfillment indices that characterize the 719 parameterizations, we specified that the pattern fulfillment criteria must be less than the lower 50th percentile for E^{PBG} and greater than the 50th percentile of correlation coefficients for group size, connectivity, and minimum genetic distance. Twenty parameterizations were able to satisfy all criteria. This process was repeated by adjusting the criteria to be lower than the 40th and greater than the upper 60th percentile, leaving 8 parameterizations capable of meeting all five criteria. Subsequently adjusting for the lower 30th and upper 70th percentile, we found only one parameterization met all five criteria (Table 1.6).

Table 1.6. Filter combinations used to reduce parameter uncertainty

Pattern Fulfillment Index	Filter Combination A	Filter Combination B	Filter Combination C	Filter Combination D
Error PBG	15.2	9.58	8.26	7.02
[1]Error Male Floater	7.32	7.32	7.32	7.32
[1]Error Female Floater	7.95	7.95	7.95	7.95
Pearson's r Group Size	0.558	0.659	0.662	0.667
Mantel's r Male Connectivity	0.116	0.254	0.257	0.261
Mantel's r Female Connectivity	0.065	0.097	0.1	0.103
Mantel's r Genetic Distance (Dij)	0.069	0.173	0.178	0.182
Number of parameterizations remaining	719	20	8	1

Filter Combination A = derived from random permutation testing
Filter Combination B = represents lower and upper 50th percentiles
Filter Combination C = represents lower 40th and upper 60th percentiles
Filter Combination D = represents lower 30th and upper 70th percentiles
[1]E^{Float} was not reduced for filter combinations B, C and D because in Filter A E^{mFloat} equaled the lower 10th percentile and E^{fFloat} is less than the 30th percentile.

Figure 1.5 illustrates how the parameter estimates and uncertainty change with increasing the strength of the pattern fulfillment criteria. A considerable amount of uncertainty was removed regarding floater survival. The filter most directly related to floater survival (i.e., E^{Float}) was not changed in the successive filter combinations (Table 1.6), therefore the mean value does not shift much. In contrast, perceptual distance for males did change considerably with filter combinations. POM predicts that male floaters have a much greater perceptual distance than male helpers. For females, POM predicts that perceptual distance for helpers and floaters converge to the same value. These results suggest that male helpers and floaters engage in very different behaviors while female helpers and floaters have more similar behaviors. These results seem to agree with observations of Jeffrey Walter's field crews conducting the radio telemetry study of RCWs on Fort Bragg (Jeffrey Walters, personal communication).

Uncertainty regarding male dispersal speed was not reduced in the successive filter combinations and a large shift was observed with filter combination D. However, because male floater perceptual distance was high in the simulations passing through these filters, male dispersal speed is likely not a critical parameter required to approximate patterns observed in the field. In contrast, uncertainty regarding female dispersal speed was reduced and the mean shifted lower with successive filter combinations.

Uncertainty regarding the parameter values for the HCRW was not reduced with successive filter combinations, and large shifts in parameter estimates are often observed with Filter Combination D. For example for m4, probability of entering a cell containing young pine, the mean shifts upward until inclusion of filter combination D. Similarly, for m5, probability of entering a non-forested / undeveloped cell, the mean shifts lower until inclusion of filter combination D. Therefore, we can not place much confidence in the parameter values derived from filter combination D for the HCRW.

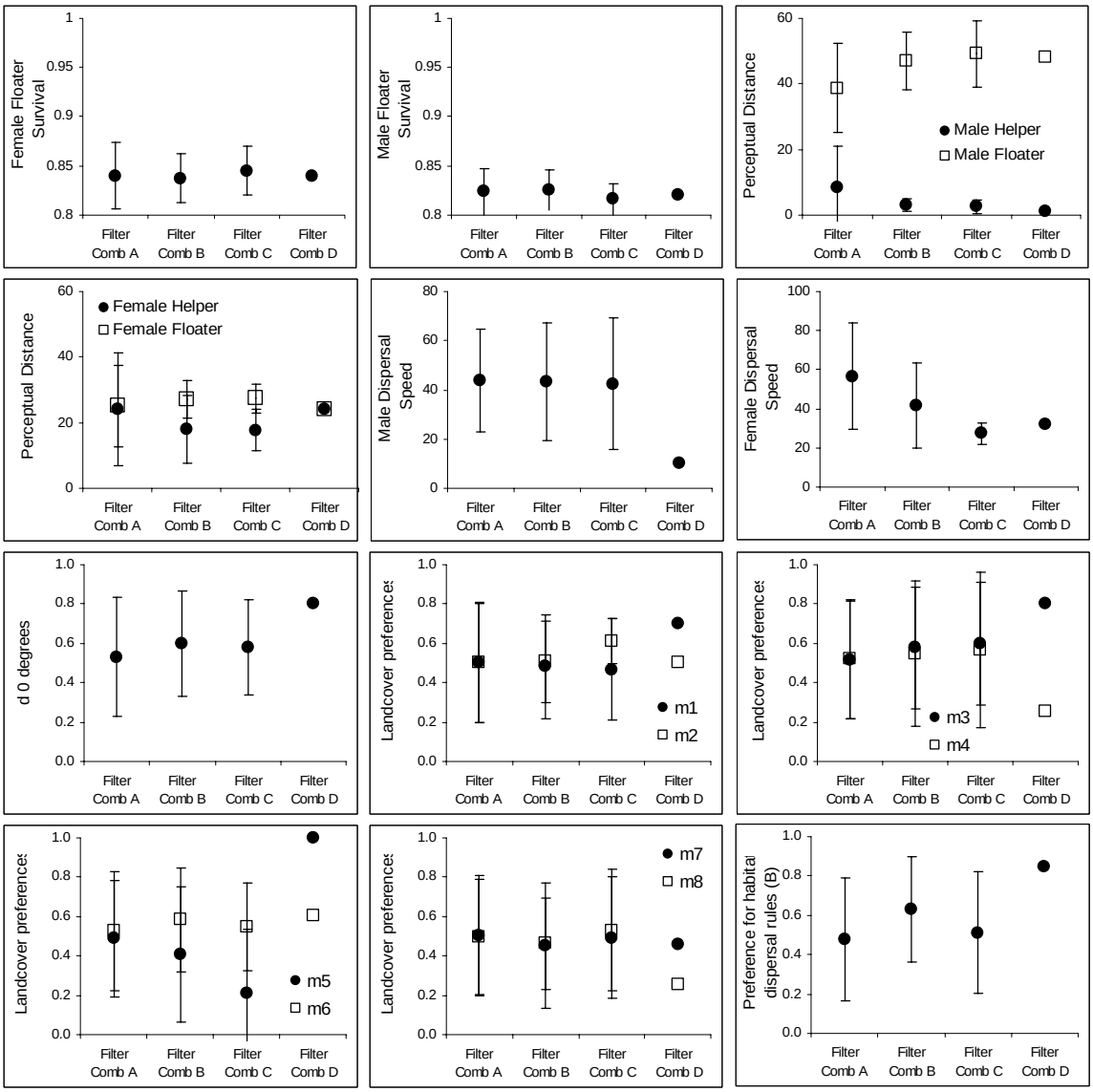

Figure 1.5. Change in parameter estimates for the uncertain dispersal parameters owing to filter optimization. Error bars represent one standard deviation. Filter Comb A, n=719. Filter Comb B, n=20. Filter Comb C, n=8. Filter Comb D, n=1 (Table 1.6).

1.5 Conclusions

POM did reduce a considerable amount of uncertainty in the RCW SEPM, especially for parameters relating to floater survival and perceptual distance. However, POM was unable to reduce uncertainty regarding the HCRW. One reason may be that the clumped distribution of habitat allows the SEPM to approximate patterns observed in the field regardless of the dispersal rules employed. Another reason may be that there is structural uncertainty in the model. Structural uncertainty refers to how the submodels simulate biological processes and how the submodels are interconnected.

While the HCRW has been successfully applied to other species (Kramer-Schadt et al. 2004), assumptions used in other submodels originally included in the Letcher model may prevent its usefulness for RCWs. For example, the Letcher competition submodel indicates that all floaters and helpers within 3 km (or 30 grid cells in our simulations) compete for a breeding vacancy. Recall that this distance reflects the bird's perceptual distance. Within a bird's perceptual distance, the intervening land cover types are assumed to have no influence on movement, keeping with the basic structural assumptions of the Letcher model.

We tested a bird's perceptual distance with POM, by allowing perceptual distance to vary independently for helpers and floaters and determining the distances that allow the simulation model to approximate multiple patterns observed in the field. For males, we found that helpers only compete for vacancies very close to their location (i.e., within 300 m) and floaters can compete for vacancies very far away from their current location (i.e., within 4.5 km) (Figure 1.5). In contrast, for females we found that both helpers and floaters can compete for vacancies very far from their current location (~2.4 km).

Perceptual distance is the main parameter in the competition submodel. The competition submodel seems to be the dominant component of the RCW SEPM that determines patterns observed on MCBCL. The HCRW simulates "searching behaviors" of floaters when no breeding vacancy is detected within their perceptual distance. The interaction between searching behaviors and competition requires further study. Searching behaviors are likely to contribute more to population viability when habitats become more fragmented. The habitat trading scenarios examined in the subsequent section may increase habitat fragmentation. Therefore, we chose to evaluate these scenarios with the 8 parameterizations that passed through filter combination C. This approach allows us to incorporate the remaining uncertainty in the HCRW by including multiple models of the influence of land cover on dispersal behaviors.

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2. Phase 2. Habitat Trading for the Red-Cockaded Woodpecker under Uncertainty Regarding Dispersal Behaviors

2.1 Objective

The objective of our SEED project was to derive a method of making decisions regarding habitat trades while incorporating uncertainty regarding how landscape pattern affects dispersal behaviors, and ultimately landscape connectivity. First, we described a landscape-scale tradable credit system designed to prevent habitat trades that exacerbate habitat fragmentation. Second, we applied the tradable credit system to hypothetical trading scenarios for MCBCL. The trading scenarios are evaluated using the Letcher model currently used for RCW management by USFWS and DoD. We also used the eight Habitat-based Correlated Random Walk models derived from POM in Phase 1 to evaluate habitat trades. Third, we applied the principles of decision analysis to weigh alternative management decisions in the face of uncertainty. By integrating Pattern-Oriented Modeling (Phase 1) with a landscape-scale tradable credit system, we described how one can determine when uncertainty is sufficiently large that collecting more data and reducing uncertainty is a better choice than trading habitat. Conversely, the approach can be used to determine when enough information has been collected and uncertainty regarding dispersal behaviors is sufficiently small to allow habitat trading.

2.2 Background

Marine Corp Base Camp Lejeune (MCBCL) is one of three management units for the Coastal North Carolina Population of Red-Cockaded Woodpeckers (RCWs). The other two include Croatan National Forest and Holly Shelter Game Lands. All three management units are located within the Onslow Bight Landscape, which stretches from Cape Lookout to Cape Fear (Fig 2.1). The Onslow Bight Partnership consists of federal and non-federal natural resource managers dedicated to preserving the biodiversity of the region. At recovery, the Coastal North Carolina population will include 350 Potential Breeding Groups (PBGs), which includes an adult male and female with or without helpers and fledglings (USFWS 2003a). To contribute to recovery, the USFWS has specified that MCBCL maintain a population growth rate of 5% per year and achieve 173 active clusters by 2025. Active clusters are defined as those which contain a solitary individual, may be captured by a neighboring group, or contain a PBG (USFWS 2003a). When MCBCL reaches the 173 active cluster goal, training restrictions due to RCWs will be eliminated or relieved (MCBCL 2007). Establishing new clusters outside of MCBCL, Croatan, and/or Holly Shelter within the Onslow Bight Landscape, through DoD's Encroachment Partnering program, will speed when regulatory relief is achieved (TNC 2006; Ralph Costa, USFWS, personal communication, 2006).

2.2.1 Habitat Trading

A quantitative method for determining incremental changes in regulatory relief thanks to Encroachment Partnering, prior to achieving population recovery goals, would benefit many DoD facilities. Due to the Base Realignment and Closure process, training on many DoD facilities has intensified. Below we discuss two important implications of using the Encroachment Partnering program to achieve regulatory relief for DoD. The first is that the Endangered Species Act (USFWS 1973) applies different standards to non-federal and federal

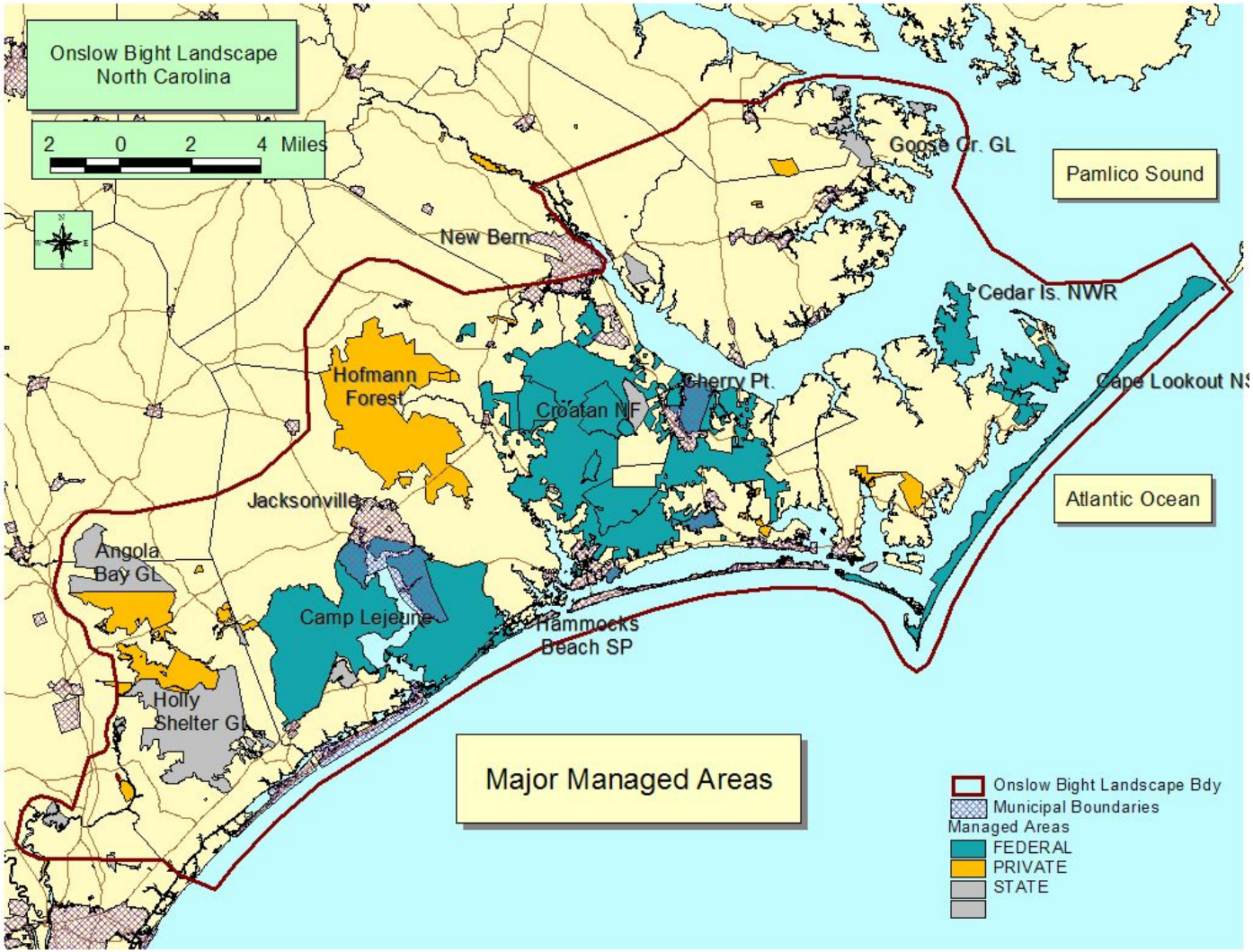

Figure 2.1. The Onslow Bight Landscape in southern coastal North Carolina.

landowners. The second is that achieving population recovery through partnerships among multiple landowners has the capacity to drastically change where habitats are located for listed species. The connectivity of habitats plays an important role in the recovery and long-term viability of many species (Hanski and Gaggiotti 2004).

The different expectations for federal and non-federal landowners are found in Sections 7, 9, and 10 of the ESA (USFWS 1973). Non-federal landowners are prevented from taking endangered species, which is defined as an action that harms, harasses, or kills a listed species (Section 9; USFWS 1973). Adverse modification to habitat that results in death or injury is included in the take provision. However, non-federal landowners are not required to manage their lands for listed species, and loss of natural disturbance regimes (e.g., fire) is often enough to decrease the probability of habitat occupancy (James et al. 2001). Under Section 10, non-federal landowners may take individuals or remove habitat if a Habitat Conservation Plan is implemented to offset the take elsewhere in the landscape (USFWS 1973). This has led to the adoption of "conservation banking," or a tradable credit system for endangered species habitat (USFWS 2003b). Tradable credit systems represent the trading of access rights to endangered species habitat. Note that federal landowners are prevented from providing habitat to offset the loss of habitat on non-federal lands (USFWS 2003b). This reflects the Section 7 requirement that federal landowners must pro-actively contribute to the recovery of listed species (USFWS 1973). Section 7 further prevents federal landowners from any action that would appreciably reduce the likelihood of survival and recovery, or jeopardize the continued existence of the species (Stanford Environmental Law Society 2001).

