Replacing Sources with Sinks: When Do Populations Go Down the Drain?

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Abstract

We investigate the scenario in which some amount of higher quality habitat is destroyed and is then replaced by some undetermined amount of lower quality habitat. We examined how much low-quality habitat would need to be created to maintain the equilibrium population abundance in the entire geographic area. Using a source–sink model, we find that (1) the number of hectares of created habitat per hectare of destroyed habitat must equal the ratio of the high-quality habitat's productivity to the low-quality habitat's productivity, however, (2) if the created habitat is a sink, then there is a threshold fraction of destroyed high-quality habitat below which the initial population abundance cannot be maintained through the creation of habitat. We illustrate these results using data on Red-winged Blackbirds (*Agelaius phoeniceus*) in two different regions where high-quality habitat is being replaced by or converted into lower quality habitat.

Key words: habitat restoration, restoration ecology, source–sink dynamics, wetland mitigation, wildlife populations.

Introduction

Since European settlement, greater than 50% of the wetlands in the United States have been lost to agriculture and development. In our region (Chesapeake Bay), there remain less than 2,000 ha of tidal wetland, of which 0.5–1% may be lost to legal development annually (reviewed in Perry et al. 2001). Wetlands have been the subject of much attempted restoration because they are highly valued for the ecological services they provide, including support of wildlife. Legislation aimed at preserving wetlands has led to the creation or restoration of many mitigation (i.e., replacement) wetlands to fulfill the official policy of no net loss (National Wetlands Policy Forum 1988).

The policy of no net loss assumes that when a wetland is destroyed, another wetland of equal or greater size will be created. However, even if new habitat is created to offset losses, this created habitat may not fully replace the ecological functions of the natural habitat. For example, created wetlands appear to support different species than natural wetlands (Melvin & Webb 1998; National Academy of Science 2001; Snell-Rood & Cristol 2003). Thus, for those with the goal of preventing population declines, it is important to determine how much mitigation habitat must be created or restored to fully replace the value of what has been destroyed.

The wetland destruction–construction paradigm is a carefully regulated form of habitat conversion, but it is by no means the only one in which land is converted into habitat with lower value to wildlife populations. When prairies are converted into grazed grasslands, or forests into fragmented woodlots, there is no legal requirement to provide mitigation, but negative ecological impacts occur, nonetheless. Many of the animals found in natural habitats can live in the new habitat created, but there is usually a reduction in both the quantity and quality (Doak 1995; Ford et al. 2001; Manolis et al. 2002). For example, conversion of pristine forests to fragmented ones has been implicated in producing sink populations of neotropical migrant songbirds in the Midwestern United States through increased nest predation and brood parasitism (Donovan et al. 1995*b*; Ford et al. 2001; Manolis et al. 2002).

Source–sink models (Pulliam 1988) are among the simplest demographic models linking habitats of differing quality (Doak 1995). Source–sink models have been used to examine the consequences of habitat degradation for populations living in high- and low-quality habitats linked by dispersal (Doak 1995; Donovan et al. 1995*a*). Assuming that individuals do not perceive differences in habitat quality, Doak (1995) found that minor habitat degradation could lead to dramatic declines in population growth rates. Regardless of the quality of the source habitat, Donovan et al. (1995*a*) found that fragmentation of the source area affected metapopulation structure and reduced population size. Unlike previous studies, we investigate how to compensate for the destruction of high-quality habitat with the creation of new lower quality habitat. The objective of this paper is to examine how much low-quality habitat would have to be created following the destruction of high-quality habitat to maintain the equilibrium abundance for a given animal population. We use natural and created salt

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marshes to examine this issue. Although our model addresses a pressing aspect of wetland conservation policy, it also has more general application to many situations in which good-quality habitat is destroyed and replaced by newly created lower quality habitat.

