DEVELOPMENT AND APPLICATION OF LANDSCAPE EQUIVALENCY ANALYSIS

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ABSTRACT

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The increasing economic value of land has been shown to be an important threat to biodiversity conservation, which is often manifested as habitat loss and fragmentation. As a possible solution, I have derived a method to scale economic incentives for habitat protection under the Endangered Species Act (ESA) based on the contribution habitat patches make to regional biodiversity service flows. The approach is termed Landscape Equivalency Analysis (LEA) and provides a link between local economic decisions and their regional ecological effects. Many endangered species persist on a regional basis through the exchange of individuals and genes among many local populations, so decisions of individual landowners at local scales may affect regional metapopulation persistence. The price of LEA credits represents the in-kind replacement value for three metapopulation services, total abundance, average genetic variance within local populations, and average genetic divergence among local populations. LEA credits can be are generated by strategically locating conservation banks to reverse the negative effects of habitat loss and fragmentation. By requiring the purchase of credits to offset the loss of metapopulation services due to economic development, landscape spatial structure can change without exacerbating the effects of habitat fragmentation. The purchase of LEA credits incorporates regional conservation values of land into local economic decisions. The approach provides a financially-based approach for directing

economic growth around critical landscape components for endangered species and a justification for protection of land deemed valuable by traditional markets.

The metapopulation services used in LEA differ in sensitivity to changes in habitat area and connectivity, according to a species' natural history. Estimating metapopulation services requires simulating the interaction between landscape pattern and metapopulation processes. Landscape indices summarize landscape pattern, providing an alternative for landscape management, but do not necessarily capture changes in biological processes important for metapopulation persistence. To compare decisions based on simulation to those based on landscape indices, a spatially-explicit population model (SEPM) was constructed for the red-cockaded woodpecker (RCW). Two habitat trades were considered, 1) losing equivalent habitat area and connectivity as provided by the bank, and 2) losing more habitat area but less habitat connectivity compared to the bank. Estimates of conservation value provided by LEA captured important interactions between landscape pattern and metapopulation processes that would have been missed had decisions been based on changes in population persistence or landscape indices. Despite the structural equivalence estimated by landscape indices, the first trade actually resulted in increased local extinction and inbreeding in habitat patches not involved in the trade. Further, two alternative hypotheses regarding dispersal behaviors were incorporated into the SEPM. The LEA credits differed in sensitivity to the alternative dispersal hypotheses. Tradable permit markets and the sustainability of the species would benefit from a mechanistic understanding of the relationship between landscape pattern and metapopulation processes provided by LEA.

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crossed during floating behaviors. Over 90% of time when a helper inherits his father's territory, the female breeder disperses to avoid inbreeding (Daniels and Walters, 2000).

Figure 2. Above: a hypothetical landscape containing old growth longleaf pine (black cells), restored second growth forest for RCWs (dark grey cells near the center), second growth forest (light grey cells), and non-forested (white cells). Each cell represents 50-ha. Below: assigning preference to cells adjacent to a bird's location (21, 34) given direction-based and forest-based dispersal rules. Under Direction-based, the vector of movement was toward the grid origin (0, 0) or southwest. Therefore, the bird was found in cell (22, 35) at t-1, this indicates that the bird will likely move to (20, 33) at t+1. At right, forest structure in the center 3x3 matrix is denoted by #1) habitat in old growth longleaf pine, #2R) habitat in restored second growth forests, #2) second growth forest, and #3) non-forested areas. The 3x3 matrix to the far right translates this forest structure into preferences for occupancy, where cell (20, 34) is the most attractive cell. Note, this landscape will be used as the mitigation landscape in later analysis, in which the dark grey cells in the center represent the conservation bank.

Figure 3. a) Fragmented or status quo landscape with 50 territories scattered throughout the region. b) Support landscape with 50 territories clustered together.

Figure 4. Total number of adults belonging to a breeding group. Closed circles denote the support landscape with direction-based dispersal. Open circles denote the support landscape with forest-based dispersal. Closed squares denote fragmented or status quo landscape with direction-based dispersal. Open squares denote fragmented or status quo landscape with forest-based dispersal. Average values taken from 100 simulations. Error bars represent one sample standard deviation.

Figure 5. Inbreeding coefficients and fixation indices for status quo and support landscapes under contrasting assumptions of dispersal. Closed circles: support landscape & direction-based dispersal. Open circles: support landscape & forest-based dispersal. Closed squares: status quo landscape & direction-based dispersal. Open squares: status quo landscape & forest-based dispersal.

Figure 6. a) Surface plot of connectivity values per territory in the status quo landscape; values range from 0-5. b) Surface plot of connectivity values per territory in the mitigation landscape, in which 12 cells in the center of the landscape are restored for RCWs to increase connectivity across the landscape; values range from 0-13. Landscape is also depicted in Figure 6.

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CHAPTER 1

LANDSCAPE EQUIVALENCY ANALYSIS: METHODOLOGY FOR CALCULATING SPATIALLY-EXPLICIT BIODIVERSITY CREDITS

Bruggeman, D. J., M. L. Jones, F. Lupi, and K. T. Scribner, in press. Landscape Equivalency Analysis: Methodology for Calculating Spatially-Explicit Biodiversity Credits. Environmental Management.

Abstract

We propose a biodiversity credit system for trading endangered species habitat designed to minimize and reverse the negative effects of habitat loss and fragmentation, the leading cause of species endangerment in the U.S. Given the increasing demand for land, approaches that explicitly balance economic goals against conservation goals are required. The Endangered Species Act balances these conflicts based on the cost to replace habitat. Conservation banking is a means to manage this balance, and we argue for its use to mitigate the effects of habitat fragmentation. Mitigating the effects of land development on biodiversity requires decisions that recognize regional ecological effects resulting from local economic decisions. We propose Landscape Equivalency Analysis (LEA), a landscape-scale approach similar to HEA, as an accounting system to calculate conservation banking credits so that habitat trades do not exacerbate regional ecological effects of local decisions. Credits purchased by public agencies or NGOs for purposes other than mitigating a take, create a net investment in natural capital leading to habitat defragmentation. Credits calculated by LEA use metapopulation genetic theory to estimate sustainability criteria against which all trades are judged. The approach is rooted in well-accepted ecological, evolutionary, and economic theory, which helps compensate for the degree of uncertainty regarding the effects of habitat loss and fragmentation on endangered species. LEA requires application of greater scientific rigor than typically applied to endangered species management on private lands but provides an objective, conceptually sound basis for achieving the often conflicting goals of economic efficiency and long-term ecological sustainability.

Introduction

Habitat loss and fragmentation are the leading causes of species endangerment in the United States (Wilcox and Murphy 1985; Noss and others 1997; Wilcove and others 1998). Economic goals of the expanding human population serve as the primary driver of land development (Czech and others 2000; Liu and others 2003). Private landowners have the potential to contribute significantly to biodiversity conservation or loss. Roughly 80% of endangered species occur on private lands and 50% of these rely exclusively on privately owned habitat for survival (Noss and others 1997; Wilcove and others 1998). The increase in per capita demand for land (commonly referred to as sprawl) has been shown to be a better predictor of biodiversity loss than the rate of human population growth (Liu and others 2003). Rates of land conversion from habitat to development increases with economic value of land.

Economic incentives have been promoted as a mechanism to mitigate habitat loss on private land (Kennedy and others 1996; Shogren and others 1999). Conservation easements (Section 170(h) of the Internal Revenue Code) and conservation banking (United States Fish and Wildlife Service (USFWS) 2003) represent two approaches allowing private landowners to partially offset the cost of protecting habitat. The financial benefits of developing habitat are still often greater than cost savings provided by these policies, and Section 10 Incidental Take Permit applications are increasing (Harding and others 2001).

Mitigating the effects of habitat loss and fragmentation is challenging, as it requires accounting for the regional ecological effects resulting from local economic decisions (Fahrig and Merriam 1994; Dreschsler and Wissel 1998; Cox and Engstrom

2001). Many endangered species persist through regional exchange of individuals and genes between local populations or subpopulations (Homes and Semmens 2004). Some exist as metapopulations, or a group of subpopulations sharing immigrants at a sufficiently low rate, permitting the exchange of genes while preventing spatially correlated demographic cycles (Hanski and Gaggiotti 2004). To prevent local economic decisions from reducing metapopulation persistence, Section 10 mitigation requirements should specify that local economic decisions should not change subpopulation growth rates and migration rates estimated at the regional (or metapopulation) scale. However, current mitigation planning often ignores *regional* ecological effects of *local* economic decisions owing to a lack of resources and data (Harding and others 2001; Smallwood and others 1999).

Economic incentives that account for the regional ecological effects of local decisions may minimize and reverse the effects of habitat loss and fragmentation and may even provide justification for increased data collection and analysis. Metapopulations provide ecological services, and changes in metapopulation services are externalities of a local economic decision. We propose basing local economic incentives for habitat protection on changes in these externalities estimated at the regional scale which provides a conservative approach to mitigating the effects of habitat loss and fragmentation on endangered species. Costs of habitat protection will differ among landowners, and their land will also differ in its contribution to ecological service flows that derive from metapopulations utilizing their land. Habitat trades based on both economic and ecological considerations are more likely to adequately balance conflicts between economic efficiency (often measured financially) and environmental sustainability (often estimated biologically). Such incentives would require linking ecological, evolutionary, and economic theory within existing policy to scale incentives appropriately.

In this paper we present a method which connects scientific theory with environmental policy to allow private landowners to profit from habitat protection while directing development (sprawl) around critical habitats within the landscape. By integrating the legal mechanism of the Endangered Species Act (ESA) with ecological, evolutionary, and economic theory, the influence of sprawl on biodiversity can be incorporated into the market value of land. We propose Landscape Equivalency Analysis (LEA), a derivation of Habitat Equivalency Analysis (National Oceanic and Atmospheric Administration (NOAA) 1999), as a method to make tradeoffs between regional conservation goals and local economic decisions. This paper first outlines the theoretical basis for examining regional externalities resulting from land conversion at local scales. Then, the conservation value of a patch is defined in a manner congruent with the goals of the ESA and metapopulation theory. Finally, we synthesize theory and policy within LEA, outlining spatially-explicit credits for habitat trades intended to minimize and reverse the effects of habitat loss and fragmentation.

Externalities from Land Conversion

Ecological functions can be treated as goods and services when a direct or indirect benefit to humans can be demonstrated (deGroot and others 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 metapopulation also provides indirect benefits for humans. Adaptive genetic variance is required for population persistence (Fisher 1930). Neutral genetic variance is useful for determining how habitat loss or restoration affects gene flow, genetic drift, and inbreeding (Hedrick 2001). Thus, endangered species habitat is a form of natural capital, defined as a stock of resources providing useful services (deGroot and others 2000). In this analysis we assume that the ecological services that provide these benefits are abundance and genetic variance (deGroot and others 2002).

Although total social costs of endangered species protection often fall well below total social benefits (Loomis and White 1996), the actual cost of endangered species protection often falls on relatively few households. An economic opportunity cost is incurred by private landowners based on the foregone revenue from not developing due to the presence of an endangered species (Shogren and others 1999). We define this as an economic opportunity cost due to habitat protection, OC-P. A private landowner's use of an Incidental Take Permit (Section 10; USFWS 1988) will be based on the size of OC-P compared to costs to meet mitigation requirements preventing take and jeopardy defined by the ESA as harming, harassing, or killing individuals and decreasing the likelihood of species survival. The ESA effectively assigns an infinite economic value to endangered species habitat as no otherwise lawful activity justifies causing a take or increasing jeopardy (Brown and Shogren 1998). In this way the ESA theoretically prevents the loss of abundance services from endangered species habitat.

Externalities result when we are unable to protect and restore habitat at a local scale in a manner that prevents the loss of abundance and genetic variance at a larger scale. In endangered metapopulations externalities may result from removal or addition of habitat within the landscape or changes in landuse among habitat patches. Strategic protection of habitat is necessitated when migration rates among subpopulations are affected by distance or landuse (e.g., roads or residential development). The contribution of a habitat patch to metapopulation service flows is not only determined by the size and vegetative composition of the patch, but also by the location of that patch relative to other patches, roads, and residential development (i.e., its spatial context). Instead of basing restoration decisions on the cheapest land to restore, metapopulation sustainability may benefit from restoration or protection of land deemed valuable for traditional economic development (i.e., high OC-P).

Defining Patch Conservation Value Inclusive of Landscape Spatial Structure

We believe that integrating population genetic theory with demographic observations would be an effective approach for defining patch conservation value. Under the ESA, habitat conservation value is often defined as its ability to maintain or decrease the probability of population extinction (Montgomery and others 1994; National Research Council (NRC) 1995). Take is typically estimated by changes in abundance, but adverse changes to habitat have also been interpreted as a take (Dwyer and others 1995). Thus, for metapopulations, the conservation value of a patch should reflect its contribution to sustainability measured at the regional scale.

The goal of the ESA is protection of enough habitat to achieve sustainable populations justifying delisting (USFWS 1988). Many believe the goal of conservation should be to protect land such that evolutionary processes are maintained (i.e., protect functional landscapes) (Frankel 1974; Meffe 1996; Moritz 2002). From a metapopulation perspective a functional landscape would be the allocation of habitat providing rates of subpopulation growth and migration rates similar to those observed prior to habitat loss and fragmentation (Meffe 1996). As habitat patches are reduced in size and/or become isolated the probability that deleterious recessive mutations will be expressed due to mating among related individuals, or inbreeding depression, will increase (Higgins and Lynch 2001). Conversely, changes in habitat spatial structure that increase migration rates may cause the disruption of co-adapted gene complexes, or outbreeding depression (Dudash and Fenster 2000).

Given existing uncertainties of landscape-scale management, we propose that recovery goals should incorporate genetic criteria to help define spatial allocation of habitat most likely to support sustainable metapopulations. Studies only examining abundance have not been able to resolve the relative importance of the loss of total habitat (amount) versus the change in habitat connectivity (pattern) in driving the decline or recovery of a metapopulation (Wiegand and others 1999; Fahrig 2001; Flather and Bevers 2002). Based on existing empirical evidence, the effect of changing habitat area versus connectivity on extinction risk will depend on both landscape- and species-specific variables (Debinski and Holt 2000; MacNally and others 2000).

Metapopulations must achieve a balance between growth within each subpopulation and migration between subpopulations to prevent 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). Field studies have demonstrated that mammalian metapopulations have evolved behaviors to simultaneously prevent loss of genetic variance within while maintaining genetic variance among subpopulations (Dobson and others 1997; Storz 1999; Coltman and others 2003). In a disturbed landscape, the ability of a metapopulation to balance genetic variance within and among subpopulations is likely impaired due to loss of habitat area and connectivity. Changes in landscape spatial structure have been shown to affect how genetic variance is partitioned over space (Hale and others 2001; Mech and Hallet 2001) and result in inbreeding depression (Bouzat and others 1998; Saccheri and others 1998).

Moritz (2002) stipulates that protecting the environmental context that produced existing patterns of biodiversity is the best way to maintain evolutionary processes. We can define a 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). This recovery objective meets the definition of a functional landscape for a metapopulation given above. Given existing loss of habitat, 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.

If the natural history of the organism is well known, demographic-behavioral models (Sugg and others 1996; Lacy 2000) could be used to reconstruct the spatial distribution of neutral genetic variance prior to habitat loss and fragmentation (i.e., baseline levels). This would save the expense of conducting genetic analysis. However, baseline levels of neutral genetic variance within and among subpopulations may also be estimated by integrating genetic analysis of museum specimens and extant conspecifics (Bouzat 2001; Matocoq and Villablanca 2001) with demographic-behavioral models.

The degree to which variance in neutral genetic markers as measured using molecular or biochemical markers and variance in quantitative genetic traits of adaptive significance are positively correlated is unresolved (Hedrick 2001; Reed and Frankham 2001). Positive correlations between levels of neutral and adaptive genetic variance are expected to be greater when the effects of drift exceed natural selection as the dominant evolutionary force, as is expected in populations of small size (Reed and Frankham 2001); a common problem for endangered species. While estimates of neutral variance are available for some endangered species, estimates of adaptive genetic variance for endangered populations are often unavailable and difficult to acquire (Neel and Cummings 2003). Subpopulation growth rates, an adaptive trait (Fisher 1930; Wright 1940), can be estimated by tracking changes in abundance and will be useful for estimating the correlation between neutral and adaptive variance.

We propose that comparing observed or predicted levels of abundance and neutral genetic variance within and among subpopulations to baseline levels will allow a more thorough assessment of the tradeoffs between habitat area and connectivity than abundance alone. We thus define conservation value of habitat patch as its contribution to the maintenance of three services: (1) abundance and genetic variance (2) within and (3) among subpopulations. By incorporating baseline estimates of neutral variance both within and among subpopulations into the definition of conservation value, the spatial allocation of habitat that permitted adaptive evolution now serves as an explicit goal. This approach may replace general "rules of thumb" (e.g., one migrant per generation; Mills and Allendorf 1996) used to prescribe adequate levels of migration for endangered metapopulations. The definition of conservation value may be viewed as a species-specific and spatially-explicit version of Karr and Dudley's (1981) definition of biotic integrity. In the context of metapopulation management, a balanced, integrated, adaptive assemblage of subpopulations having the functional organization comparable to that of a natural landscape would have a high level of biotic integrity.

In summary, the conservation value of a habitat patch derives from its incremental (marginal) contribution to metapopulation sustainability. Recovery goals for the metapopulation can be translated into species-specific sustainable service flows of abundance and genetic variance. A patch's conservation value would then equal its marginal contribution toward meeting the recovery goal, or, in the case of mitigation, the marginal decline in service flows that would result if the patch were removed (e.g., Petit and others 1998). The latter is a negative externality at the regional scale, and its magnitude provides an estimate of the ecological opportunity cost resulting from a change in landscape structure. We define this as the opportunity cost due to habitat disturbance, OC-D. Using the three estimates of metapopulation services, the OC-D represents lost opportunities for population growth and adaptive evolution.

Resource-based Compensation

A common way to balance economic activities with conservation goals is through "service-to-service" compensation (NOAA 1999). When natural capital is injured (e.g., wetland impacted by oil spill) ecological restoration or enhancement can increase ecological service flows in a manner to equate an individual's well-being before habitat destruction with their well-being after habitat destruction (Mazzotta and others 1994; Jones and Pease 1997). This is called resource-based compensation and is used to plan ecological mitigation to prevent the loss of social welfare. When environmental regulations stipulate in-kind replacement of ecological resources, as in the ESA, compensation must be made using the same type of resource and services that were lost (Mazzotta and others 1994).

Habitat Equivalency Analysis (HEA) is the most widely used service-to-service approach (NOAA 1999; Penn and Tomasi 2002; Strange and others 2002). HEA is a "scaling methodology" that equates losses in services due to destruction of an ecological resource in one location (injury) to gains in said services provided by an ecological resource at another location (compensatory restoration). This permits comparison of different ecological resources based on the level of service flows they provide (King 1997). The social time preference for capital assets is incorporated into HEA by discounting ecological service flows over time (Mazzotta and others 1994; NOAA 1999). The rate of discounting reflects a society's willingness to substitute future "consumption" for present "consumption" of the ecological service (NOAA 1999).

Managing Externalities with Cap and Trade Policies

Creating a market for the exchange of positive and negative externalities at local scales is one way to prevent negative externalities at a regional scale. Marketable permit systems, or "cap and trade", must first set a limit on the amount of externalities allowed.

