

Should Habitat Trading Be Based on Mitigation Ratios Derived from Landscape Indices? A Model-Based Analysis of Compensatory Restoration Options for the Red-Cockaded Woodpecker

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Abstract Many species of conservation concern are spatially structured and require dispersal to be persistent. For such species, altering the distribution of suitable habitats on the landscape can affect population dynamics in ways that are difficult to predict from simple models. We argue that for such species, individual-based and spatially explicit population models (SEPMs) should be used to determine appropriate levels of off-site restoration to compensate for on-site loss of ecologic resources. Such approaches are necessary when interactions between biologic processes occur at different spatial scales (i.e., local [recruitment] and landscape [migration]). The sites of restoration and habitat loss may be linked to each other, but, more importantly, they may be linked to other resources in the landscape by regional biologic processes, primarily migration. The common management approach for determining appropriate levels of off-site restoration is to derive mitigation ratios based on best professional judgment or pre-existing data. Mitigation ratios assume that the ecologic benefits at the site of restoration are independent of the ecologic costs at the site of habitat loss. Using an SEPM for endangered red-cockaded woodpeckers, we show that the spatial configuration of habitat restoration can simultaneously influence both the rate of recruitment within breeding groups and the rate of migration among groups, implying that simple mitigation ratios may be inadequate.

Keywords Conservation banking · Landscape ecology · Mitigation ratios · Population viability analysis · Private lands · Uncertainty

Introduction

Continuing pressure to develop terrestrial and aquatic landscapes in the United States has led to provisions in several environmental regulations (e.g., the Endangered Species Act [USFWS 1988], the Clean Water Act [33 USC § 1251], the Oil Pollution Act [33 USC § 2701], and the Comprehensive Environmental Response, Compensation, and Liability Act [USC §§ 9601 to 9675]) for the restoration of ecologic resources at some point on the landscape to compensate for lost ecologic resources caused by development. These provisions require a means by which to determine the appropriate level of off-site compensation and therefore effectively mitigate the loss of ecologic resources at the point of development. Most notably for wetlands (Stein and others 2000), this has led to the specification of mitigation ratios. Mitigation ratios are intended to capture dissimilarities in ecologic function between natural and created ecosystems (Stein and others 2000). In practice these ratios have most often been based on best professional judgment, which means that the relation between these ratios and the sustainability of ecologic structure and function tends to be implicit and not clearly articulated.

Further complicating decision making, compensatory restoration changes how ecologic resources are allocated in a landscape. Currently mitigation ratios do not consider spatial dynamics. For example, the removal of one habitat site and the restoration of another mitigation ratio-equal site may still result in a change in the aggregate level of ecologic function produced because of spatial dynamics. If we wish to conserve a decreasing wildlife population that requires migration to maintain regional persistence (Hanski and Gaggiotti 2004), then the change in spatial distribution of ecologic resources caused by compensatory restoration will affect the sustainability of local populations elsewhere in the region. Ensuring

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that changes in landscape pattern do not impede movement among resource patches or decrease landscape connectivity (Taylor and others 1993) should be an important factor in determining where to place restoration efforts. However, we are often uncertain how changes in landscape pattern affect the movement of individuals (Ricketts 2001).

Due to ignorance regarding dispersal behaviors, landscape connectivity is often managed from a structural perspective (i.e., spatial association of different land cover classes; Goodwin 2003; Calabrese and Fagan 2004). Landscape indices summarize the area, shape, and contiguity of different land cover types (i.e., geometric descriptors of habitat) and are easily derived from map layers of land cover patterns (Turner and others 2001). Some landscape indices have been successfully correlated with biologic patterns (Fahrig 2003). Researchers have extended landscape indices to include aspects of an organism's natural history, including minimum habitat area required for local persistence and interpatch distance within a species' expected dispersal distance (Vos and others 2001; Polasky and others 2005). It would seem that landscape indices could serve as a basis for extending mitigation ratios so that off-site compensatory restoration is implemented without decreasing movement of individuals across resource patches (USFWS 2001).

There are two problems associated with applying these indices for determining appropriate mitigation ratios that protect landscape processes. First, despite evidence for empiric correlations, landscape indices have proven to be poor surrogates for measures of ecologic function, such as population growth and migration rates (Calabrese and Fagan 2004; Li and Wu 2004; Winfree and others 2005). This may result from landscape indices failing to capture the complex interaction between population growth and migration (e.g., migration rates often depend on population density and vice versa: Travis and others 1999). Landscape indices have often been developed based on analyses that focus on dispersal and landscape pattern, but they ignore the interaction between recruitment, dispersal, and landscape pattern (e.g., Bender and others 2003). Assigning value to habitat area and connectivity requires a good understanding of a species' movement and migration dynamics.

Second, off-site mitigation results in changing landscape patterns over time (i.e., dynamic landscapes) (Schrott and others 2005). In dynamic landscapes, we may observe a temporal delay between when a change in landscape pattern occurs and the demographic response of the population, which has been referred to as the "extinction debt" (Tilman and others 1994). Because of this, correlations between landscape indices and biologic patterns that have been observed in static landscapes may not be capable of predicting population dynamics when landscape structures change over time. For example, in a study that compared species-specific responses

to landscape attributes in different landscapes, MacNally and others (2000) observed that differences in the timing of land use change prevented accurate predictions regarding the impact of fragmentation based on an organism's natural history. Therefore, both landscape history and an organism's natural history are likely critical for predicting fragmentation effects and thus defining appropriate mitigation ratios for landscape-scale habitat change.