The RCW Recovery Plan discusses recovery goals and conditions required for offsetting a take in terms of PBGs and active clusters (USFWS 2003a), supporting the broader regulatory goal of preventing the net loss of habitat area for endangered species (USFWS 1973). However, changing the connectivity of RCW clusters can also affect RCW population viability (Cox et al. 2001; Letcher et al 1998). Landscape connectivity can be defined as "the degree to which the landscape facilitates or impedes movement among resource patches" (Taylor et al. 1993). While there are no regulatory criteria for managing changes in habitat connectivity in the ESA, the RCW Recovery Plan does consider this problem under the Private Lands Conservation Strategy (USFWS 2003a). RCW Recovery Plan specifies that only isolated clusters, defined as those sharing few migrants with other clusters, can be traded for new clusters that are more connected. Further, the location where new clusters are established must have capacity for at least 10 highly connected RCW groups. However, defining levels of connectivity at which habitat trading is a viable management option is an important area of research (USFWS 2003a). To achieve military readiness, the DoD will often wish to change the allocation of habitat for endangered species prior to reaching scientific consensus regarding dispersal behaviors.

2.2.2 Considering Landscape Processes when Trading

Parcels will differ in their contribution to total (meta)population growth, rates of migration, and maintenance of genetic variance, based not only on the size and quality of the habitat patch, but also the landscape context of a parcel (i.e., its location relative to all other land uses). For example, even if habitat patches of equivalent size, shape, and quality are traded, habitat trading will likely change the rates of migration among other patches within the region. The change in regional, landscape structure may subsequently change rates of local extinction and erosion of

genetic variance in subdivided populations such as RCWs (Bruggeman 2005). A measure of conservation value that captures the interaction between local and regional biological processes is needed to ensure that an ecologically equivalent trade in habitat is made (Bruggeman et al. 2005). A tradable credit system that accounts for differences in conservation value among habitat patches is more likely to achieve sustainable populations at the least cost.

We argue that that population genetic theory provides a robust approach for avoiding trades that increase habitat fragmentation and, subsequently, decrease population viability. Subdivided populations must achieve a balance between growth within each breeding group and migration between breeding groups to prevent local extinction, inbreeding and outbreeding depression, and to maintain genetic variance needed for adaptation through natural selection at both individual and group levels (Harrison and Hastings 1996; Mills and Allendorf 1996). Neutral genetic variance is useful for determining how habitat loss or restoration affects gene flow, genetic drift, and inbreeding (Hedrick 2001). Field studies have demonstrated that mammalian populations have evolved behaviors to simultaneously prevent loss of genetic variance within while maintaining genetic variance among local populations (Dobson et al. 1997; Storz 1999; Coltman et al. 2003). Using a computer simulation, Bruggeman (2005) showed that the complex mating system of RCWs (as described by Walters 1988) is very efficient at maintaining genetic variance within and among breeding groups when a continuous distribution of habitat exists, but habitat fragmentation increased rates of inbreeding and local extinction. In a population of 220 RCW groups, Daniels and Walters (2000) observed that short dispersal distances can result in the mating between closely related individuals, causing inbreeding depression, measured as a reduction in recruitment.

The spatial distribution of genetic variance is a reflection of the rates of growth within local populations, migration, and local extinction. The spatial apportionment of genetic variance observed in a landscape with an allocation of habitat observed prior to habitat loss and fragmentation, a baseline condition, is indicative of rates of migration and population growth that maintain adaptive genetic variance and prevent inbreeding and outbreeding depression. Therefore, we can quantify changes in fragmentation by comparing the spatial apportionment of genetic variance before and after the trade to that observed in this baseline condition (Bruggeman et al. 2005). If trading leads to greater genetic variance among local populations, compared to this baseline condition, then rates of migration, recolonization, and/or local population growth have decreased and genetic drift, inbreeding depression, and local extinction may threaten viability. If trading leads to greater genetic variance within local populations then outbreeding depression and lost opportunities for local adaptations may threaten viability.

2.2.3 Landscape Equivalency Analysis (LEA)

By integrating population genetic theory and natural resource economics, we have devised a tradable credit system to incorporate the influence of changing habitat area and connectivity on the viability of endangered species (Bruggeman et al. 2005). We developed Landscape Equivalency Analysis (LEA) as a generally applicable, landscape-scale accounting system to calculate the conservation value of tradable credits for endangered species habitat to minimize and reverse the negative effects of habitat fragmentation (Bruggeman et al. 2005). Endangered species management may benefit from incorporating habitat defragmentation into recovery goals. Therefore, LEA adds a “spatially-explicit” recovery objective as the allocation of habitat

yielding the spatial apportionment of genetic variance (e.g., as would be determined using neutral genetic markers) observed prior to habitat loss and fragmentation (Meffe 1996; Bruggeman et al. 2005). Given existing loss of habitat in most landscapes, this goal will often be unachievable, but it does serve as an objective criterion for defragmenting endangered species habitat to protect evolutionary processes at the landscape scale.

LEA is an extension of resource-based compensation applied to a landscape-scale. When environmental regulations stipulate in-kind replacement of ecological resources, as in the ESA, compensation must be made using the same type of resources that were lost (Jones and Pease 1997; Zafonte and Hampton 2007). Resource-based compensation determines the amount of restoration required to equate an individual's well-being before loss of an ecological resource with their well-being after habitat destruction. A "service-to-service" approach is used wherein adequate compensation is made to the public if the habitats restored provide equivalent types and levels of ecological services as the habitats lost. Ecological functions can be treated as goods and services when a direct or indirect benefit to humans can be demonstrated (deGroot et al. 2002). The direct human benefits of protecting endangered species include use value (e.g., seeing the species), option value (e.g., possibility that genetic variance provided by the species may contribute to medical or agricultural advances), existence value (i.e., knowing the species exists), and bequest value (i.e., knowing the species will be present for future generations) (Loomis and White 1996). Genetic variance of an endangered population also provides indirect benefits for humans. Adaptive genetic variance is required for population persistence (Fisher 1930). As previously discussed, neutral genetic variance provides useful information regarding how populations respond to changes in habitat area and connectivity. Thus, endangered species habitat is a form of natural capital, defined as a stock of resources providing useful services (deGroot et al. 2000). In this analysis we assume that the ecological services that provide these benefits are abundance and genetic variance (Bruggeman et al. 2005).

The goal of LEA is to account for habitat fragmentation by directing the trade of endangered species habitat toward the provision of the ecological services provided by the spatial allocation of habitat in which the organism evolved. Under LEA, the financial value of tradable credits equals the in-kind replacement costs of ecological services that are differentially affected by changes in habitat area and connectivity (Bruggeman et al. 2005). LEA estimates the equivalency of habitat patches traded in a fragmented landscape based on changes in three ecological services, 1) abundance and genetic variance 2) within and 3) among local populations, measured at the regional scale. Therefore, a patch restored is equivalent to a patch lost if the alternative landscape structures are equivalent in all three ecological services. A "LEA credit" represents the marginal contribution a change in landscape structure (i.e., taking or restoring of breeding or dispersal habitat) makes toward moving the ecological service closer to or away from service levels observed prior to habitat loss and fragmentation.

2.3 Method for Evaluating Hypothetical Trades with LEA under Alternative Dispersal Models

2.3.1 Step 1. Constructing Alternative Landscapes

In order to estimate LEA credits, ecological service flows from alternative landscape configurations must be projected. LEA credits were estimated by comparing three different landscape configurations: baseline, withdrawal, and mitigation. The baseline landscape was

determined using MCBCL RCW habitat restoration program, which is designed to meet their contribution to the Coastal North Carolina Population recovery goal. The restoration program is focused on the Main Base and will provide a highly clumped reference landscape. Levels of genetic variance within and among breeding groups expected to result from the restoration program were used as the baseline levels for calculating LEA credits. This represents an adjustment from the "prior to habitat loss and fragmentation" condition for a baseline described in Bruggeman et al. (2005) for trading among private landowners. The baseline trajectory of genetic services expected by the restoration plan represents the improvement in rates of recruitment, migration, and local extinction that result from meeting yearly recovery objectives and are feasible given soil types and existing land use. Therefore, habitat trading that moves genetic services away from the baseline levels has resulted in moving rates of migration, drift, inbreeding, and local extinction away from levels achievable along the recovery trajectory. Application of the "prior to habitat loss and fragmentation" condition applies to private landowners because they trade around the "take standard". In contrast, Federal landowners trade around a "recovery standard". Therefore, baseline service trajectories play a more prominent role in credit calculations and application of the "prior to habitat loss and fragmentation" condition would result in any Federal landowner owing credits due to the loss of endangered species habitat prior to the ESA being promulgated.

The withdrawal landscape represents the landscape condition that would occur due to training intensification on the Main Base, which would result in taking existing clusters or not restoring clusters that were planned to contribute to recovery. This landscape condition can be compared with a landscape in which new clusters are established outside of the Main Base to examine the contribution Encroachment Partnering makes to population viability in light of expected takes. This landscape will be referred to as the mitigation landscape. Below we describe how these landscapes were constructed and included in the RCW SEPMs.

2.3.1.1 Baseline Landscape. MCBCL plans to add 112 new clusters on the Main Base, for a total of 198 clusters (Fig. 2.2), to meet the RCW recovery objective of 173 active clusters. Five of the 112 were added in 2006, but these were treated as planned clusters because our project began before monitoring data on the occupancy of these new sites were available. Using MCBCL's "SppRePopPt" GIS layer, we determined the cluster locations and year when the cluster is expected to be made available. Within the RCW SEPMs, we added the cluster at the time and location planned by MCBCL. We simulated restoration by turning immature pine and mixed pine-hardwood pixels into the predominantly pine classification (Table 1.1) to provide 100-hectares of foraging habitat (USFWS 2003a). We later learned that the restoration plan present in the GIS layer was a rough draft, which has since been modified to restore habitat more quickly (Craig Ten Brink, MCBCL ECON, personal communication).

2.3.1.2 Withdrawal Landscape: Proposed Takes. Due to training intensification, MCBCL has identified RCW habitats that will be reduced or removed in order to achieve military readiness. MCBCL provided shapefiles of the areas to be affected and a list of territories likely to be lost (Fig. 2.2). Two different development projects are examined (Table 2.1).

The first development project is to build the new Marine Special Operations Center (MARSOC), in the southwest corner of the Main Base, beginning in 2007 (Fig. 2.2). MARSOC will result in developing 88 hectares, most of which represents immature forest, previously slated for restoration of Longleaf pine savannah in 2020 to contribute to RCW recovery on base. Development of MARSOC will result in loss of one planned cluster. We also analyzed a worse case scenario to help determine how sensitive LEA is for analyzing habitat trades. Therefore, we assumed that 3 other adjacent clusters planned for installation in 2020 would not be included in the simulation (Table 2.1).

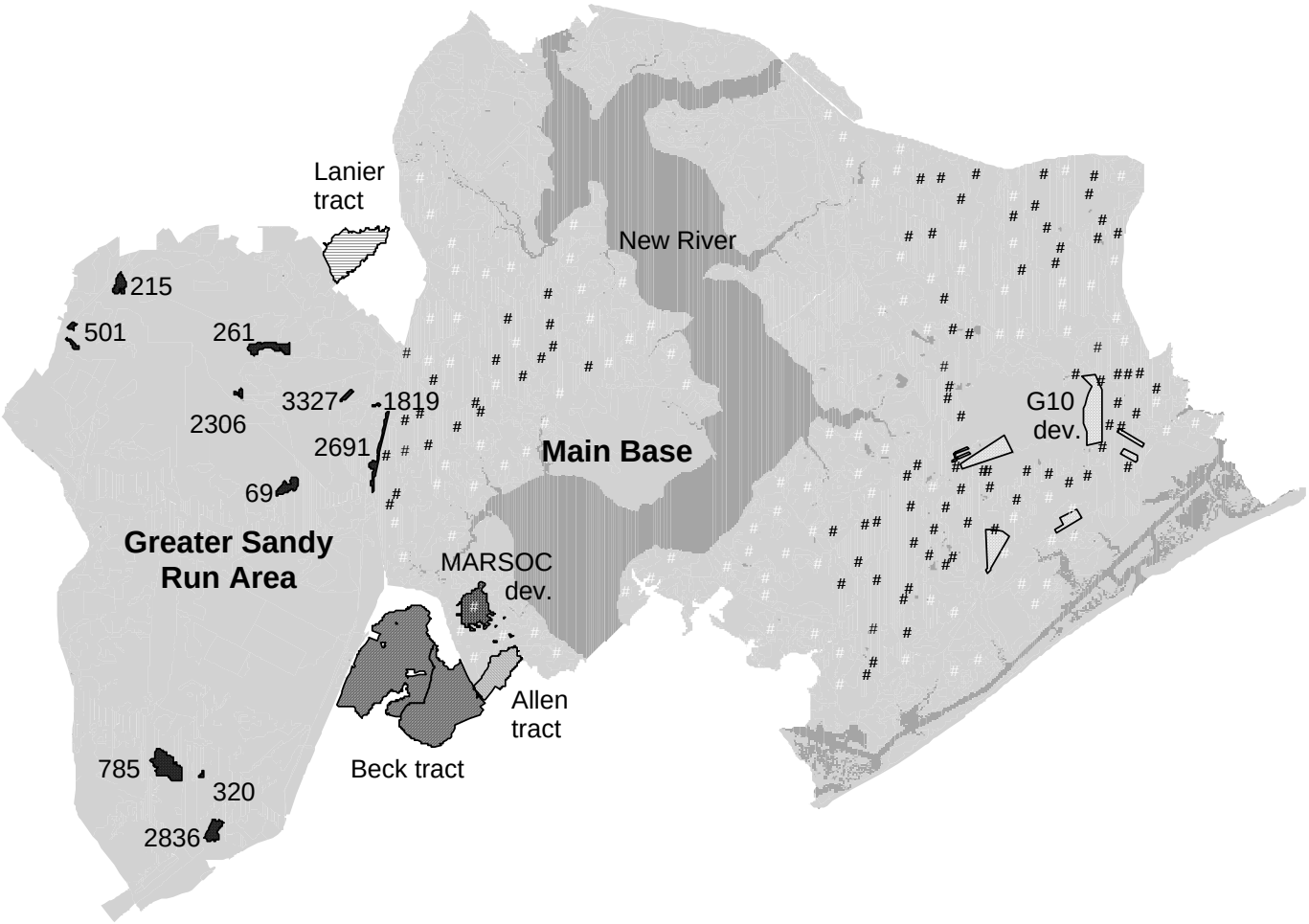

Figure 2.2. Silhouette of Camp Lejeune used to highlight proposed changes in allocation of RCW habitat. Main Base: existing RCW cluster locations are indicated with black #s and planned clusters in white #s; development of MARSOC and the G10 Area shown with stippled areas. Greater Sandy Run Area: 12 potential cluster locations are numbered; the numbers report MCBCL's Forest Object ID for stands of either Loblolly or Longleaf Pine containing at least 2 pines greater than 10" dbh. Off-base: parcels purchased through Encroachment Partnering (Beck, Allen, and Lanier) are striped.

The second development project is the installation of new ranges near the G10 area on the east side of the Main Base (Fig. 2.2). Several areas of existing forest stands will be developed, totaling 232 hectares. The G10 development is expected to begin in 2010 and impact 3 existing clusters. We also developed a worse case scenario to support a sensitivity analysis for LEA by assuming that 5 more clusters near these development sites would be lost (Table 2.1).

Table 2.1. Description of proposed takes examined with Landscape Equivalency Analysis.

Development Project	**MARSOC**	**G10 Area**
Hectares affected	88	232
Year initiated	2007	2010
Clusters lost – Best case	SB H11	23,50,55
Clusters lost – Worst case	SB H8, SB H10, SB H11, SB H14	13,15,23,37,50,55,70,75

Note: planned cluster locations are identified as alpha-numeric, while existing clusters are defined numerically.

2.3.1.3 Mitigation Landscapes: Encroachment Partnering and Restoration of Greater Sandy Run Area. Three different mitigation landscapes were evaluated with LEA. We evaluated the conservation benefit of restoring three of the five parcels already purchased through MCBCL's Encroachment Partnering program. These parcels were chosen due to their close adjacency to the Main Base and potential for allowing habitat trades without exacerbating fragmentation. The parcels included the Beck, Allen, and Lanier tracts (Fig 2.2). We also considered the conservation benefit of restoring the Greater Sandy Run Area (GSRA), which is adjacent to the Main Base and solely owned by MCBCL.

Mitigation Choice 1: Restore only the Beck and Allen tracts. The Beck and Allen tracts are adjacent to each other and lie south of MCBCL and west of the New River (Fig. 2.2). The Beck tract is 976 hectares and was acquired in cooperation with NC Wildlife Resources Commission (NCWRC). NCWRC contributed $3,396,000 and MCBCL contributed $5,236,000, for a total cost of $8,632,000. The Allen tract, sometimes referred to as Testamentary, is 68 hectares, and was acquired with cooperation with North Carolina Coastal Land Trust (NCCLT). MCBCL and NCCLT both contributed $1,732,500 (total cost = $3,465,000). In total, the Beck and Allen tracts comprise 1,044-ha.

The vegetative composition of these lands has not yet been quantified. Based on an aerial photograph, these tracts contain mixed pine-hardwood forests and bottomland hardwood forests. MCBCL estimates that 8 RCW clusters can be located on the Beck tract and one on the Allen tract in about 30 years, with an average territory size of 100-ha (USFWS 2003a). A GIS shape file with property boundaries was provided. Based on soil classification, MCBCL provided a photo of the approximate areas where Longleaf could be restored. We used this information to estimate cluster centers and integrated the current and expected habitat conditions, derived from viewing an aerial photograph and soils map, into the landscape simulation model.