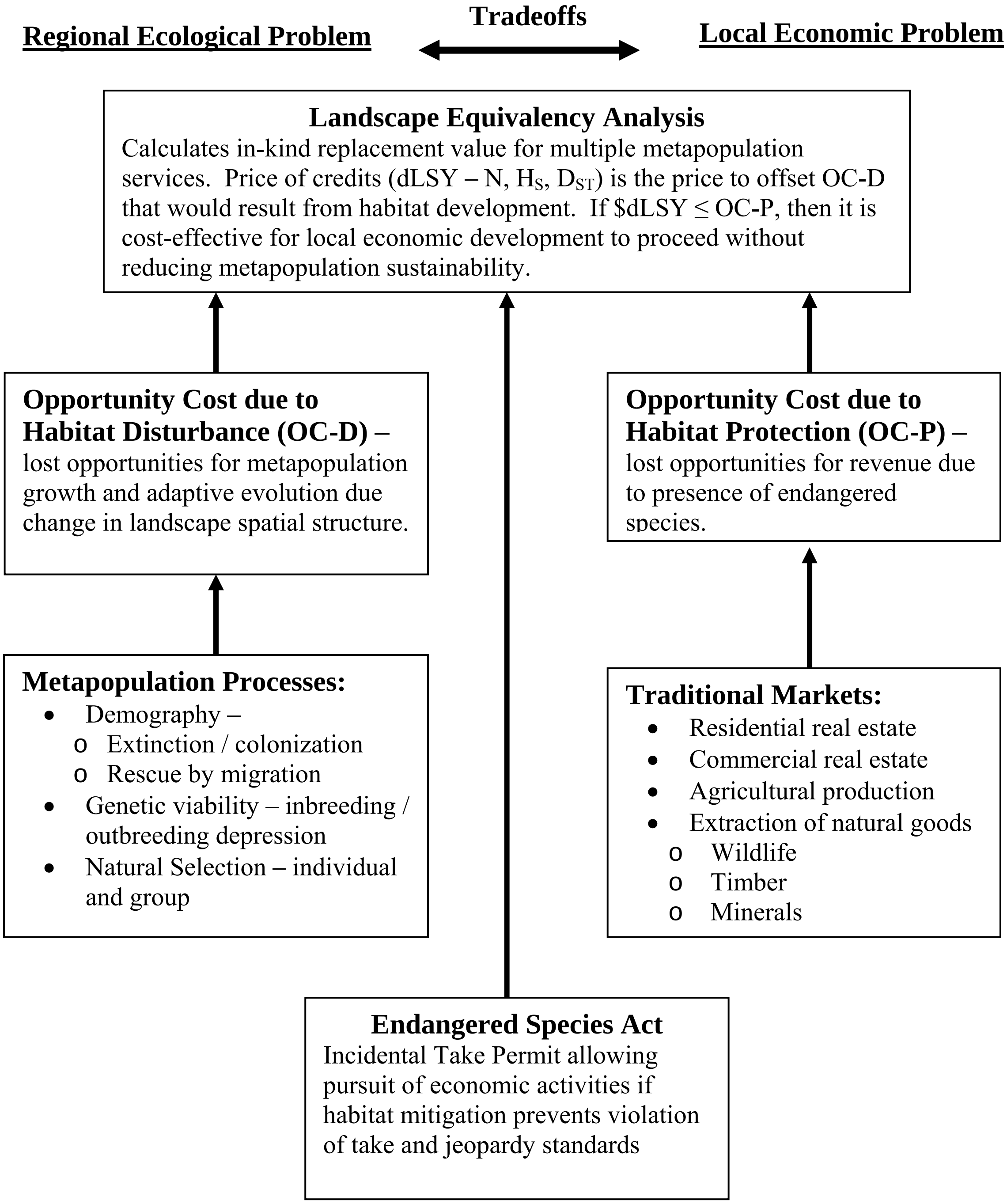
A regulated entity with high compliance costs of meeting the cap can purchase permits from those with low compliance costs. The increased flexibility reduces the economic costs of the meeting the cap, and the limited number of permits assure that the cap is met. In essence, a market is created so that some of the external (social) costs are incorporated into the price of the good or service that created the externality (e.g., Air Pollution Trading; Tietenberg 2004).

The ESA can be thought of as imposing a cap on further loss of abundance, as represented by the take and jeopardy standards. Conservation banking provides a system similar to a cap and trade system, wherein the purchase of a credit from the bank represents trading of access rights to endangered species habitat (USFWS 2003). Issuance of an Incidental Take Permit requires that the take be mitigated to the greatest extent practicable and no appreciable reduction in the likelihood of species survival results (Stanford Environmental Law Society 2001). Recognizing the importance of metapopulation processes for many endangered species, Federal guidance stipulates locating a conservation bank within the landscape to minimize the effects of habitat loss and fragmentation (USFWS 2003). Also, it is critical that an accounting system be developed to ensure that credits are not oversold by a bank (i.e., creating a take or otherwise increasing risk of extinction). Since all “trades” under conservation banking are individually evaluated and subject to regulator conditions, these are not pure market systems (Shabman and Scodari 2004), but this pseudo-market system can enhance flexibility and lower compliance costs while ensuring trades do not decrease regional service flows. We propose resource-based compensation as the basis for a landscape-scale tradable permit system.

Landscape Equivalency Analysis

HEA does not include any ecological interaction between site of injury and site of compensatory restoration or between these sites and adjacent patches. Therefore, it is not suitable for managing metapopulations. By applying a landscape perspective to resource-based compensation, we provide a method for making tradeoffs between changes in patch conservation value, estimated as changes in OC-D at the regional scale, and OC-P at the local scale, as described in Figure 1. Applying the principles of landscape ecology to HEA will capture externalities that result from changes in habitat spatial structure. An equitable habitat trade is one which prevents OC-D from being incurred at the regional scale when economic development is pursued. We call this new formulation of HEA Landscape Equivalency Analysis (LEA).

LEA treats the landscape as a single unit of ecological resource providing a set of services. A goal of LEA is to identify landscape configurations that provide equivalent levels of services despite changes in landscape structure that result from losing a patch or changing matrix quality. As with HEA, calculation of equivalency is based on expected changes in services over time, appropriately discounted. HEA allows adjustment for differences in efficiency (differences in service levels) across two sites by adjusting the total acreage (size of the resource) (NOAA 1999). The level of service is summarized per unit of resource (e.g., sediment retention per wetland acre) and the quality of the two sites are compared based on discounted Service Acre Years (dSAYs). dSAYs are a time-integrated estimate of resource quality based on area-weighted service flows emanating from the resource.



Landscape Equivalency Analysis

Calculates in-kind replacement value for multiple metapopulation services. Price of credits (dLSY – N, H_S, D_{ST}) is the price to offset OC-D that would result from habitat development. If \$dLSY $\leq$ OC-P, then it is cost-effective for local economic development to proceed without reducing metapopulation sustainability.

Opportunity Cost due to Habitat Disturbance (OC-D) – lost opportunities for metapopulation growth and adaptive evolution due change in landscape spatial structure.

Opportunity Cost due to Habitat Protection (OC-P) – lost opportunities for revenue due to presence of endangered species.

Metapopulation Processes:

- Demography –
  - Extinction / colonization
  - Rescue by migration
- Genetic viability – inbreeding / outbreeding depression
- Natural Selection – individual and group

Traditional Markets:

- Residential real estate
- Commercial real estate
- Agricultural production
- Extraction of natural goods
  - Wildlife
  - Timber
  - Minerals

Endangered Species Act

Incidental Take Permit allowing pursuit of economic activities if habitat mitigation prevents violation of take and jeopardy standards

Figure 1. Flow chart of proposed integrative decision analysis to mitigate the negative effects of habitat loss and fragmentation at the regional scale due to economic decisions at the local scale. Landscape Equivalency Analysis (LEA) estimates credits as discounted Landscape Service Years (dLSYs) for three metapopulation services including abundance (N), average expected heterozygosity (H_S), and average genetic divergence (D_{ST}).

Landscape components must be classified so that their role in metapopulation growth and migration can be estimated (McIntyre and Hobbs 1999). Habitat within the landscape can be defined as the "resources and conditions present in an area that produce occupancy – including survival and reproduction – by a given organism" (Hall and others 1997, pg 175). Habitat patches are distinguished by greater habitat quality than surrounding areas. Areas outside of the habitat patch which allow low occupancy rates (lower habitat quality) are classified as the matrix and may be differentially permeable to migration among subpopulations. For our purposes, a landscape is defined as the patches and matrix that interact and contribute to the same set of landscape services that we wish to manage.

When the resource is a landscape it can not be merely assumed that differences in levels of service over time can be compensated by adjusting the total area of patches that contribute to the service. The level of landscape services will also depend on the spatial associations of patches (i.e., connectivity), and the relationship between connectivity and service flows is not necessarily monotonically increasing. No simple spatial variable (e.g., area or connectivity) will sufficiently predict changes in landscape services (Crow 2002). Therefore, LEA will use discounted Landscape Service Years (dLSYs), in which the quantification of landscape services implicitly includes the spatial aspects (area and location) of the action being considered.

The conservation value of tradeoffs between habitat amount and connectivity can be assessed by changes in dLSYs estimated at the landscape (regional) scale. LEA estimates marginal changes in externalities at the metapopulation-scale based on the marginal decision to destroy or restore another patch or change matrix quality within the landscape. dLSYs is a time-integrated estimate of the externality caused by marginal changes in landscape spatial structure. LEA can also be used to estimate positive externalities resulting from habitat restoration or enhancement that cause service flows to move closer to sustainability goals.

Externalities at the regional scale due to local decisions can be estimated with spatially-explicit population models (SEPMs). SEPMs describe the interaction among landscape structure and metapopulation processes (Turner and others 1995) and have been used to predict the effects of landscape management on endangered metapopulations (Liu and others 1995; Letcher and others 1998). SEPMs have also been used to predict changes in genetic variance within and among subpopulations (Lacy and Lindenmayer 1995). For example, VORTEX is an individual-based model that tracks the movement and reproductive success of each genotype (or individual) in a metapopulation (Lacy 2000). Making predictions at the subpopulation (patch) level with a SEPM is challenging due to the number of parameters required to link demography (subpopulation growth rate) and behaviors (rates and patterns of migration) to habitat quality and structure in fragmented landscapes (Ruckelshaus and others 1997; South 1999). Verifying and updating models using both demographic and genetic observations has been suggested as one approach to reduce uncertainty (Lindenmayer and Lacy 2002).

LEA provides a mechanism for integrating demographic and genetic data for decision analysis. Including genetic variance as an ecological service flow in resource-based compensation will increase our ability to make tradeoffs between local economic decisions and regional ecological effects.

Quantifying Genetic Variance for LEA

Species and populations within species may differ from each other in their baseline level of genetic variance (Matocq and Villablanca 2001). Genetic markers (e.g., allozymes, mitochrondrial haplotypes, or microsatellites) provide estimates of whether neutral genetic variance within and among subpopulations have departed from baseline due to a changes in the spatial structure of habitat (Hedrick 2001). Nei (1973) describes how data from genetic markers can be used to estimate the apportionment of neutral genetic variance at different spatial scales. When two levels of spatial organization are present (i.e., at subpopulation and metapopulation levels), Nei's theory can be summarized as:

$$H_T = H_S + D_{ST} .$$

H_T equals the total genetic diversity in the metapopulation and represents the probability that any two alleles chosen at random, one from each of two individuals, are independent (Nei 1973). The average expected genetic diversity within a subpopulation can be estimated as the average frequency of heterozygotes in a subpopulation (H_S) under Hardy-Weinberg Equilibrium. The remaining genetic variance in a metapopulation is due to divergence in allele frequencies among subpopulations, which is estimated using a measure of average minimum genetic distance (D_{ST}). Levels of average expected heterozygosity (H_S), the average genetic divergence (D_{ST}), and abundance (N) will serve as estimates of metapopulation services, which will be estimated at the regional scale.

Applying LEA to an Endangered Metapopulation

At each point in time when a decision is made regarding habitat restoration or habitat loss, an investment or withdrawal of natural capital results, changing the rate of appreciation or depreciation. A withdrawal that drives services below current levels violates ESA, representing a take and may increase the risk of extinction. Sufficient investment above current levels, without withdrawals, eventually leads to species recovery. LEA facilitates a tradable credit market that is driven by private landowners' interest in maximizing land values but is constrained by the Federal goal of achieving sustainable populations (by ensuring credit trades do not violate ESA take and jeopardy standards). The uniqueness of this approach lies in the ability of LEA to incorporate the unequal contribution of habitat patches and landscape matrix to multiple metapopulation service flows.

In the remainder of this section, we illustrate the LEA approach using several simple qualitative descriptions of the effects of spatial structure on metapopulation services. A fully quantitative approach would require development and description of a SEPM, which is beyond the scope of this paper. The critical output from a quantitative analysis would be expected levels of abundance (N), average expected heterozygosity (H_S), and average genetic divergence (D_{ST}) over time under different landscape configurations. To illustrate LEA, Figure 2 presents three hypothetical landscape structures. For the illustration, several assumptions are made which need not hold for general applications of LEA. Habitat patches in the landscape differ in the amount of habitat destruction they experienced and in ownership (patches with a G or P represent government or private land respectively). Even though patches differ in level of connectivity and habitat area, the illustration assumes equal habitat quality across patches for all extant subpopulations. We make the simplifying assumption that the matrix is homogeneous, and dispersal is only limited by the distance between extant patches. In a real landscape, habitat and matrix quality will vary. We also assume that movement of individuals across proximate subpopulations is constant over time. We do not consider that metapopulations often require empty but suitable habitat patches to colonize when local extinction occurs elsewhere (Thomas and Hanski 1997).

Figure 2A displays a landscape structure meeting the sustainability (recovery) goal, in which the combined shaded and non-shaded areas represent the historic geographic range of the species. Expected service levels from this landscape are referred to as the b-trajectory (baseline) in Figure 3. Here we assume that the recovery goal is to restore the historic geographic range of the species. Figure 2A also displays habitat remnants (shaded areas) that provide the status quo level of services (j-trajectory in Figure 3). The status quo services will reflect service levels below which constitute a take. In general, as populations become subdivided, gene flow is restricted and genetic drift increases, causing a loss of genetic variance within a subpopulation but an increase in genetic divergence among populations (Whitlock 2004). Given the habitat loss and fragmentation indicated in Figure 2A, we can expect a large reduction in abundance within the metapopulation, a decrease in average heterozygosity within subpopulations, and an increase in average genetic divergence among subpopulations (Figure 3).

Figure 2B indicates that a conservation bank has been added to the metapopulation at a later time (M in Figure 3). Assuming a SEPM can be constructed,

Figure 2. Change in spatial structure of hypothetical landscape over time with multiple landowners. Patches labeled “P” are each owned by different private parties and those labeled “G” are owned by the Federal government. Open areas represent endangered species habitat that has been lost to economic development. Filled areas represent habitat supporting the endangered population. Length of double-sided arrows equal the species maximum dispersal distance, indicating connectivity. The matrix is homogeneous and dispersal is only limited by the distance between patches. A) Shaded and non-shaded areas combined represent the baseline habitat distribution that would provide a sustainable metapopulation (b-curve in Figure 3). Shaded areas represent the current remnant subpopulations (j-curve in Figure 3). B) Conservation bank is added to metapopulation (m-curve) changing landscape spatial structure. C) Three possible choices for economic growth leading to an endangered species take are displayed (withdrawal of credits: w1, w2, and w3-curves in Figure 3). Open arrows represent connectivity lost due to economic development.

Figure 2A

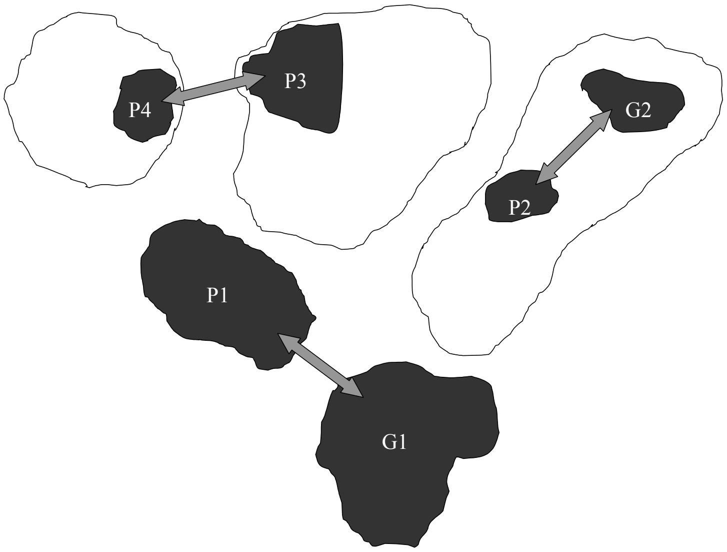


Figure 2B

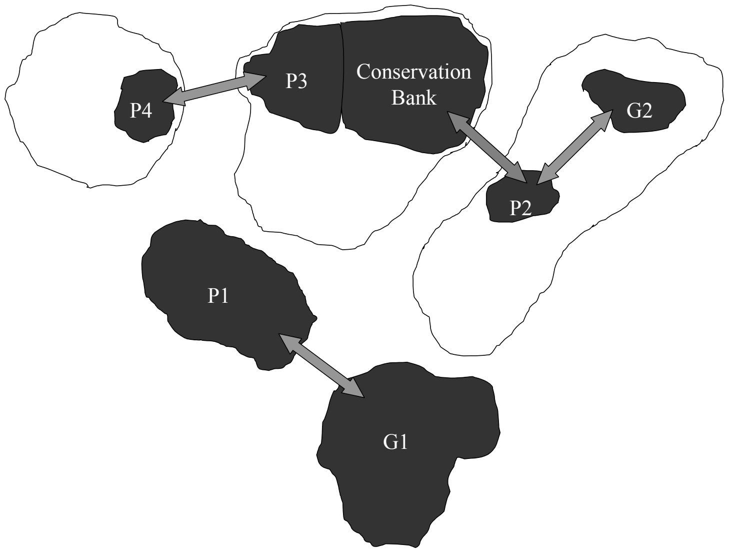
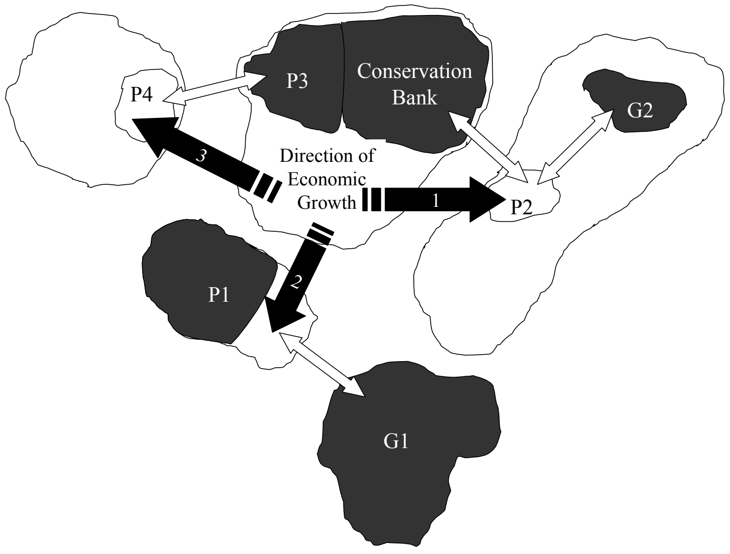


Figure 2C



the interaction between a species' natural history and landscape structure can be modeled. Therefore, the SEPM can be used to estimate metapopulation services resulting from the restoration of different sites, given landscape- and species-specific conditions, in order to find the best location for the bank. The bank location in the hypothetical landscape was chosen because it has a high probability of being colonized by individuals from adjacent habitat (P3) and sharing migrants with the smallest habitat remnants (i.e., patches with highest probabilities of extinction, G2, P2, and P4). Figure 3 illustrates that the placement of the bank should move services closer to sustainability goals, helping to reverse the negative effects of habitat loss and fragmentation (m-trajectory).