In this study, we assessed the importance of these issues in a relatively well-understood species system: red-cockaded woodpeckers (*Picoides borealis*; RCW) in a longleaf pine savannah ecosystem. Our goal was to assess whether landscape indices could actually provide a good basis for determining mitigation ratios in this case. We used a spatially explicit mechanistic population model (SEPM) to assess the demographic effects of habitat restoration and removal decisions. By explicitly modeling the effects of changes to landscape structure, we were able to determine whether simple indices adequately reflect the processes that ultimately govern population dynamics on the landscape. Our premise was that this well-understood system is broadly representative of spatially structured populations that require dispersal to maintain regional persistence (Thomas and Kunin 1999).

RCWs, a monogamous, cooperative breeding species endemic to old-growth longleaf pine forests in the southeastern United States (Conner and others 2001), are especially well-suited for this analysis because an individual-based and SEPM already exists (Letcher and others 1998). These models simulate how landscape pattern affects variation in recruitment and migration over space and time. Based on applications of the Letcher model to static landscapes, RCWs appear to be sensitive to habitat fragmentation at low-habitat densities (Schiegg and others 2002, 2005; Walters and others 2002). For the purposes of dynamic landscape modeling (i.e., simulating changes to habitat patterns in the landscape), we increased the spatial realism of Letcher's model by incorporating four different land cover types. A critical and relevant uncertainty for RCWs concerns their dispersal behavior. We considered two alternative hypotheses about dispersal behavior, including how environmental and demographic factors affect the probability of male natal dispersal (Pasinelli and Walters 2002), to assess the robustness of our conclusions to this uncertainty. For simplicity we confined our analysis to a single fragmented landscape and contrasted the ability of one off-site mitigation action to compensate for two habitat-removal scenarios. The habitat-removal scenarios were designed to be representative of typical but contrasting strategies for habitat trading.

We evaluate the ability of mitigation ratios to capture population dynamics in the context of conservation banking, in which habitat is restored before habitat loss, and subsequent habitat loss results in a withdrawal from the bank (USFWS 2003b). Habitat trading for endangered

species is allowed as long as mitigation is implemented to prevent the “harming, harassing, or killing of individuals,” commonly referred to as “take standard,” and the likelihood of species survival is not decreased, commonly referred to as “jeopardy standard” (USFWS 1988). The minimum mitigation ratio enforced by USFWS thought to prevent violation of take and jeopardy standards for RCWs is one active territory for one active territory (USFWS 2003a). Furthermore, isolated groups must be traded for less isolated groups. The site of restoration must have the capacity for at least 10 clustered groups. However, defining levels of isolation at which habitat trading is a viable management option is an important area of research.

Methods

We start by describing the landscapes used in our simulations and two alternative ways in which to summarize the landscape (i.e., landscape indices or with an SEPM). Next, we describe the technical basis for including two alternative dispersal behaviors into the SEPM. The stylized trades are presented describing how landscape structure changes over time. Finally, we describe the simulations and how we summarized outputs to capture the interaction between landscape change and biologic processes.

Landscape Composition

The model was constructed in Matlab 7 (The MathWorks, Inc., Natick, MA) and was constrained to a square grid. Each cell was designated either as old-growth habitat, restored habitat, matrix, or nonforested. Old-growth habitat cells are assumed to be actively managed for RCWs by applying yearly burns and maintaining 3 to 4 cavities/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 re-establishing a natural fire regime (James and others 2001). Restoration of second-growth pine forest will constitute a bank for this analysis. However, we assumed that birds do not establish new territories in second-growth pine forests containing a hardwood understory on their own; therefore, budding and pioneering behaviors were not included (Schiegg and others 2005). The average RCW territory size observed in old-growth longleaf pine communities is 47 ha (Engstrom and Sanders 1997). Landscapes representing 125,000 ha were generated with 2,500 cells, each representing 50 ha.

Landscape Indices and Mitigation Ratios

As an alternative to SEPMs, landscapes before and after mitigation were summarized using two landscape indices.

First, we used the number of territories to summarize the changes in habitat area because all territories had equal size and shape. Second, we estimated the connectivity of each territory, as recommended by the RCW Recovery Plan (USFWS 2003a), as the number of territories within 3.5 km. Analysis of historic data suggests that this value reflects a helper’s search radius (Pasinelli and Walters 2002). Mitigation ratios were developed for habitat area and connectivity separately. A 1:1 ratio implies that territories exchanged had equal habitat area or connectivity.

RCW SEPM

The model simulates a cooperative mating system of RCWs and has been described in detail elsewhere (Letcher and others 1998). RCW breeding groups consist of a reproductively active male and female, nestlings or fledglings, and, occasionally, helpers, who are usually male and full or half-siblings to the fledglings (Fig. 1) (Walters and others 1988). Helpers play a critical role in population dynamics by participating in defending territory, feeding nestlings, and inheriting their natal territory on the death of the male breeder (Conner and others 2001). Floaters of both sexes are present in the region, which move continuously, seeking a breeding vacancy in a territory (Walters and others 1988). Helpers will preferentially inherit their natal territory on the death of the breeding male, out-competing floaters, and helpers in adjacent territories. Female floaters only compete for territories containing solitary males wherein the oldest female within 3.5 km wins the vacancy (Letcher and others 1998).