Modeling Source–Sink Dynamics

We model the dynamics of a population living in a network of habitat patches of differing quality. Each patch contains a fixed number of breeding sites and belongs to one of two categories: high quality or low quality (Fig. 1a). The average number β_1 of female offspring produced by a female in a high-quality breeding site is greater than the average

(a)

(b)

WINTER

Survival through non-breeding season

Immigration/ emigration
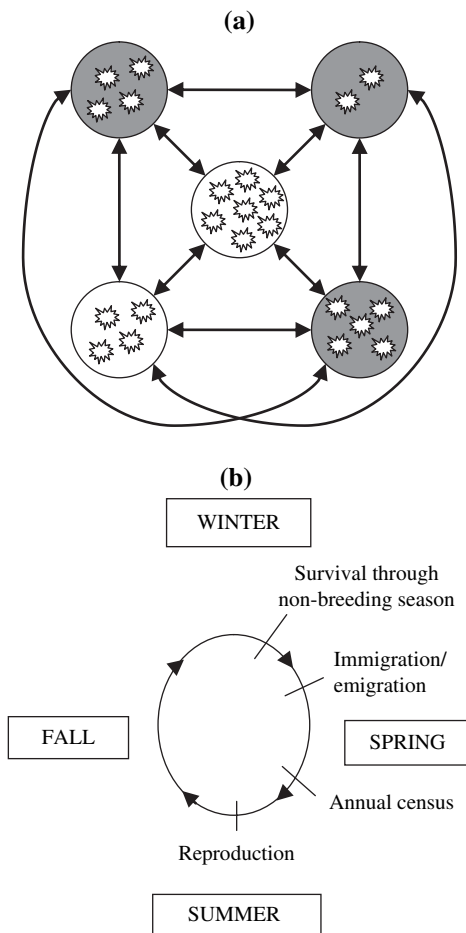
FALL

SPRING

Annual census

Reproduction

SUMMER

Figure 1. Overview of system of interest. (a) High-quality (white) and low-quality (gray) habitat patches are located in various parts of a greater geographical area. Various numbers of breeding sites (indicated by the starburst symbols) are located in each patch. (b) An annual census is taken in each habitat patch in the spring at the initiation of the breeding season (summer). Each female breeding in the habitat produces β female juveniles by the end of the breeding season. There is no adult mortality during the breeding season. Adults survive the nonbreeding season (winter) with probability P_A and juveniles survive with probability P_J.

number β_2 of female offspring produced by a female in a low-quality breeding site. An annual census recording the population abundance z_n in the nth season is taken prior to reproduction. On average, a fraction P_J of juveniles and a fraction P_A of adults survive the nonbreeding season. After the nonbreeding season, individuals are free to disperse to a different habitat patch, and the census is then repeated (Fig. 1b). Juveniles mature into adults after 1 year. Because the low-quality patches have a fixed number of breeding sites, our model generalizes the source–sink dynamics model of Pulliam (1988) where low-quality patches have an infinite number of breeding sites.

Following Pulliam (1988), we assume that individuals can distinguish between the high- and low-quality habitat patches and show preference toward high-quality patches (e.g., Delibes et al. 2001). A limited number of breeding sites are available in each habitat patch, and individuals unable to secure breeding sites are nonbreeding "floaters" who have the same probability of surviving as breeding adults. Any individual potentially has the same chance of securing a breeding site in a given year, that is, there is no age or prior-residence effect. To describe the distribution of nesting sites, it suffices to keep track of $\hat{n}_1$, the number of breeding sites in high-quality patches, and $\hat{n}_1$, the number of breeding sites in low-quality patches. Under these assumptions, the model is given by

$$z_{n+1} = P_A z_n = P_J \overline{\beta}_z z_n \qquad (1)$$

where

$$\overline{\beta}_z = \begin{cases} \beta_1 & \text{if } z_n \leq \hat{n}_1 \\ \dfrac{[\beta_1 \hat{n}_1 + \beta_2 (z_n - \hat{n}_1)]}{z_n} & \text{if } \hat{n}_1 \leq z_n \leq \hat{n}_1 + \hat{n}_2 \\ \dfrac{(\beta_1 \hat{n}_1 + \beta_2 \hat{n}_2)}{z_n} & \text{if } z_n \geq \hat{n}_1 + \hat{n}_2 \end{cases}.$$