The number of credits available in a bank is conditional upon the ability of the mitigation plan to increase conservation values (USFWS 2003), estimated in our analysis as increased service flows. Sale of credits represents a decrease in service flows due to the decision of another private landowner to develop a habitat patch. Figure 2C displays three possible directions of economic growth each resulting in a take. The SEPM is used to estimate the change in service flows due to each possible direction of growth (the w-trajectories in Figure 3). Expected changes in genetic variance will depend on interactions between organismal and landscape history. Further, the magnitude of changes in average expected heterozygosity (H_S) and average genetic divergence (D_{ST}) should be especially sensitive to changes in landscape structure.

Direction 1 results in losing a habitat patch that recently connected organisms inhabiting private and public land (i.e., a stepping stone is lost, P2) due to conservation banking. The subpopulation in G2, which is publicly owned, would then suffer from increased genetic drift and inbreeding due to the loss of gene flow. In this example, the

Figure 3. Trajectories of metapopulation services used to calculate Landscape Equivalency Analysis (LEA). Figure 2 reports the landscape spatial structure hypothesized to give each service flow trajectory. The expected service flow trajectories are represented by lower case letters. When time = M, a conservation bank is added to the metapopulation. When time = W, services flows resulting from one of three possible withdrawal of credits from the bank is projected. Each time the landscape structure is changed (i.e., time = M and time = W), service flows are estimated assuming no changed occurred, as indicated by the dotted lines. These estimates are required so that LEA can calculate the change in appreciation or depreciation of service flows from natural capital.

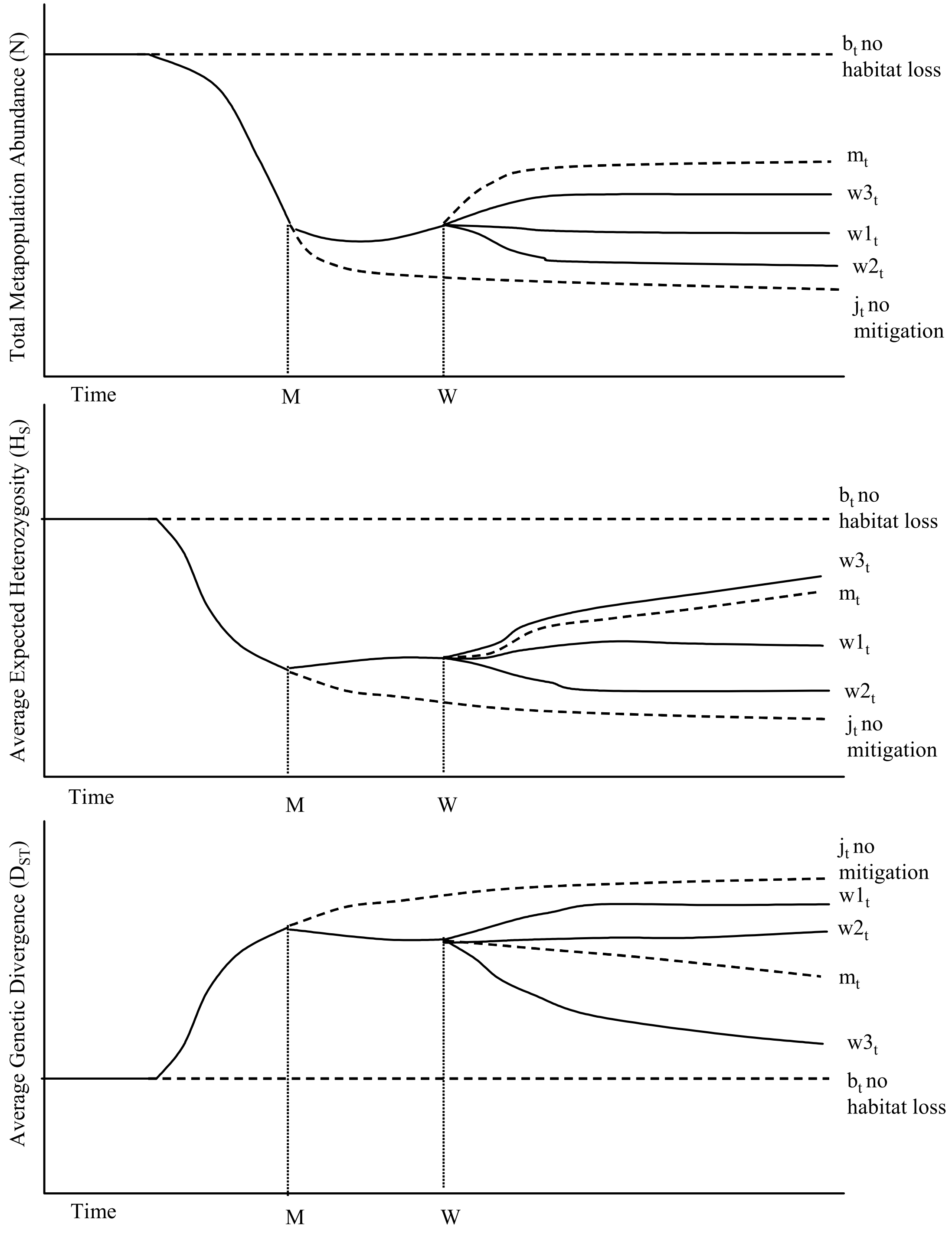

Total Metapopulation Abundance (N)
b_t no habitat loss
m_t
$w3_t$
$w1_t$
$w2_t$
j_t no mitigation
Time
M
W
Average Expected Heterozygosity (H_S)
b_t no habitat loss
$w3_t$
m_t
$w1_t$
$w2_t$
j_t no mitigation
Time
M
W
Average Genetic Divergence (D_{ST})
j_t no mitigation
$w1_t$
$w2_t$
m_t
$w3_t$
b_t no habitat loss
Time
M
W

Figure 3

service most affected by this trade would be average genetic divergence among subpopulations, because the increased connectivity provided by the bank is lost. Also, metapopulation abundance and average expected heterozygosity would be reduced (Figure 3, trajectory w_1).

Direction 2 results in reducing the size of a historically large subpopulation (P1). Also, gene flow between the two largest subpopulations is lost. The services most likely affected by this trade are abundance and average expected heterozygosity within each subpopulation. This larger subpopulation contributed disproportionately to abundance and average expected heterozygosity measured at the regional scale, but contributed little to average genetic divergence, owing to its larger subpopulation size and comparatively high exchange of migrants with another large subpopulation. Because the subpopulation experiencing the take has been historically outbred, it may be more susceptible to inbreeding depression due to harboring more deleterious recessive mutations than smaller, peripheral subpopulations (Frankham and others 2001). Therefore, there is a greater probability that inbreeding depression will threaten population persistence in both P1 and G1, which is why the development scenario is projected to have the biggest impact on metapopulation abundance (Figure 3). Average genetic divergence will also increase over time, but more slowly, compared to the smaller peripheral patches.

Direction 3 results in losing the most isolated patch (P4). Subpopulation P4 is likely the most genetically distinct and its loss has a disproportionate effect on average genetic divergence at the metapopulation scale, bringing the subpopulation closer to baseline (Figure 3). Though Nei's (1973) estimates of genetic variance are weighted by population size, loss of the isolated patch may slightly increase the average expected heterozygosity at the metapopulation scale. The reduction in metapopulation abundance is expected to be relatively small compared to the other possible takes (w1 and w2). Even though the area of habitat lost in direction 1 and 3 are very similar, a greater decline in abundance is expected under direction 1 because the extinction risk for the subpopulation G2 is increased by the loss of the stepping stone (P2). This simple example described how each metapopulation service differs in sensitivity to changes in habitat area and connectivity.

If the loss of any habitat results in loss of alleles only found in that subpopulation (i.e., private alleles), Nei's estimates of total genetic diversity may be inadequate for decision making and measures of allelic richness should be considered (Petit and others 1998; Neel and Cummings 2003). In this case, translocation of organisms may also be considered (Moritz 1999). These topics are beyond the scope of this paper, however.

Calculating Biodiversity Credits using LEA

The number of credits the private landowner must purchase to offset externalities that result from habitat alterations can be calculated by comparing changes in service trajectories. The number of credits required to offset the local and regional loss of abundance due to losing a habitat patch can be calculated as discounted Landscape Service Years - Abundance (dLSY^N):

$$E\left[dLSY^{\ N}\right] = \sum_{t=W}^{\infty} \frac{1}{(1+r)^t} \left(\frac{m_t{}^N - w_t{}^N}{b_t^N} \right)$$

where loss of service flows due to habitat loss for the endangered metapopulation begins at year W, r is the social discount rate, b_t^N is the expected abundance for the metapopulation at year t (representing the recovery goal), m_t^N is the expected abundance at year t inclusive of adding or enhancing the bank patch that will sell credits, and w_t^N is the expected abundance at year t reflecting anticipated loss of habitat or connectivity.

dLSY^N represents the marginal conservation value of the lost patch given it's spatial context within the metapopulation relative to a recovery goal (i.e., the negative externality in abundance that results from losing that patch to development). The credit represents the fraction of problem solved by mitigation minus the fraction of the solution lost due to take elsewhere in the landscape. Because the public has a positive time preference for services from capital assets, discounting modifies the number of credits associated with the change in abundance, as in HEA. In other words, the more slowly the withdrawal decreases population size, the fewer credits must be purchased.

Calculating credits associated with changes in genetic variance is more complex. The management goal is to approximate the distribution of habitat in which the organism evolved (baseline landscape) (Meffe 1996; Moritz 2002). Greater genetic diversity within a subpopulation or greater genetic divergence among subpopulations is not always better for sustainability (Bouzat 2001). As estimates of genetic variance within and among subpopulations move farther away from baseline levels due to losing a patch or connectivity, the larger the credit purchased from the bank will have to be. The credit representing the magnitude of externality in genetic services due to losing a patch elsewhere can be calculated as discounted Landscape Service Years – Genetic Variance (dLSY^G):

$$E\left[dLSY^G\right] = \sum_{t=W}^{\infty} \frac{1}{(1+r)^t}\left(\frac{\left|b_t{}^G - w_t{}^G\right|}{b_t{}^G}\right) - \sum_{t=W}^{\infty} \frac{1}{(1+r)^t}\left(\frac{\left|b_t{}^G - m_t{}^G\right|}{b_t{}^G}\right)$$

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 representing the recovery goal or baseline levels, m_t^G is the expected level of genetic variance at year t inclusive of adding or enhancing the bank patch that will sell credits, and w_t^G is the expected level of genetic variance at year t reflecting anticipated loss of habitat or connectivity.

For any positive discount rate, the more slowly a landscape change moves the population away from baseline, the fewer credits per change in service level are incurred. Conversely, habitat changes resulting in a large departure from baseline in the immediate future will be charged many credits per change in service level.

Assuming that neutral variance serves as a surrogate for adaptive variance in a small population, when H_S and D_{ST} are close to baseline the probability of inbreeding and outbreeding depression will be reduced, while opportunities for natural selection at individual and group levels are protected. Conversely, if we assume no correlation between neutral and adaptive variance, when H_S and D_{ST} are close to baseline, subpopulation growth rates and migration rates (i.e., metapopulation processes) observed prior to habitat loss and fragmentation have been closely approximated.

It is possible for m_t^G, j_t^G, or w_t^G to oscillate about b_t^G and each other over time. The amplitude in the oscillations and average distance from b_t^G will be reflected in the credit estimate using the equation above. If the loss of a patch (w^G) produces large oscillations and pushes genetic variance farther away from b^G than previously observed under mitigation-level scenario (m^G), $dLSY^G$ will be large.

Due to the denominator, the smaller the baseline level of genetic variance (b^G), the larger $dLSY^G$ would be per change in service levels. Therefore, sensitivity of the

$dLSY^G$ measure increases as the baseline genetic variance moves closer to zero. If the baseline average expected heterozygosity within a subpopulation were low ($b^{Hs} \to 0$), genetic drift caused by habitat loss and fragmentation may quickly drive H_S to zero. Conversely, if mitigation increased H_S well above baseline due to immigration, disruption of locally adaptive gene complexes may result in outbreeding depression (Dudash and Fenster 2000). If the baseline level of genetic divergence were low ($b^{Dst} \to 0$), the metapopulation historically experienced high rates of gene flow among patches. Therefore, $dLSY^{Dst}$ would be more sensitive to changes in habitat connectivity.

Recommendations for Basic Conservation Banking Scenario

In the simple example described in Figures 2 and 3, the size of credits can be estimated by examining the graphs regardless of the discount rate, because trajectories of service levels do not cross. Economic development in direction #3 would require the smallest number of credits to be purchased from the bank for each metapopulation service. Direction #2 results in the largest externalities as estimated by abundance and average expected heterozygosity, but a relatively smaller externality as estimated by changes in genetic divergence when compared to direction #1. Direction #1 results in an intermediate externality for abundance and average expected heterozygosity, but the largest externality for genetic divergence credits.

Results from the hypothetical example are obvious because only the influence of the organism's maximum dispersal distance and previous landscape structure are considered. Incorporating more details on landscape structure and an organism's natural history may lead to a different placement of the bank and/or a different recommended direction for economic growth. However, even in our simple example, we show that by only examining patch-level changes in abundance at the site of take and bank, and ignoring metapopulation dynamics, all three directions of growth are likely to be considered equally undesirable, because the habitat area lost for each direction of growth is roughly equal. LEA incorporates information on existing service levels which will help capture previous loss of connectivity, reduction in population size, and extinction of subpopulations, occurring at different times, that would be missed if trades were based solely on demographics (e.g., Frankham 1995; Luikart and others 1998).

Trading Metapopulation Credits

A private landowner wishing to purchase an Incidental Take Permit from the conservation bank would have to buy credits for each service individually. The price of the credit represents the in-kind replacement value for each service inclusive of landscape spatial structure. Applying resource-based compensation to habitat trades within a metapopulation will require institutional arrangements that outline how the Federal government, conservation bank, and private landowners interact to achieve sustainability goals. A market for metapopulation service flows from a landscape will likely be a centralized market (i.e., a pseudo-market) in which Federal oversight is needed to ensure sufficient scientific certainty for trading exists and that banks do not over sell credits (USFWS, 2003; Shabman and others 1996). Federal oversight will be especially important when managing metapopulations due to the potential for a neighbor reducing habitat quality, subsequently reducing the marginal conservation value of adjacent patches (i.e., an unmitigated take). Trading rules enforced by regulators should promote trading of credits (i.e., allowing development) while not further endangering the population (Shabman and others 1996). Some preliminary rules are listed below:

Rule #1. Trades must not violate take and jeopardy standards. Two necessary conditions for all trades could be that no take results from the action (i.e., mean-w^N > mean-j^N, where j^N is expected abundance under status quo conditions) or the probability of extinction under the j-trajectory (E^j) must be greater than or equal to the probability of extinction under the w-trajectory (E^w) (i.e., $P[E^J] \geq P[E^w]$). Violation of these conditions (i.e., take and jeopardy, respectively) means that the trade would result in overdrawing credits (i.e., cap is exceeded). This indicates that the bank has not yet provided a sufficient increase in ecological services to make the trade. More time and/or restoration are required before trading would be allowed, or a different 'w-action' could be considered.

Rule #2. Trades should not produce an allocation of habitat that drives the spatial apportionment of genetic variance farther away from baseline levels. If the projected maximum absolute difference between b^G (baseline levels of the genetic variance component) and w^G across all time is greater than that between b^G and j^G (i.e., $\max |b^G - j^G| \leq \max |b^G - w^G|$, where j^G is the expected level of genetic variance in status quo landscape), then the loss of the patch may move the metapopulation farther away from baseline than was observed under status quo conditions. Changes in spatial distribution of genetic variance are not currently used to define a take. However, habitat trades that drive genetic variance farther away from baseline may exacerbate effects of habitat loss and fragmentation. Accordingly, we recommend that trades among genetic services (e.g., $dLSY^{Hs}$ for $dLSY^{Dst}$) should not be allowed. Genetic variance within and among subpopulations both contribute to evolution in but different ways (i.e., natural selection at individual v. group level), and we are uncertain of the long-term effects of such tradeoffs (Moritz 1994). Under certain circumstances, for example moving D_{ST} farther away from baseline to alleviate inbreeding depression (increase H_S), these tradeoffs may be advised. LEA provides a framework for managing these long-term and short-term goals.

Rule #3. Private investment in natural capital leads to marketable credits, while public investment in natural capital leads to species recovery. The trading of habitat patches among private parties using LEA minimizes the effect of habitat loss and fragmentation. Private landowners are only legally responsible for not increasing the probability of extinction or otherwise causing a take relative to the status quo of the population (i.e., increasing the current rate of depreciation) (Harding and others 2001). However, purchase of credits by public agencies or NGOs for reasons other than mitigating a take represent a net investment in natural capital leading to habitat defragmentation. This would be a cost-effective approach to promote species recovery.

Rule #4. Begin discounting of service flows from the time the trade occurs. Our goal is to meet the preferences of the current generation without sacrificing the welfare of future generations. Each time a trade is made the credit will be estimated with the current estimate of that generation's rate of positive time preference. The welfare of future generations is protected at a minimum level by preventing trades that cause a take or increase jeopardy.

Rule #5. Monitoring data must be continually used to update the SEPM, so that conservation banking helps reduce uncertainty. Conservation banking provides a financial incentive for reducing uncertainty. Conservation banking guidance (USFWS

2003) indicates that the size of the endowment used to fund perpetual management should be proportional to the risk the banker is accepting and the cost of maintaining that account should be incrementally offset by the sale of each credit. If uncertainty regarding an endangered species' natural history were too great, conservation banking should be cost-prohibitive. Increasing OC-P would provide economic drivers for collecting data to reduce uncertainty, facilitating market entry.

SEPMs have been heavily criticized because detailed datasets are required to parameterize the models (Beissinger 2002). Beissinger (2002) observed that when large opportunity costs are associated with species protection (OC-P), analysis of management scenarios using detailed datasets often result. Examples include models for the northern spotted owl (Lamberson and others 1994), California gnatcatcher (Akcakaya and Atwood 1997), Florida scrub jay (Breininger and others 1999), red cockaded woodpecker (Letcher and others 1998), and Bachman's sparrow (Liu and others 1995). The ever increasing economic value of real estate and human population growth (Liu and others 2003), suggests that the OC-P will increase in the future for most species. In other words, despite the uncertainties associated with SEPM, modeling should become financially feasible in the future for more species as the economic value of land increases.

Differences in mitigation costs result from the influence of landscape spatial structure on metapopulation services (i.e., patches differ in influence on OC-D) and from differences in land values as determined by traditional markets (i.e., OC-P; Ando and others 1998). The mitigation costs for externalities (price of dLSY for three metapopulation services - N, H_S, D_{ST}) relative to the expected financial benefit of economic growth ultimately determines the spatial allocation of habitat (Figures 1 and 2).