Alternative Hypotheses About RCW Ecology

We examined the influence of two sources of uncertainty in Letcher’s SEPM: the influence of landscape pattern on dispersal and the probability of a male fledgling delaying

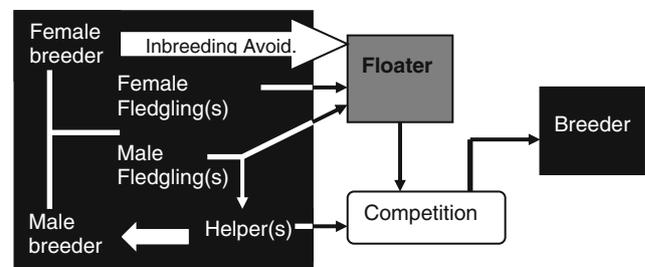


Fig. 1 Breeding group structure and demographic transitions for RCWs. Black boxes denote breeding territories, and the grey box denotes the matrix crossed during floating behaviors. All female fledglings leave their territorial nest within the first year, but some male fledglings stay as helpers. More than 90% of time when a helper inherits his father’s territory, the female breeder disperses to avoid inbreeding (Daniels and Walters 2000)

dispersal to remain as a helper. The Letcher and others SEPM assumed that dispersing birds choose a direction at random and disperse in a straight line. However, it has been observed that nonforested areas, or gaps, act as barriers to movement for many small to medium-sized forest bird species (Belisle and Desrochers 2002). An alternative model of RCW dispersal would allow the direction of movement to be influenced by the surrounding habitat (Kramer-Schadt and others 2004). Letcher's SEPM used a constant probability that male fledglings stay as helpers and delay dispersal. However, Pasinelli and Walters (2002) found that the probability of staying as a helper is mediated by demographic and landscape factors. These results suggested that fledglings acquire knowledge of habitat availability, referred to as "prospecting behaviors," before deciding to leave. To reflect these sources of uncertainty, we compared two models: the "random-straight model," to parallel the model of Letcher and others (1998), and the "forest-based model," in which movement direction is affected by landscape pattern, and the probability that a male fledgling will stay as a helper is mediated by demographic and landscape factors (Appendix). These sources of uncertainty provide the critical link between recruitment and dispersal behaviors, which have been predicted to have a large influence on the accuracy of SEPMs (South 1999).

Mitigation Scenarios

We confined our analysis to a landscape with approximately 50 territories, which is the population size at which habitat fragmentation is expected to considerably decrease population growth (Letcher and others 1998). We compared five landscape configurations: current conditions ("status quo"), a sustainability goal ("baseline"), habitat restoration to create a bank ("mitigation"), and two habitat removals ("withdrawals 1 and 2"). Although optimal placement of a mitigation bank is an interesting question regarding many species, the importance of a clumped distribution of habitat is well known for RCWs (Letcher and others 1998). Therefore, we only considered one mitigation landscape and two different withdrawals.

The status quo condition represents a highly fragmented landscape in which the land cover types are distributed randomly (Fig. 2A). The baseline landscape represents one of the many possible landscape configurations of clumped breeding territories (Fig. 2B), thus meeting the Private Lands Conservation goal for RCWs (USFWS 2003a). This landscape was included to contrast results between our efforts and those previously published (Letcher and others 1998). The status quo and baseline landscape differed only in spatial associations of land cover types and comprised equal amounts of all three land cover types: old growth

longleaf pine (3% of the landscape), second-growth pine (52%), and nonforested (45%).

We derived the mitigation landscape to maximize the contribution restoration makes to regional population sustainability. Based on simulation studies with Letcher's SEPM, it is best to increase connectivity of breeding groups across the entire landscape. Territories with the greatest connectivity tend to be in the northeast and southwest 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 and increase connectivity from the northeast to the southwest (mitigation landscape, Fig. 2C).

Two possible scenarios for the loss of habitat (take or withdrawal) within the landscape were determined to illustrate extreme changes in landscape structure based on a one-time trade. In the first scenario, withdrawal 1 (Fig. 2D), 12 territories with the greatest connectivity values (i.e., 4 or 5 territories within 3.5 km) among old-growth pine were cleared for development. In withdrawal 2 (Fig. 2E), 24 territories with the lowest connectivity values (0 to 3 nearby territories) were cleared for development. These scenarios create development patterns that are not inconsistent with the low-density residential development often pursued in southern pine forests.

Simulations

The RCW SEPM was run for 100 years for all landscapes. The model is stochastic; therefore, we repeated each simulation 100 times and examined the distribution of outcomes. Simulations were run for 2 static landscape conditions (i.e., territory configuration remained constant): baseline and status quo. For the mitigation landscape, we assumed that the 12 restored territories were added to the status quo landscape at year 20 (Table 1), 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. Results for mitigation landscape were summarized assuming that no later changes occurred to landscape structure. For the two withdrawal landscapes, it was assumed that the withdrawals occurred at year 25 from the mitigation landscape (Table 1). We assumed that if a territory within the conservation bank was 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.

Fig. 2 Hypothetical landscapes used in simulation study. Each cell represents 50 ha. **(A)** Fragmented or status quo landscape, containing old-growth longleaf pine (black cells, covering 3%), second-growth forest (light grey cells, 52%), and nonforested (white cells, 45%). **(B)** Baseline landscape with 50 territories clustered together, which served as our sustainability goal. **(C)** Mitigation landscape with 12 cells in the center restored as second-growth habitat (dark gray cells), making an incremental contribution toward the baseline landscape. **(D)** Withdrawal 1 landscape, in which 12 cells that were more connected old-growth habitat were lost to development. Connectivity was defined as the number of old-growth habitat cells within 3.5 km. **(E)** Withdrawal 2 landscape, in which 24 cells that were less connected old-growth habitat were lost to development