Model Analysis

If $\beta_1 P_J + P_A < 1$, then the high-quality habitat is a sink and the entire metapopulation is doomed to extinction. Thus, we will assume that the high-quality habitat type is always a source, that is, $\beta_1 P_J + P_A > 1$. Solving for the nonzero equilibrium z^* of Eq. (1), we find that if $(\beta_1 \hat{n}_1 * \beta_2 \hat{n}_2 / \hat{n}_1 + \hat{n}_2) P_J + P_A \geq 1$,

$$z^* = \frac{P_J}{1 - P_A} (\beta_1 \hat{n}_1 + \beta_2 \hat{n}_2), \qquad (2)$$

otherwise,

$$z^* = \frac{P_J \hat{n}_1 (\beta_1 - \beta_2)}{1 - P_A - P_J \beta_2}. \qquad (3)$$

To examine the consequences of destroying a natural habitat patch and replacing it with some unknown amount of lower quality created or degraded habitat, consider a situation where there are initially N high-quality breeding sites and no low-quality habitat (i.e., $\hat{n}_1 = N$ and $\hat{n}_2 = 0$). Although today this pristine situation is extremely unlikely, it is a useful starting point in the investigation of

this model. The equilibrium abundance under these pristine conditions is

$$\frac{P_J}{1 - P_A}\beta_1 N. \quad (4)$$

Now, suppose that some high-quality habitat is destroyed, leaving only $\hat{n}_1$ breeding sites in high-quality patches. Ideally, conservation efforts should maintain the pristine population abundance (Eq. 4) by creating sufficiently many low-quality habitats to offset the destruction of natural habitat. If the created habitats are sources (i.e., $\beta_2 P_J + P_A > 1$), then it is possible to maintain the pristine equilibrium abundance in Eq. (4) by creating low-quality habitat that supports

$$\hat{n}_2 = \frac{\beta_1}{\beta_2}(N - \hat{n}_1) \quad (5)$$

breeding sites. Notice that this is a simple linear relationship that depends only on the ratio of the per capita reproductive success of the high-quality habitat type to the per capita reproductive success of the low-quality habitat type. The "rate of mitigation" can be defined as the number of low-quality breeding sites needed to replace the destruction of a single high-quality breeding site:

$$\text{rate of mitigation} = \frac{\beta_1}{\beta_2}. \quad (6)$$

This is simply the ratio of the reproductive successes of both types of habitat.

When the created habitats are sinks (i.e., $\beta_2 P_J + P_A < 1$), we show in the Appendix that there is a "point of no return" defined by

$$F = \frac{\beta_1(1 - P_A - P_J\beta_2)}{(1 - P_A)(\beta_1 - \beta_2)}. \quad (7)$$