If we assume all participants are price takers (i.e., the banker will try to maximize profit and purchaser will minimize mitigation costs) and share perfect information, the market would prevent the spatial allocation of habitat from moving farther away from the allocation of habitat that permitted adaptive evolution. Bank patches strategically located will be able to sell many credits. Patches that contribute greatly to metapopulation size and genetic variance will cause a greater withdrawal from the bank if lost to development. LEA provides an effective accounting system for conservation banking while linking regional ecological effects to local economic decisions (Figure 1). Trading habitat credits with LEA will distribute the cost to comply with the ESA more evenly among private landowners (Olson and others 1993).

Discussion

We have introduced a novel approach for calculating biodiversity credits that are sensitive to landscape spatial structure, a species' natural history, existing service levels, and society's rate of positive time preference (i.e., discount rate). The price of the credit represents the in-kind replacement value for three metapopulation services. Purchase of a credit includes the influence of sprawl on biodiversity at the regional scale, such that a local economic decision will only proceed if the price of the biodiversity credit is sufficiently less than the expected net economic benefit of destroying habitat (Figure 1). We have summarized information so that a private landowner's decision reflects the tradeoff between OC-P and mitigation costs to prevent loss of conservation value measured at the regional scale (OC-D).

Whenever off-site mitigation compensates for habitat loss, management decisions change the spatial structure of the landscape (Huxel and Hastings 1999). Incorporating spatial biological processes into decision making may indicate tradeoffs between habitat area and connectivity (Lamberson and others 1994; Cox and Engstrom 2001). These tradeoffs may find habitat allocations that protect endangered species without preventing economic growth. This paper provides a conservative approach for assessing these tradeoffs while providing an economic incentive for greater data collection and analysis.

Usually, the number of credits available in a conservation bank are based on habitat suitability indices, size of habitat, and/or number of individuals observed within the patch (USFWS 2003). This approach ignores the importance of spatial structure. Calculation of conservation credits for a bank for red legged frog in California included habitat connectivity, habitat shape, and habitat location criteria (USFWS 2001). These indices are based on generalizations relating the natural history of vertebrate organisms to landscape structure (i.e., bigger habitat with less edge and more connectivity is always best). However, we lack a theory describing the effects of habitat loss and fragmentation on populations (Fahrig 2003). Further, evolutionary theory and empirical data indicate that some isolation between subpopulations plays an important role in adaptive evolution (Lesica and Allendorf 1995). The effects of habitat loss and fragmentation vary based on species- and landscape-history. Thus, no prior generalizable approach for calculating spatially-explicit credits has been derived.

The lack of theory and presence of uncertainty has not stopped economic decisions that change the landscape spatial structure (Wilcove and others 1998; Smallwood and others 1999; Harding and others 2001). In lieu of analytical models, we propose a solution that integrates case-specific landscape simulation models with resource-based compensation. For some endangered species use of the best available science and data (Smallwood and others 1999) entails constructing a SEPM so that demography, behavior, and genetics can be related to landscape structure. Simulation modeling may reveal critical landscape components not identified by ignoring interactions between natural history and spatial structure. LEA could be used to justify protecting and restoring these critical landscape components and directing sprawl around these areas.

The Federal government requires monitoring of conservation values in a bank, because ecosystems will not be static over time (USFWS 2003) suggesting that conservation banking may benefit from Adaptive Management. Adaptive Management is a method of incorporating the role of uncertainty in decision-making by treating decisions as hypotheses regarding the system’s response to management actions (Walters 1986). Monitoring data are used to test the validity of alternative hypotheses given existing knowledge of the system. Using monitoring data to continually improve our understanding of the system improves future decisions. LEA would benefit from SEPMs incorporating different hypotheses relating genetic variance to demographic parameters. However, the curse of dimensionality (Ludwig and Walters 2002) and difficulty of comparing replicate metapopulations (Dunning 2002) are significant barriers to applying Adaptive Management to conservation banking at the landscape scale.

Previous authors have recognized the need for a tool like LEA. Kennedy and others (1996) outlined an incentive system to permit trading of endangered species habitat. These authors recognized that demographic and genetic characteristics would be important measures of conservation value upon which the incentive system would be based, but provided no mechanistic approach for meeting this goal. The NRC emphasized the need for explicit decision making tools that incorporate the influence of uncertainty when making tradeoffs between economic and conservation values under ESA (NRC 1995). NRC (1995) also recommended using a landscape perspective when making management decisions despite the scientific uncertainties associated with the large geographic scale of analysis. Similarly, an NRC study of wetland mitigation banking stressed the need to site banks within a landscape so that trading of credits prevents the loss of wetland function necessary for ecological sustainability (NRC 2001). Wetland scientists may find LEA useful for meeting this goal.

Conclusion

Ecological goods and services are often not given adequate consideration during decision making because we lack markets to value them. A market for trading habitat, as provided by conservation banking, could serve as a market for trading ecological services (Daily and Ellison 2003) such as abundance and genetic variance of an endangered species. Applying a landscape perspective to conservation banking also provides a means for conservationists to justify the protection of real estate that is considered valuable by the traditional market. Protected lands have historically been low in economic value, or lands provided by individuals with a strong conservation ethic (i.e., opportunistic protection). Strategic methods of habitat protection sensitive to economic behavior will be critical to the success of biodiversity conservation. Strategic decisions incorporating economic, ecological, and evolutionary components can be made by comparing development scenarios with LEA. We can now apply an evolutionary perspective to describe the biophysical implications of economic growth.

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CHAPTER 2

TRADING RED-COCKADED WOODPECKER HABITAT AT THE LANDSCAPE-SCALE WITH LANDSCAPE EQUIVALENCY ANALYSIS

Abstract

Tradable permits for endangered species habitat is one form of mitigation that is increasingly being used to resolve conflicts between economic growth and biodiversity conservation. Conservation banking has been proposed as a method to consolidate mitigation efforts to minimize and reverse the effects of habitat fragmentation. We have developed Landscape Equivalency Analysis (LEA) as a generalizable, landscape-scale accounting system to organize these trades, which allows tradeoffs between habitat area and connectivity without exacerbating the effects of habitat fragmentation. LEA estimates tradable credits based on three metapopulation services, total abundance, average expected heterozygosity within breeding groups, and average genetic divergence among breeding groups. LEA credits capture changes in functional connectivity and represent a scientifically defensible habitat trading system. In this study, we applied LEA to the red-cockaded woodpecker by increasing the spatial realism of the spatially-explicit population model (SEPM) most widely used for management. We demonstrated that landscape indices and probability of population persistence do not necessarily provide the best estimates of the ecological equivalence of habitats traded.

We show that tradable permit markets and the sustainability of the species would benefit from a mechanistic understanding of the relationship between landscape pattern and metapopulation processes provided by LEA. Compared to the current assumptions regarding dispersal used for landscape-management, incorporating an alternative dispersal hypothesis, supported by empirical data, increased the conservation value of a bank.

Introduction

Conflicts between economic growth and endangered species habitat protection have benefited from a tradable permit system commonly referred to as conservation banking (Fox and Nino-Murcia, 2005). A bank is a parcel of land protected in perpetuity, through a Conservation Easement, based on its conservation values. Purchase of credits from a bank facilitates issuance of an Incidental Take Permit, allowing landowners to pursue alternative uses of endangered species habitat (USFWS, 2003a). The tradable permit market provides a mechanism to incorporate some of the social value of habitat protection into a landowner's decision to develop or protect habitat (Tietenberg, 2004).

The financial value of the credits is determined by the market and represents the replacement costs of endangered species habitat. However, a measure of conservation value is needed to scale the exchange of credits to ensure that an ecologically equivalent trade in habitat is made (Brown and Shogren, 1998). The first comprehensive review of the conservation banking industry observed that the number of credits was based on habitat area alone for 91% of banks, while the remaining banks incorporated the number of breeding pairs into their credit estimate (Fox and Nino-Murcia, 2005). Fox and Nino-Murcia (2005) found that 94% of banks were preservation banks, or lands already containing the species prior to initiating the bank. Therefore, unless species are threatened by loss of natural disturbance regimes, preservation banks result in a net loss of habitat (Fox and Nino-Murcia, 2005; Wilcove and Lee, 2004). Fox and Nino-Murcia (2005) observed that only 44% of banks were adjacent to other protected lands, suggesting that most banks are isolated, remnant populations. Despite the expressed intention of conservation banking to reduce habitat fragmentation (USFWS, 2003a), currently, bankers lack incentives to reduce the effects of habitat fragmentation through strategic habitat restoration.

The preference for preservation banks over restoration banks resulted from the uncertainty regarding the colonization and quality of restored habitat (Bonnie, 1999). Directing the exchange of habitat for already small and isolated populations when uncertain regarding the species natural history is a daunting task. The USFWS has proposed the use of landscape indices when valuing credits for the California red legged frog to minimize the effects of fragmentation (USFWS, 2001). While such approaches represent a large step forward for the banking community, we caution the uncritical use of these indices. Landscape indices capture the changes in geometric patterns of habitat, but are not necessarily representative of important biological processes (Li and Wu, 2004). Rather, landscape indices allow us to ignore the uncertainty regarding the influence of landscape pattern on the behavior and demography of at-risk species. While landscape indices may be useful for establishing correlative relationships between geometric patterns and biological patterns, they should be used as an initial step toward understanding the underlying biological process (Li and Wu, 2004) and should not serve as the basis of decisions whose ultimate goal is to sustain biological processes.

Many endangered species are metapopulations, exchanging genes and individuals over many local populations to achieve regional persistence (Homes and Semmens, 2004). Therefore, banks could be located to mitigate the effects of altered migration patterns among local populations (USFWS, 2003a). This would require estimates of an organism's vagility and how the landscape mosaic affects dispersal patterns (Wiens, 1997). Conservation banking guidance suggests that the size of the endowment used to fund perpetual management of the habitat should be proportional to the risk of local extinction to offset the costs of corrective action if the initial management plan was insufficient to prevent a take (USFWS, 2003a). Similarly, the cost of credits should be more expensive when uncertainty regarding probability of local extinction is greater to offset the larger endowment required for management (USFWS, 2003a). For banks to meet these criteria, alternative models of hypothesized relationships between landscape pattern and a species' behavior and demography are needed to estimate the equivalency of habitats exchanged and uncertainty associated with the trade.

Failure to incorporate metapopulation dynamics and uncertainty associated with habitat trades reduces the economic efficiency of the tradable permit market. Metapopulations are a network of interacting local populations, so actions of self-interested landowners can have consequences for populations found on other properties. If we recognize that endangered species provide ecological services (Loomis and White, 1996) the loss of these services due to changes in the spatial association of habitat represents a network externality (Parkhurst et al., 2002). We argue that the conservation value of credits in a bank should be based on the marginal changes in network externalities caused by a trade. Tradable permit systems for endangered metapopulations could then lead to an economically efficient allocation of protected habitat if the economic benefit of developing habitat were more than the cost to prevent negative network externalities through off-site mitigation (Bruggeman et al., in press).

Ideally, estimates of network externalities should be based on changes in population persistence (Montgomery et al., 1994). However, we often lack empirical relationships to describe how changes in the correlation of genes within and among local populations affect viability (i.e., inbreeding and outbreeding depression) (Hedrick, 2002; Dudash and Fenster 2000). The isolation of local populations that result from habitat fragmentation may increase the mating among closely related individuals, or inbreeding. Recent studies have demonstrated that metapopulations may be particularly vulnerable to loss of fitness due to inbreeding owing to a larger genetic load (i.e., deleterious recessive mutations) (Higgins and Lynch, 2001; Saccheri et al., 1998). Therefore, unless estimates of probability of persistence include accurate models of dispersal behaviors and demographic-genetic feedbacks, it is likely that important network externalities resulting from a habitat trade would be missed.

Recently, Bruggeman et al. (in press) proposed Landscape Equivalency Analysis (LEA) as a method to calculate the conservation value of tradable credits for endangered species habitat to minimize and reverse the negative effects of habitat fragmentation. LEA estimates the equivalency of habitat patches traded in a fragmented landscape based on changes in three metapopulation services, 1) abundance and genetic variance 2) within and 3) among local populations, measured at the regional scale. This approach forces us to recognize the uncertainty regarding landscape processes and defines the conservation value of habitat patches based on their contribution to functional connectivity (i.e., exchange of individuals; Goodwin, 2003).

The goal of LEA is to account for habitat fragmentation by directing the trade of endangered species habitat toward the provision of the metapopulation 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 value of metapopulation services that are differentially affected by changes in habitat area and connectivity

(Bruggeman et al., in press). Discounted changes in metapopulation services relative to services observed at the population recovery goal provide an estimate of the change in network externalities due to the trade. LEA provides a link between the regional ecological effects and local economic decisions by scaling trades based on changes in metapopulation services. Therefore, LEA may serve as an ecological-economic tool for directing development around critical landscape components for endangered species.

This paper is a case study for the application of LEA to a red-cockaded woodpecker (*Picoides borealis*; RCW) population inhabiting a hypothetical landscape. The RCW was chosen because much is known about its behavior and demography and the species has benefited from novel partnerships with private landowners. First, we describe the natural history and management of RCWs. Second, we describe a spatially-explicit population model (SEPM) that integrates previous modeling efforts with alternative hypotheses regarding the influence of landscape pattern on RCW population dynamics. Third, we use the SEPM to estimate LEA credits exchanged in two different habitat trades, contrasting LEA credits with estimates of conservation value based on probability of persistence, habitat area, and habitat connectivity. We show that tradable permit markets and the sustainability of the species would benefit from a greater understanding of the relationship between landscape pattern and metapopulation processes provided by LEA.

Red Cockaded Woodpeckers

RCW are a monogamous, cooperative breeding species endemic to old growth longleaf pine forests in the southeastern US (Conner et al., 2001). The pre-settlement range of longleaf pine forests included the lower Atlantic and Gulf Coastal Plains, but have been reduced by over 97% (Frost, 1993). The loss of longleaf pine habitat resulted in an approximately 99.5% reduction in the number of RCWs (Costa, 2004). The RCW has been listed as endangered since 1968 under the Endangered Species Preservation Act (Jackson, 2004).

Private landowners have made important contributions toward recovery of RCWs (Costa, 2004). The USFWS has established cooperative partnerships with 49% of private landowners containing RCW groups for the active management of habitat (Costa, 2004). Safe Harbor Agreements are one such cooperative agreement that encourage landowners to manage their property for endangered species (Bonnie, 1999). Landowners are allowed to cease active management of habitat knowing that Endangered Species Act's (ESA; USFWS, 1988) take prohibition will not be enforced for any additional occupancy by endangered species provided by their actions. Conservation banks have already been established for RCWs. These are typically lands protected with Safe Harbor Agreements that are moving toward banking agreements to ensure long term management of habitat (Fox and Nino-Murcia, 2005; R. Costa, USFWS, personal communication).

RCWs require fire-maintained ecosystems. James et al. (2001) observed that fire suppression and encroachment of hardwoods in the understory decreased the probability of habitat occupancy. The number of individuals within a breeding group has been shown to vary with the size distribution and density of longleaf pine, the height and composition of the understory, and number of cavity trees (James et al., 2001; Walters et al., 2002b). Each RCW breeding group defends a breeding territory containing a cluster of older pines (>50 years) with cavities used for nesting and roosting (Conner et al., 2001). Cavity excavation occurs in live pines, is estimated to take 6-10 years, and is often performed by a single individual. Cavity trees are the critical limiting resource for the population.

RCW breeding groups consist of a reproductively active male and female, nestlings or fledglings, and, occasionally, helpers who are usually full or half-sibs to the fledglings (Figure 1) (Walters et al., 1988). Floaters of both sexes are also present in the region, which move continuously seeking a breeding vacancy in a territory (Walters et al., 1988).

Helpers play a critical role in population dynamics by participating in the defense of the territories and feeding of nestlings, but make no direct reproductive contribution to the group (Conner et al., 2001). Walters et al. (1988) observed that females remain as helpers on their natal territory only 1% of the time, usually dispersing to become floaters. In contrast, males stay as helpers 81% of the time (Letcher et al., 1998). Male's may prefer to stay as helpers to gain access to breeding territories, either their natal territory upon the death of the breeding male or an adjacent territory (Walters et al., 1992). Males that inherit a territory by staying as helpers are estimated to have greater fitness, even without the fitness benefits of kin selection, than males that disperse to a different territory (Walters et al., 1992). When a helper takes over a territory after the male's death, over 90% of the time the adult female disperses to avoid inbreeding (Daniels and Walters, 2000).

In addition to vegetation characteristics within a patch, the spatial associations of habitat patches have also been shown to affect RCW populations. The isolation of RCW breeding groups and adjacency of habitat to non-forested areas has been observed to decrease the probability of habitat occupancy (Connor and Rudolph, 1991; Thomlinson, 1995; Cox et al., 2001). Conner and Rudolph (1991) hypothesized that habitat loss and fragmentation reduces the probability that dispersing birds find a mate.

Landscape Heterogeneity and RCWs

Several authors report on a SEPM for RCWs that was constructed from 15 years of demographic and behavioral observations in a population of over 200 breeding groups of marked birds in the Sandhills Region of North Carolina (Letcher et al., 1998; Daniels et al., 2000; Schiegg et al., 2002; Walters et al., 2002a). The hypothetical landscapes used in these studies contained RCW territories separated by non-habitat, the distribution of which did not affect the dispersal behaviors of individuals. Based on behavioral observations in the Sandhills Region of North Carolina, Letcher's SEPM assumed that birds pick a direction at random and disperse in a straight line.

Letcher et al. (1998) found that the degree of territory clumping can have a dramatic effect on population persistence at small population sizes (≤ 100 territories). Daniels et al. (2000) observed that moderate levels of territory clumping and small population size (25-49 territories) resulted in a substantial accumulation of inbreeding, but the addition of two or more migrants per year kept the coefficient of kinship (f, probability two alleles chosen at random from separate individuals are identical by descent) below 0.1. Schiegg et al. (2002) concluded that habitat fragmentation reduced the probability of locating mates, and at small population sizes helpers contributed disproportionately to male breeder recruitment when territories were clumped. Walters et al. (2002a) incorporated the influence of environmental stochasticity and levels of territorial clumping at different spatial extents. Walters et al. (2002a) concluded that small, highly clumped populations can be expected to be relatively stable because environmental stochasticity has only minor effects on occupancy of territories owing to the recruitment of helpers as breeders. Results from Letcher's SEPM suggest that population recovery may benefit from protecting smaller populations that are capable of exchanging migrants (Walters et al., 2002a).

However, we are still uncertain about how land use patterns affect RCW dispersal behaviors (J. Walters, Virginia Polytechnic Institute and State University, personal communication). Some researchers have suggested that forest stands not suitable for nesting or roosting, but suitable for foraging represent conditions favorable to movement. Based on observations in Florida, Azevedo et al. (2000) indicated that pine stands older than 16 years may be suitable for movement. Connor and Rudolph (1991) observed that habitat loss and fragmentation forced birds to travel through occupied territories to gain access to foraging habitat in eastern Texas. Results from Thomlinson's (1995) study in eastern Texas corroborated the idea that RCW show preference for forested areas during movement. Assuming that birds preferentially disperse through pine stands, including second growth, Thomlinson (1995) found that occupied territories were more often connected to other occupied territories by pine forests, and pine forests were more often absent between occupied and unoccupied territories. It has been observed that non-forested areas, or gaps, act as barriers to movement for many small to medium-sized forest bird species (Belisle and Desrochers, 2002).