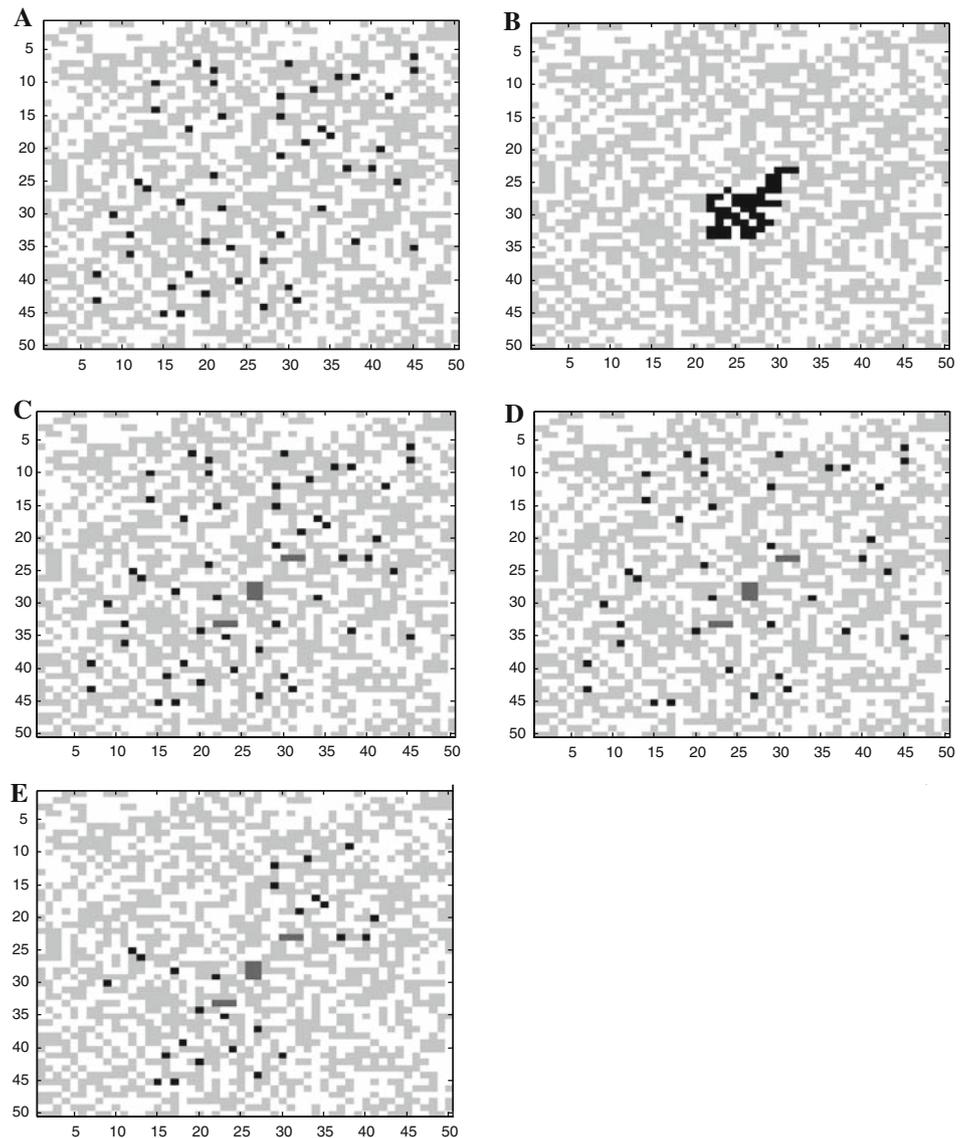


Table 1 Change in probability of persistence resulting from landscape change (e.g., transitioning from status quo to mitigation resulted in increased persistence)

Landscape	A: Status quo ^a	C: Mitigation ^b	D: Withdrawal 1	E: Withdrawal 2
A: Status quo ^a		Increased		
C: Mitigation ^b	Increased		Decreased	Increased
D: Withdrawal 1		Decreased		
E: Withdrawal 2		No change		

Letters assigned landscapes in Fig. 2 are included here. Results for the random-straight dispersal model are reported below the diagonal and for forest-based dispersal are reported above the diagonal for forest-based dispersal

^a At year 20, status quo landscape transitions into the mitigation landscape

^b At year 25, mitigation could transition to either withdrawal 1 or withdrawal 2 landscapes, but withdrawal 1 never transitions into the withdrawal 2 landscape

Population extinction occurred when only one breeding group remained, and no subsequent breeding groups formed. Numbers of breeding groups and helpers were also

tracked in the simulations. We computed the change in probability that an individual territory would be occupied at year 75 to understand how landscape change may affect

population structure. We compared the occupancy of territories after a withdrawal occurred to the occupancy of territories assuming that no withdrawals occurred (i.e., withdrawal minus mitigation). This analysis was applied separately to all original old-growth territories not involved in the trade and to the restored territories. Negative values indicated that the probability of habitat occupancy would have been greater had no withdrawal occurred. A zero value indicated that the change in landscape structure had no impact on probability of occupancy. Positive values indicated that a change in landscape structure occurring elsewhere in the landscape actually increased territory occupancy.

Results

Withdrawal 1 represents a 1:1 mitigation ratio for habitat area and a 2:1 mitigation ratio for connectivity (i.e., the restored territories had roughly twice as much connectivity as territories lost) (Table 2). In contrast, withdrawal 2 represents 1:2 mitigation ratio for area and a 5:1 mitigation ratio for connectivity.

First we considered how habitat trading affects the probability of persistence under the random-straight dispersal model. Restoring habitat in the center of the landscape (mitigation landscape, Fig. 2C) increased the probability of population persistence by 47% (Table 3).