Mitigation Choice 2: Restore only the Lanier tract. The Lanier tract is a 177-hectare parcel and lies in between the Main Base and GSRA to the north (Fig. 2.2). It was purchased with a cooperative agreement between MCBCL and NCWRC for a total cost of $2,032,500. Based on aerial photograph, the Lanier tract is comprised mostly of mixed pine-hardwood forests and, secondarily, bottomland hardwood forests. We estimated that two clusters could be located on the Lanier tract in 30 years.

Mitigation Choice 3: Restore Beck, Allen, Lanier, and Greater Sandy Run Area. We did not consider restoration of GSRA without the other three parcels because the Beck, Allen, and Lanier tracts will increase the connectivity of clusters in GSRA with those on the Main Base. MCBCL has initiated the restoration of Longleaf Pine in GSRA with the hopes of better connecting their RCW population with birds in the Holly Shelter Games Lands and other parcels under consideration for the Encroachment Partnering program (Fig 2.1). GSRA was acquired in 1991 by MCBCL from International Paper primarily for military training.

Placement of new clusters in the Greater Sandy Run Area was based on the best available data from MCBCL's Forestry Coverage GIS Layer and the RCW Foraging Habitat Guidelines (USFWS 2003a). The Foraging Habitat Guidelines require information on the basal area of specific size class distributions of pine. However, these data were often not available for the older stands of Longleaf and Loblolly pines in the GSRA. One basic requirement of the guidelines is that good quality foraging habitat should have 40 pines per hectare (or 16 pines per acre) of pines at least 36 cm dbh and cover 51 hectares. Available data from Forestry Coverage GIS Layer allowing us to infer these characteristics included birth year of a representative pine, total pine basal area, primary species, number of pines greater than 25 cm dbh, and size of stand (Table 2.2).

We identified 12 forest stands in GSRA dominated by Longleaf or Loblolly Pine and containing at least 2 pines greater than 25 cm dbh (Table 2.2; Fig 2.2). These stands tended to be small in size and surrounded by Longleaf and Loblolly stands that were much younger. Therefore, we assumed that stands with a birth year less than 1960, would not be suitable for both reproductive and foraging habitat for another 30 years. For the remaining six stands, we assumed that they would be suitable within 50 years. Restoration was simulated by turning immature pine and mixed pine-hardwood pixels within 800 m of cluster center into the predominantly pine classification (Table 1.1) to provide 100-hectares of foraging habitat (USFWS 2003a).

Table 2.2. Forest attributes describing stands in Greater Sandy Run Area that may be suitable locations for RCW nesting cavities.

Year cluster include in Simulation	Stand Object ID	Birth year of Stand	Pine basal Area	Hardwood basal Area	Number of pines greater than 25 cm dbh	Primary Species	Hectares
2035	320	1939	83	0	2	Longleaf	2
2035	2306	1948	70	0	4	Loblolly	4
2035	2691	1948	76	0	2	Loblolly	20
2035	3327	1948	70	0	2	Longleaf	4
2035	501	1953	68	0	3	Longleaf	4.5
2035	1070	1956	95	0	3	Longleaf	3.6
2045	69	1968	75	0	2	Loblolly	18
2045	261	1968	99	0	4	Loblolly	28
2045	215	1970	100	0	6	Loblolly	15
2055	1819	1973	80	0	4	Loblolly	1.2
2055	785	1976	150	0	2	Loblolly	53
2055	2836	1980	90	0	2	Loblolly	22

2.3.2 Step 2. Projecting Ecological Services under Uncertainty

In order to predict ecological services in the future for each landscape configuration, we used the Letcher model and eight separate models of the new HCRW SEPM identified in Phase 1. Each of the eight HCRW models represents a different parameterization that passed through all five pattern fulfillment criteria using Pattern-Oriented Modeling. Using multiple models allows us to incorporate how uncertainty regarding a species' behavior and demography might affect decision making.

Each SEPM was initiated with the population structure observed on MCBCL in 2005, including the number of observed breeders, helpers, fledglings, and floaters. Initial population size was 316 individuals. All models included an infinite alleles model of genetic variance (Lacy 2000). The infinite alleles model assumes that every founding individual is heterozygous and contains two unique alleles (i.e., total alleles = 2 x number of breeders in the founding population). We compiled a pedigree using MCBCL's RCW monitoring data provided by Jeffrey Walters. Using the pedigree we simulated the transmission of alleles from parents to offspring assuming Mendelian inheritance (i.e., their offspring had an equal probability of inheriting each of the two alleles) for the years 1986-2005, at the start of each simulation. Simulating Mendelian inheritance under an infinite alleles model allows us to estimate the spatial distribution of genetic variance in the initial population.

Population dynamics were projected 100 years into the future. At the start of each year, eight immigrants, or floaters, were added. The average number of immigrants observed each year in MCBCL over the past five years was 8.2. We assumed that each immigrant was unrelated to each other and all individuals on MCBCL. Therefore, each immigrant was heterozygous, containing two unique alleles. Immigrants were added within the simulation to parallel the manner in which Jeffrey Walters' field crews first observe new floaters. Floaters of unknown

parentage are observed in the spring near a cluster. Therefore, we placed each new floater at a location randomly selected from all possible clusters available in a year, whether occupied or not. At that point the immigrant can either compete for a breeding vacancy within their perceptual distance or begin their stepwise search for breeding vacancies elsewhere.

In order to estimate LEA credits, ecological services in the baseline, withdrawal, and mitigation landscapes were calculated. We estimated abundance as the number of PBGs due to the biological and regulatory significance of this estimate (USFWS 2003a). Recall that MCBCL's contribution to recovery will be estimated based on number of "active clusters". Due to the difficulty of estimating when neighboring groups merely capture a cluster but do not use it for breeding within a computer simulation, we used PBGs instead. The expected apportionment of genetic variance within and among breeding groups under the assumption of Hardy-Weinberg Equilibrium was estimated by the method of Nei (1973; as described in Appendix A). Nei's theory relates the total expected heterozygosity in the population (H_T) to the average expected heterozygosity within breeding groups (H_S) and average genetic divergence among breeding groups (D_{ST}), $H_T = H_S + D_{ST}$. The SEPMs include stochastic effects when determining the number of fledglings produced, individual survival, and dispersal behaviors as previously discussed in Phase 1. Therefore, we took an average for PBG, H_S, and D_{ST} at each year from 100 replicate simulations.

2.3.3 Step 3. Estimate Spatially-explicit Debits and Credits with LEA

LEA estimates debits and credits using a time-integrated estimate of proportional differences in ecological services expected under alternative landscape configurations, called Landscape Service Years (LSYs). LSYs provide an estimate of the change in landscape function due to changing habitat area and/or connectivity.

The debit in abundance is estimated as the proportional change in PBG due to habitat removal relative to number of PBG expected under the recovery trajectory. The debit in abundance services due to habitat loss (LSY_d^{PBG}) represents the marginal conservation value of the clusters lost, given their spatial context within the population.

$$E\left[LSY_d{}^{PBG}\right] = \sum_{t=W}^{100}\left(\frac{r_t{}^{PBG} - j_t{}^{PBG}}{r_t^{PBG}}\right) \quad \text{(eqn 2.1)}$$

Where the expected loss of services due to habitat loss begins at year W, r_t^{PBG} is the expected number of PBGs at year t under the USFWS recovery trajectory, j_t^{PBG} is the expected number of PBGs at year t given the loss of habitat (Table 2.1).

Next we estimate the increase in services due to restoring habitat elsewhere. The expected number of abundance credits generated by the mitigation landscape (LSY_c^{PBG}) is estimated as:

$$E\left[LSYc^{PBG}\right] = \sum_{t=W}^{100}\left(\frac{m_t{}^{PBG} - j_t{}^{PBG}}{r_t^{PBG}}\right) \quad \text{(eqn 2.2)}$$

where m_t^{PBG} is the expected number of PBGs at year t given the loss of habitat on the Main Base and restoration of habitat outside of the Main Base (i.e., service trajectory from mitigation

landscape). If ($LSY_c^{PBG} - LSY_d^{PBG}$) is greater than or equal to zero, then off-site restoration provides enough abundance credits to justify the habitat trade.

Calculating tradable credits associated with changes in genetic variance is more complex. The management goal is to approximate ecological services provided by the distribution of habitat in which the organism evolved (Meffe 1996; Moritz 2002). Greater genetic diversity within a breeding group or greater genetic divergence among breeding groups is not always better for sustainability (Bouzat 2001). The levels of genetic service provided by the baseline landscape will be used to direct trading toward this goal. The spatial distribution of the clusters in the baseline landscape have been planned to be as clumped in distribution as vegetative composition will allow.

As estimates of genetic variance within and among breeding groups move farther away from baseline levels due to losing a patch or connectivity, the larger the debit in genetic services that accrues. To account for changes in genetic diversity either greater than or less than baseline levels, LSY_d^G uses the absolute distance between service trajectories:

$$E\left[LSY_d{}^G\right] = \sum_{t=W}^{100}\left(\frac{\left|b_t{}^G - j_t{}^G\right|}{b_t{}^G}\right) \quad \text{(eqn 2.3)}$$

where G is the genetic variance component estimated (H_S or D_{ST}), b_t^G is the expected level of genetic variance at year t provided by the baseline landscape, and j_t^G is the expected level of genetic variance at year t provided by the withdrawal landscape.

To estimate the contribution restoring habitat off-base would make toward maintaining the spatial allocation of genetic variance observed in the baseline landscape, LSY_c^G is estimated as:

$$E\left[LSY_c{}^G\right] = \sum_{t=W}^{100}\left(\frac{\left|b_t{}^G - j_t{}^G\right|}{b_t{}^G}\right) - \sum_{t=W}^{100}\left(\frac{\left|b_t{}^G - m_t{}^G\right|}{b_t{}^G}\right) \quad \text{(eqn 2.4)}$$

where m_t^G is the expected level of genetic variance at year t provided by the mitigation landscape, which includes the loss of clusters on the Main Base. LSY_c^G is large when mitigation moves genetic services close to baseline (i.e., value on right hand side of minus sign equals zero). The best outcome is that LSY_c^G equals LSY_d^G, meaning that clusters on-base can be traded with clusters outside of the Main Base without exacerbating the effects of habitat fragmentation. In other words, restoration has been provided so that the baseline and mitigation landscapes provide equivalent genetic services. If LSY_c^G is positive but less than LSY_d^G, then mitigation off-base did help ameliorate the effects of habitat fragmentation caused by the take, but rates of recruitment and migration in the baseline and mitigation landscapes are not equivalent. If LSY_c^G equals zero then the withdrawal and mitigation level genetic services are equally distant from baseline levels and mitigation did not help to reduce the effects of fragmentation. If LSY_c^G is negative then mitigation moves genetic services farther away from baseline than observed under the withdrawal landscape indicating that off-base mitigation has exacerbated functional fragmentation.

2.4 Results and Discussion

2.4.1 Mitigation Choice 1: Restore Only Beck and Allen Tracts

First, we discuss the extent to which restoring 9 clusters on the Beck and Allen tracts will mitigate the loss of clusters on the Main Base (Table 2.1), including the secondary effects of changes in habitat connectivity. The temporal trajectories of ecological services are illustrated in Figures 2.3 to 2.5. Recall that MCBCL is required to reach its recovery goal by 2025. However, habitat loss begins in 2007 while habitat restoration outside of the Main Base does not begin until 2035.

We observed that the withdrawal landscape will still provide enough clusters to exceed the recovery goal by 2025 (Fig 2.3), thanks to the aggressive RCW habitat restoration plan on Main Base. However, the rate of recovery in the withdrawal landscape is a little slower when compared to the baseline landscape, especially in the Letcher model. A high rate of habitat occupancy was observed for the Letcher model and all 8 parameterizations of the HCRW SEPM. Therefore, the debit in services estimated by comparing the PBG-trajectory under the withdrawal landscape to the PBG-trajectory given the recovery goal (eqn 2.1) resulted in a negative LSY_d^{PBG} value, because the j-trajectory exceeds, on average, the r-trajectory from the time the loss of habitat begins (W=2007) (Table 2.3). In other words, despite the loss of habitat area in both the best and worst case scenarios, all models predict that more than enough clusters are provided and occupied by RCWs on the Main Base to meet MCBCL's contribution to recovery by 2025.

The conservation benefit of establishing new clusters on the Beck and Allen tracts in 2035, estimated by the m-trajectory, indicates occupancy of these new clusters shortly after they were made available in 2035 (Fig 2.3). Therefore, LSY_c^{PBG} values indicate a further accrual of PBG credits relative to the recovery goal, for all models (eqn. 2.2; Fig 2.3).

The differences in LEA credits between the new RCW HCRW and the Letcher SEPMs are not large for PBGs (Table 2.3). Both indicate that more credits remain under the best case development scenario. The Letcher model predicts that habitat loss will have a slightly worse effect on PBGs than the HCRW models. Further, the Letcher model predicts that habitat restoration will have a slightly stronger benefit for habitat occupancy than predicted by HCRW models. The net result is that both the Letcher and HCRW models predict roughly the same number of LSY^{PBG} credits will remain after the trade.

Proportional changes in genetic services due to the loss of clusters on the Main Base were small (Table 2.3; Figs. 2.4 and 2.5). Comparing the average expected heterozygosity within breeding groups (H_S) in the baseline landscape to that observed in the withdrawal landscape (i.e., eqn. 2.3 reporting LSY_d^{Hs}) suggested that the loss of clusters on the Main Base may only slightly change rates of genetic drift and inbreeding (Table 2.3; Fig 2.4). The Letcher model predicts LSY_d^{Hs}-values that fall within the range expected from the eight HCRW models. The rather small debit for H_S is not surprising given the density of RCW clusters that remain on the Main Base after the MARSOC and G10 development projects, and the number of immigrants expected to arrive each year to MCBCL.

When including the comparison of the baseline landscape to the mitigation landscape (eqn. 2.4), differences between the Letcher and HCRW models emerge. The Letcher model predicts that off-base restoration will help move H_S closer to baseline levels (i.e., LSY_c^{Hs} values are positive). However, LSY_c^{Hs} values are not as large as LSY_d^{Hs} values, so a small habitat fragmentation effect may remain despite mitigation efforts. In contrast, the HCRW models predict that off-base mitigation will move H_S farther away from baseline (i.e., LSY_c^{Hs} values are negative). Therefore, off-base mitigation has increased the effects of habitat fragmentation compared to the withdrawal landscape. The negative values for LSY_c^{Hs} are small, but they suggest that the 9 off-base clusters do not make an equivalent contribution to rates of recruitment as those that may be lost on the Main Base. Recall the Letcher model does not allow land cover to affect dispersal behaviors. Therefore, breeding vacancies may be filled at a greater rate in the Letcher model.

For average genetic divergence among breeding groups (D_{ST}), we observed a small debit due to the loss of clusters on the Main Base (LSY_d^{Dst}; Fig. 2.5). The loss of these clusters often resulted in an increase in genetic differences among groups. In other words, the loss of the clusters on the Main Base likely changed patterns of migration among groups, leading to an increase in the degree of genetic differentiation among groups. When comparing D_{ST} values observed in the baseline, withdrawal, and mitigation landscapes (eqn. 2.4), a small increase in habitat fragmentation effects is observed in all models (Table 2.3). Therefore, the 9 clusters restored off-base do not make equivalent contributions to migration among clusters as those that may be lost on the Main Base. However, the net increase in habitat fragmentation effects is small (Fig 2.5). The Letcher model predicts the smallest increase in genetic divergence because its dispersal rules allow for relatively higher rates of gene flow among distant clusters.

Table 2.3. Landscape Service Years (LSYs) that evaluate the ability of restoring 9 clusters on the Beck and Allen tracts to offset habitat loss and fragmentation effects resulting from the loss of 4 clusters (best case) or 12 clusters (worst case) on the Main Base.

	Landscape Service Years (LSYs)								
	[2]LSY_d^{PBG}	LSY_c^{PBG}	PBG Credits remaining	LSY_d^{Hs}	[3]LSY_c^{Hs}	[4]H_S Credits remaining	LSY_d^{Dst}	[3]LSY_c^{Dst}	[4]D_{ST} Credits remaining
[1]HCRW SEPM					**Best Case**				
minimum	-8.38	3.17	9.83	0.084	-0.212	-0.297	0.203	-0.498	-0.705
median	-7.60	3.34	11.00	0.097	-0.146	-0.251	0.228	-0.392	-0.635
maximum	-6.54	3.55	11.92	0.154	-0.080	-0.195	0.288	-0.259	-0.514
Letcher SEPM	-6.63	3.60	10.23	0.096	0.004	-0.092	0.173	-0.119	-0.293
[1]HCRW SEPM					**Worst Case**				
minimum	-4.13	2.83	5.26	0.068	-0.271	-0.375	0.183	-0.581	-0.900
median	-3.31	3.21	6.52	0.104	-0.141	-0.236	0.251	-0.343	-0.599
maximum	-2.43	3.38	7.51	0.126	-0.068	-0.161	0.327	-0.195	-0.429
Letcher SEPM	-2.46	3.43	5.89	0.096	0.022	-0.074	0.226	-0.035	-0.262

[1] Range of values taken from results of running eight different parameterizations of the RCW HCRW SEPM derived from Phase 1.
[2] Proportional loss of ecological services relative to the recovery goal (eqn 2.1). If negative, a gain in ecosystem services has occurred above that required by the recovery criteria.
[3] Mitigation exacerbated the effects of fragmentation when values are negative (eqn 2.4).
[4] When values are close to zero, habitat trading did not exacerbate the effects of fragmentation.