RCWs will disperse long distances, but rarely (i.e., female maximum = 31.5 km) (Walters et al., 1988). As a result, it is likely that they will cross non-forested areas when covering great distances, but only if no breeding vacancies can be found near their natal territory (USFWS, 2003b). Daniels and Walters (2000) observed that the clustering of closely related RCW males around natal territories due to delayed male dispersal (i.e., helping behaviors) does not increase female dispersal distance, which would reduce the probability of consanguineous mating. Females were observed to only migrate an average 2.8 territories away from natal sites. Short dispersal distances resulted in mating between closely related individuals ($f \geq 0.125$), which produced 44% fewer offspring than unrelated pairs ($f=0$, relative to the rooting of the pedigree in 1980).

This suggests that costs of distant female dispersal are greater than costs from inbreeding depression (Daniels and Walters 2000). Costs of long-distance dispersal through an inhospitable matrix include loss of foraging opportunities and increased risk of predation (Belisle and Desrochers, 2002; Zollner and Lima, 1999). As forest cover is reduced and populations become smaller and more isolated, costs of both short-distant and long-distant dispersal will increase. Recovery of smaller populations threatened by habitat fragmentation will require understanding how land use affects dispersal behaviors of RCWs (Ruckelshaus et al., 1997; South, 1999).

RCW SEPM for the Application of LEA

We developed an RCW SEPM based on Letcher's models, but with modifications to increase spatial realism. We incorporated results from a recent empirical study which estimated the demographic and spatial factors affecting male natal dispersal (Pasinelli and Walters, 2002). We used the individually-based model to compare two alternative models of dispersal behaviors.

Landscape Composition

The model was constructed in MatLab 7 and was constrained to a square grid. Each cell was designated as either old growth habitat, restored habitat, matrix, or non-forested. Old growth habitat cells are assumed to be actively managed for RCW by applying yearly burns and maintaining 3-4 cavities per territory. We assume that matrix areas are second growth pine forests that can be restored for RCW habitat by thinning the hardwood understory, establishing cavities in larger pines, and establishing a yearly fire regime (Walters et al., 2002b). The average RCW territory size observed in old-growth longleaf pine communities is 47-ha (Engstrom and Sanders, 1997; Walters et al., 2002b). Landscapes representing 80,000-ha were generated with 1600 cells each representing 50-ha. A 5-cell buffer zone was added around the central 1600-cell area. The buffer zone consisted of only matrix or non-forested areas, but no habitat. Addition of the buffer zone removed edge effects during fledgling prospecting behaviors (see below) and provided an opportunity for birds that float away from the central habitat areas to wander back before being lost as an emigrant (Zollner and Lima, 1999), depending on which dispersal rules are used.

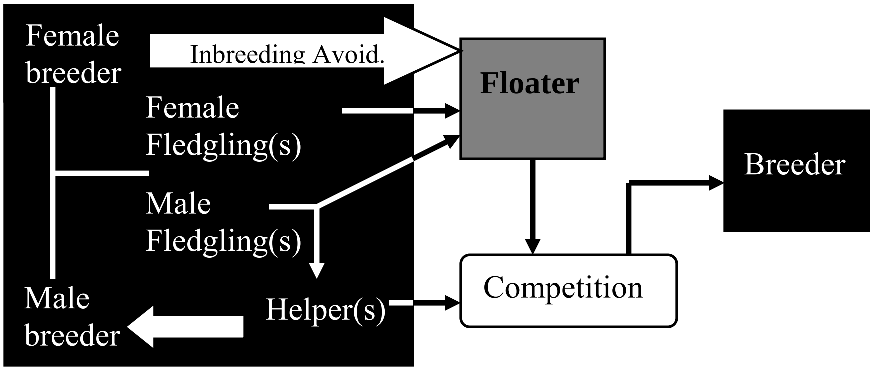


Figure 1. Breeding group structure and demographic transitions for the red-cockaded woodpecker. Black boxes denote breeding territories and the grey box denotes the matrix crossed during floating behaviors. Over 90% of time when a helper inherits his father's territory, the female breeder disperses to avoid inbreeding (Daniels and Walters, 2000).

Initial Conditions

We assumed that all old growth habitat cells start with a breeding pair. The age of each breeder was randomly chosen from a normal distribution with mean of 4 and variance of 1. Four was chosen as the average because it equals the generation length for RCWs (Reed et al., 1988). An infinite alleles model of genetic variance was used, assigning two unique alleles to one locus for each breeder (Lacy and Lindenmayer, 1995). Assuming Mendelian inheritance, their offspring had an equal probability of inheriting each of the two alleles. By assuming that every individual is heterozygous and contains two unique alleles (i.e., total alleles = 2 x number of breeders in the founding population), we can examine how the processes of genetic drift and gene flow interact in a spatially subdivided population. The average number of helpers observed in old-growth longleaf pine habitat, based on two years of observations, were 1 and 1.6 helpers per territory (Engstrom and Sanders, 1997). We randomly selected half of the territories for the addition of 2 helpers. It was assumed that the helper was one-year old.

Model Flow

The model is both age- and stage-structured, uses a seasonal time step (3 months per step), and assumes that biological processes proceed in the following order: reproduction (season 1 only), mortality, natal dispersal, territorial competition, and then migration.

Reproduction

The equations used to model reproduction were derived by Letcher et al. (1998). Variation in reproduction was modeled by drawing two u[0,1] random numbers and comparing them to probabilities of breeding and of producing eggs respectively. The probability that a pair attempts to breed is:

$$P(nest\_attempt) = 1 - e^{-\alpha Age_f}$$

Where Age_f is the age of the female breeder. All model parameters are defined in Table 1. If an attempt was made, the probability of nest success was generated by a logit function:

$$P(nest\_success) = \frac{e^{b_0 + b_1 e^{-Age_m} + b_2 e^{-Age_f} + b_3 e^{-HP}}}{1 + e^{b_0 + b_1 e^{-Age_m} + b_2 e^{-Age_f} + b_3 e^{-HP}}},$$

where Age_m is the age of the male breeder and HP is the number of helpers in the territory. If the nest is not successful, birds renest with probability 0.319, and if the second nest is not successful, no subsequent attempts are made for that year (Letcher et al., 1998). Fecundity has been shown to vary based on the ages of the male and female breeder and the number of helpers (Letcher et al., 1998). If the nest is successful the average number of fledglings (FL) was estimated as:

$$FL = b_4 + b_5 e^{-Age_m} + b_6 e^{-Age_f} + b_7 HP$$

The actual number of fledglings was modeled as a normally distributed random variable with mean = FL and standard deviation = 0.05, estimated from the Sandhills population (Letcher et al., 1998). A 50/50 progeny sex ratio was used (Reed et al., 1993).

Table 1. 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	2.0657	Letcher et al., 1998
b_5 Mean fledgling male's effect	-1.18634	Letcher et al., 1998
b_6 Mean fledgling female's effect	-1.03431	Letcher et al., 1998
b_7 Mean fledgling helper's effect	0.28401	Letcher et al., 1998
Seasonal probability of survival – Male Fledgling	0.841	Letcher et al., 1998
Seasonal probability of survival – Helper	0.946	Letcher et al., 1998
Seasonal probability of survival – Male Breeder	0.937	Letcher et al., 1998
Seasonal probability of survival – Male Floater	0.887	Letcher et al., 1998
Seasonal probability of survival – Solitary Male	0.901	Letcher et al., 1998
Seasonal probability of survival – Female Fledgling	0.805	Letcher et al., 1998
Seasonal probability of survival – Female Breeder	0.918	Letcher et al., 1998
Seasonal probability of survival – Female Floater	0.887	Letcher et al., 1998
Maximum age	17	Conner et al., 2001
d_0 Male natal dispersal intercept	-1.930	Pasinelli and Walters, 2002
d_1 Male natal dispersal number of male fledglings	0.700	Pasinelli and Walters, 2002
d_2 Male natal dispersal territory quality within 1 km	-0.399	Pasinelli and Walters, 2002
d_3 Male natal dispersal quality of natal territory	-0.082	Pasinelli and Walters, 2002
d_4 Male natal dispersal vacancies within 3.5 km	0.044	Pasinelli and Walters, 2002
Maximum number of helpers	4	Pasinelli and Walters, 2002
Group size high habitat quality – old growth	3.6	Engstrom and Sanders, 1997
Group size lower habitat quality – secondary growth	2.6	James et al., 2001
Search radius of birds	3.5 km [5 cells]	Pasinelli and Walters, 2002
Female floater & Male natal dispersal speed (per season)	4.9 km [7 cells]	Letcher et al., 1998
Male floater dispersal speed (per season)	2.1 km [3 cells]	Letcher et al., 1998

The probability an individual survives into the next season is determined based on stage-specific mortality estimates derived by Letcher et al. (1998) (Table 1). The maximum age recorded for RCW is 17 years (Conner et al., 2001), so birds were not allowed to live past this age.

Natal Dispersal

The probability of an individual's transition among life stages depends on the interaction between demography, behavior, and landscape spatial structure. The transition from fledgling to floater has been observed to occur in seasons 2, 3, or 4 for both males and females (Conner et al., 2001). We assigned an equal probability (0.33) that an individual will depart during one of these seasons (Letcher et al., 1998). The model assumed that all female fledglings surviving the first year became floaters or breeders, but never helpers.

A recent study examined the demographic and environmental factors mediating male natal dispersal using monitoring data from populations in the Sandhills Region, Camp Lejeune Marine Base, and Croatan National Forest in North Carolina (Pasinelli and Walters, 2002). Multiple logistic regression with backward elimination (α=0.05) was used to simultaneously examine the influence of several factors on the probability of male natal dispersal. The probability of male natal dispersal was positively associated with the number of males in a brood but not the number of helpers already present in the territory, suggesting that only within brood competition plays a role. Relative nestling mass, indicative of dominance relationships within broods, was negatively associated with the probability of dispersal. The probability of dispersal was negatively related to the quality of natal territory and quality of territories within 1 km of the natal territory. Probability of dispersal was positively associated with number of vacant territories within 3.5 km. This suggests that fledglings acquire knowledge of habitat availability prior to deciding to leave, referred to as prospecting behaviors.

Incorporating the results of Pasinelli and Walters (2002) into our SEPM was straightforward for number of male fledglings within a brood and number of vacant territories within 3.5 km (5 cells, intercentroid distance). Relative nestling mass was excluded because no estimates for the variation in nestling mass within broods are available. Based on a Spearman rank correlation, relative nestling mass was not found to be correlated with any of the other independent variables (Pasinelli and Walters, 2002), so excluding this variable should not significantly bias model results. For territory quality, we assumed that all old growth remnants were of equal quality, estimated by average group size of 3.6 (Engstrom and Sanders, 1997). We assumed that second growth pine stands restored for RCWs are perceived by the birds has having an average group size of 2.6 (i.e., lower habitat quality), based on observations made in restored second growth stands at the Apalachicola National Forest (James et al., 2001). Therefore, the probability of male natal dispersal ($P[D_{m,nat}]$) can be estimated as:

$$P\left[D_{m,nat}\right] = \frac{e^{d_0 + d_1 FL_m + d_2 T_{1km} + d_3 T_{nat} + d_4 T_{vac3km}}}{1 + e^{d_0 + d_1 FL_m + d_2 T_{ikm} + d_3 T_{nat} + d_4 T_{vac3km}}}$$

where T_{1km} is the number of territories in old growth pine within 1 km of the natal territory, T_{nat} is the quality of the natal territory, and T_{vac3km} is the number of vacant territories within 3.5 km. When this equation was incorporated into our model, unnaturally large number of helpers were retained within a territory (i.e., up to 10) when density of old growth longleaf pine was high in the landscape. In the Sandhills Region only 30% of groups contained at least one helper and 5% of groups contained more than one helper with 3 being the maximum number of helpers (Walters et al., 1988). Even though Pasinelli and Walters (2002) found that number of adults within a group did not affect the probability of male natal dispersal, they indicated that the maximum number of helpers observed in any RCW group is 4. The probability of male natal dispersal was calculated with the equation above when less than 3 helpers are present but set to unity otherwise, which created a maximum of 4 helpers when habitat density was high.

Territory Competition

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 perceptual range the model uses assumptions thought plausible by Letcher et al. (1998), who assumed that all fledglings, helpers, floaters, and solitary males can compete for breeding vacancies within 3.5 km of their current location. We assumed that birds are able to detect vacancies within this area and are willing to cross non-forested gaps to acquire a breeding vacancy (e.g., Norris and Stutchbury 2001). This assumption is plausible for fledglings and helpers given their hypothesized prospecting behaviors (Pasinelli and Walters, 2002). However, further research is required to determine if floaters and solitary males have an equivalent perceptual range. Some researchers believe that female floaters can detect distant solitary males due to the drumming behaviors on pine trees often observed in solitary males (Conner et al., 2001).

Male-Male Competition

First, we assume that all helpers will preferentially inherit their natal territory upon the death of the breeding male. If more than one helper is present in a territory when the male breeder dies, we assume the oldest helper wins the territory (Letcher et al., 1998). When a helper inherits his natal territory, the female breeder becomes a floater to avoid incest. If the male breeder dies and no helpers are present, it has been observed that 83% of the time the female breeder remains in the territory and acquires a new mate (Daniels and Walters, 2000). It is assumed that widowed females remain in territories until a new male can be established (Letcher et al., 1998). Next competition for widowed female breeders occurs. The model assumes that helpers, male floaters, and solitary male breeders within 3.5 km of the widowed female will compete. The closest male wins the breeding vacancy, if equidistant the oldest male wins (Letcher et al., 1998). Third, competition for vacant territories occurs within 3.5 km of all helpers and male floaters in the area, applying the same rules stated above.

Female-Female Competition

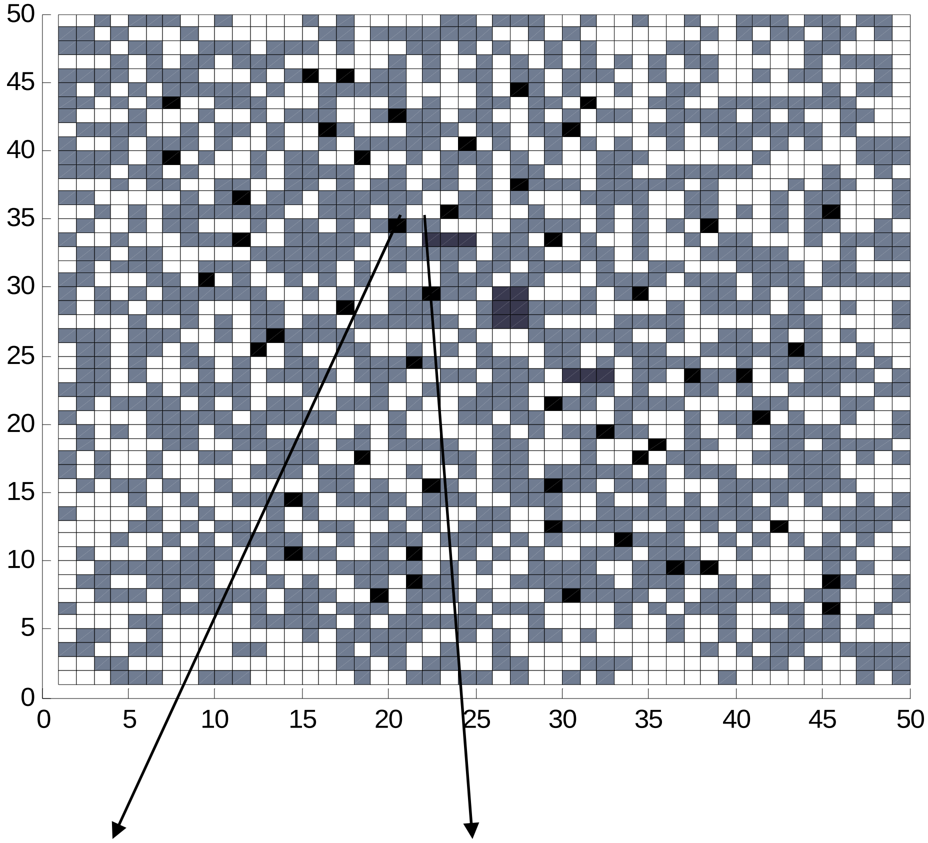
We assume that females only compete for territories containing solitary males and do not defend territories as solitary females (Lether et al., 1998). The pool of female competitors includes all fledglings, displaced female breeders due to inbreeding avoidance, and floaters within 3.5 km of the solitary male. The oldest female wins the vacancy, following Letcher et al. (1998). If there is more than one female of that maximum age, the winner is selected at random.

Floating Behaviors

After seasonal competition is completed, floating behaviors are modeled. Based on Pasinelli and Walters (2002), we assume that fledglings are aware of the forest structure within a 3.5 km radius of their natal territory, which will be referred to as their natal neighborhood. Therefore, we assume that birds choose their initial direction of travel based on the density of habitat at the edge of their natal or, for displaced female breeders, breeding neighborhood. If no habitat was found at the 3.5 km perimeter, the birds will orient to the greatest density of secondary growth. This differs from Letcher et al., (1998) and subsequent studies which assumed that birds choose their direction of dispersal randomly. We assume that birds then begin making directional choices based on either forest structure (Connor and Rudolph, 1991), the tendency to disperse in a straight line (Letcher et al., 1998), or a combination of both factors.

Dispersal speed for all female floaters averaged 4.8 km per season and for first year male floaters (natal dispersal) was estimated at 5.1 km per season (Letcher et al., 1998). Our model assumes that all females and first year male floaters disperse 4.9 km per season, or 7 cells. Older male floaters on average moved 2.3 km per season (Letcher et al., 1998). We assumed that male floaters move 2.12 km per season, or 3 cells. Each floater is allowed to compete for territorial vacancies in cells adjacent to its current location before taking the next step.

Assuming no vacancies exist, each of the 8 adjacent cells is assigned a probability of occupancy based on plausible dispersal rules (Zollner and Lima, 1999). We assigned



Direction-based

	20	21	22
35	0.08	0.02	0
34	0.2	0	0.02
33	0.4	0.2	0.08

Forest-based

	20	21	22
35	2	3	3
34	1	2	2
33	2	3	2R

	20	21	22
35	0.08	0.02	0.02
34	0.4	0.08	0.08
33	0.08	0.02	0.2

Figure 2. Above: a hypothetical landscape containing old growth longleaf pine (black cells), restored second growth forest for RCWs (dark grey cells near the center), second growth forest (light grey cells), and non-forested (white cells). Each cell represents 50-ha. Below: assigning preference to cells adjacent to a bird's location (21, 34) given direction-based and forest-based dispersal rules. Under direction-based, the vector of movement was toward the grid origin (0, 0) or southwest. Therefore, the bird was found in cell (22, 35) at t-1, this indicates that the bird will likely move to (20, 33) at t+1. At right, forest structure in the center 3x3 matrix is denoted by #1) habitat in old growth longleaf pine, #2R) habitat in restored second growth forests, #2) second growth forest, and #3) non-forested areas. The 3x3 matrix to the far right translates this forest structure into preferences for occupancy, where cell (20, 34) is the most attractive cell. Note, this landscape will be used as the mitigation landscape in later analysis, in which the dark grey cells in the center represent the conservation bank.

four levels of preference to adjacent cells in which the first level was twice as attractive as the second, the second was 2.5 times as attractive as the third, and the third was 4 times as attractive as the fourth (Figure 2). The level of preference assigned to each cell was based on two contrasting sets of rules for dispersal: direction-based versus forest-based. If the birds show preference for straight movement (direction-based), the model assumes that four directions of travel in the next step are possible (0° [straight ahead], 45°, 90°, 135° - i.e., backwards movement will not occur). If the birds choose their next step based on habitat quality in adjacent cells (forest-based), the model recognizes four levels of habitat quality: #1 designates old growth longleaf pine forests, #2R designates secondary growth pine restored for RCWs, #2 is secondary growth pine forests, and #3 is non-forested.