Table 2 Comparison of habitat trades using landscape indices and mitigation ratios

Landscape index	Withdrawal 1 ^a (12 most connected)	Withdrawal 2 (24 least connected)
No. of territories ^b	12 : 12 [1:1]	12 : 24 [1:2]
Average territory connectivity ^c	10.3 : 4.5 [2:1]	10.3 : 1.9 [5:1]

^a Meets USFWS (2003a) criteria of 1:1 trade for habitat area and bank parcels having higher connectivity than habitats lost due to take (i.e., 2:1 ratio for connectivity)

^b Ratio of territories restored to territories lost due to take

^c Ratio of average connectivity of restored territories to average connectivity of territories lost. Connectivity of a territory is estimated as the number of territories within 3.5 km, providing an estimate of adjacency as recommended by USFWS (2003a)

Withdrawal 1 subsequently decreased persistence by 11%, whereas withdrawal 2 resulted in no change in persistence. Examining changes in the probability of territory occupancy within the bank before and after the trade indicated that withdrawal 1 decreased the probability of occupancy slightly for half of the territories in the bank (Fig. 3B). For withdrawal 2, territory occupancy increased slightly for approximately 25% of the territories within the bank. In contrast, the probability of territory occupancy outside of the bank (Fig. 3A) was reduced considerably for some territories for withdrawal 1 but not for withdrawal 2. For withdrawal 2, a small increase in territory occupancy outside of the bank was observed. In general, for random-straight dispersal, withdrawal 1 was more detrimental than withdrawal 2, despite the larger loss of habitat area caused by withdrawal 2.

When we compared the two withdrawals under alternative model assumptions, our results still suggested that withdrawal 2 is the better trade (Table 3), based on changes in probability of persistence. Despite these qualitative similarities, there are potentially important quantitative differences. First, a lower probability of persistence can be expected under the random-straight model in the mitigation landscape (Fig. 2C; 74% vs. 98%, Table 3). In contrast, the conservation value of restoration is lower under forest-based dispersal (i.e., increase in probability of persistence caused by the bank: 25 vs. 47%, Table 3). Under both dispersal models, withdrawal 1 decreased the probability of persistence by roughly an equal proportion (approximately 20%) of the conservation value added by the bank. In contrast, withdrawal 2 actually increased the probability of persistence slightly under forest based dispersal (+2%), compared with no change for random-straight dispersal.

The probability of occupancy in territories not involved in the trade was also sensitive to dispersal assumptions (Fig. 3A). Withdrawal 1 decreased the probability of occupancy by as much as 0.7 to 0.8 for 3 territories under forest-based dispersal but no greater than 0.5 under random-straight dispersal. Under withdrawal 2, assuming forest based dispersal, no appreciable change in probability of territory occupancy was observed.

To further explore why such differences were observed under the random-straight and forest-based models, we contrasted demographic and behavioral results under the

Table 3 Results of simulation and comparison of habitat trades under alternative dispersal models using probability of persistence

Dispersal	Withdrawal 1 (12 most connected)		Withdrawal 2 (24 least connected)	
	Random-straight	Forest-based	Random-straight	Forest-based
Mitigation–status quo	74–27 = 47	98–73 = 25	74–27 = 47	98–73 = 25
Withdrawal–mitigation	63–74 = (–11)	93–98 = (–5)	74–74 = 0	100–98 = 2
Conservation value remaining in bank	36	20	47	27

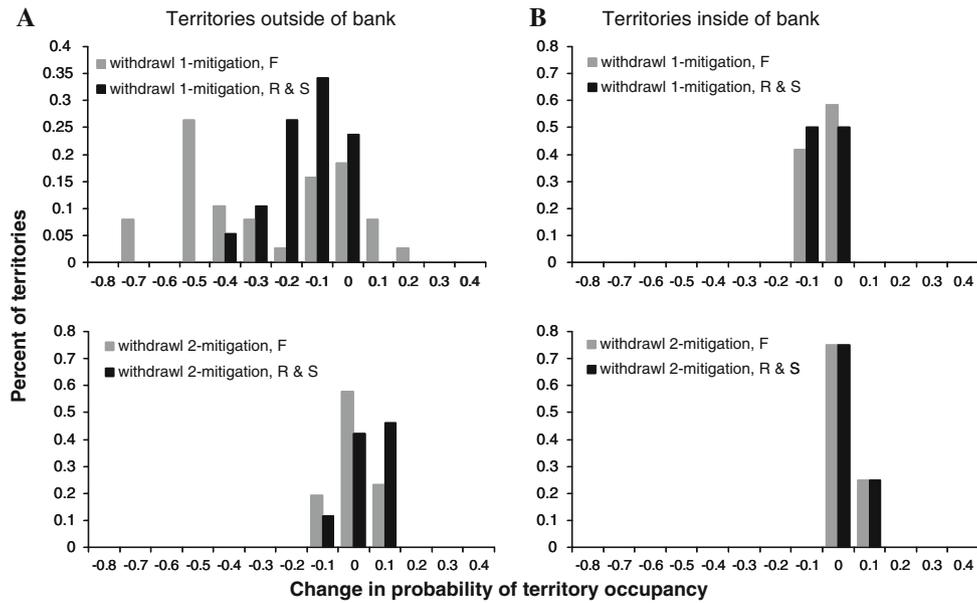


Fig. 3 Change in probability of occupancy of a territory by a breeding pair at time = 75 averaged over 100 simulations. (A) Change in occupancy for all territories in old-growth forest not involved in the trade. (B) Change in occupancy for territories in restored second-growth forest (i.e., the bank). The decrease in habitat

occupancy (change in probability of occupancy <0) after the trade compared with the mitigation landscape, suggested that habitat occupancy would have been greater had no trade occurred. R&S = random-straight dispersal model; F = forest-based dispersal model; W1 = withdrawal 1; W2 = withdrawal 2

Fig. 4 Demographic trends in baseline and status quo landscapes. (A) Number of breeding groups and (B) average number of helpers per group. Average values taken from 100 simulations. Error bars represent one sample SD. R&S = random-straight dispersal model; F = forest-based dispersal model