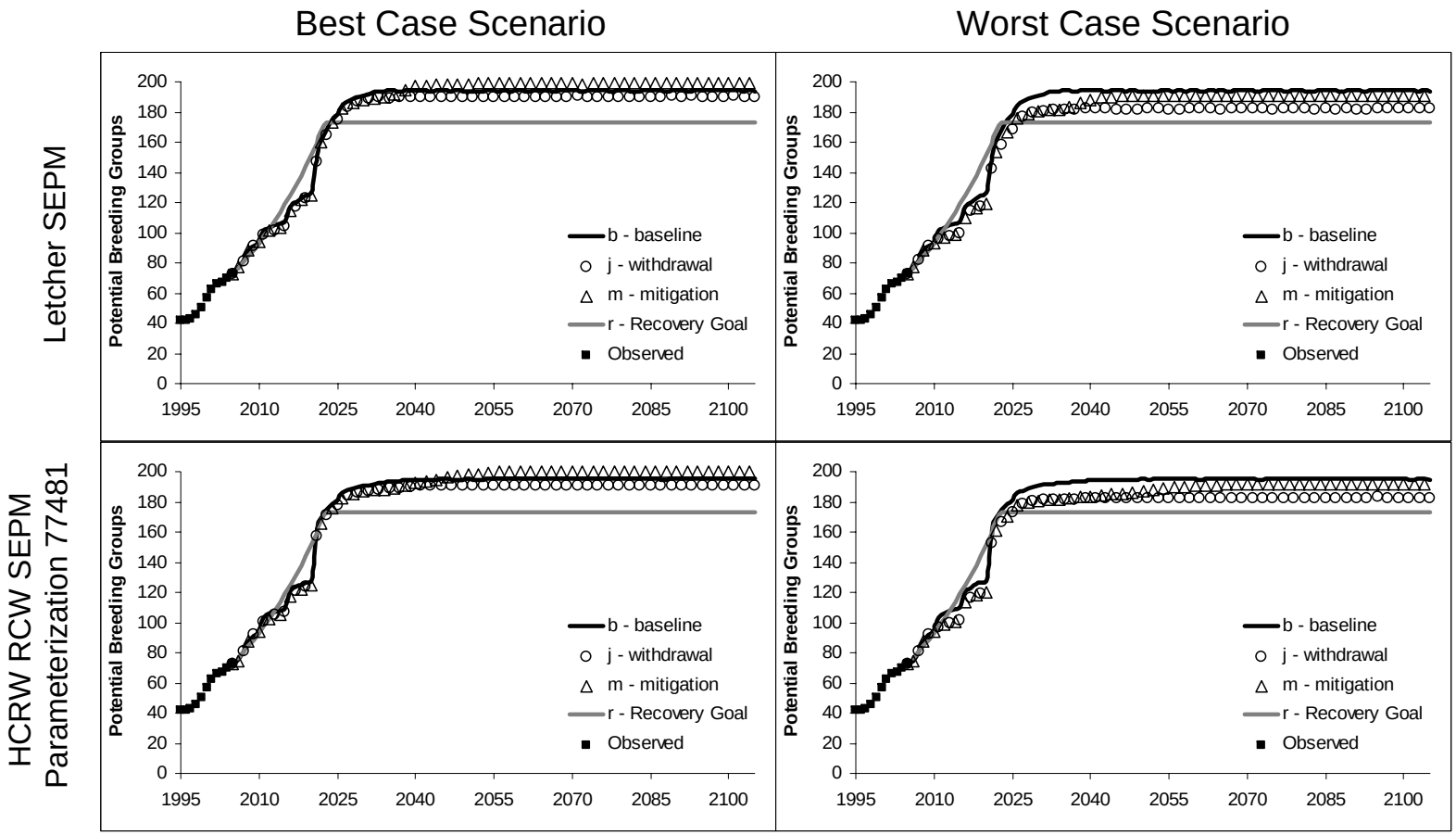

Figure 2.3. Trajectories of Potential Breeding Groups used to estimate LEA credits derived from the original Letcher SEPM and one parameterization of the Habitat-correlated Random Walk SEPM. Baseline landscape includes the addition of 112 new clusters by 2025. Withdrawal landscape represents the baseline landscape minus the loss of clusters due to MARSOC (t=2007) and G10 (t=2010) development. The best and worst case scenarios are defined in Table 2.1. The mitigation landscape represents the withdrawal landscape plus the addition of clusters on the Beck and Allen tracts (t=2035) thanks to Encroachment Partnering. The recovery trajectory represents USFWS's expectation for MCBCL's contribution to recovery of the Coastal North Carolina RCW Population.

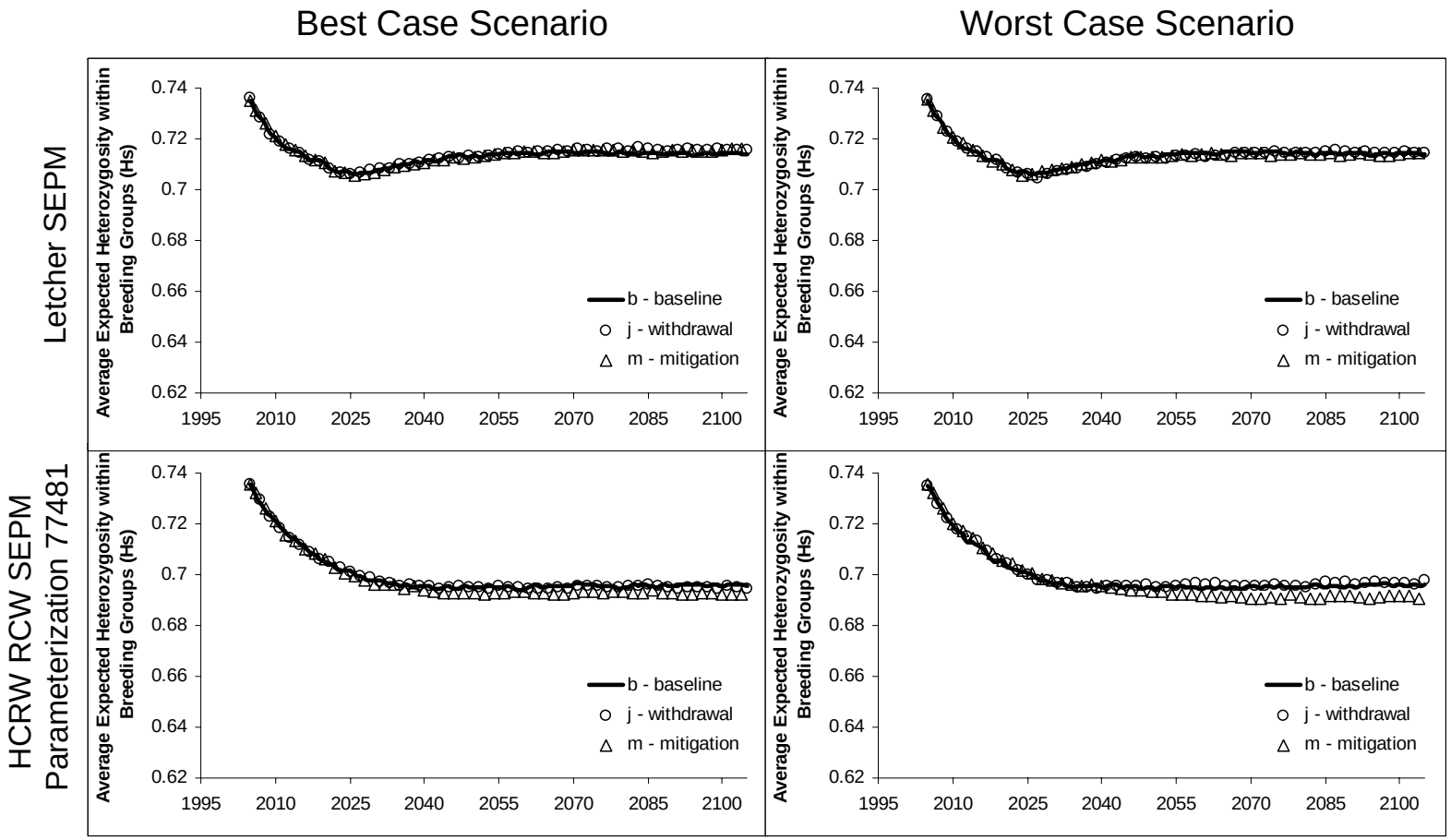

Figure 2.4. Trajectories of average expected heterozygosity within breeding groups (H_S) used to estimate LEA credits derived from the original Letcher SEPM and one parameterization of the Habitat-correlated Random Walk SEPM. Parameterization 77481 is displayed because the biggest change in genetic diversity was observed in this simulation. Baseline landscape includes the addition of 112 new clusters by 2025. Withdrawal landscape represents the baseline landscape minus the loss of clusters due to MARSOC (t=2007) and G10 (t=2010) development. The best and worst case scenarios are defined in Table 2.1. The mitigation landscape represents the withdrawal landscape plus the addition of clusters on the Beck and Allen tracts (t=2035) thanks to Encroachment Partnering.

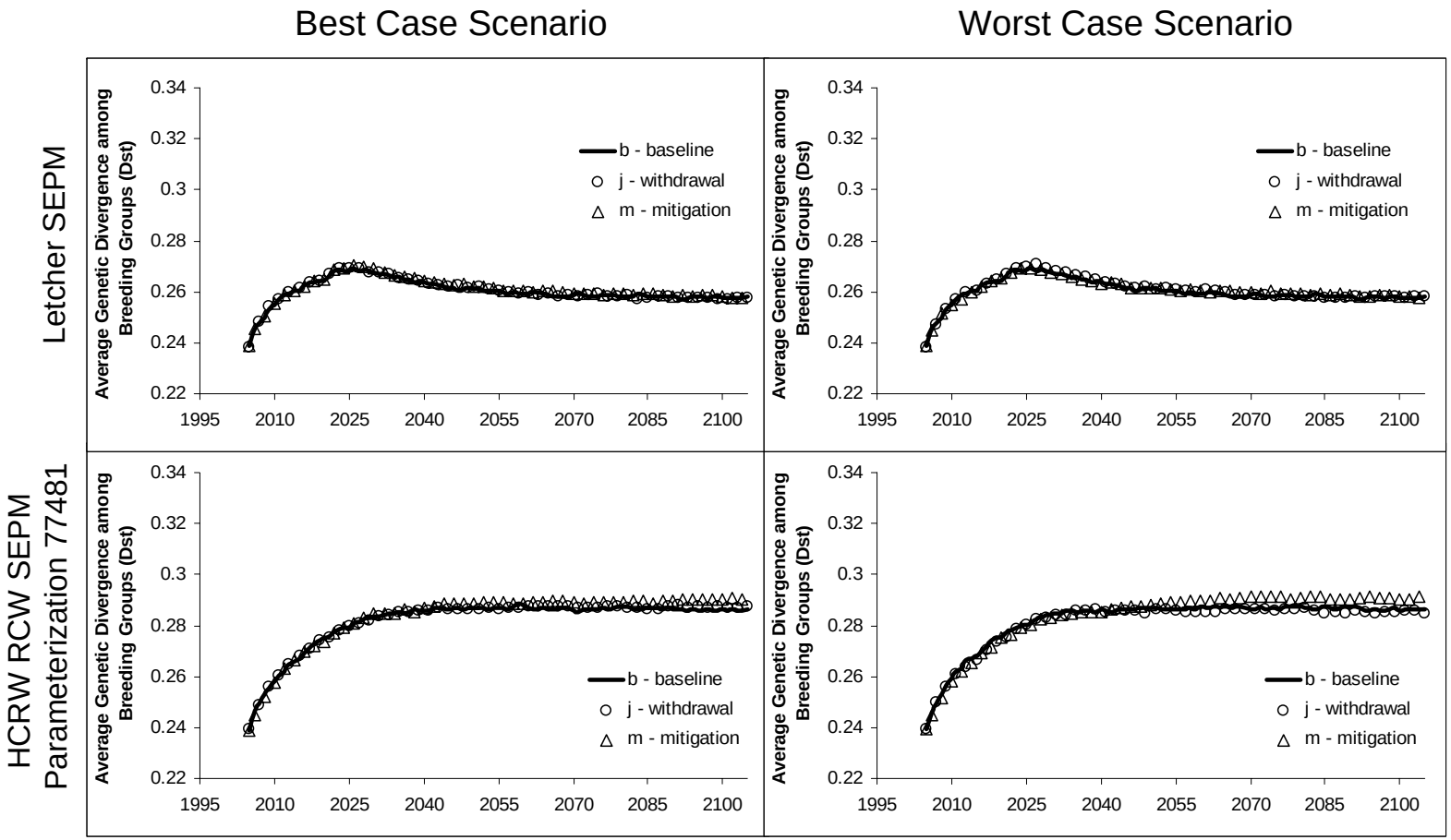

Figure 2.5. Trajectories of average genetic divergence among breeding groups (D_{ST}) used to estimate LEA credits derived from the original Letcher SEPM and one parameterization of the Habitat-correlated Random Walk SEPM. Parameterization 77481 is displayed because the biggest change in genetic diversity was observed in this simulation. Baseline landscape includes the addition of 112 new clusters by 2025. Withdrawal landscape represents the baseline landscape minus the loss of clusters due to MARSOC (t=2007) and G10 (t=2010) development. The best and worst case scenarios are defined in Table 2.1. The mitigation landscape represents the withdrawal landscape plus the addition of clusters on the Beck and Allen tracts (t=2035) thanks to Encroachment Partnering.

2.4.2 Mitigation Choice 2: Restore only Lanier

Next we contrast the conservation benefit of restoring only the Beck and Allen tracts with the choice to restore only the Lanier tract. The trades are compared based on the number of LSYs remaining after a trade (i.e., $LSY_d - LSY_c$), which represents the net gain or loss of ecological services due to a change in landscape pattern.

As expected, restoring only 2 clusters on the Lanier tract will leave fewer LEA credits for PBGs than would be possible if the Beck and Allen tracts were restored (Fig 2.6). These results do indicate that the Lanier clusters also have a high probability of maintaining breeding groups ($LSY_c^{PBG} > 0$ for all models). For all off-base habitat trading, the number of LSYs remaining for PBGs reported by the Letcher model is within the range of values expected from the eight HCRW models (Fig 2.6).

Changes in genetic services indicate that habitat fragmentation effects are smaller when restoring the Lanier tract than the Beck and Allen tracts (Fig. 2.6). In other words, restoring only 2 clusters on Lanier provided more equivalent contributions to the rates of recruitment and migration, compared to those lost on Main Base, than the 9 clusters that could be restored on the Beck and Allen tracts. Therefore, while the Lanier tract represents a smaller increase in habitat area, it provides clusters that are more strongly connected with other clusters in the landscape. The Letcher model suggests that the apportionment of genetic variance is fairly insensitive to changes in landscape structure that result from trading (Fig 2.6). In contrast, the HCRW models suggest that restoration of Lanier will result in smaller changes in population genetic structure, compared to the restoration of the Beck and Allen tracts. The changes in genetic services due to mitigation is often very small (i.e., the largest possible change in genetic structure for these comparisons is displayed in Figs. 2.4 and 2.5).

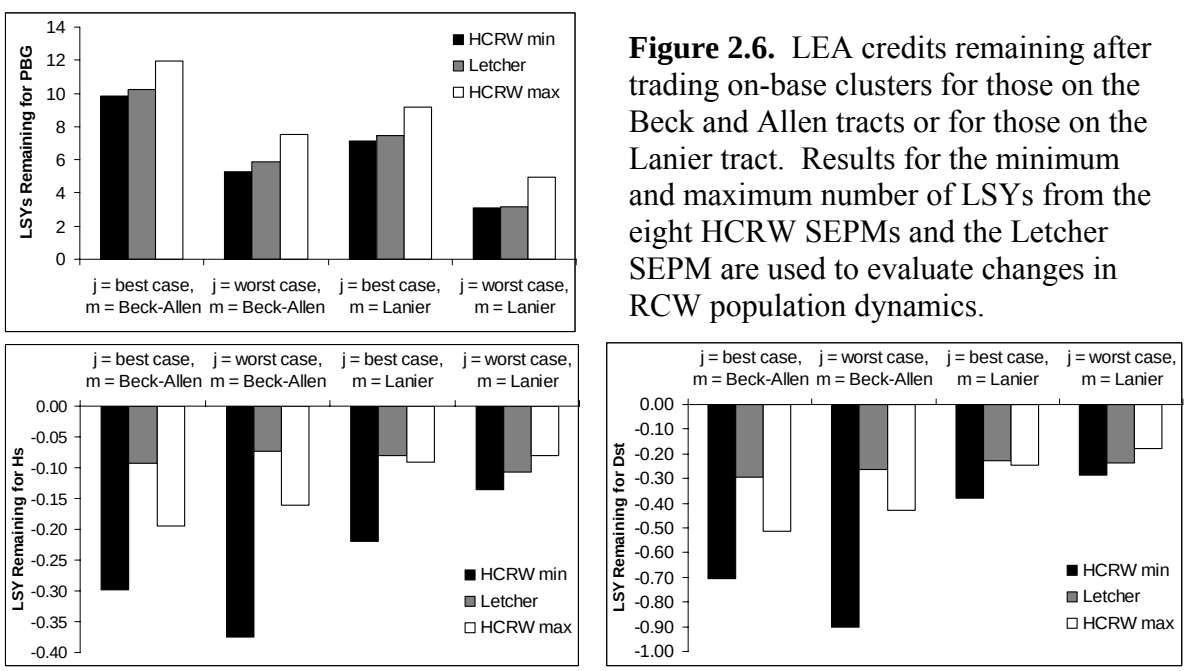

Figure 2.6. LEA credits remaining after trading on-base clusters for those on the Beck and Allen tracts or for those on the Lanier tract. Results for the minimum and maximum number of LSYs from the eight HCRW SEPMs and the Letcher SEPM are used to evaluate changes in RCW population dynamics.