Figure 2 summarizes how the model assigned the 4 levels of preference based on direction-based and forest-based dispersal rules. The values for matrices V (direction-based) and HQ (forest-based) are reported in Figure 2. The matrices are combined within the following equation to estimate the probability the individual will move to each cell given its location in the previous time step (L_t) and surrounding forest structure (HQ):

$$P[L_{t+1} \mid L_t, HQ] = d_v V + d_{hq}\left(HQ / \sum HQ\right)$$

Where d_v and d_{hq} are the (0-1) weighting factors assigned to each matrix ($d_v + d_{hq} = 1$). Matrix $P[L_{t+1}|L_t,HQ]$ was transformed into cumulative probability distribution and compared to a u[0,1] random number to determine the bird's location in the next time step.

Landscapes used in Simulations

Simulations were conducted to illustrate the contribution LEA could make to the Private Lands Conservation Strategy outlined in the Recovery Plan for RCWs (USFWS, 2003b). The objective of the Private Lands Conservation Strategy is to provide support populations of 40-100 territories which are clumped together. The support populations are to provide immigrants to larger RCW populations (250-500 territories), or recovery populations, protected on State and Federal lands. Based on results from Letcher's SEPM, recovery populations should be large enough to minimize extinction risks due to environmental and demographic stochasiticity, as well as inbreeding, but too small to offset the loss of genetic variance through drift (USFWS, 2003b). While support populations will be vulnerable to threats from drift and environmental stochasticity, they should not be vulnerable to demographic stochasticity and inbreeding, if sufficiently clumped. Support populations are intended to provide connectivity among recovery populations and increase the retention of locally adapted gene complexes (USFWS, 2003b).

Fragmented versus clumped habitats

We confine our analysis to a landscape with approximately 50 territories, which is the population size where habitat fragmentation is expected to considerably reduce population growth and increase inbreeding (Letcher et al., 1998; Daniels et al., 2000). Figure 3a illustrates a landscape in which the three land cover types are distributed randomly simulating a highly fragmented landscape. These include old growth longleaf pine (covering 3% of the landscape), secondary growth pine (52%), and non-forested

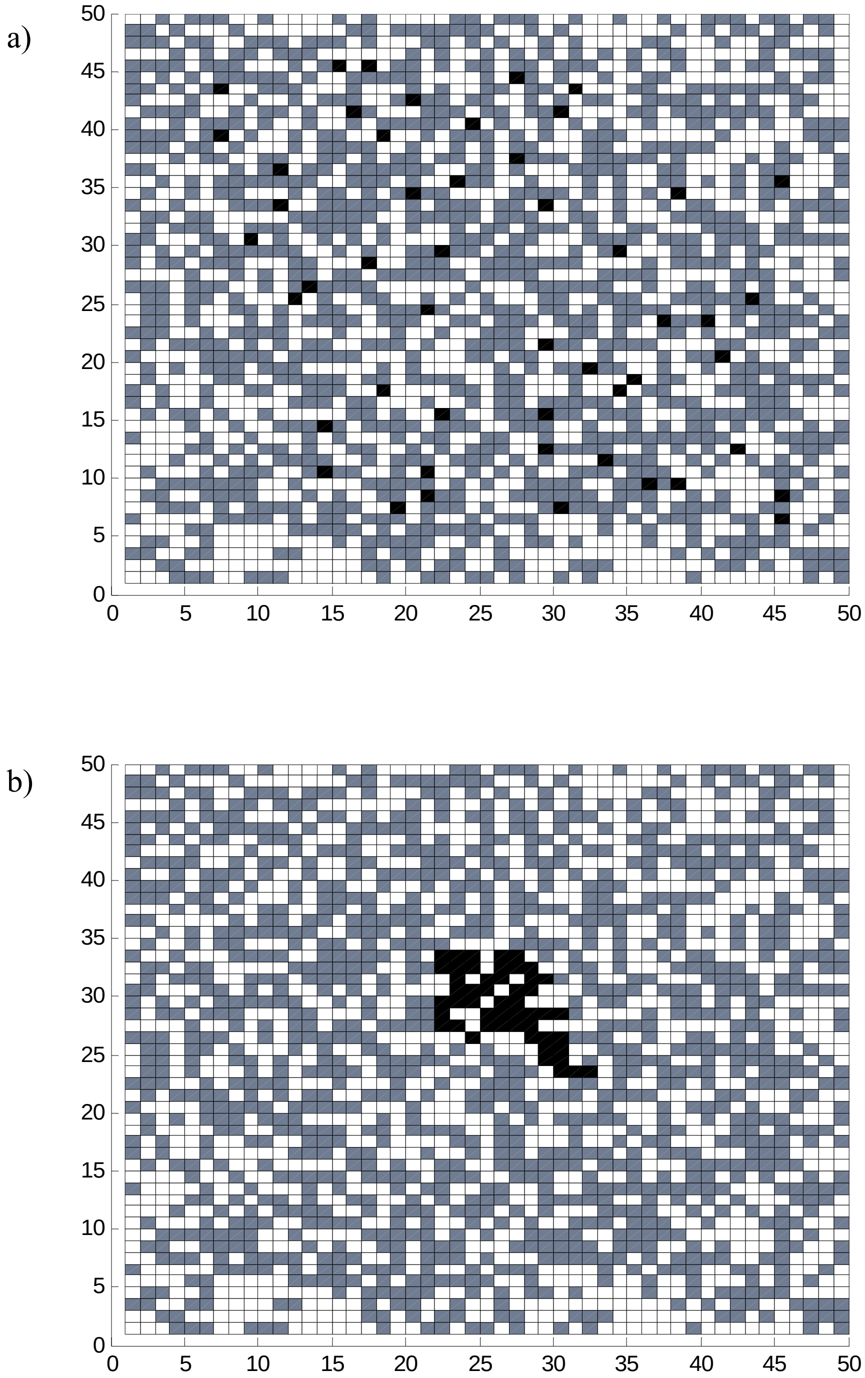


Figure 3. a) Fragmented or status quo landscape with 50 territories scattered throughout the region. b) Support landscape with 50 territories clustered together.

(45%). We assumed that all land is privately owned and the requirements of a support population could be met if the 50 territories were clumped (Figure 3b). This was defined as the support landscape, or one of the many possible landscapes meeting the Private Lands Conservation goals for the region.

To examine if the 50 clumped territories satisfy the Private Lands Conservation Strategy for support populations, the RCW SEPM was run for 100 years for both landscapes under the assumption of strictly direction-based ($[d_v, d_{hq}] = [1, 0]$) and forest-based [0, 1] dispersal for 100 iterations. Total number of adults within a breeding group and number of individuals lost as emigrants per year were averaged across all simulations. Time to quasi-extinction was estimated as the time when only one breeding group remains and no subsequent breeding groups are formed. 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), summarized in the Appendix. Nei's theory relates the total expected heterozygosity in the metapopulation (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 average observed frequency of heterozygous individuals within a breeding group, weighted by breeding group size, was also calculated (H_O).

Demographic outputs indicated that habitat fragmentation resulted in a large decrease in abundance, regardless of which dispersal model was applied (Figure 4). Larger variance about the mean abundance in the fragmented landscape resulted from the interaction between demographic stochasticity and landscape pattern. In both landscapes, abundance is slightly greater for forest-based dispersal, which resulted from a greater

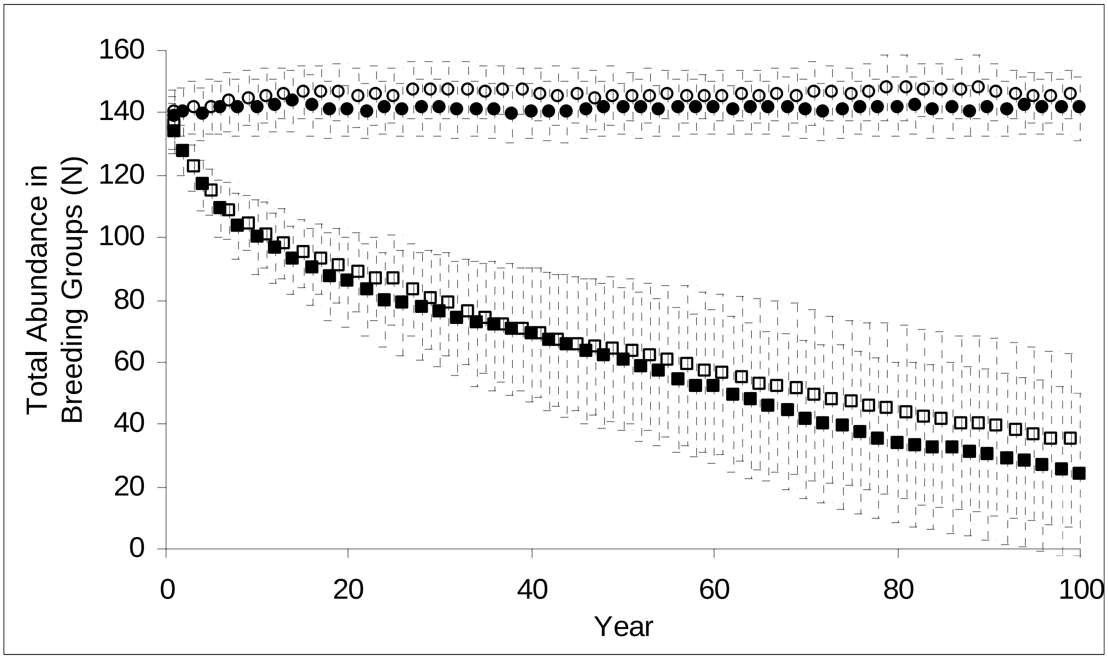


Figure 4. Total number of adults belonging to a breeding group. Closed circles denote the support landscape with direction-based dispersal. Open circles denote the support landscape with forest-based dispersal. Closed squares denote fragmented or status quo landscape with direction-based dispersal. Open squares denote fragmented or status quo landscape with forest-based dispersal. Average values taken from 100 simulations. Error bars represent one sample standard deviation.

Table 2. Average number of male and female floaters lost as emigrants per year from the support and status quo landscapes under alternative dispersal hypotheses.

	Direction-based		Forest-based	
	Males	Females	Males	Females
Support	0.22	2.41	0.00030	0.017
Status quo	0.34	1.08	0.13	0.45

retention of floaters (Table 2). For the support landscape, populations were persistent in all simulations regardless of dispersal assumptions (Table 3). In the fragmented landscape, differential retention of floaters affected probability of quasi-extinction (direction-based P[qE] = 0.4; forest-based P[qE] = 0.23).

Fixation indices were calculated to estimate how landscape structure and dispersal assumptions affect the correlation of alleles within and among breeding groups relative to expectations under random mating (Nei, 1977). Under an infinite alleles model Wright's inbreeding coefficient, the probability that two alleles chosen at random from within a breeding group are identical by descent, was estimated as: $F = 1 – H_O$ (Miller and Lacy, 2005). F equals the average coefficient of kinship (f) of mated pairs. Wright's fixation indices were estimated with observed and expected heterozygosities following Nei (1977). Fis, or the correlation of alleles within an average individual relative to the correlation of alleles expected in an average subpopulation mating randomly, is estimated as $Fis = 1 – H_O/H_S$. Fit, or the correlation of alleles within an average individual relative to correlation of alleles expected if the entire population were mating randomly, is estimated as $Fit = 1 – H_O /H_T$. Fst, or correlation of two alleles drawn at random from different subpopulations, is estimated as $Fst = 1 – H_S /H_T$.

Figure 5 indicates that the inbreeding coefficient remains below 0.125 in the support landscape under both dispersal models. However, inbreeding accrues quickly in the fragmented landscape, especially under the forest-based dispersal model. The greater accrual of inbreeding results from the redundant search path of floaters moving based on forest-structure in a fragmented landscape, resulting in increased mating among relatives despite the mother-son inbreeding avoidance behaviors included in the model. Fis

Figure 5. Inbreeding coefficients and fixation indices for status quo and support landscapes under contrasting assumptions of dispersal. Closed circles: support landscape & direction-based dispersal. Open circles: support landscape & forest-based dispersal. Closed squares: status quo landscape & direction-based dispersal. Open squares: status quo landscape & forest-based dispersal.

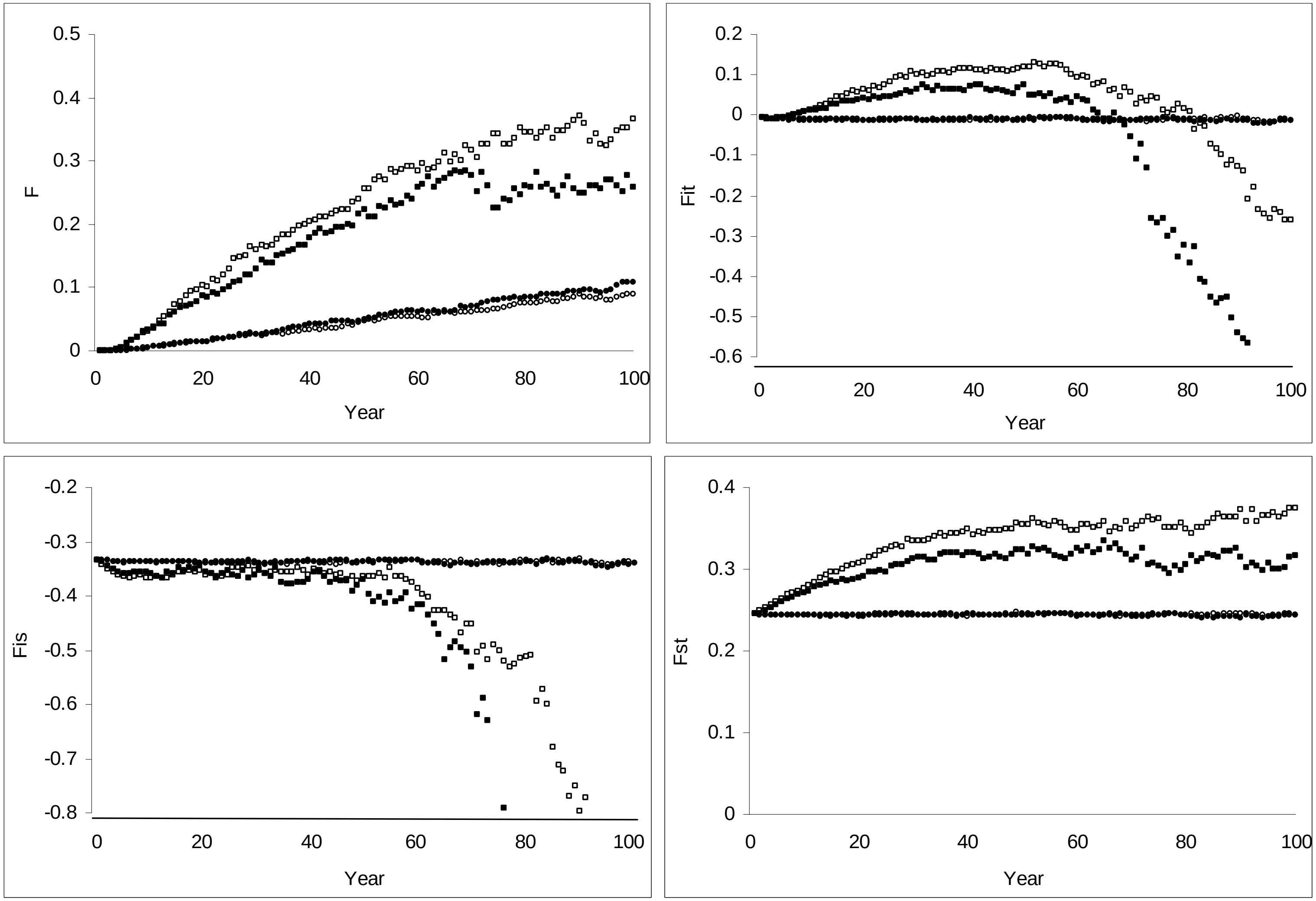

0.5
0.4
0.3
0.2
0.1
0
F
0
20
40
60
80
100
Year
0.2
0.1
0
-0.1
-0.2
-0.3
-0.4
-0.5
-0.6
Fit
0
20
40
60
80
100
Year
-0.2
-0.3
-0.4
-0.5
-0.6
-0.7
-0.8
Fis
0
20
40
60
80
100
Year
0.4
0.3
0.2
0.1
0
Fst
0
20
40
60
80
100
Year

Figure 5.

indicates that individuals within a breeding group are more outbred than expected under the assumption of random mating within subpopulations due to the mating system. In the fragmented landscape, as F increases, Fis decreases because inbreeding avoidance behaviors resulted in greater H_O than expected under random mating (H_S). Fit is slightly less than zero in the support landscape indicating that when territories are clumped the mating system is able to reduce the level of inbreeding within an individual compared to expectations if the entire population were mating randomly. However, habitat fragmentation reduces the effectiveness of the mating system such that a spatially subdivided population experiences higher inbreeding than expected if the entire population were mating randomly (Fit>0). Again, the accrual of inbreeding is faster under forest-based dispersal. Fit decreased well below zero in the fragmented landscape at $t > 65$, because the combined influence of the extinction of breeding groups and inbreeding avoidance behaviors increased the ratio of H_O/H_T. Therefore, as more breeding groups and alleles are lost, random mating would reduce total expected heterozygosity in the metapopulation (H_T) lower than observed in the average breeding group (H_O). In the support landscape Fst is maintained at a positive equilibrium value of ~0.24, regardless of the dispersal assumption, due to male philopatry and female biased dispersal (Sugg et al., 1996). In the fragmented landscape, more variance is partitioned among breeding groups under forest-based dispersal, suggesting that direction-based dispersal led to greater sharing of alleles across the landscape.

While demographic outputs also indicate the importance of clumped territories, genetic outputs and analysis with Fixation Indices provide a mechanistic understanding of how territory spatial structure, the mating system, and alternative hypotheses of dispersal behaviors interact. If landscape spatial structure is altered under the Section 10 permitting process of the ESA (USFWS, 1988), the ability of metapopulations to balance genetic variance within and among breeding groups, to prevent inbreeding and outbreeding depression and maintain adaptive variance, is altered (reviewed in Bruggeman et al., in press). The complex mating system of RCWs is able to achieve this balance when a continuous habitat distribution exists. Habitat fragmentation reduces the effectiveness of the mating system and increased the accrual of inbreeding, especially under the forest-based dispersal model.

To prevent trades from exacerbating habitat fragmentation, LEA estimates the equivalency of different landscape patterns resulting from a habitat trade based on levels of abundance (N), average expected heterozygosity within breeding groups (H_S), and average genetic divergence among breeding groups (D_{ST}) relative to landscape patterns in which the organism evolved.