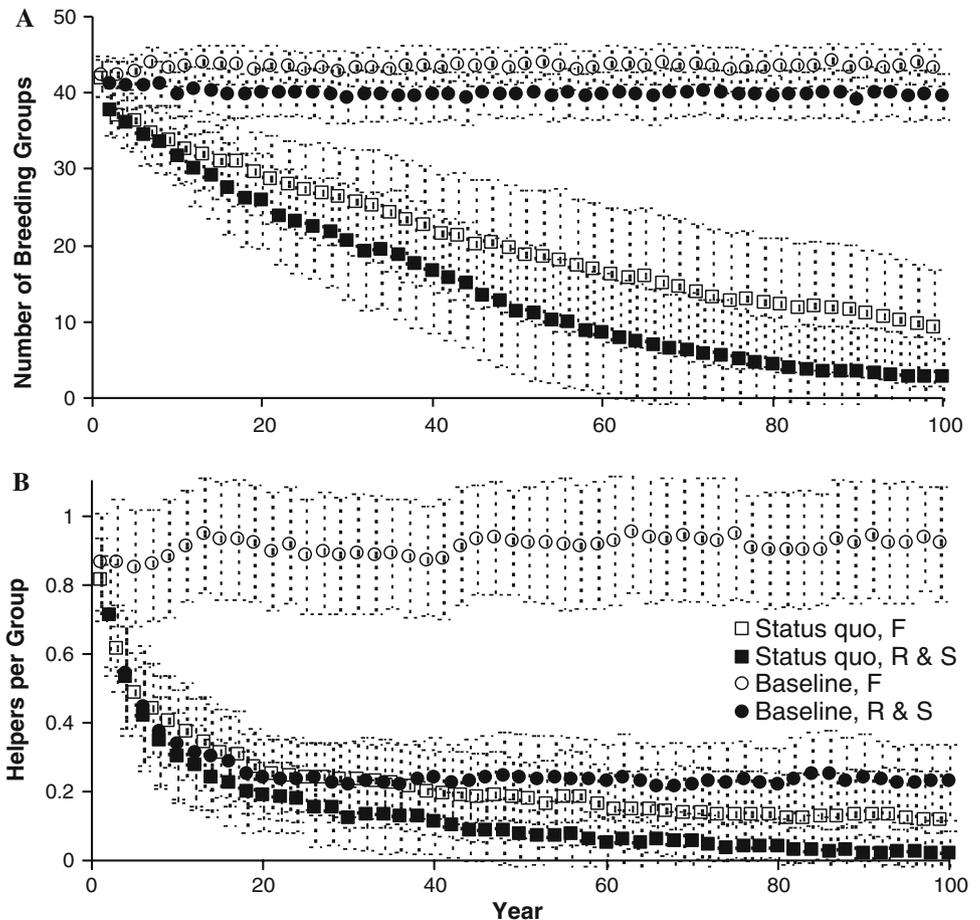


Table 4 Average number of male and female floaters lost as emigrants per year and average dispersal distances (m) from the baseline and status quo landscapes (one sample SD)

Landscape		Random-straight		Forest-based	
		Male RCWs	Female RCWs	Male RCWs	Female RCWs
Baseline	Emigration rate	0.66 (0.15)	1.95 (0.29)	0.0003 (0.002)	0.018 (0.013)
	Average dispersal distance	1,230 (77)	2,844 (31)	497 (38)	3,341 (41)
Status quo	Emigration rate	0.39 (0.45)	1.18 (1.1)	0.12 (0.12)	0.41 (0.32)
	Average dispersal distance	3,252 (110)	4,467 (134)	2,861 (112)	4,135 (101)

alternative models for the baseline and status quo landscapes. Under forest-based dispersal we observed a greater number of breeding groups in both baseline and fragmented landscapes (Fig. 4A). More striking differences among dispersal assumptions were observed when examining the average number of helpers in a territory (Fig. 4B).

Large differences in dispersal behaviors were observed in the simulations congruent with the dispersal assumptions included. Average dispersal distance and emigration rate of the landscape tended to be greater under random-straight dispersal (Table 4). However, in the baseline landscape, female RCWs travel longer distances under forest-based dispersal compared with random-straight dispersal (Table 4). Longer dispersal distances for female RCWs under forest-based dispersal results from retaining female RCWs longer in the region where territories are located, so the probability of sharing migrants between territories at the edges of landscape is greater.

Discussion

Our simulation results suggest that landscape indices and mitigation ratios may not be capable of capturing biologic processes that underlie the sustainability of spatially structured populations. These points are explored later in light of existing policy, specifically the USFWS (2003a) Private Lands Conservation Strategy for RCWs.

Withdrawal 1 meets the USFWS criteria of no net loss of habitat and trading isolated groups for more connected groups based on results of mitigation ratios using landscape indices (Table 2). Probability of persistence for withdrawal 1 did not decrease below the value observed in the status quo landscape under either dispersal assumption (Table 3), indicating that the jeopardy standard was not violated. However, the USFWS may be uncomfortable with withdrawal 1 because it increases the probability of local extinction on lands not involved in the transaction (Fig. 3). This would also affect private landowners outside of the bank who have established safe harbor agreements (Bonnie 1999). Safe harbor agreements provide incentives for individuals to actively manage their lands for endangered

species because the USFWS does not enforce the take prohibition for any additional occupancy by endangered species provided by their actions. In other words, private landowners' efforts to increase occupancy would be rendered ineffective due to changes in landscape spatial structure occurring elsewhere in the landscape. Such effects are not captured by a landscape index approach.