This is the minimum fraction of high-quality sites that must remain to maintain the pristine population abundance (Eq. 4). When $(\hat{n}_1/N) < F$, it is possible, just like in the previous case, to maintain the pristine population abundance (Eq. 4) by creating low-quality habitats with $\hat{n}_2 = \beta_1/\beta_2(N - \hat{n}_1)$ nesting sites. However, when $(\hat{n}_1/N) > F$, the pristine state is irretrievably lost because even creating low-quality habitats with an innumerable number of nesting sites will not result in a system that achieves the pristine equilibrium abundance. Equation (7) implies that the greater the quality of the pristine habitat, the less of it that can be destroyed in order to maintain the pristine equilibrium abundance. Alternatively, increasing β_2 results in a decrease in the minimum number of high-quality breeding sites that must remain, as might be expected (Fig. 2). Increasing P_A and P_J have similar effects.
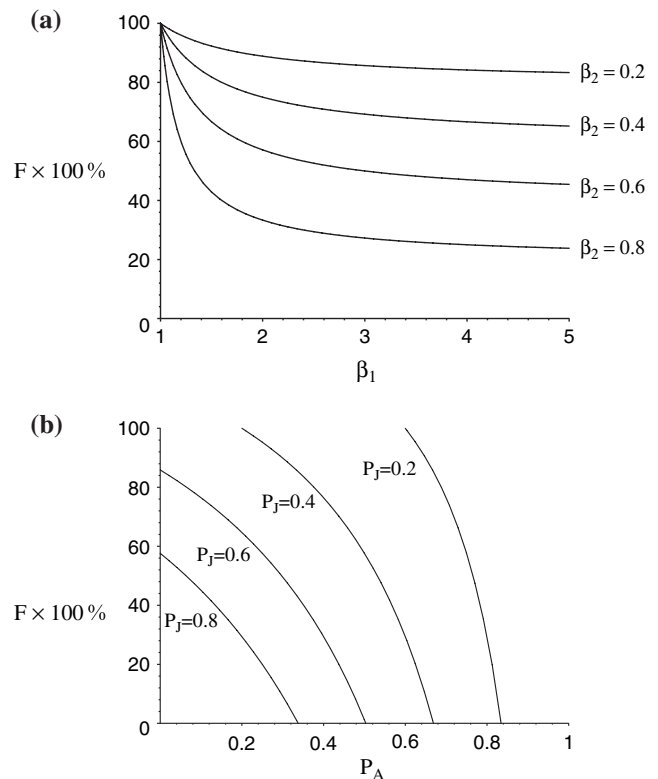

Figure 2. Point of no return. This figure displays the minimum percentage of higher quality breeding sites, $F \times 100\%$, that must remain for the initial equilibrium abundance to be maintained as (a) a function of the per capita reproductive success in the higher quality habitat (β_1) and (b) as a function of the adult survivorship (P_A). The function is plotted for different values of reproductive success in the lower quality habitat (β_2) and juvenile survivorship (P_J).

Case Study: Red-Winged Blackbirds

We applied this modeling framework to two independent datasets on populations of Red-winged Blackbird (*Agelaius phoeniceus*). The Red-winged Blackbird is not a species of conservation concern, but it serves as a good model because it is perhaps the best-studied bird in North America (Yasukawa & Searcy 1995). The first dataset is ours and was recently collected on natural and created salt marshes in southeastern Virginia. The model is of great interest here because of questions pertaining to policy decisions about the destruction and replacement of wetlands, which are important to many bird populations. The second dataset was collected by Vierling (2000) on Red-winged Blackbird populations inhabiting tallgrass prairies and hayfields in Boulder County, Colorado. These data are of interest because it is another example of a higher quality natural habitat being "replaced" by a lower quality habitat—in this case through conversion rather than mitigation. In cases of habitat conversion, it may be possible to compensate for the reduction in habitat quality by restoring or creating additional habitat elsewhere, as is done when wetlands are negatively impacted by development.

Our model can be used to determine, in theory, the amount of compensation needed after habitat conversion or degradation.

Natural and Created Salt Marshes

Seven natural and seven created salt marshes (9–20 years postcreation), matched for size, shape, and surrounding land uses, were surveyed May–August 2002. Each site was visited every 10 days. We searched for nests on each visit, and this was facilitated by behavioral observations of males and females coming and going from nests. Vegetation several meters from each nest was marked with numbered flagging tape to facilitate relocation, and on each visit, the condition and contents of each nest were noted. We used the Mayfield method to determine nesting success (Mayfield 1975; Hensler 1985). This method corrects for upward bias that can occur when using the more intuitive apparent estimator method (successful nests/total nests). The mean number of female offspring per adult female per year (β, hereafter, "per capita reproductive success") was determined using methods described by Donovan et al. (1995*b*), with the following assumptions (which were supported by our data): (1) females could fledge a maximum of one brood per year and (2) females would renest up to two times if two consecutive nesting attempts failed. Adult and juvenile survivorship values (P_A and P_J, respectively) were taken from the literature on Red-winged Blackbirds. Estimates of annual adult survivorship, which does not differ by sex, ranged from 40.3 to 63% (Frankhauser 1967, 1971; Searcy & Yasukawa 1981; Yasukawa 1987; Yasukawa & Searcy 1995; Vierling 2000). Juvenile survivorship estimates range from 49 to 65% (Vierling 2000).