Adding a Conservation Bank & Making Withdrawals

The goal of LEA is to direct the trading of habitat toward an allocation that provides the same metapopulation services as the one in which the organism evolved. Therefore, a banker would be advised to increase connectivity of breeding groups across the entire landscape to maximize the number of LEA credits accrued (Bruggeman et al., in press). The connectivity of each territory was estimated as the number of territories within 3.5 km, the average helper search radius (Letcher et al., 1998; USFWS, 2003b). Figure 6a illustrates the territory connectivity values of the fragmented landscape used in the previous analysis – here we will refer to this as the status quo landscape for comparison to some landscape alteration scenarios. The average territory connectivity for the status quo landscape was 2.88 (Table 3). Territories with the greatest connectivity tend to be in the northwest and southeast quadrants of the landscape and a gap of no territories is found in the middle between these high connectivity areas. We assumed the banker purchased 12 cells with secondary growth forest for restoration. In our scenario the banker chose cells in the center of the landscape, to fill the gap in connectivity observed in Figure 6a (Figure 6b; Figure 2). This was referred to as the mitigation landscape, in which average territory connectivity increased to 4.9.

Two possible scenarios for the loss of habitat within the landscape were determined to illustrate extreme changes in landscape structure based on a one-time trade. When applied in a real landscape, trades would be made on an individual basis and the conservation value assigned to any trade will be dependent on the previous trades in the landscape. In the first scenario, withdrawal 1 (W1), 12 territories with the greatest connectivity values (i.e., 4 or 5) were cleared for development. Therefore, the landscape resulting from W1 contained 50 territories with the average connectivity value of 3.16 (Table 3). In withdrawal 2 (W2), 24 territories with the lowest connectivity values (0, 1, 2, or 3) were cleared for development. The landscape resulting from W2 contained 38 territories with the average connectivity value of 3.55.

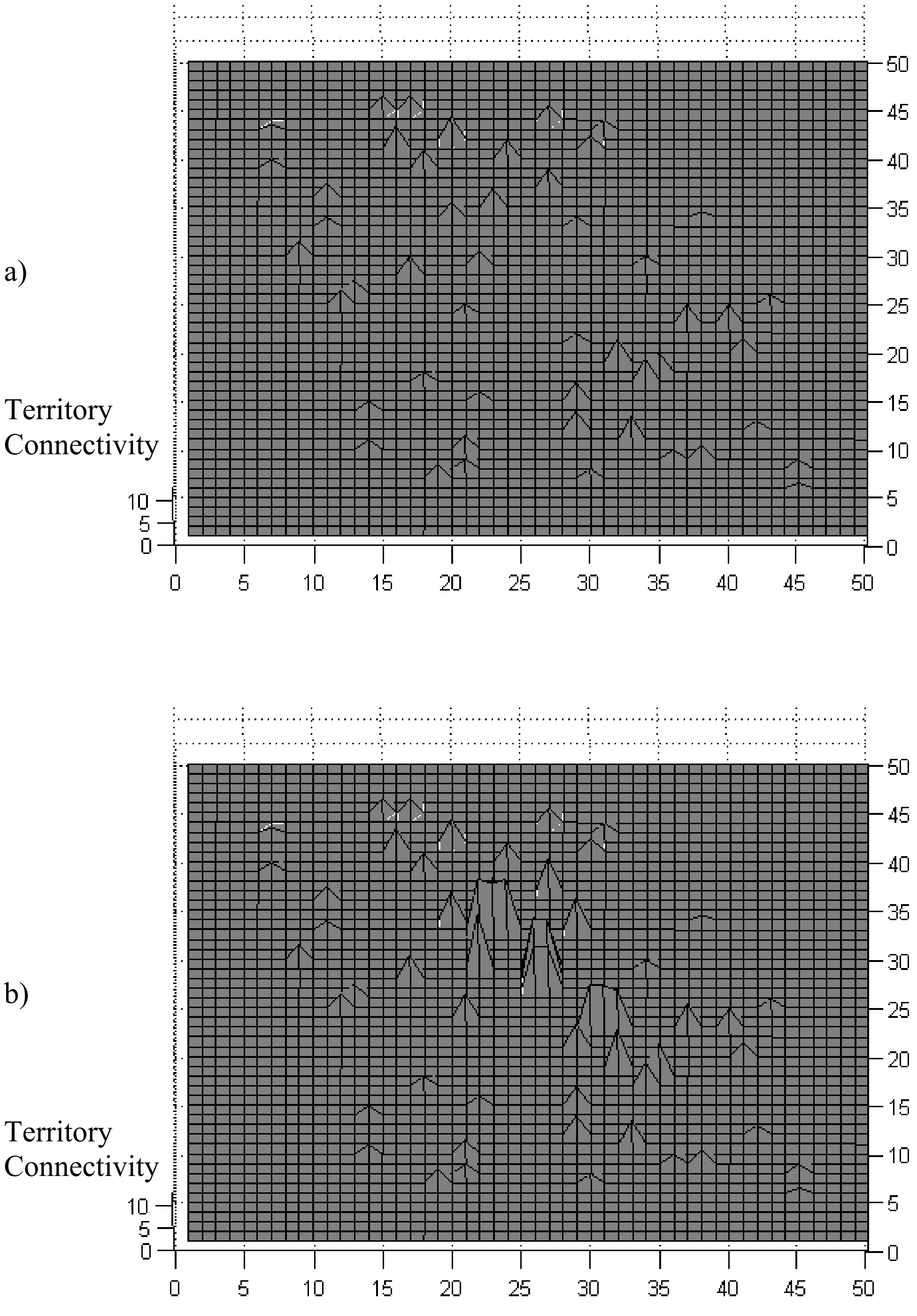


Figure 6. a) Surface plot of connectivity values per territory in the status quo landscape; values range from 0-5. b) Surface plot of connectivity values per territory in the mitigation landscape, in which 12 cells in the center of the landscape are restored for RCWs to increase connectivity across the landscape; values range from 0-13. Landscape is also depicted in Figure 2.

Table 3. Results of Landscape Equivalency Analysis applied to the red-cockaded woodpecker in hypothetical landscapes.

Landscapes	**Support**		**Status quo**		**Mitigation**		**Withdrawal 1**		**Withdrawal 2**	
Dispersal Model	Direction	Forest	Direction	Forest	Direction	Forest	Direction	Forest	Direction	Forest
Number of territories	50		50		62		50		38	
Average territory connectivity	34.88		2.88		4.9		3.16		3.55	
Probability of Persistence	1	1	0.60	0.77	0.95	0.97	0.93	0.97	0.95	0.99
Discount rate (r) = 0										
dLSY - N					24.60	22.74	-20.86	-22.63	-14.72	-13.48
dLSY - Hs					11.41	10.31	-4.03	-1.97	-0.29	+1.71
dLSY - Dst					9.88	2.63	-4.49	+2.70	+1.28	+5.80
Discount rate (r) = 0.03										
dLSY - N					7.21	7.04	-6.88	-7.50	-5.49	-5.06
dLSY - Hs					2.56	2.62	-0.83	-0.42	-0.11	+0.72
dLSY - Dst					2.58	2.10	-0.15	+1.48	+1.28	+2.34

Evaluating Trades with LEA

The RCW SEPM was run to compare the service trajectories for the three metapopulation services used in LEA for the status quo, support, mitigation, withdrawal 1, and withdrawal 2 landscapes. The bank was not added until year 20, at which time the territories are assumed to be suitable for colonization by floaters and helpers already present in the landscape; no birds were translocated from outside populations. It was assumed that the withdrawals occurred 5 years after the bank is established. We assumed that if a territory within the conservation bank were vacant at the time of the trade, a breeding pair from one of the habitats slated for development was selected at random for translocation. All helpers and remaining breeding pairs were assumed to become floaters within the landscape.

Addition of the bank at year 20, assuming no subsequent withdrawals, increased the probability of population persistence for both dispersal models and moved total abundance in breeding groups (N), average expected heterozygosity within breeding groups (H_S), and average genetic divergence among breeding groups (D_{ST}) closer to service levels observed in the support landscape (Table 3; Figure 7).

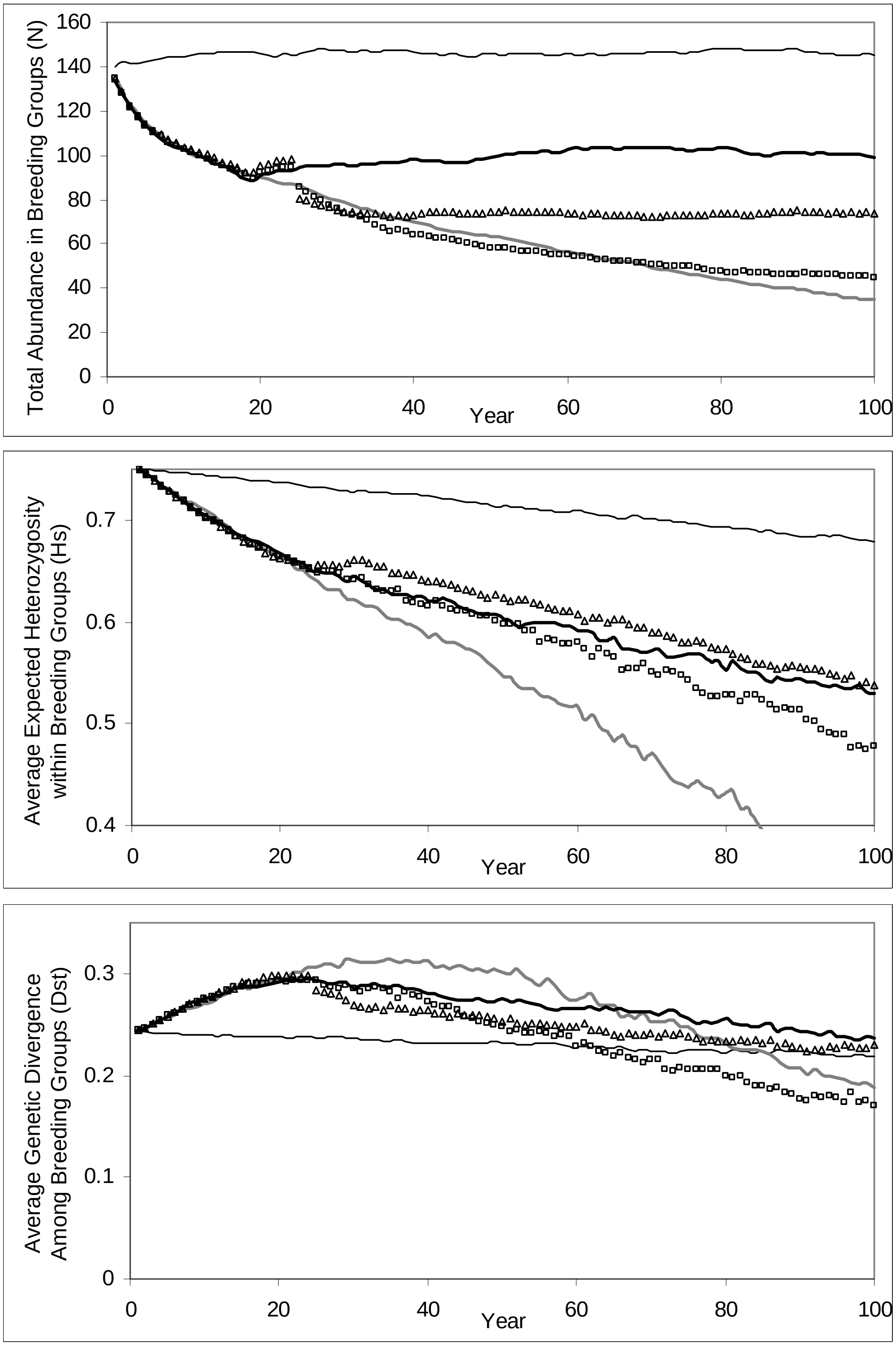


Figure 7a. Assuming forest-based dispersal, metapopulation service trajectories for support (b, thin black line), status quo (j, thick grey line), mitigation (m, thick black line), withdrawal 1 (w1, squares), and withdrawal 2 (w2, triangles) for the two models of dispersal (forest- and direction-based).

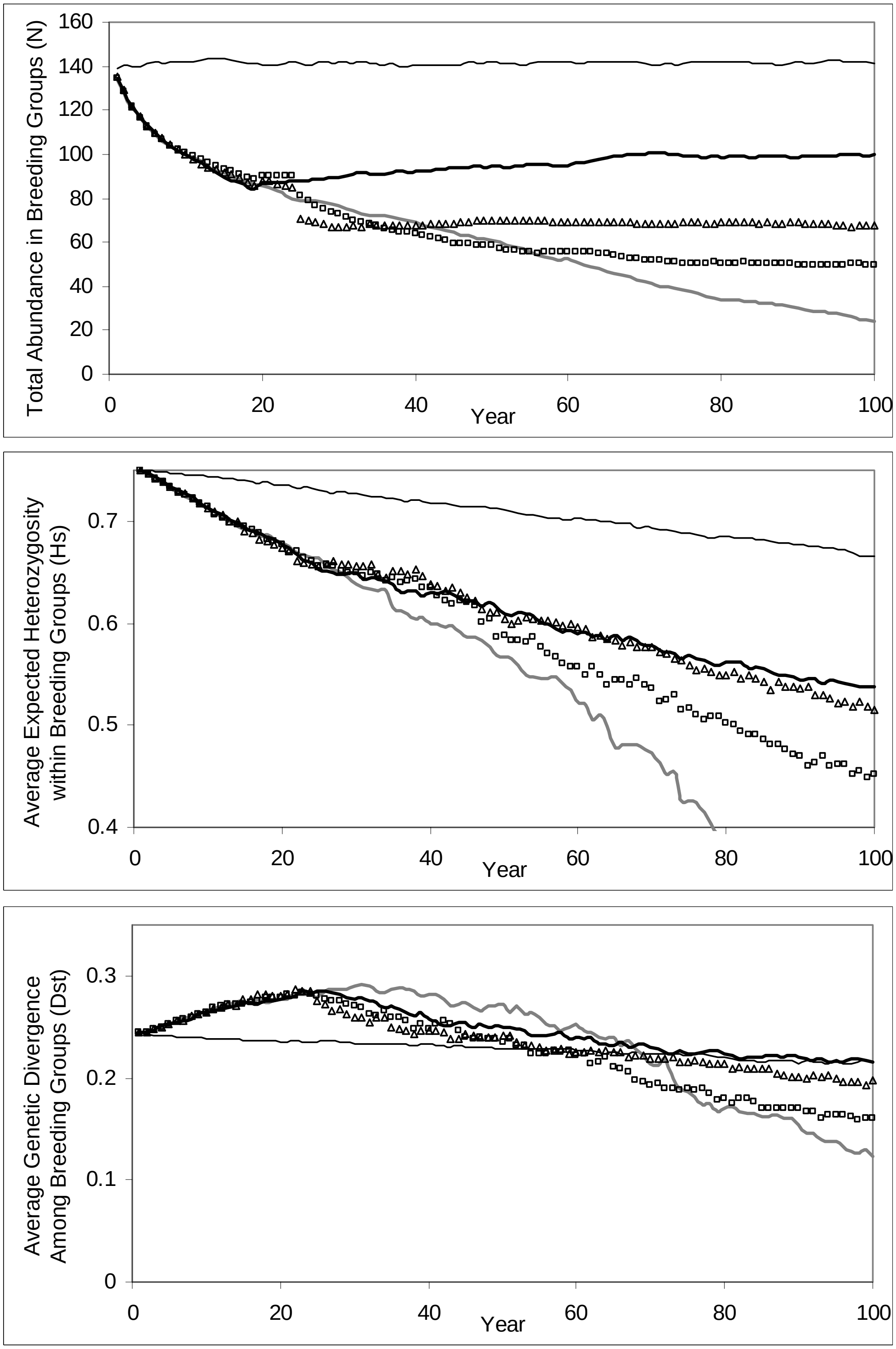


Figure 7b. Assuming direction-based dispersal, metapopulation service trajectories for support (b, thin black line), status quo (j, thick grey line), mitigation (m, thick black line), withdrawal 1 (w1, squares), and withdrawal 2 (w2, triangles) for the two models of dispersal (forest- and direction-based).

The number of LEA credits available in the bank at the time of the trade (t=25) was estimated following Bruggeman et al. (in press), which estimates the marginal change in network externalities given the bank's location relative to all other territories and other land cover types (i.e., its spatial context) and the species' natural history. The expected number of abundance credits is estimated as discounted Landscape Service Years - Abundance ($dLSY_C^N$):

$$E\left[dLSY_C{}^N\right] = \sum_{t=W}^{\infty} \frac{1}{(1+r)^t}\left(\frac{m_t{}^N - j_t{}^N}{b_t^N}\right)$$

where W is the time the trade occurs, r is the social discount rate, b_t^N is the expected total abundance in breeding groups at year t provided by the support landscape, m_t^N is the expected total abundance in breeding groups at year t provided by the mitigation landscape, and j_t^N is the expected total abundance in breeding groups at year t provided by the status quo landscape.

The number of credits purchased to offset the local and regional loss of abundance due to a withdrawal (i.e., marginal change in network externality due to take) can be calculated as discounted Landscape Service Years - Abundance ($dLSY_D^N$):

$$E\left[dLSY_D{}^N\right] = \sum_{t=W}^{\infty} \frac{1}{(1+r)^t}\left(\frac{m_t{}^N - w_t{}^N}{b_t^N}\right)$$

where w_t^N is the expected abundance at year t provided by the withdrawal landscape. Because the public has a positive time preference for services from capital assets, discounting modifies the number of credits associated with the change in abundance. In other words, the more slowly the withdrawal decreases population size, the fewer credits must be purchased.

Calculating credits associated with changes in genetic variance is more complex. The management goal is to approximate metapopulation 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 support landscape will be used as the baseline service levels to direct trading toward this goal. As estimates of genetic variance within and among subpopulations move closer baseline levels due to restoring habitat area or connectivity, the more credit is accrued in the bank. The credit representing a marginal, positive change in network externality estimated by genetic services due to restoring 12 territories can be calculated as discounted Landscape Service Years – Genetic Variance ($dLSY_C{}^G$):

$$E\left[dLSY_C{}^G\right] = \sum_{t=W}^{\infty} \frac{1}{(1+r)^t} \left(\frac{\left| b_t{}^G - j_t{}^G \right|}{b_t{}^G} \right) - \sum_{t=W}^{\infty} \frac{1}{(1+r)^t} \left(\frac{\left| b_t{}^G - m_t{}^G \right|}{b_t{}^G} \right)$$

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 support landscape, $j_t{}^G$ is the expected level of genetic variance at year t provided by the status quo landscape, and $m_t{}^G$ is the expected level of genetic variance at year t provided by the mitigation landscape.

The number of credits purchased to offset the negative network externality due to a withdrawal or departure of genetic variance away from baseline-levels relative to mitigation-levels can be calculated as discounted Landscape Service Years – Genetic Variance ($dLSY_D{}^G$):

$$E\left[dLSY_D{}^G\right] = \sum_{t=W}^{\infty} \frac{1}{(1+r)^t}\left(\frac{\left|b_t{}^G - w_t{}^G\right|}{b_t{}^G}\right) - \sum_{t=W}^{\infty} \frac{1}{(1+r)^t}\left(\frac{\left|b_t{}^G - m_t{}^G\right|}{b_t{}^G}\right)$$

where $w_t{}^G$ is the expected level of genetic variance at year t reflecting anticipated loss of habitat area or connectivity. For any positive discount rate, the more slowly a landscape change moves the genetic variance away from baseline, the fewer credits per change in service level are incurred. Conversely, habitat changes resulting in a large departure from baseline in the immediate future will be charged many credits per change in service level.