Withdrawal 2 could be interpreted as a take because of the net loss of habitat area (Dwyer and others 1995), and contradiction of the "no net loss of groups" policy enforced by USFWS (2003a). However, withdrawal 2 does not violate the jeopardy standard (Table 3). Rather, we observed that withdrawal 2 had no effect or a positive effect on persistence, even when examining two different assumptions regarding dispersal. Therefore, the relation between habitat area and population viability is unclear when habitat connectivity is also changing over time. Exchanging twice as many territories with lower connectivity for the territories in the bank (i.e., withdrawal 2), often increased the habitat occupancy of territories outside of the bank (Fig. 3). Although the mitigation ratio for connectivity increased greatly for withdrawal 2 and the connectivity index was based on the empiric evidence of the helpers' search radius (Pasinelli and Walters 2002), there is no theoretical basis for relating this geometric change to population processes (Fahrig 2003), and, therefore, no determination of take or jeopardy.

These results suggest that setting policy based simply on structural connectivity will likely be inadequate. Applying mitigation ratios, based on landscape indices, to coordinate the trading endangered species habitat in dynamic landscapes may result in unintended takes occurring elsewhere in the landscape. If mitigation ratios are used, trades must employ new ratios for each trade to account for the change in occupancy that occurred across the landscape because of the previous trade. We argue that the best way to estimate mitigation ratios that incorporate landscape processes important for population viability is to use an SEPM and perform dynamic landscape modeling for each trade individually.

We recognize that it takes much more effort to construct an SEPM than to calculate landscape indices. However, techniques for building and validating such models are

improving rapidly (Grimm and others 2005) despite initial criticism (Beissinger and Westphal 1998). The most complex SEPMs are constructed as individual-based models. A recent science-based Web search yielded >900 citations for individual-based models in ecology (DeAngelis and Mooji 2005). Because of uncertainty associated with the impact of landscape patterns on recruitment and/or migration for many species, many SEPMs may not be able to discern the conservation value of individual land parcels. Conversely, we may be able to estimate mitigation ratios for habitat area and connectivity. The difference between these approaches is that the former requires expressing existing knowledge mathematically and incorporating uncertainty into decision making, whereas the latter allows decision makers to ignore uncertainty, a practice that generally leads to poor decision making (Morgan and Henrion 1990). Furthermore, landscape indices ignore the temporal component of habitat trading, which is troubling because the rate of landscape change can have a large impact on extinction risk (Schrott and others 2005). Because uncertainty is not a sufficient reason to forego decision making under the Endangered Species Act (USFWS 1973), landscape indices will invariably be used in the interim. However, research could be conducted to relate occupancy patterns to landscape patterns before and after the trade to provide the initial steps toward building mechanistic, nonequilibrium models.

Broader Spatial Linkages

Subdivided populations often share migrants with populations in other regions, which has recently been referred to as “metalandcape connectivity” (With and others 2006). The USFWS (2003b) guidance for conservation banking focuses on increasing connectivity at smaller scales (i.e., connectivity within a metapopulation). However, habitat loss and fragmentation occurring outside of a tradable credit market can affect the demographic (With and others 2006) and genetic (Wang 2004) viability of the metapopulation considered. The metalandscape connectivity for endangered species is often unknown, but it can be estimated, even at different time scales, using molecular genetic approaches (Johnson and others 2003). Managing metapopulation and metalandscape connectivity within tradable credit systems would benefit from population genetic approaches (Bruggeman and others 2005), such as Nei’s (1973) theory of gene diversity, which can be applied to multiple spatial scales.

Alternative Dispersal Assumptions

We observed more persistent populations under forest-based dispersal but with stronger isolation effects leading to lower occupancy rates at local scales (i.e., withdrawal 1).

This resulted because territory occupancy and retention of helpers was greater for forest-based dispersal, and individuals tend to disperse shorter distances (Table 4). The average number of helpers retained in the baseline landscape (Fig. 4B) under forest-based dispersal slightly underestimates the number observed in clustered territories of old-growth forests in Georgia (Engstrom and Saunders 1997). In contrast, when using the point estimate for the probability of natal dispersal derived from the Sandhills Population in North Carolina (Letcher and others 1998), the average number of helpers retained in the baseline landscape under random–straight dispersal closely approximated that observed for the Sandhills Population. Therefore, updating model assumptions to include recent hypothesis regarding demographic and landscape factors (Pasinelli and Walters 2002), may help extend the Letcher model to new landscapes.

Conclusion

Had the trades been evaluated by existing technology and policy, withdrawal 1 would have been favored over withdrawal 2. We argue that withdrawal 1 is the wrong decision because of the lower probability of persistence and lower probability of habitat occupancy outside of the bank. The alternative would be to apply an SEPM to determine how best to implement restoration at the landscape scale to prevent violation of take and jeopardy standards at the local and regional scales. This would increase transaction costs. However, if results indicate that the banker could double the size of his or her market and increase occupancy in territories outside of the bank (i.e., withdrawal 2), such transaction costs may be acceptable by the USFWS and private landowners. In other words, by recognizing the strong interaction between recruitment and migration observed in RCWs, trades that benefit the species and private landowners can be made.

We believe that a scientifically defensible habitat-trading system designed to mitigate habitat fragmentation (USFWS 2003b) must recognize the uncertainty regarding the relation between the landscape pattern and (meta)population processes (Bruggeman and others 2005). Habitat trading can have negative consequences for RCW groups remaining after a trade, outside of a bank, even if the extinction risk for the entire population is not increased and no decrease in habitat area occurs. We found that if bankers strategically locate their restoration efforts, changes in landscape structure should not appreciably affect levels of occupancy within the bank (Fig. 3).