2.4.3 Mitigation Choice 3: Restore Beck, Allen, Lanier and GSRA

We examined the conservation benefit of restoring Beck, Allen, Lanier, and GSRA for the best case and worst case development scenarios. Restoring all possible areas outside of the Main Base should help increase connectivity of RCWs across the Onslow Bight Landscape. However, loss of forested areas due to economic growth is occurring rapidly across the Onslow Bight Landscape. Therefore, we included a new question: how might further development in the Onslow Bight Landscape affect future trading options for MCBCL? We tested this by varying the number of immigrants added per year to the simulation. Recall that eight floaters of unknown origin are added to the landscape at eight randomly selected clusters each year to parallel field observations. To simulate how development may affect landscape function we evaluated trades assuming 8, 2, and 0 immigrants per year.

First, we compare the results of the three mitigation choices by assuming eight immigrants per year. The restoration of Beck, Allen, Lanier, and GSRA provides an increase in credits remaining for PBGs (Fig. 2.7), compared to the decisions to develop only the Beck and Allen tracts or only the Lanier tract (Fig. 2.6). However, comparing Figures 2.6 and 2.7, we see that the increase in credits is not linear. In other words, if the Beck, Allen, and Lanier tracts achieved the same level of habitat occupancy when all mitigation sites were restored, then we would expect that we could simply stack the histograms from Figures 2.6 and 2.7. In the best case scenario, if we stacked the histograms, we would get 18-22 LSYs remaining for PBGs instead of 12 to 16 (Fig 2.7). Therefore, providing more clusters that are dispersed may help decrease occupancy previously observed under the Beck and Allen or Lanier only mitigation scenarios (Pulliam 1988). When immigration into MCBCL is decreased (Fig. 2.7), a small decline in the number of LSYs remaining for PBGs results in both the best and worst case scenarios.

By restoring all sites outside of the Main Base, we observed that habitat fragmentation effects increased notably in the HCRW models. Assuming eight immigrants per year, the decrease in credits remaining observed for H_S under mitigation choice 3 (Fig 2.7), compared to the other mitigation choices (Fig. 2.6), indicate that the new, dispersed clusters do not make equivalent contributions to rates of recruitment as those that may be lost from the Main Base. The Letcher model also indicates increased fragmentation effects due to mitigation choice 3 compared to choices 1 and 2, but the effects are often smaller compared to the HCRW models. The HCRW models further indicate that increased fragmentation effects should be expected if immigration into MCBCL is reduced. These results suggest that maintaining migration into MCBCL from the Onslow Bight Landscape will help provide flexibility when determining how to change the allocation of habitat to relieve training restrictions. Immigrants help reduce influences of genetic drift and inbreeding that erode genetic variance within breeding groups.

Average genetic divergence among groups (D_{ST}) was more sensitive to changes in landscape structure than H_S. More genetic differences among groups accrue due to the restoration of dispersed clusters under mitigation choice 3. Therefore, the restored clusters do not make equivalent contributions to rates of migration among breeding groups as those that may be lost on the Main Base.

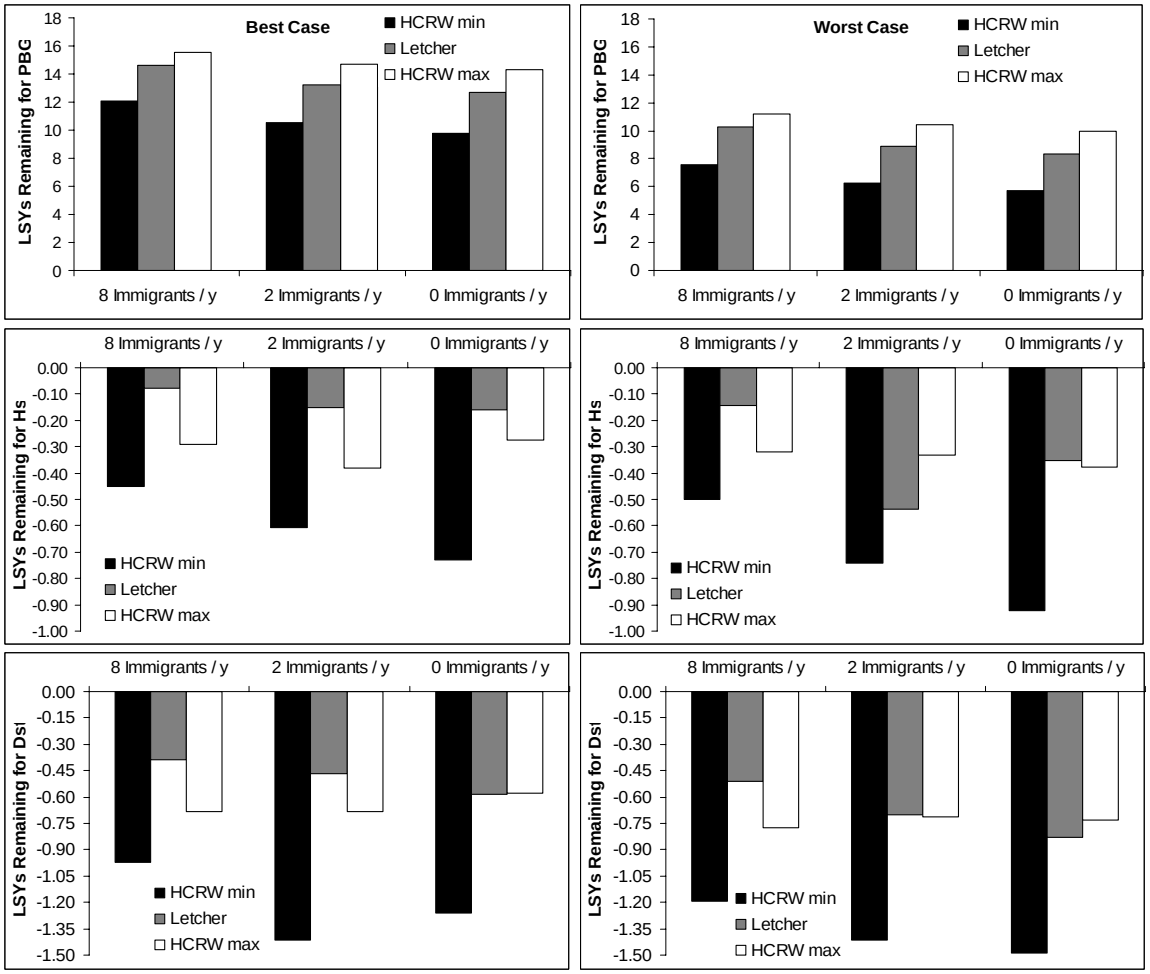

Figure 2.7. LEA credits remaining after trading on-base clusters for those on the Beck, Allen, Lanier, and Greater Sandy Run Area (GSRA), for all SEPMs used to evaluate changes in RCW population dynamics. Number of immigrants per year from Onslow Bight Landscape were reduced to examine how outside development might affect habitat trading.

2.4.4 Making Cost-effective Decisions under Uncertainty

2.4.4.1 Decision Making under Uncertainty. Our results report a range of possible effects that changing habitat area and connectivity might have on RCWs on and near MCBCL. We used decision analysis to more formally incorporate the role of uncertainty into habitat trading or mitigation choices (Raiffa and Schlaifer 1961; Clemen and Reilly 2001). We assumed that the best trade could be determined based on the number of LSYs remaining for each of the three ecological services. Number of LSYs remaining is a time-integrated estimate of the net gain or loss of ecological services due to the change in landscape structure. The expected value of a trade given uncertainty in dispersal behaviors captured by the eight SEPMs is estimated as:

$$EV[Trade \mid M] = \sum_{M=1}^{8} P[M] * LSY_{M,Trade} \qquad \text{(eqn. 2.5)}$$

Where, M is the index for the eight uncertain SEPMs, P[M] is the prior probability that SEPM "M" is true, $LSY_{M,Trade}$ is the number of LSYs remaining after the trade observed under model "M". All eight models passed through Filter Combination C from Phase 1, therefore, we assumed that each model has an equal probability of being true, P[M]=0.125. The trade with the greatest expected value is referred to as the preferred trade ($EV[Trade^{p}|M]$). For PBGs the preferred trade, given uncertainty in dispersal behaviors, is to restore all possible locations outside of the Main Base (Table 2.4). In contrast, for both genetic services, the preferred trade, given uncertainty in dispersal, is to restore only the Lanier tract, which reduced fragmentation effects relative to the other choices.

Next we wish to know the expected LSYs remaining assuming that the best trade is made given the expectations under each model. This value equals the expected value of knowing the true dispersal behaviors (i.e., the true SEPM) given the possible trades available:

$$EV[M \mid Trade] = \sum_{M=1}^{8} P[M] * \max(LSY_{M,Trade}) \qquad \text{(eqn. 2.6)}$$

Where, $\max(LSY_{M,Trade})$ is the largest number of LSYs remaining from the three possible trades for each SEPM. If EV[M|Trade] does not equal EV[Trade|M] for all M, then at least one of the eight models indicates that a greater conservation benefit can be achieved by making a different trade than suggested when considering all models to be equally likely.

The expected value of learning the true dispersal behaviors can now be estimated as the expected value of perfect information (EVPI = EV[M|Trade] - $EV[Trade^{p}|M]$). If EVPI is positive then reducing uncertainty may lead to a different mitigation choice that provides greater conservation benefits. The EVPI is zero for each service in the best and worst case scenarios (Table 2.4). In other words, for genetic services, reducing uncertainty would likely not lead to a decision to restore other parcels besides Lanier, because the expected conservation value of knowing the true model is no greater than the conservation value of only restoring Lanier. We conclude that the value of learning is

Table 2.4. Results of Decision Analysis applied to habitat trading using Landscape Equivalency Analysis under uncertainty regarding dispersal. The preferred mitigation choice is highlighted in gray.

	Remaining LSY^{PBG}			Remaining LSY^{Hs}			Remaining LSY^{Dst}		
Mitigation Choices	EV [Trade|M]	EV [M|Trade]	EVPI	EV [Trade|M]	EV [M|Trade]	EVPI	EV [Trade|M]	EV [M|Trade]	EVPI
	Best Case								
1. Beck and Allen	10.98			-0.248			-0.615		
2. Lanier	8.33			-0.145	-0.145	0	-0.292	-0.292	0
3. Restore All	13.87	13.87	0	-0.385			-0.886		
	Worst Case								
1. Beck and Allen	6.51			-0.251			-0.615		
2. Lanier	4.07			-0.108	-0.108	0	-0.241	-0.241	0
3. Restore All	9.46	9.46	0	-0.367			-0.875		

EV[Trade|M] = expected conservation value of trade given uncertainty in the SEPMs.
EV[M|Trade] = expected conservation value of knowing the true SEPM given the possible trades.
EVPI = EV[M|Trade] - EV[$Trade^P$|M]

Table 2.5. Projected management costs for the three mitigation choices (Beck and Allen Only, Lanier Only, and Restore All Possible outside Main Base). Costs of land purchase include contributions from DoD and Encroachment Partners. Management costs were taken from Table 16 in RCW Recovery Plan (USFWS 2003a).

Mitigation Choices	**Number of Clusters**	**[1]Cost of Land Acquisition**	**[2]Initial Restoration**	**[3]Prescribed Burning**	**[4]Cavity Installation**	**Total Cost**	**Cost per Cluster**
1. Beck and Allen	9	$ 12,097,000	$ 225,000	$ 787,500	$ 7,200	$ 13,116,700	$ 1,457,411
2. Lanier	2	$ 2,032,500	$ 44,250	$ 154,875	$ 1,600	$ 2,233,225	$ 1,116,613
GSRA[5]	12	$ -	$ 300,000	$ 1,050,000	$ 9,600	$ 1,359,600	$ 113,300
3. Restore All	23					$ 16,709,525	$ 726,501

[1]The cost of acquiring the Greater Sandy Run Area was not included because this acquisition was made to provide land for military training.
[2]Initial clearing of understory at $250/ha
[3]Prescribed burning costs $50/ha to be applied every 4 years over a 70 year planning horizon.
[4]Assumes that 4 cavities are installed for each cluster at a total cost of $800
[5]GSRA clusters were not evaluated as a mitigation choice alone because they were the most isolated clusters. Therefore, we included restoration of Beck, Allen, and Lanier tracts in the "Restore All" mitigation choice to increase connectivity with GSRA

zero given the uncertainty about dispersal behaviors that emerged from Phase 1 and for the trades we examined in Phase 2. We stress that this conclusion is specific to the dispersal behaviors and trades that we considered – there may be value to learning about the dispersal uncertainties we considered for other landscape configurations and trading scenarios.

2.4.4.2 Cost-effectiveness. LEA organizes habitat trading based on the in-kind replacement costs of the three ecological services. Replacement costs of ecological services were estimated using the total cost of land acquisition and costs associated restoring and managing habitat reported in the RCW Recovery Plan (USFWS 2003a) (Table 2.5). Therefore, LEA allows us to incorporate habitat fragmentation effects into cost-effectiveness analysis. We define the most cost-effective trade as the one providing the greatest conservation benefits at the lowest cost (Wätzold and Schwerdtner 2005). Specifically, the most cost effective trade has the lowest cost per LSY. However, the restoration choices available were unable to replace genetic services and actually created a small net increase in habitat fragmentation. No trade considered provided a cost effective approach for preventing habitat fragmentation. For discussion purposes, we present cost effectiveness in terms of allocating PBGs, an index of total habitat area.

Table 2.6 indicates that the most cost effective trade, ignoring habitat fragmentation effects, is to develop Beck, Allen, Lanier, and GSRA. Both the Letcher model and the HCRW model indicate that this is the most cost-effective trade for PBGs. The price of credits is a little lower under the Letcher model than the HCRW models, because the Letcher model predicted greater rates of habitat occupancy in GSRA. The price of credits is higher under the worse case development scenarios, because fewer LSY_c^{PBG} accrue (Table 2.3). Note that because this analysis does not include genetic services, it is biased against mitigation choice 2 which resulted in less fragmentation that the other choices.

Table 2.6. Cost effectiveness of alternative mitigation choices using the Letcher SEPM and the expected value of the trade given uncertainty in the HCRW SEPM (EV[Trade|M]).

Mitigation Choices	[1]Letcher LSY_c^{PBG}	Cost / LSY_c^{PBG}	[1]HCRW LSY_c^{PBG}	Cost / LSY_c^{PBG}
		Best Case		
1. Beck and Allen	3.60	$3,639,726	3.38	$3,879,209
2. Lanier	0.85	$2,625,378	0.73	$3,077,291
3. Restore All	7.97	$2,096,282	6.28	$2,660,246
		Worst Case		
1. Beck and Allen	3.43	$3,825,628	3.16	$4,146,555
2. Lanier	0.70	$3,195,708	0.72	$3,105,351
3. Restore All	7.78	$2,147,619	6.07	$2,752,915

[1]equation 2.2

We found that the price of a LEA credit for PBGs varies from roughly $2 to $4 million due to land values in coastal North Carolina. Therefore, had decision analysis indicated that there was value in reducing uncertainty regarding dispersal (i.e., positive EVPI), then

a cost-effect research study would be one that requires less than (EVPI*Cost/LSY) dollars.

2.5 Conclusions

LEA indicates that mitigation choices available to MCBCL will lead to different conservation benefits and costs, measured as Landscape Service Years (LSYs) for three ecological services. The number of LSYs remaining captured the contribution individual land parcels make to maintaining rates of habitat occupancy, recruitment, and migration observed under a clumped distribution of habitat. If habitat trades were based solely on exchanging equal numbers of occupied clusters, then MCBCL would be advised to restore all possible locations outside of the Main Base, as this provided the greatest number of credits at the least cost. In contrast, if habitat trades were based on ensuring equivalent rates of recruitment and migration are maintained after a trade, then none of the mitigation choices fully satisfy this condition. However, only restoring the Lanier tract led to the smallest fragmentation effects.

Our analysis suggests that habitat fragmentation effects due to trading will likely be small. Model assumptions reducing habitat fragmentation effects include implementation of an aggressive restoration program on the Main Base, increasing habitat density, and constant rates of immigration into MCBCL from the Onslow Bight Landscape. These model conditions suggest that significant habitat fragmentation effects over ecologically relevant time scales, such as inbreeding depression and increased rates of local extinction, are not likely to result from trading.

In general, habitat fragmentation effects were exacerbated by restoring parcels outside of the Main Base (i.e., baseline and withdrawal landscapes were more functionally equivalent than the baseline and mitigation landscapes). It is important to emphasize that this was a consequence of the spatial scale of the analysis and the fact that adjacency of clusters increases the probability of immigration. The baseline condition was defined only based on the spatial association of clusters on the Main Base. In the future, the baseline condition should be determined at a larger scale to understand how habitat trading will change levels of fragmentation for the entire Coastal North Carolina Recovery Unit.

Landscape-scale tradable credit systems must balance uncertainty regarding biological processes occurring at large spatial scales with management costs. Integrating Pattern-Oriented Modeling with Decision Analysis provided a means to determine if existing knowledge of behavior and demography is sufficient to inform decision making. Despite existing uncertainty in dispersal behaviors, discussed in Phase 1, it is unlikely that reducing this uncertainty will lead to a different recommendation for habitat trading, given the mitigation choices considered. Uncertainty regarding dispersal behaviors did double the magnitude of habitat fragmentation effects under mitigation choices 1 and 3 under the worst case development scenario (Figs. 2.6 and 2.7). Therefore, when restored clusters are more dispersed, uncertainty regarding attractiveness of land cover for dispersal may lead to stronger fragmentation effects. If the spatial scale of analysis is increased to include the entire Coastal North Carolina Recovery Unit, then prioritization of land acquisitions in the Onslow Bight Landscape may benefit from further reducing uncertainty regarding dispersal.