Natural salt marshes had a higher per capita reproductive success than created salt marshes (natural: 1.11 ± 0.48, created: 0.46 ± 0.46; $t_{11} = -2.533$, $p = 0.028$; $n = 13$ marshes, one natural marsh excluded due to uncertain nest fates). This is a conservative estimate because sites that are too poor to have any nests did not contribute to this calculation. Depending on the adult and juvenile survivorship values used, natural and created salt marsh habi-

tat could be classified as either source ($\beta P_J + P_A > 1$) or sink ($\beta P_J + P_A < 1$) habitat. Using the maximum juvenile and adult survivorship values, all six of the natural salt marshes were classified as sources and three of the seven created salt marshes were classified as sources. Because our model focused on differences between two habitat types, rather than separate sites within each habitat type, we recalculated per capita reproductive success values using all nests within each habitat type (natural: $\beta_1 = 1.1283$, created: $\beta_2 = 0.8277$). We considered the results for all combinations of maximum, minimum, and mean adult and juvenile survivorship values.

Three possible scenarios exist: (1) Natural salt marshes and created salt marshes are both sinks; (2) natural salt marshes are sources and created salt marshes are sinks; and (3) natural salt marshes and created salt marshes are both sources. The first scenario results in extinction of the entire metapopulation; hence, there is no rate of mitigation (Table 1). A rate of mitigation can be calculated for scenarios 2 and 3. This rate is the same regardless of the adult and juvenile survivorship values used (Table 1). In this situation, one would need to create or restore 1.36 times the area of natural salt marsh destroyed (assuming that the number of breeding sites is proportional to area) to maintain the Red-winged Blackbird metapopulation. If created salt marshes are sinks, there is a point of no return. If any additional natural salt marsh habitat is destroyed beyond this point, no amount of newly created salt marsh habitat can result in the same initial equilibrium abundance of blackbirds. A great deal of variation exists in the point of no return (14–79% of the original habitat must be preserved) because of the variation in survivorship estimates; thus, it would be difficult, in practice, to pinpoint the point of no return without being extremely confident about the adult and juvenile survivorship values (Table 1).

Natural Prairie and Converted Hayfield

Vierling (2000) monitored a variety of breeding habitats of Red-winged Blackbirds, including tallgrass prairies and agricultural hayfields. Nest searches were conducted three

Table 1. Model predictions using our data from created and natural salt marshes.

Scenario	P_A	P_J	λ_1	λ_2	Rate of Mitigation = β_1/β_2	Point of No Return
1	0.403	0.490	0.9559	0.8086	N/A	N/A
2	0.403	0.570	1.0461	0.8748	1.3632	0.7872
2	0.403	0.650	1.1364	0.9410	1.3632	0.3709
2	0.510	0.490	1.0629	0.9156	1.3632	0.6467
2	0.510	0.570	1.1531	0.9818	1.3632	0.1395
3	0.510	0.650	1.2434	1.0480	1.3632	N/A
3	0.630	0.490	1.1829	1.0356	1.3632	N/A
3	0.630	0.570	1.2731	1.1018	1.3632	N/A
3	0.630	0.650	1.3634	1.1680	1.3632	N/A

P_A = adult survivorship; P_J = juvenile survivorship; λ_1 = growth rate of natural salt marsh; λ_2 = growth rate of created salt marsh ($\lambda_i = P_A + P_J\beta_i$, if $\lambda_i < 1$, habitat i is a sink). $\beta_1 = 1.1283$; $\beta_2 = 0.8277$. The point of no return is the minimum fraction of high-quality sites that must remain to maintain the pristine population abundance.

to four times per week from April to July of 1995, 1996, and 1997. Vierling (2000) used the same methods as we did for calculating nesting success and per capita reproductive success. Using her maximum juvenile and adult survivorship values, one of the five tallgrass prairies and none of the five hayfields could be classified as sources.