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Appendix: Modeling RCW Dispersal

We used the equations and parameters described in Letcher and others (1998) to model probability of nesting, the probability of nest success, and the number of fledglings produced. The model is both age and stage structured, uses a seasonal time step (3 months per step), and assumes that biologic processes proceed in the following order: reproduction (season 1 only), mortality, natal dispersal, territorial competition, and then dispersal.

We assumed that all old-growth habitat cells in our landscape start with a breeding pair. Letcher's model assumes that fecundity is only a function of the ages of male and female breeders and the number of helpers in a territory. The age of each breeder was randomly chosen from a normal distribution with a mean of 4 (Reed and others 1988) and variance of 1. The average number of helpers observed in old-growth longleaf pine habitat, based on 2 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 two helpers.

The probability of an individual's transition among life stages depends on the interaction between demography, behavior, and landscape spatial structure. The model assumed that all female fledglings surviving the first year became floaters or breeders but never helpers. Male RCWs stay as helpers approximately 81% of the time to gain access to breeding territories, either their territory or an adjacent territory (Letcher and others 1998). Walters and others (1988) observed that female RCWs remain as helpers on their natal territory only 1% of the time, usually dispersing to become floaters. When a helper takes over a territory after the male RCW's death, >90% of the time the adult female RCW disperses to avoid inbreeding (Daniels and Walters 2000). 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).

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 empiric estimates of a bird's perceptual range, the model uses assumptions thought plausible by Letcher and others (1998), who assumed that all fledglings, helpers, floaters, and solitary male RCWs can compete for breeding vacancies within 3.5 km of their current location.

The alternative model describing the probability that male fledglings delay dispersal for the forest-based SEPM was based on the study by Pasinelli and Walters (2002). The simulation model already predicted the 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 were 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); therefore, excluding this variable should not significantly bias model results. For territory quality, we assumed that all old-growth remnants were of equal quality, as 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 as 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 and others 2001). Therefore, the probability of male natal dispersal ($P[D_{m,nat}]$) can be estimated as (Eq. A1):

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

where FL_m is the number of male fledglings, 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. Table A1 reports the parameter values fitted to the logit function by Pasinelli and Walters (2002). When this equation was incorporated into our model, unnaturally large number of helpers were retained within a territory (i.e., ≤ 10 helpers) when density of old-growth longleaf pine was high in the landscape. In the Sandhills Region, only 30% of groups contained at least 1 helper, and 5% of groups contained >1 helper, with 3 being the maximum number of helpers (Walters and others 1988). Although Pasinelli and Walters (2002) found that the number of adults within a group did not affect the probability of male RCW natal dispersal, they indicated that the maximum number of helpers observed in any RCW group is 4. The

Table A1 Parameter values used to estimate probability of male natal dispersal (Eq. A1)^a

Parameter	<i>p</i>
d_0 Male natal dispersal intercept	-1.930
d_1 Male natal dispersal number of male fledglings	0.700
d_2 Male natal dispersal territory quality within 1 km	-0.399
d_3 Male natal dispersal quality of natal territory	-0.082
d_4 Male natal dispersal vacancies within 3.5 km	0.044

^a Pasinelli and Walters (2002)

probability of male natal dispersal was calculated with the previous equation when <3 helpers are present but set to unity otherwise, which created a maximum of 4 helpers when habitat density was high. To more closely approximate Letcher's SEPM, the random-straight model assumes the probability of male RCW natal dispersal is a constant equaling 0.19 (Letcher and others 1998).

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 is found at the 3.5-km perimeter, the birds will orient to the greatest density of secondary growth. Therefore, the forest-based model assumed that both sexes choose their initial direction of travel during natal dispersal based on the direction providing the greatest density of RCW habitat. In contrast, the random-straight model assumed that birds choose their initial direction of travel at random, as included in Letcher and others (1998).

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 and others 1998). Our model assumes that all female RCWs and first year male floaters disperse 4.9 km per season (i.e., seven cells). Older male floaters on average moved 2.3 km per season (Letcher and others 1998). We assumed that male floaters move 2.12 km per season or (three cells). Each floater is allowed to compete for territorial vacancies in cells adjacent to its current location before taking the next step.

We assume that birds make directional choices based on either forest structure (Connor and Rudolph 1991), the tendency to disperse in a straight line (Letcher and others 1998), or a combination of both factors. Assuming that no vacancies exist, each of the eight adjacent cells is assigned a probability of occupancy based on plausible dispersal rules (Zollner and Lima 1999). We assigned 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 (Table A2). The level of preference assigned to each cell was based on two contrasting sets of rules for dispersal: straight versus forest based. If the birds show preference for straight movement, the model assigns four levels of preferences for the direction of travel in the next step based on the direction of travel in the previous time step (Table A2). If the birds choose their next step based on habitat quality in adjacent cells (forest based), the model recognizes four levels of habitat quality (Table A2). The values in Table A2 are assigned to the eight-cell neighborhood providing matrices V (straight) and HQ (forest-based). Both preferences assign a zero probability of a bird not moving, and the straight-dispersal approach prevents backward movement. The matrices are combined within the following equation to estimate the probability that the individual will move to each cell given its location in the previous time step (L_t) and surrounding forest structure (HQ) (Eq. A2):

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

where d_v and d_{hq} are the (0 to 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 with a $u[0,1]$ random number to determine the bird's location in the next time step. For the present analysis we constrained the model to simulate forest-based dispersal only, [d_v, d_{hq}] = [0, 1] or straight-dispersal, [d_v, d_{hq}] = [1, 0].

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Table A2 Preferences assigned in alternative models of dispersal behaviors (Eq. A2)

Random-straight model	Preference	Forest-based model
0° (straight)	0.4	Old-growth longleaf pine
45°	0.2	Restored second-growth longleaf pine
90°	0.08	Pine–hardwood mixed
135°	0.02	Nonforested

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