3. Phase 3: Exploring Habitat-Fitness Relationships with Pre-Existing Data

3.1 Objective

The objective of this phase is to derive a new recruitment submodel that can be initialized without knowing the age-structure of the population, so that the SEPM can be applied at a broader spatial scale. We describe how habitat-fitness relationships can be determined using the foraging habitat data collected in 1998-2000 by J.H. Carter & Assoc. and MCBCL (GEC 2000). These data do not meet all the requirements of USFWS's updated Foraging Habitat Guidelines (USFWS 2003a), because they did not collect information on groundcover. While it is important to use USFWS guidelines for managing RCWs, new methods that lead to cost-effective approaches of landscape-scale management should continue to be investigated. We introduce a new approach that summarizes forest attributes within different lag distances from the cavity trees. Our analysis also includes the effect of year into habitat-fitness relationships. Year of observation was included because there seems to be large yearly fluxes in recruitment that may be due to climatic effects such as rainfall.

3.2 Background

A major benefit of using individual-based, spatially-explicit population models (SEPMs) is their ability to simulate interactions among population processes and changes in landscape pattern that result from habitat trading. We might call such models mechanistic and non-equilibrium models. If we wish to trade habitat across the entire geographic extent of the Coastal North Carolina population, then the model's ability to predict population dynamics across this entire area should be incorporated into decision making. In other words, population monitoring data collected outside of Marine Corps Base Camp Lejeune (MCBCL) should serve as patterns used to initialize the model as well as to estimate and reduce uncertainty, as described in Phases 1 and 2. Model calibration and validation should be an integral part of any decision making process that relies on SEPMs, due to their reliance on uncertain parameters and structural assumptions (Beisinger and Westphal 1998; Wiegand et al. 2004).

As previously presented, the SEPMs used in this study and by DoD and DOI for managing Red-Cockaded Woodpeckers (RCWs) rely on information regarding the age structure and social structure of RCW populations to initialize the model and simulate population dynamics. While this quality of data is available for MCBCL, it is not available for other management units of the Coastal North Carolina population. For example, data on the age structure of the entire population is not available. The RCW SEPMs (Phases 1 and 2) predict the number of fledglings in a territory based on the ages of the male and female breeder and number of helpers (Letcher et al. 1998). The age- and helper-based recruitment model is based on a statistically significant regression equation ($p<0.0001$), but only accounts for 8% of the observed variance in fledglings (D. Bruggeman, Phase 1).

It may be more cost-effective to collect data on habitat attributes than to continue bird banding studies that lead to estimates of age structure, especially as the population size increases toward recovery. Previous attempts to establish a statistically significant relationship between the number of fledglings produced and vegetative characteristics of Red-Cockaded Woodpecker (RCW) territories (i.e., fitness-habitat relations) have not been successful (James et al. 2001;

Walters et al. 2002). However, many biologists have observed that groups in mature Longleaf pine forests that are regularly subjected to burning tend to have more productive groups.

Convery (2002) did successfully relate recruitment to habitat attributes in 23 territories on MCBCL. Based on the observations of James et al. (1997; 2001), Convery (2002) supplemented previous surveys of RCW foraging habitat (GEC 2000) by collecting data on ground cover, because it is strong indicator of fire history. Convery (2002) also conducted behavioral observations to estimate size and location of home ranges. With this approach, Convery derived statistically significant relationships between forest attributes, based on USFWS's updated Foraging Habitat Guidelines (USFWS 2003a), and recruitment using linear regression. The work of Convery provides hope, but the efforts required to estimate home ranges and quantify ground cover have not been replicated across MCBCL and would be time consuming to implement across the entire Coastal North Carolina population.

3.3 Methods

3.3.1 Foraging Habitat Data for MCBCL

Concerns regarding changes in forest structure on MCBCL due to hurricanes and pine beetle infestations led to a major effort to characterize RCW foraging habitat across the entire base from 1998-2000 (GEC 2000). Initially, 5,670 0.04-hectare plots were laid out across MCBCL on a standard grid of five chains north to south by 12 chains east to west. Sampling focused on managed pine and pine-hardwood stands that were at least 30 years old, but some younger stands were also sampled. A total of 5,374 forested plots were characterized.

During the foraging habitat survey the number of stems per hectare was estimated in 5 cm dbh classes, for pines and hardwoods. Following Convery (2002), we condensed these data into three size classes for pines to parallel USFWS Foraging Habitat Guidelines (Table 3.1). Similarly, we condensed data for hardwoods into two size classes.

3.3.2 Spatially Integrating Foraging Habitat Data

Home ranges for all territories on MCBCL have not been estimated. To characterize habitat attributes corresponding to individual RCW groups, we developed a new approach. USFWS Foraging Habitat Guidelines specifies that foraging habitat should be within 800 m of a cluster's center. Convery (2002) estimated average home range size as 80.2 ha based on 23 territories on MCBCL by analyzing the movement data using the Animal Movement Analysis extension in ArcView GIS. This suggests that foraging habitat tends to be within 800 m even if the cavity trees were located at a border of a home range. We summarized foraging habitat data using a moving window approach to integrate forest attributes at different lag distances from cluster centers. This approach helps control uncertainty regarding the borders of home ranges and the influence of forest fragmentation on habitat quality. It may lead to a useful approach for determining how loss of forest near clusters may affect population dynamics. Three sizes of windows were employed: 100 ha, 400 ha, and 1,225 ha (Table 3.1). These windows correspond to 500 m, 1,000 m, and 3,500 m lag distances from the cluster center. Note, the last lag distance corresponds to estimated 3.5 km search radius of helpers (Pasinelli and Walters 2002). To characterize habitat attributes within a window, we calculated the average density of each size class of pines and hardwoods:

$$PSw = \frac{1}{w} \sum_{j=1}^{s} PineSmall(stems/ha)_j \quad \text{(eqn. 3.1)}$$

where PS means small pines (Table 3.1), w is the size of the window in hectares, and s is the number of times small pines were detected within a window.

3.3.3 Regression Approach

Simple linear regression was used to parallel other studies (Convery 2002; James et al. 2001; Walters et al. 2002). Figure 3.1 indicates that the number of fledglings per cluster approximate a normal distribution, so simple linear regression is appropriate. However, unlike previous studies we chose to include the intercept term during model fitting. Biologically it makes sense to exclude the intercept because areas with no trees will not contain fledglings. However, omitting the intercept inflates the estimate of model fit, R^2, and increases prediction bias. Ideally, the relationship between group fitness and the independent variables predicted by the model should remove the intercept from the model (i.e., the intercept should not be significantly different from zero).

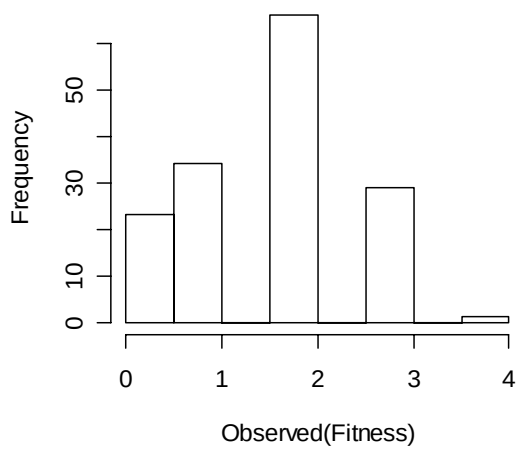

Figure 3.1. Frequency distribution of fledglings per group (fitness) observed from 1998 to 2000 on MCBCL.

Independent variables used in the regression were based on the foraging habitat survey described previously and other variables that may be easily collected across the extent of the Coastal North Carolina population. It is well accepted that clusters with more helpers tend to produce more fledglings (Walters et al. 2002; James et al. 2001; Letcher et al. 1998), so we supplemented habitat variables with observed number of male and female helpers per cluster. Also, Charles Clarkson (VPI&SU), who manages the RCW monitoring program at MCBCL, indicated that rainfall patterns likely have a large impact on recruitment. To conduct a preliminary analysis of this hypothesis, we included year of observation as an independent variable (Table 3.1).

Table 3.1. Derivation of independent variables for use in habitat-fitness relationships.

[1]Abbreviation	Independent Variable	Converting data from MCBCL Foraging Habitat Survey	Corresponding USFWS (2003) Recommendation
PL1, PL4, PL12	Large Pines	No. pine stems/ha ≥ 35 cm dbh	2a. ≥ 45 stems/ha of pine at least 35 cm dbh
PM1, PM4, PM12	Medium Pines	No. pine stems/ha 25.4 to 35 cm dbh	2b. basal area of pines 25.4 to 35 cm dbh between 0 and 9.2 m^2/ha
PS1, PS4, PS12	Small Pines	No. pine stems/ha < 25.4 cm dbh	NA
HL1, HL4, HL12	Large Hardwoods	No. hardwood stems/ha ≥ 25.4 cm dbh	2g. Canopy hardwoods <10% of canopy in longleaf stands, and < 30% of canopy in loblolly stands
HS1, HS4, HS12	Small Hardwoods	No. hardwood stems/ha < 25.4 cm dbh	2f. Hardwood midstory < 2.1 m
HP	No. Helpers	NA	NA
YR	Year of Observation	NA	NA

e.g., PL1 = density of large pines within 100-ha window.

Statistical analyses were completed in the software R version 2.2.0 (Venables and Smith 2005). Three sets of full regression equations were compiled. The first included only the habitat variables. The second included all the habitat variables and number of helpers per group. The third included habitat, helpers, and year of observation.

Stepwise model selection was performed using the Akaike Information Criterion (AIC). AIC uses the Kullback-Leibler distance to quantify the discrepancy between the distribution describing the true outcomes of an environmental process and the distribution of outcomes predicted by the model (Burnham and Anderson 2002). Because the distribution of true outcomes can never be known, the AIC method estimates the Kullback-Leibler distance by using maximum likelihood to fit observed data to the model. Unlike the more traditional statistical estimate "R^2", which only estimates model fit based on the proportion of the sum of squares explained by a model, AIC incorporates the number of parameters into the assessment of model fit (Richards 2005). The most parsimonious model, capable of explaining the largest amount of variance in the data with the fewest parameters, is given the lowest AIC score. The "stepAIC" procedure in the R 2.2.0 software package was used to determine the model with the lowest AIC score using forward and backward elimination. However, when models differ in AIC scores by 2 units or less, then we say that the two models are equivalent (Richards 2005). Therefore, we also report the most parsimonious model within 2 AIC units of the model selected by the stepAIC procedure.

3.4 Results

Regressing group fitness against only habitat variables did not lead to a statistically significant relationship (p=0.063; Model A, Table 3.2). However, AIC model selection indicated that four habitat variables explained 3.3% of the variation in group fitness. Density of small pines within a 100-ha window about the cluster center was positively related to group fitness. In contrast, the density of medium pines within this same window was negatively related to group fitness. Within a 400-ha window, the density of small pines was negatively related to group fitness. Similarly, within a 1,225-ha window the density of small hardwoods is negatively related to group fitness. Even though the model is not significant, these results suggest that group productivity may be sensitive to forest structure well outside of home ranges. When we simplified the model further without increasing the AIC score greater than 2 units, we found that only density of medium pines within 100 ha was retained.

Model B summarizes the results of including the number of helpers and stem densities for pines and hardwoods at different lag distances (Table 3.2). Model B explained 8.9% of the variance in group fitness and resulted in a large decrease in the AIC score compared to Model A. AIC model selection resulted in excluding all habitat variables except the density of large hardwoods within a 100-ha window and the density of small pines and medium pines within a 1,225-ha window (Model B, Table 3.2). The model predicts that density of large hardwoods near the cavity trees is negatively related to group fitness. At the largest window size, the model indicates that the density of small pines is positively related with group fitness, but density of medium pines is negatively related to group size. The correlation between PS12 and PM12 was -0.62, which is sufficiently small to include both variables. Further simplifying Model B indicated that an equivalent model would be one that includes only number of helpers.

When the effect of year was added into AIC model selection, we observed a significant improvement in model fit and the same habitat variables were retained (Model C, Table 3.2). Helpers still play a dominant role in determining the number of fledglings, but the influence of year was more significant than the habitat variables. With the inclusion of more independent variables the adjusted R^2 value increased from 0.089 (Model B) to 0.12 in Model C, which is expected because we have more variables present to account for variance. However, the AIC score dropped by 5 units, indicating that the increased model complexity does provide useful information regarding the relationship between environmental variables and fitness. However, the predicted distribution of fledglings per group (Fig. 3.2) underestimates the observed number of fledglings per group (Fig. 3.1). When we further simplified the model, only number of helpers and year was retained.

Table 3.2. Habitat-fitness relationships predicted by linear regression and AIC model selection. Data analyzed represent 154 Potential Breeding Groups observed from 1998 to 2000.

[1]**Model A**	**p-value**	**Adj R^2**	**AIC**
Fit = 2.50 + 0.0079 PS1 – 0.036 PM1 – 0.0102 PS4 – 0.019 HS12	0.063	0.033	426
Parameter	**p-value**	**t-value**	
Intercept	<0.0001	8.23	
PS1	0.125	1.54	
PM1	0.038	-2.10	
PS4	0.107	-1.62	
HS12	0.063	-1.88	
Model A – Most Parsimonious	**p-value**	**Adj R^2**	**AIC**
Fit = 2.02 – 0.03 PM1	0.053	0.018	427

[1]**Model B**	**p-value**	**Adj R^2**	**AIC**
Fit = 1.93 + 0.247 HP – 0.238 HL1 + 0.0085 PS12 – 0.043 PM12	0.0014	0.089	418
Parameter	**p-value**	**t-value**	
Intercept	<0.0001	4.66	
HP	0.003	2.99	
HL1	0.042	-2.06	
PS12	0.163	1.40	
PM12	0.043	-2.04	
Model B – Most Parsimonious	**p-value**	**Adj R^2**	**AIC**
Fit = 1.40 + 0.28 HP	0.0007	0.067	419

[1]**Model C**	**p-value**	**Adj R^2**	**AIC**
Fit=1.51+0.252HP+0.228YR–0.253HL1+0.009PS12–0.047PM12	0.0002	0.120	413
Parameter	**p-value**	**t-value**	
Intercept	0.0007	3.44	
HP	0.0023	3.11	
YR	0.013	2.52	
HL1	0.028	-2.22	
PS12	0.142	1.48	
PM12	0.028	-2.22	
Model C – Most Parsimonious	**p-value**	**Adj R^2**	**AIC**
Fit = 0.96 + 0.29 HP + 0.21 YR	0.0002	0.093	415

[1]Inclusion of all other independent variables only increased AIC scores.

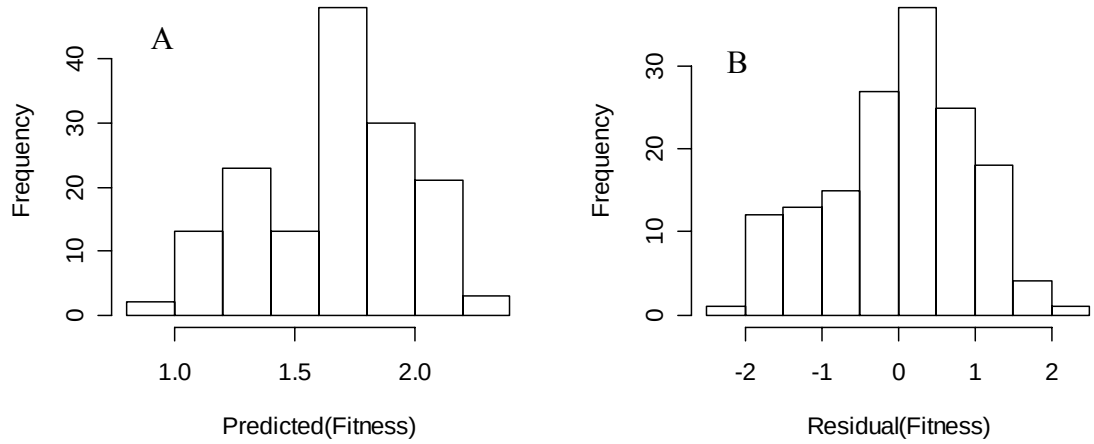

Figure 3.2. (A) Frequency distribution of fledglings per group (fitness) predicted by Model C. (B) Frequency distribution of residuals from Model C.

3.5 Discussion

We have demonstrated that integrating data describing vegetative characteristics at different spatial scales, number of helpers, and differences among years can lead to a better prediction of fledglings than the age- and helper-based recruitment model already used for decision making. However, there is still much room for improvement, because at most only 12% of the variation in recruitment was explained by the model. Two observations made by the current work suggest that further research might improve our prediction of fledglings. First, density of vegetation outside of home ranges is important. Second, yearly variation in environmental conditions should be taken into account. These are further discussed below.

The importance of continuous old growth Longleaf pine forests has been well articulated by other researchers (Conner and Rudolph 1991; Cox et al. 2001; James et al. 2001; Walters et al. 2002). However, quantitative analysis of forest fragmentation effects have been limited to an 800-m lag distance from the cluster center (Conner and Rudolph 1991; Cox et al. 2001; James et al. 2001), based on USFS and USFWS guidelines. In contrast, this study included a 500-m, 1,000-m, and 3,500-m lag distance, corresponding to 100-ha, 400-ha, and 1,225-ha square window. This approach provided interesting results. Within the 100-ha and 1,225-ha windows, AIC model selection suggested that the density of small pine was positively related to fitness. However, high densities of small pines in a 400-ha window was negatively related to fitness. While the coefficients describing the influence of small pines were not statistically significant ($p>0.05$), AIC model selection indicated that they do contribute to model fit.