The number of credits accrued by the bank ($dLSY_C$) depends on which migration model is used to describe the behavior of RCWs (Table 3). A larger number of credits accrue under the assumption of direction-based dispersal because the loss of abundance and genetic services due to habitat fragmentation (i.e., status quo landscape) is expected to be greater compared to forest-based dispersal. In other words, under the assumption of straight dispersal, habitat fragmentation had a larger impact on the population because the birds are less likely to find new territories and more likely to leave the landscape compared to forest-based dispersal (Table 2). When a discount rate of 3% is applied (NOAA, 1999b), the accrual of credits is smaller as differences in service trajectories in the distant future are weighted less than differences in service trajectories in the near future.

The number of LEA credits withdrawn ($dLSY_D$) represents the change in network externalities due to an economic decision to develop habitat. Under the assumption of direction-based dispersal behaviors and a zero discount rate, W1 resulted in a large withdrawal of credits available in the bank for abundance [change in $dLSY^N = 24.60 - 20.86 = 3.74$]. Therefore, the bank has retained a balance of 3.74 credits for abundance.

Similar results were observed for W1 under the forest-based dispersal model, but the withdrawal of credits was larger. For example, when a positive discount rate was applied to the model, W1 resulted in credits for abundance to be overdrawn [change in $dLSY^N = 7.04 - 7.50 = (-0.46)$]. This resulted from an initial decline in the number of birds in a breeding group in the first few years after the transaction, indicating that time is required for helpers to be established in the new territories before equivalent reproductive output was achieved (Figure 7). In the absence of discounting, the greater abundance observed at $t>70$ compensates for the initial decline in abundance due to the take and a small net balance for abundance is retained by the bank, +0.11.

W2 results in a larger initial decline in abundance but a smaller withdrawal of credits (Table 3). As expected, application of a positive discount rate increased the number of available credits withdrawn. Even with the application of discounting, the benefits of the 12 well connected bank territories provides sufficient credits to justify the withdrawal of 24 of the least connected territories.

Average expected heterozygosity within a territory decreased with the loss of the 12 most connected territories (W1), but not greater than observed in the status quo landscape under both dispersal models (i.e., credits are not overdrawn). Application of the direction-based model resulted in a larger withdrawal of credits compared to the forest-based model, because more floaters and alleles are lost under direction-based dispersal.

Loss of the 24 least connected territories (W2) resulted in a slight increase in Hs under the forest-based model, which resulted in accrual of more credits within the bank for this metapopulation service (positive network externality). Thus, the least connected territories contributed less to the average expected heterozygosity compared to the other territories (Petit et al., 1998). Under the direction-based model for W2, average expected heterozygosity service levels closely approximated those observed prior to the take. W2 resulted in a small withdrawal of credits regardless of the discount rate. The difference in dLSY – H_S for W2 observed for the alternative dispersal models likely resulted from greater inbreeding which accrues in isolated territories under forest-based dispersal. Under direction-based dispersal, migrants from farther territories are more likely to reach the isolated territories. Therefore, the more isolated territories do not negatively weight the average expected heterozygosity as substantially under direction-based dispersal.

Under direction-based dispersal, W1 resulted in a withdrawal of dLSY – D_{ST} credits regardless of the discount rate. Figure 8 indicates that average breeding group size decreased in some territories not involved in trade W1. These territories may be defined as having lower functional connectivity due to the trade. The increased local extinction of these isolated breeding groups along with the loss of the 12 territories with high structural connectivity decreased genetic divergence averaged across the landscape. Under forest-based dispersal a similar trend in D_{ST} service flows are predicted, but LEA indicates a net accrual of credits. In this scenario, the positive network externality provided by the bank is lower (i.e., mitigation services do not as closely approximate baseline services; Figure 7). The smaller positive network externality results because more genetic differences are

Figure 8. Change in average breeding group size (N, grey bars) and average inbreeding coefficient (F, black bars) for each territory not involved in the habitat trade at time = 75, averaged over 100 simulations. The decrease in habitat occupancy (change in N<0) and increase in rate of inbreeding (change in F>0) after the trade compared to the status quo landscape, suggested that negative network externalities were created by applying conservation banking to the region. Positive network externalities were also observed, especially for withdrawal 2 and forest-based dispersal.

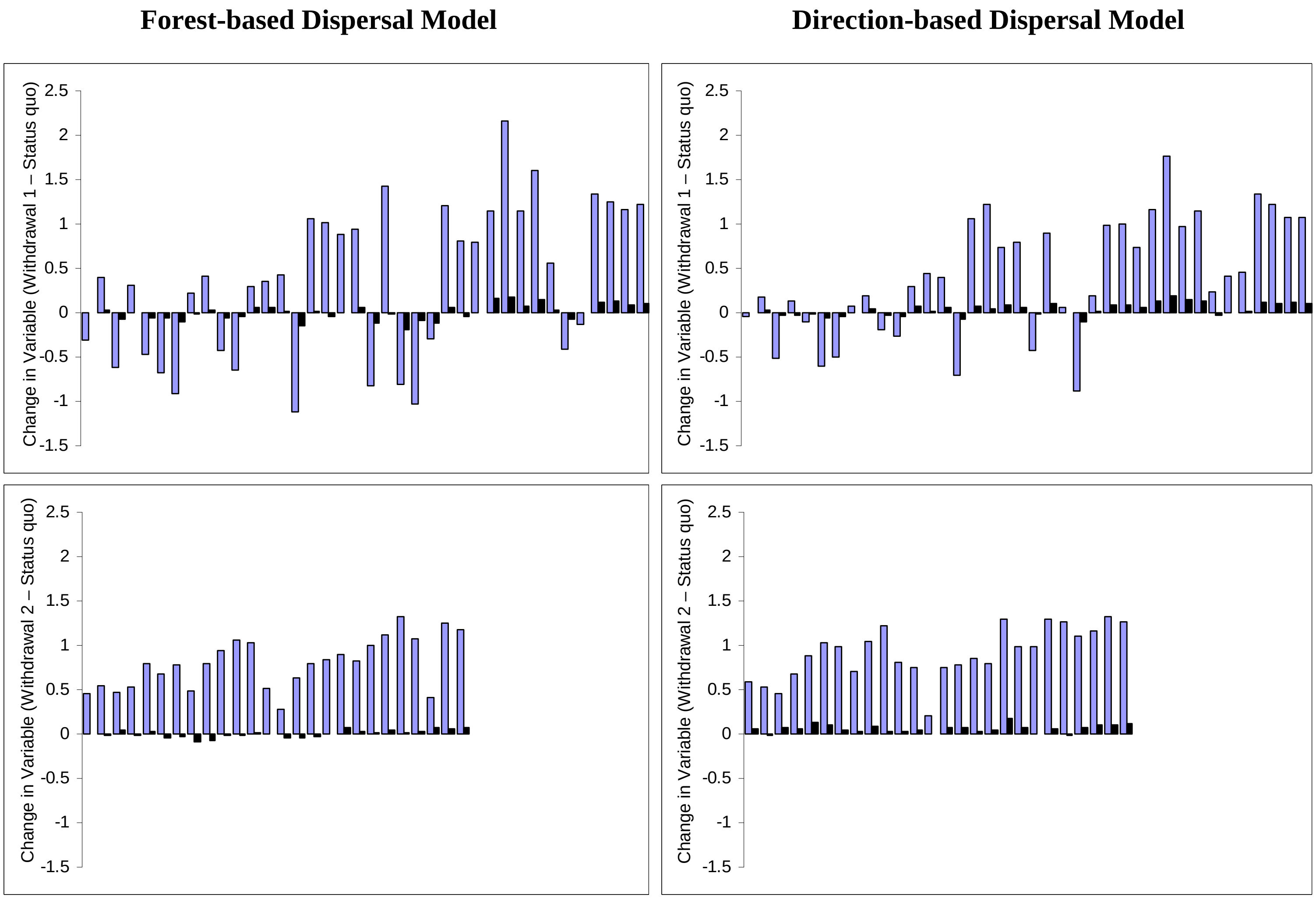

Forest-based Dispersal Model
Direction-based Dispersal Model
Change in Variable (Withdrawal 1 – Status quo)
Change in Variable (Withdrawal 2 – Status quo)
2.5
2
1.5
1
0.5
0
-0.5
-1
-1.5

Figure 8

retained among breeding groups due to the redundant search paths of floaters under forest-based dispersal.

The net result of W2 under both dispersal models was the accrual of dLSY – D_{ST} credits. Therefore, regardless of the dispersal model W2 resulted in a positive network externality as estimated by average genetic divergence. The accrual of credits is greatest under the forest-based dispersal model with no discounting. This suggests that the 24 isolated territories contributed significantly to the average genetic divergence among territories under forest-based dispersal.

Discussion

LEA estimates tradable credits for endangered species management that capture the interaction between landscape pattern and metapopulation processes. By estimating the equivalency of territories traded based on metapopulation services that differ in sensitivity to changes in habitat area and connectivity, trades that exacerbate the effects of functional fragmentation can be avoided.

Simulations revealed that W2 was the preferred habitat trade regardless of which dispersal hypothesis was used and whether marginal changes in conservation value were based on LEA credits or probability of persistence. However, habitat trades based on changes in probability of persistence may indicate that certain landscapes are equivalent when in fact metapopulation services generated by different configurations are not equivalent (Table 3; Figure 7). For example, no change in the probability of persistence is observed between the mitigation and withdrawal 1 landscape under the assumption of forest-based dispersal, nor between mitigation and withdrawal 2 under the assumption of direction-based dispersal. Examination of the expected metapopulation service trajectories indicated that the different landscape structures and assumptions regarding dispersal produce different population structures.

It may be argued based on changes in probability of persistence and total abundance in breeding groups, assuming a zero discount rate, that W1 is a viable trade. After all, W1 was based on an equivalent exchange of habitat area, and the average habitat connectivity was still greater than that observed in the status quo landscape (Table 3). However, the change in landscape spatial structure has created negative network externalities on some territories, which are offset by positive network externalities on other territories (Figures 7 and 8). The USFWS may be uncomfortable with a trade that results in a take occurring on lands not involved in the transaction, especially if they are being actively managed for RCWs (e.g., land with a Safe Harbor Agreement). However, if patch-based landscape indices (i.e., number of territories and territory connectivity; Turner et al., 2001) are used to estimate the equivalency of a trade, ignoring metapopulation processes, such unintended consequences may occur. These results suggest that habitat area and connectivity should not be traded on a 1:1 basis because the relationship between landscape pattern and metapopulation processes is likely not linear (Kareiva and Wennergren, 1995).

Bruggeman et al. (in press) proposed some trading rules to relate LEA to existing endangered species policy (USFWS, 1988; 2003a), population genetic theory, and adaptive management. Rule #1 stated that trades can not violate ESA's take and jeopardy standards (USFWS, 1988). Table 3 indicates that the probability of persistence after both trades remained greater than that observed under the status quo landscape, so the jeopardy standard was not violated. Figure 7 indicates that the total abundance in breeding groups decreased below the status quo levels immediately after the trades under both dispersal models, but increased above status quo over the long-term. This could be interpreted as a take.

Rule #2 stated that trades should not produce an allocation of habitat that drives the spatial apportionment of genetic variance farther away from baseline levels, exacerbating the effects of fragmentation. Specifically, if the projected maximum absolute difference between b^G and w^G across all time is greater than that between b^G and j^G, then the withdrawal may exacerbate effects of habitat fragmentation (i.e., $\max |b^G - j^G| \geq \max |b^G - w^G|$ to allow trade). Figure 7 indicates that this rule was not violated; the trades did not skew the spatial allocation of variance farther away from support (baseline) compared to the status quo landscape.

However, the expected D_{ST} for the withdrawal 1 landscape ($w1^{Dst}$) is farther from D_{ST} for the support landscape (b^{Dst}) than the D_{ST} values for the status quo landscape (j^{Dst}) at certain times (i.e., $60<t<75$ for direction-based dispersal and $t>75$ for forest based dispersal). Average genetic divergence among breeding groups may be reduced either through migration among extant breeding groups or extinction of isolated breeding groups. The LEA equations and rules are useful for directing the trade of habitat to reapportion genetic variance within and among groups assuming no change in the probability of breeding group extinction (Bruggeman et al., in press). Examination of territory specific-data revealed that occupancy for some territories not involved in the trade decreased for withdrawal 1, indicating the increased occurrence of local extinction

(Figure 8). The dLSY – D_{ST} remaining after W1, under both dispersal models, therefore did not reflect a positive network externality due to increased migration.

It is critical to also examine changes in territory occupancy to understand how the apportionment of genetic variance within and among groups is affected by the processes of local extinction, gene flow, drift, and inbreeding when applying LEA. Loss of genetic variance due to local extinction may be detected by reduction in total expected heterozygosity (H_T). However, H_T in W1 is still greater than that observed in the status quo landscape (data not shown), because W1 increased average expected heterozygosity within breeding groups (H_S) substantially relative to the status quo landscape (Figure 7). We add to LEA Rule #2 by specifying that the expected genetic variance, both within and among local populations, resulting from a trade must not be less than the expected genetic variance under the status quo and support landscapes at any time (i.e., $w1_t^G < j_t^G < b_t^G$ would prevent trades).

Rule #3 stated that private investment in natural capital leads to marketable credits, whereas public investment leads to species recovery. In most cases, Federal lands should not be used to supply credits for habitat trades (USFWS, 2003a). However, public agencies or NGOs interested in contributing to endangered species recovery may wish to invest in LEA credits. For example, the banker used knowledge of the organism's natural history when selecting habitat restoration sites and credits exchanged under W2 for genetic services represented a relatively small withdrawal or a net accrual of credits. The banker now has increased flexibility when considering future land transactions. In other words, when considering how to increase bank area, the new bank parcels will not have to have high connectivity, or when considering future withdrawals, territories with high connectivity may be offset due to the bank's strategic restoration, which increased functional connectivity. If a public agency or an NGO decided to buy remaining genetic variance credits (i.e., defragmentation credits) this would force the banker to continue to defragment habitat when expanding the bank. Purchase of credits results in service trajectories for withdrawal 2 (w2) becoming the status quo service trajectories (j) for all future trades (Figure 7) (USFWS, 2003a). Purchase of defragmentation credits would lead to a conservation bank that is clumped, thus meeting the first requirement of a support population as defined under the Recovery Plan (USFWS, 2003b). The second requirement of support populations is connectivity to larger recovery populations (USFWS, 2003b). The conservation value of support populations relative to nearby recovery populations can also be estimated with LEA by adding one level to the spatial hierarchy in Nei's theory to estimate average genetic divergence among populations (Nei, 1977).

Rule #4 stated that discounting of service flows should begin from the time the trade occurs. A discount rate equal to interest rates of Treasury Bills is typically used when applying resource-based compensation because it describes the government's time preference for capital (~3%) (NOAA 1999a). Application of a positive discount rate resulted in overdrawing credits for W1 under forest-based dispersal. Therefore, if the public's rate of positive time preference for seeing the endangered species, for example, were to be incorporated into decision making W1 would not be allowed, but W2 would.

Rule #5 indicated that if SEPMs are to be used to estimate the equivalency of habitats traded, that monitoring data must be used to continually update model assumptions. Our model results did not incorporate uncertainty due to sampling (or observational) error nor, for the most part, parameter (or process) error. We have increased the ecological realism of Letcher's SEPM by incorporating 2 alternative dispersal models and assumed the birds interact with four land cover types, not just two. Our model contains many parameter uncertainties besides directional choices during dispersal. First, mortality estimates for floaters was not affected by land cover type occupied (Belisle and Desrochers, 2002). Second, more research is required to estimate the ability of floaters to find breeding vacancies (i.e., perceptual range). We suspect assuming that floaters have equivalent search radius as helpers (3.5 km) reduces the sensitivity of model results to the dispersal models used. Third, feedback between demographic and genetic parameters was not incorporated. Further research into the relationship between fitness of offspring and kinship coefficient of the parents is needed before inbreeding depression can be adequately included in a simulation study (Daniels et al., 2000). Fourth, the influence of environmental stochasticity was not included, as those data were not available in the primary literature (Walters et al., 2002a).

A SEPM represents a hypothesis of landscape processes (i.e., how landscape pattern affects metapopulation processes). We have used expectations from 2 alternative hypotheses to evaluate two possible habitat trades. The proportional change in credits available in the bank after W2 differed for the three metapopulation services for each dispersal model. As we expected the largest difference in exchange of LEA credits based on the alternative dispersal models was observed for dLSYs – Dst (Table 4). Therefore, the metapopulation services used in LEA differ in sensitivity to assumptions regarding

Table 4. Percent change in number of Landscape Equivalency Analysis credits (dLSYs) for each metapopulation service available in the bank after withdrawal 2 for each dispersal model and rate of discount (r).

	r = 0		r = 0.03	
	Direction	Forest	Direction	Forest
dLSY - N	40	41	24	28
dLSY - Hs	97	117	96	127
dLSY - Dst	113	321	150	211

biological processes. If we assume that RCWs disperse straight regardless of land cover, fewer credits remain in the bank after the trade compared to the forest-based dispersal assumption.

Landscapes are heterogeneous and the costs associated with protecting and restoring a parcel relative to conservation benefits will vary over space. Differences in costs and benefits of habitat management provide profitable opportunities for trading habitat among landowners. There is still much uncertainty associated with estimating the role a single habitat patch plays within a landscape for population persistence (Lindenmayer and Lacy, 2002). We argue that a scientifically defensible habitat trading system designed to mitigate habitat fragmentation requires recognizing uncertainty regarding the relationship between landscape pattern and metapopulation processes. However, when appropriately implemented, tradable permit systems provide financial mechanisms for reducing uncertainty.

Decisions regarding whether land should be protected due to it's high conservation value or developed due to it's high economic value, under Section 10 of the ESA (USFWS, 1988), can not be appropriately made if uncertainty regarding a species' habitat requirements for foraging, reproduction, or migration is great. When making habitat trades under great ecological uncertainty it is difficult to discern the contribution a habitat patch makes to species persistence (i.e., all patches have equivalent conservation value). Further, uncertain habitat trades would not necessarily lead to increased conservation benefits, but may increase the probability of extinction.

The required monitoring of the outcomes of mitigation under ESA's Section 10 (USFWS, 1988) provides an opportunity to learn about interactions between landscape patterns and metapopulation processes. Wilhere (2002) proposed direct payments or tax breaks to private landowners for monitoring data when habitat trades under ESA occur because monitoring is often not enforced. Similarly, a performance bond may be required when uncertainty regarding equivalency of habitats is great, which may be partially remitted when a banker demonstrates that risks are less than previously expected due to data collection (Wilhere, 2002). USFWS (2003a) proposed incorporating risks associated with a habitat trade into the price of the credits to offset the cost of the endowment used for management.

We have developed a landscape-scale accounting system for making tradeoffs between habitat area and connectivity, which incorporates uncertainty regarding a species' natural history that would have otherwise been ignored by landscape indices. Compared to the current assumptions regarding dispersal used for landscape-scale management, incorporating an alternative dispersal hypothesis, supported by empirical data, increased the conservation value of a bank.

Conclusion

The opportunity costs of protecting RCW habitat ranges from \$100-200K per territory based on lost revenues from timber harvest and real estate development (R. Costa, USFWS, personal communication). Therefore, trading 12 well connected restored territories for 24 isolated old growth territories (W2) may provide a net financial benefit for all private landowners and reduce the negative effects of fragmentation on the species. These results confirm the conclusion of Cox and Engstrom (2001). They found that if a Conservation Easement program used a SEPM for RCWs to direct strategic habitat protection, an equivalent probability of persistence would be achieved with 22,000 hectares less protected habitat than would be observed under random habitat protection.

Appendix: 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 where 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 individuals 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 subpopulations (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).

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