James et al. (2001) found that density of small pines (15-25 cm dbh) was negatively related to number of fledglings, but that the difference in large to small pines was positively related to fitness. Walters et al. (2002) suggests that RCWs tend to avoid areas with small pines, are indifferent to medium pines, and prefer large pines during foraging. These results seem to contradict our observations. We attempt to reconcile these observations below, by stressing the

conclusion of James et al. (2001) that the structure of pine forest is critical, not just the densities of individual sizes classes of pines.

Recall that almost all plots characterized on MCBCL were managed pine stands 30 years or older. Therefore, presence of small pines near cavity trees (i.e., within a 100-ha window) is likely indicative of natural pine regeneration and fire history. Management of longleaf pine forests through prescribed burning leads to uneven-aged forest stands, in which low densities of larger pines are interwoven with small areas with higher densities of smaller pines able to regenerate in gaps created by the loss of an older tree, absent competition from hardwoods in the understory (James et al. 2001). In contrast, high density of small pines within a 400-ha window, farther from cavity trees, would suggest the presence of even aged forest due to a recent planting. Similarly, high density of medium pines within a 100-ha window may be indicative of an even aged forest near cavity trees, which the model predicts will lead to lower fitness. Model A suggests that density of small hardwoods within 1,225-ha was negatively related to fitness. This suggests that maintaining historical fire regimes well outside of a group's home range could contribute to group fitness.

When number of helpers were included, variables describing pine in the smaller two windows dropped out of the model. This suggests that number of helpers is a good surrogate for attributes of pine structure describing good quality habitat close to cavity trees and home ranges. Model B does include density of larger hardwoods within a 100-ha window. The negative relationship between fitness and HL1 corresponds to observations of other researchers that RCWs avoid forested areas with large hardwoods when foraging (Walters et al. 2002). The positive relationship between density of small pines in the largest window (1,225-ha) and fitness in Model B may be indicative natural pine regeneration at large spatial scales, but this variable does not contribute greatly to model fit (t-vale = 1.4). The negative relationship between density of medium pine in the largest window and fitness may reflect the presence of large even aged stands. It is curious that these larger scale habitat variables are introduced only after including the effect of helpers. Perhaps the structure of pine forests within a 1,225-ha window may affect the probability that a breeding vacancy is filled by a floater? Recall that Phase 1 attempted to characterize habitat effects on dispersal, but used much cruder estimates of forest structure (i.e., size class distributions were ignored).

Yearly environmental variation contributed considerably to fitness (Model C). The t-value for year provided the third largest absolute value. Further, inclusion of the year effect helped to increase the significance of all other independent variables, suggesting a possible interaction between year and habitat quality. To the best of our knowledge yearly variation in recruitment has not been considered in previous studies. When multi-year data were available, researchers averaged fitness within territories across years before performing regression analysis (Convery 2002; Walters et al. 2002). Arguably, including year as a factor is not the best surrogate for environmental variables that could affect recruitment such as rainfall and temperature. One confounding factor could be that the number of territories increased from 46 in 1998 to 56 in 2000. However, the presence of these new clusters could have reduced the number of helpers per group due to new breeding vacancies. We strongly encourage future research that examines how climatic variables might contribute to recruitment.

In the SERDP SEED grant contract modified proposal, we indicated that the new habitat-fitness relationship derived here would be included into the RCW SEPM. However, this investigatory research discovered that yearly variation in environmental factors is key for providing a relationship that is at least as good as the age- and helper-based recruitment model currently being used. Due to uncertainty regarding what those factors are (e.g., rainfall levels during which months), we were unable to update the SEPM.

3.6 Conclusion

Linear regression modeling including a moving window approach and yearly variation in recruitment did improve the prediction of group fitness. Observations including numbers of helpers within groups, forest structure at multiple scales, and climatic variables could be collected without instituting a bird banding study across the Coastal North Carolina population of RCWs.

The forest attributes included in this study were collected at great expense to MCBCL and were not being used for management. Replicating this effort in Croatan National Forest, Holly Shelter State Game Lands, and smaller areas considered for acquisition under the Encroachment Partnering program may be expensive. Remotely sensed data describing vegetative structure may also be integrated with climatic data and may be more cost-effective. In Phase 3, we have been able to devise an approach to bring value to existing data while directing future data collection efforts.

4. Overall Conclusions and Recommendations

4.1 Summary of Significant Results

The use of Encroachment Partnering to relieve training restrictions due to the presence of endangered species highlights the importance of understanding how changing landscape patterns may affect recruitment and migration. Individually-based, spatially-explicit population models (SEPMs) can be used to determine how changing habitat area and / or connectivity will affect population viability. These models allow interaction between rates of recruitment within patches with rates of migration among patches. We applied new techniques to improve how SEPMs can be used for Encroachment Partnering. The major methodological advances and conclusions are summarized below:

1. Pattern-Oriented Modeling (POM) provides a strong inference approach for reducing uncertainty regarding parameter values in SEPMs. Out of 100,000 alternative dispersal submodels tested, only 8 were able to simultaneously reproduce all RCW patterns observed on MCBCL.
2. Of the 8 parameter sets remaining, estimates of landscape friction and turning angles varied greatly. We proposed two possible reasons for this result. One, POM was applied over too small an area. In other words, the ability of simulation model to reproduce patterns observed on MCBCL was not affected by large differences in land use. Two, the model does not accurately describe how dispersing birds make decisions to maximize survivability and to find a breeding vacancy (i.e., structural uncertainty remains in the model).
3. Landscape Equivalency Analysis (LEA) provides a quantitative approach for determining how much regulatory relief can be achieved from specific Encroachment Partnering decisions. By calibrating the new dispersal submodel to patterns observed on MCBCL, we found that Encroachment Partnering may lead to less regulatory relief than would be projected using the dispersal submodel found in the Letcher model.
4. Integrating uncertainty analysis (POM) with a landscape-scale tradable credit system (LEA) indicated that we have sufficient knowledge to prioritize habitat restoration decisions.
5. We used decision analysis to describe how DoD can determine when it is cost effective to forego cooperative purchase of off-base parcels and collect more biological data to ensure that Encroachment Partnering will lead to regulatory relief without decreasing population viability.
6. Habitat-fitness relationships were found by applying a moving window approach to quantify forest structure at multiple spatial scales. We found that yearly variation in environmental conditions contribute significantly to observed variation in recruitment. This approach accounted for more of the total variance in recruitment (Adj. R^2=0.12) than the age-base recruitment submodel (Adj. R^2=0.08) currently used by the SEPM.

In conclusion, by examining habitat trading opportunities on and near MCBCL, we found that POM reduced enough uncertainty regarding dispersal to prioritize trading decisions. However, we also observed that examining habitat trades at this spatial extent always resulted in increasing habitat fragmentation effects.

It is critical to determine if Encroachment Partnering will increase or decrease habitat fragmentation for the entire recovery population. MCBCL is one of three Management Units (MUs) within the Coastal North Carolina RCW recovery population. The other two include Croatan National Forest and Holly Shelter Game Lands, and the three MUs are found in the Onslow Bight Landscape. Habitat trades that increase habitat fragmentation relative to the current population on MCBCL may actually decrease fragmentation across the entire Coastal North Carolina recovery population inhabiting the Onslow Bight landscape. Further, the remaining uncertainty in dispersal would likely affect habitat trading decisions over the entire Onslow Bight Landscape. Given the high rate of sprawl in coastal North Carolina, MCBCL has initiated an aggressive Encroachment Partnering program. For instance, MCBCL is working to protect lands for RCWs that are closer to Holly Shelter Game Lands than MCBCL's Main Base. Determining how much regulatory relief can be achieved through such actions indicates that increasing the spatial scale of our model is a critical area of future research.

4.2 Priorities for Future Research

4.2.1 Habitat Trading for RCWs in Onslow Bight (Bruggeman, JR Walters et al.)

In order to determine if DoD can spread RCW liability across the Onslow Bight landscape without jeopardizing recovery, we need to understand how landscape patterns affect recruitment and migration at a broad geographic extent. Results from Phase 3 (habitat-fitness analysis) are currently being explored in collaboration between Douglas Bruggeman and Jeffrey Walters under SI-1472. Climatological data have been collected for Fort Bragg and MCBCL and will be integrated with the foraging habitat quality data Dr. Walters' group has been compiling. This effort should shed light on the cause of the strong "year-effect" observed in Phase 3. Dispersal uncertainty is being addressed in a radiotelemetry study (SI-1471) through collaboration between Aaron Moody and Jeffrey Walters. Douglas Bruggeman has recently shared results of the POM analysis of dispersal uncertainty (Phase 2) to help guide the integration of the radiotelemetry studies with the RCW SEPM. Despite this increased collaboration, there is still one critical research question not being addressed under any existing proposal:

What are the historic and current rates of migration among the three Management Units in the Onslow Bight (Croatan National Forest, MCBCL, and Holly Shelter Game Lands)? Understanding historic and current landscape function at this scale is critical for determining how much regulatory relief can be achieved through Encroachment Partnering.

In order capture habitat fragmentation effects, LEA assigns a conservation value to trades at a local scale based on marginal changes in ecological services at the landscape (regional) scale, relative to service levels expected in an unfragmented or baseline landscape. We defined baseline for MCBCL as the apportionment of genetic variance within and among breeding groups afforded by their recovery plan. By applying the concept to the entire Onslow Bight, we might define baseline as the apportionment of genetic variance within and among breeding groups, averaged across all three management units (MUs), afforded by reaching property-specific recovery goals (USFWS 2003a). **In contrast to the baseline defined for MCBCL, the baseline for the Onslow Bight does not provide the most clumped distribution of habitat possible, merely the most clumped distribution possible on public lands.** We propose

research to determine if this provides adequate levels of connectivity for RCWs. The work would also determine if restoration of private land would increase population viability, justifying the use of Encroachment Partnering to provide regulatory relief.

Landscape Genetic Study of Coastal North Carolina RCW Recovery Population
We propose to conduct a landscape genetics study in the Onslow Bight landscape. Tissues will be collected from RCWs located on MCBCL, Croatan National Forest, and Holly Shelter. These data will be used to address the following objectives.

1. **Estimate levels of connectivity prior to habitat loss and fragmentation.** The tissues will be assayed for genetic variability using allozymes and microsatellites, because these two classes of nuclear DNA have very different properties. Microsatellites mutate frequently but are selectively neutral. In contrast, allozymes mutate much less frequently and the genotypes may be associated with differences in fitness among individuals, breeding groups, or MUs. Therefore, we can estimate habitat fragmentation effects at different time scales by contrasting the spatial apportionment of allozymes to microsatellites.

   The spatial apportionment of microsatellite markers provides an opportunity to test the implicit assumption of the RCW recovery plan that land use changes in between MUs will not affect recovery. In contrast, the spatial apportionment of allozyme markers will be descriptive of migration rates prior to fragmentation. We predict that the baseline levels of genetic services provided by the RCW recovery plan will likely be an inadequate representation of an unfragmented condition. Knowledge of historic apportionment of genetic variance reported by allozymes may help justify increasing migration among MUs through Encroachment Partnering.

2. **Determine the degree of genetic divergence among the three MUs.** MUs are defined genetically as independent populations in which the rate of population growth is independent of rates of migration (Moritz 1994; Palsboll et al. 2007). MUs are identified by examining the level of genetic divergence among local populations within a landscape. The goal is to identify and manage units in a way that will help maintain the potential to adapt to environmental conditions while not necessarily protecting all current adaptations (Moritz 1994). This is a practical objective because it is impossible to identify and protect the genetic basis of traits that will be adaptive to environmental conditions in the future.

   Allozyme data will likely predict only one population unit in the Onslow Bight, but the microsatellite data may predict several units, because their spatial distribution will be indicative of recent changes in migration-drift processes due to their high mutation rate and selective neutrality. If population units display significant divergence in allozyme markers, then genetic differences among population units may have adaptive significance. Therefore, habitat trading that increases migration would still increase population viability up to a point, but high rates of migration may cause outbreeding depression. While we doubt this will be the case, LEA would account for this contingency by including three genetic services: average expected heterozygosity within

breeding groups (HS), average genetic divergence among breeding groups within an MU (Dcs), and average genetic divergence among population units within the Onslow Bight landscape (Dst).

3. **Generate RCW patterns at a broader scale to apply Pattern-Oriented Modeling.** POM could be used to calibrate the RCW dispersal submodel derived from radiotelemetry studies at Fort Bragg (SI-1471) to the Onslow Bight population. Evaluation of parameter uncertainty in the RCW SEPM benefited greatly from the long-term monitoring program on MCBCL. In contrast, the only consistent pattern across all three MUs is restricted to number of active clusters dating back to 1999. Historical data on the number of individuals shared among the three MUs is virtually absent, except for a few banded birds that moved between Croatan and MCBCL. Statistical techniques for summarizing population genetic patterns are rapidly developing (e.g., Geneland: Guillot et al. 2005; Structure: Pritchard et al. 2000; and Bayesassnm: Jehle et al. 2005). We will develop techniques to link genetic patterns observed in the Onslow Bight to those predicted by the RCW SEPM, thereby providing an empirical basis for applying POM across the Onslow Bight.

The RCW SEPM with the empirically-derived dispersal submodel will be used to predict baseline levels of genetic variance within and among population units expected under the RCW recovery plan. However, the SEPM can also be used to estimate the historic levels of genetic services congruent with the spatial distribution of allozymes, indicative of historic rates of migration among population units. Illustrating how Encroachment Partnering can be used to move rates of migration closer to levels observed historically will provide the basis for shifting the spatial distribution of RCW clusters away from that required under the current recovery plan.

4.2.2 Development of SEPMs for other Species (Bruggeman, T Wiegand et al.)

It has recently been argued that habitat fragmentation is a poorly defined concept (Fahrig 2003; Lindenmayer and Fischer 2007). Researchers have not used a consistent approach for quantifying geometric, or structural, changes in the spatial distribution of habitat. Changes in the biological system are also quantified in different ways including patch occupancy, total abundance, migration distances or rates, and, sometimes, changes in spatial apportionment of genetic variance. The field of landscape ecology has also been hindered by summarizing patterns observed in nature and then proposing theories for the biological processes that generated the patterns (i.e., process is inferred from pattern). Inferring process from pattern while using inconsistent methodology has led many scientists to conclude that habitat fragmentation effects are species- and landscape-specific, which can not be generalized (Wiegand et al. 2005). This represents a large technological hurdle for military installations wishing to shift the allocation of threatened and endangered species habitat to ensure military readiness. Below we present some surprising results that will provide a step forward.

Prior to beginning research on our SEED grant, the Helmholtz Centre for Environmental Research – UFZ funded collaboration between Douglas Bruggeman and Thorsten Wiegand to establish relationships between structural and biological descriptors of habitat fragmentation (Bruggeman et al. submitted). We already have a hypothesis regarding how landscape pattern

affects biological processes for RCWs based on 20 years of empirical observations on military lands (i.e., the Letcher model). Below we describe a method that allowed us to replace that hypothesis of process with a set of indices describing land use patterns (i.e., pattern was inferred from process). We argue that this method will provide a generally applicable and scientifically rigorous approach for inferring process from pattern for other species and should be used as a starting point for building SEPMs.

Methods: Inferring Pattern from Process

The RCW SEPM with a HCRW dispersal submodel was simulated on 60 different hypothetical landscapes that varied from clumped to fragmented. Three land use classes were employed including old growth Longleaf pine, mixed pine-hardwood, and non-forested. The HCRW submodel assumed that dispersing birds avoid crossing non-forested areas and showed greatest preference for Longleaf pine. Both the first and second order effects of landscape structure were included in the analysis (Bailey and Gatrell 1995). First order effects summarize the mean density of RCW habitat across the entire landscape. We used three densities of old growth Longleaf pine or RCW breeding habitat (2.5%, 5%, and 7%). Second order effects, which summarize the spatial dependence of land use classes at small spatial scales, were summarized using Ring Indices based on the fundamental the physical theory of point pattern phenomenon (Wiegand et al. 2005). Ring Indices report the probabilities of finding land use type 1 at location X conditioned on the occurrence of finding land use type 2 at location Y. Where r = X - Y, or the lag distance between two points, Ring Indices are symbolized as O12(r). In our study, land use type 1 represents RCW habitat, 2 represents mix pine-hardwood, and 3 represents non-forested. For example, O12(r) represents the probability of finding mixed pine-hardwood at lag distance r from RCW habitat, providing an estimate of the contribution mixed pine-hardwood forest makes to habitat fragmentation at lag distance r. In contrast, O11(r) provides a measure of habitat adjacency at small spatial lags or habitat dispersion at large spatial lags.

The influence of first and second order effects of landscape structure on biological structure was estimated by running the RCW SEPM for 100 years to achieve equilibrium between landscape pattern and biological processes. Biological results were summarized as N (census population size or number of adults found across all clusters), F (Wright's inbreeding coefficient), and F_{ST} (average coancestry within a breeding group due to population subdivision).

We used multiple linear regression to determine if the dependent variables describing population structure could be predicted by independent variables describing first and second order effects of landscape structure. Analysis began with null regression models relating population structure to known first order effects. For abundance, $N = \beta * f_1$ (Fahrig 2003), where f_1 = percent of RCW habitat. For genetic indices, $G = \beta * \log(N)$ (Frankham 1996; Wang 2004). We then regressed the residuals from these null models against Ring Indices O11, O12, O13 for lag distances of 1 to 16 cells (707 m to 11.3 km). Ring Index-lag distance combinations explaining most of the residual variance was assembled into a "full model" and AIC model selection was used to find the most parsimonious multiple regression equation (Burnham and Anderson 2002).

Results

Results suggested that given the assumption of equilibrium between population processes and landscape pattern, the RCW SEPM could be replaced by a series of multiple linear regression

equations. For abundance (Fig. 4.1), a strong relationship with first order effects was observed indicative of the critical role of breeding habitat for predicting population size (R^2=0.98). However, inclusion of Ring Indices, or second order effects, improved model fit considerably based on reduction in AIC scores (AIC Null Model = -296, AIC Full Model = -420).

$$N = 12.2*f_1 \qquad R^2 = 0.98$$

$$N = 14.1*f_1 - 0.07*O11(16) - 0.06*O12(1) - 0.2*O13(4) \qquad R^2 = 0.998$$

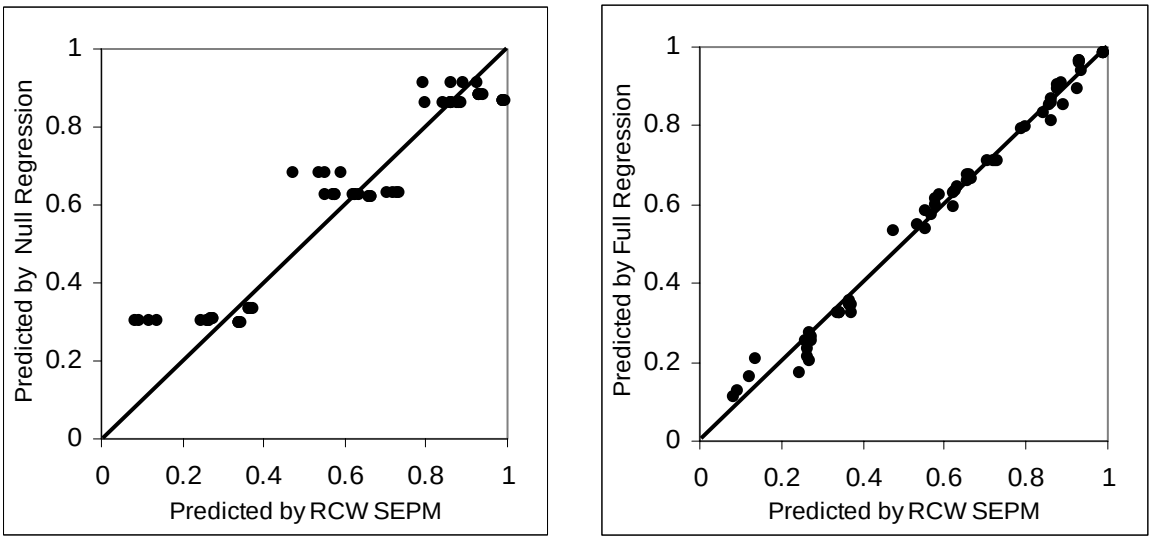

Figure 4.1. Predicted census population size (N) using the RCW SEPM assuming a HCRW, and N predicted by the null and full linear regression models. Diagonal line represents the hypothetical complete agreement between the two modeling approaches.

The strongest fragmentation effect was observed due to the presence of non-forested areas at a distance of 4 cells (2.8 km) from breeding habitat (O13(4)). The perceptual distance of RCWs was set at 5 cells for these simulations. Therefore, the presence of non-forested areas at the edge of a fledgling's, helpers, or floaters perceptual distance decreased N. Similarly, the presence of mix pine-hardwood forest adjacent to breeding habitat decreased population size (O12(1)). The dispersion of breeding habitat across the landscape, as would be expected when O11(16) is large, also decreased population size. The influence of O12(1) and O11(16) highlight the importance of habitat adjacency included in the model structure. The model rules predict that more helpers will be retained under a clumped distribution of habitat and that these helpers increase recruitment (Letcher et al. 1998; Pasinelli and Walters 2002).

Prediction of Wright's inbreeding coefficient (F) was more difficult (Fig. 4.2). Total population size only accounted for 59% of the variance in inbreeding. However, inclusion of the ring indices improved model fit considerably, increasing R^2 to 0.89 (AIC Null Model = -242, AIC Full Model = -321)

$F = 1.7 - 1.6*\log(N)$ $R^2 = 0.59$

$F = 0.98 - 1.0*\log(N) + 0.21*O12(1) - 0.3*O13(4)$ $R^2 = 0.89$

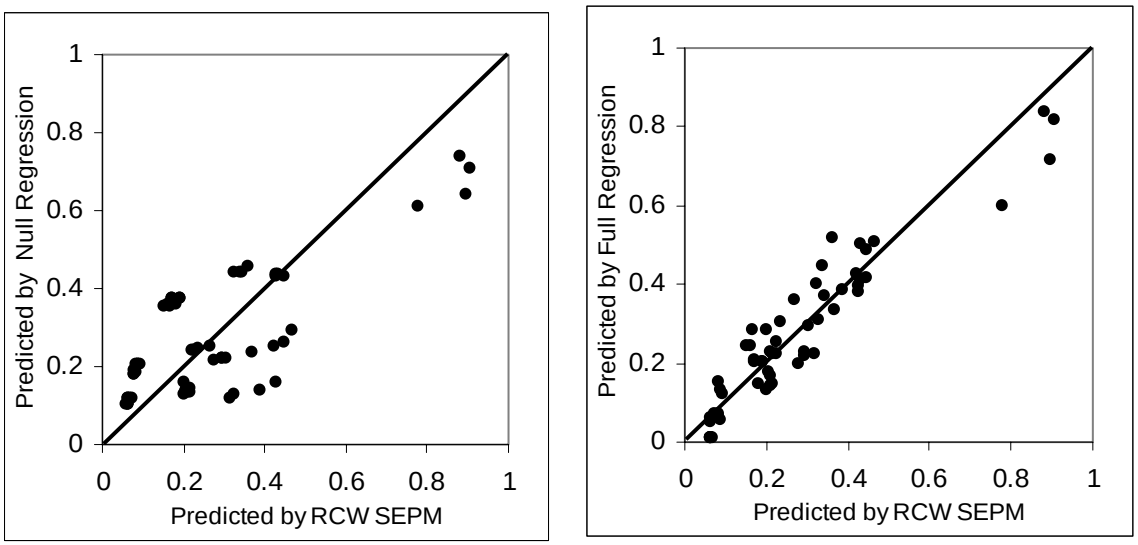

Figure 4.2. Prediction of inbreeding coefficient (F) by the RCW SEPM assuming a HCRW, and by the null and full linear regression models. Note, F values are large because the model was run for 100 years without the addition of immigrants. Diagonal line represents the hypothetical complete agreement between the two modeling approaches.

Unlike population size, a considerable portion of inbreeding can only be explained when including habitat fragmentation effects. While, O11(16) dropped out of the equation during AIC model selection procedures, the other Ring Index-lag distance combinations are consistent across the full regression models for total population size and inbreeding. Therefore, patterns detected as important descriptors of biological processes hard-wired into the SEPM were consistent across these statistical summaries of population structure.

To determine if the Ring Indices might detect the influence of landscape friction on population structure, we also ran the RCW SEPM assuming straight dispersal. We changed the model rules to decrease floater survival based on the number of steps taken in non-forested areas to simulate increased predation risks hypothesized for small forest birds (Belisle and Desrochers 2002). Comparing results across the HCRW and the straight dispersal model indicated that the Ring Index-lag distance combinations were consistent for N and F. However, the fitted coefficients varied in a manner consistent with the dispersal rules (data not shown). Average coancestry among groups (F_{ST}) is a more sensitive indicator of migration rates. Accordingly, a shift in Ring Index-lag distance combinations was observed for F_{ST}. Figure 4.3 indicates that there is no relationship between F_{ST} and population size under the null regression model. Inclusion of second order effects improved model fit considerably!

$F_{ST} = 0.82 - 0.09*\log(N)$ $R^2 = -0.003$

$F_{ST} = 0.65 + 0.33*\log(N) - 0.27*O11(2) - 0.09*O12(8)$ $R^2 = 0.75$

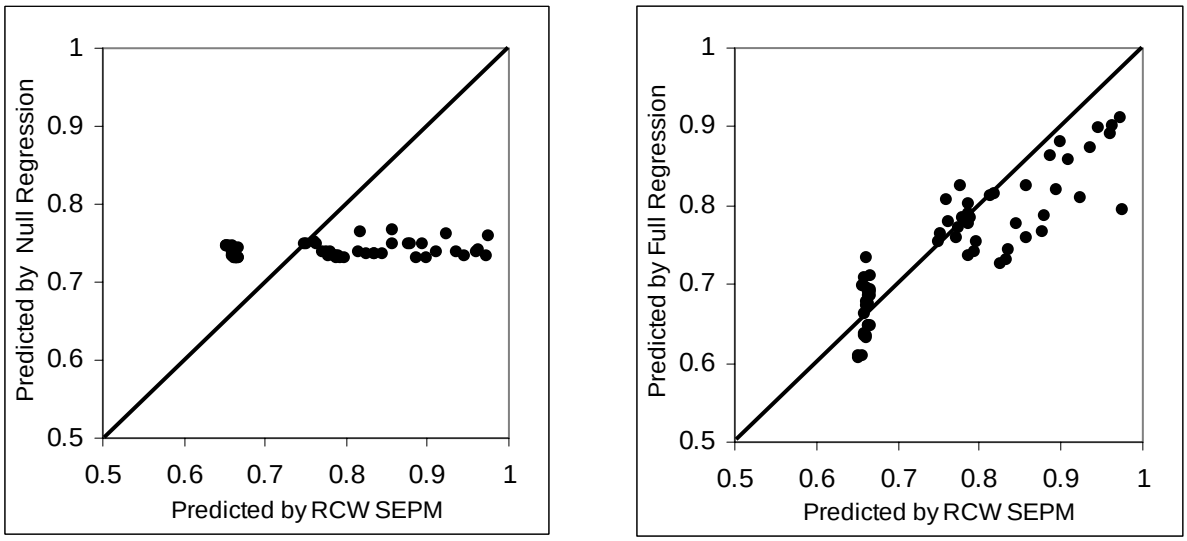

Figure 4.3. Prediction of average coancestry due to population subdivision (F_{ST}) by the RCW SEPM assuming straight dispersal, and by the null and full linear regression models. Note, F_{ST} values are large because the model was run for 100 years without the addition of immigrants. Diagonal line represents the hypothetical complete agreement between the two modeling approaches.

Population geneticist often use spatially-implicit models that hold second order effects constant by assuming equal rates of recruitment within each population unit and equal rates of migration among all population units. Such models indicate that F_{ST} is positively related with log(N) (Wang 2004). When Ring Indices are included in the full regression model this theoretical expectation holds. This suggests that variance in migration rates among population units present in a spatially-explicit model are accounted for by the Ring Indices. The shift in Ring Index-lag distance combinations is also supportive of this conclusion. Retention of O12(8) indicates that when mixed pine-hardwood forests are located at lag distance 8, F_{ST} will be lower. This result was only observed when floaters moved in a straight line and suffered a reduction in survival when crossing non-forested gaps. Therefore, landscapes containing higher densities of forested areas far away from breeding habitat increased migration rates among groups, thus lowering F_{ST}. While O11(1 to 4) accounted for a significant amount of the residual variance, only O11(2) was retained after AIC model selection. Therefore, O11(2) may be detecting a threshold of habitat adjacency associated with a decrease in F_{ST}.

Discussion & Future Directions

These results suggest that under equilibrium landscape conditions, an SEPM with 37 parameters (assuming a HCRW) can be replaced by three linear regression equations, each containing at most 5 fitted parameters. We stress that the relationships presented are very likely invalid when landscape structure is changing over time, as would be required under habitat trading programs. When changing landscape structure over time, SEPMs are is still preferred because ideally they are capable of capturing interactions between landscape pattern and biological processes that may change based on system condition in the previous time step.

SEPMs are rule-based models. The RCW SEPM incorporates rules that relate the second order spatial structure of habitat to behavior and demography. Integration of AIC model selection with the Ring Index approach was capable of detecting spatial thresholds associated with these rules. Are other species that limit military readiness sensitive to second order effects (i.e., habitat fragmentation)? If so, Encroachment Partnering and sustainability of biodiversity would benefit from deriving mechanistic, rule-based models for more species and bases.

We propose to apply this approach "in reverse" to a different endangered or threatened species. In the preliminary study just presented we inferred pattern from process, thanks to the availability of an SEPM. By performing the research "in reverse" we would infer process from pattern using a consistent and theoretically rigorous approach. The objective would be to integrate population genetic theory with the theory of point pattern phenomenon to derive rules for a new SEPM. To do so would require conducting a landscape-scale population genetic study as outlined for RCWs in the Onslow Bight above. However, the studies should be conducted in landscapes in which the classification of land cover is complete or nearly complete. Such a study would benefit from identifying a species that that has limited military readiness on several bases. We have not identified collaborators or bases well suited to the approach and look forward to discussing this with SERDP in the near future. **Our strengths lie in compiling information in a manner that is useful for determining how much regulatory relief can be achieved by trading habitat at a landscape-scale.**

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Appendix A

Apportioning Genetic Variance over Space

Estimates of biodiversity service flows in the form of genetic variance can be obtained using a method derived by Nei (1973). Nei's method estimates the frequency of heterozygous genotypes based on the frequency of alleles observed in the metapopulation. This method reports the heterozygosity expected if the metapopulation were in Hardy-Weinberg Equilibrium (i.e., alleles are assorting in offspring assuming a random mating process). This approach uses data on allele frequencies within and differences among subpopulations. Nei defines genetic diversity as the probability that any two alleles chosen at random, one from each of two individuals are independent. By assuming that individuals are mating at random, this probability is equivalent to the expected heterozygosity. The two alleles can be sampled from within an individual, from two different individuals within the same subpopulation, or from two individuals from different subpopulations within the same metapopulation. The expected heterozygosity of an individual in subpopulation i (number of subpopulations, S=1, 2, 3, …i) can be calculated from the frequency of allele m (number of alleles, k = 1, 2, 3, …m) in the subpopulation given as X_m:

$$H_i = 1 - \sum_{k=1}^{m} X_{im}^2 . \qquad \text{(A.1)}$$

H_i equals the average proportion of heterozygotes in the subpopulation. Summarized another way, H_i equals the average genetic diversity of an individual in subpopulation i. If k=2, then the maximum value of H_i is 0.5, meaning that the average individual is heterozygous at that loci. When k>2, H_i may approach unity if the frequency of alleles are similar to each other, and H_i will approach zero when the frequency of alleles are skewed. The probability that two genes are different when chosen at random from individuals in different subpopulations (e.g., subpopulation i and j, H_{ij}) is calculated as:

$$H_{ij} = 1 - \sum_{k=1}^{m} X_{im} X_{jm} . \qquad \text{(A.2)}$$

The average expected heterozygosity within each subpopulation (H_S) can be estimated by adding a weighting factor to correct for differences in subpopulation size ($w_i = n_i/N$) as:

$$H_S = 1 - \left(\sum_{s=1}^{i} \sum_{k=1}^{m} w_i X_{im}^2 \right). \qquad \text{(A.3)}$$

The average gene diversity among subpopulations (genetic divergence, D_{ST}) can be calculated as the average differences in heterozygosities between all pairwise subpopulations:

$$D_{ST} = \sum_{s=1}^{i} \sum_{s=1}^{j} w_i w_j \left[H_{ij} - \left(\frac{H_i + H_j}{2} \right) \right]. \qquad \text{(A.4)}$$

The product of $H_{ij} - (H_i + H_j)/2$ is Nei's minimum genetic distance between two populations (D_m). The total gene diversity of the metapopulation can now be estimated by the separate contribution of intra- and inter-subpopulation genetic variances (H_T):

$$H_T = H_S + D_{ST} . \qquad \text{(A.5)}$$

Or H_T can be estimated directly from allele frequencies:

$$H_T = 1 - \sum_{k=1}^{m} \left(\sum_{s=1}^{i} w_i X_{im} \right)^2 \qquad \text{(A.6)}$$

These equations do not account for the statistical bias that results when allele frequencies are estimated from a subset of individuals in a subpopulation. Adjustments to these equations to account for sampling bias have been summarized in Nei and Chesser (1983).

Appendix B

Presentations

National Mitigation and Conservation Banking Conference. St. Louis, MO. April 11-13, 2007. Emerging Tools for Conservation Banking at a Landscape-scale. Integrating Spatially-explicit Population Models with Natural Resource Economics. D. Bruggeman, M. Jones, and T. Wiegand.

SERDP and ESTCP's Partners in Environmental Technology Technical Symposium and Workshop**.** Washington, D.C. November 28-30, 2006. Trading Habitat Patches for the Red-Cockaded Woodpecker: Incorporating the Role of Landscape Structure and Uncertainty in Decision Making.

The Wildlife Society Annual Conference. Anchroage, AK. September 23-27, 2006. (Invited) Integrating Population Genetics and Tradable Permit Markets to Design Nature Reserves on Private Land. D. Bruggeman, F. Lupi, M. Jones, and K. Scribner.

Ecological Society of America 91st Annual Meeting. Memphis, TN. August 6-10, 2006. (Invited) Designing Nature Reserves on Private Land using Tradable Permit Markets. D. Bruggeman, M. Jones, F. Lupi, and K. Scribner.

Estacion Biologica de Donana, Seville, Spain. May 26, 2006. (Invited) Reconciling Structural and Functional Indices of Habitat Fragmentation. D. Bruggeman, T. Wiegand, and N. Fernandez.

Camp Lejeune. Presentation to the Onslow Bight Partnership. April 28, 2006. Habitat Trading for Red-Cockaded Woodpeckers: Incorporating Landscape Processes and Providing Incentives for Cooperation. D. Bruggeman.