We used the per capita reproductive success values reported by Vierling (2000) for the 3 years of combined data (prairie: 0.77, hayfield: 0.24). We used the maximum, minimum, and mean adult and juvenile survivorship values reported. Hayfields were sinks regardless of the adult and juvenile survivorship values used (Table 2). Therefore, when tallgrass prairie is a source, there is a rate of mitigation of 3.21. This means that for every unit of tallgrass prairie that is converted to hayfield, 3.21 units of mitigation habitat would have to be created, in addition to the new hayfield, to maintain the pristine equilibrium abundance of Red-winged Blackbirds (assuming the quality of the additional mitigation habitat is at least as good as that of the converted hayfield). When the prairie is a source, 84–99% of original prairie must be preserved to maintain the blackbird population abundance (Table 2).

Discussion

We examined how much lower quality habitat would have to be created to maintain the equilibrium abundance of a population if a specified amount of high-quality habitat is destroyed. This question has not been answered before; yet, it is a very important and useful one as a general guide for conservation management decisions such as wetland mitigation policy. Critically, we are explicitly acknowledging that newly created habitat is not of the same quality as the natural habitat it replaces. We developed a model for a network of habitat patches of differing qualities spread randomly throughout a greater geographical area. Each patch belongs to one of the two categories. One of these categories is of higher average quality than the other, where quality is defined empirically as mean number of female offspring per adult female per year.

Very striking was the finding that if the low-quality habitat is so poor that it is a sink (i.e., the population will decline without immigration), there is a point of no return at which no more high-quality habitat can be destroyed if the goal is to maintain the initial equilibrium abundance. This point of no return can be thought of as the minimum amount of the high-quality (source) habitat that must be preserved. Depending on reproductive and survival parameters, our model predicts that this point of no return may come rapidly, after little destruction of source habitat.

We found a simple equation for the rate at which low-quality habitat must replace high-quality habitat. This is the number of low-quality breeding sites that must be created in order to replace a single high-quality breeding site. This rate of mitigation is simply the ratio of the high-quality habitat's productivity to the low-quality habitat's productivity. Therefore, for this metric, juvenile and adult mortality rates are inconsequential. However, the point of no return does depend on such parameters, so the rate of mitigation suggested by the model would have to be used with caution unless survivorship values could be estimated with confidence. This is because the model shows that once the point of no return has been reached, no amount of replacement will maintain the population at its original level.

Adult and juvenile mortality rates can have great influence on the behavior of the metapopulation because they determine source or sink classification. As simulation with data from Red-winged Blackbirds showed, for some estimates of survivorship, the entire metapopulation may act as a sink and decline deterministically to extinction. For other estimates of survivorship, the low-quality site is a source and there is not a point of no return. Because it is often very difficult to determine adult and juvenile mortality rates for long-lived, wide-ranging animals, in practice it would be difficult to pinpoint the point of no return. Consequently, even if habitat was replaced at the rate prescribed by this model, the point of no return could be crossed without realizing it, resulting in a population decline. It must also be recognized that the methodology used to calculate per capita reproductive success (Donovan

Table 2. Model predictions using data from tallgrass prairies and hayfields (from Vierling 2000).

P_A	P_J	λ_1	λ_2	Rate of Mitigation	Point of No Return
0.450	0.490	0.8273	0.5676	N/A	N/A
0.450	0.580	0.8966	0.5892	N/A	N/A
0.450	0.650	0.9505	0.6060	N/A	N/A
0.560	0.490	0.9373	0.6776	N/A	N/A
0.560	0.580	1.0066	0.6992	3.2083	0.9932
0.560	0.650	1.0605	0.7160	3.2083	0.9377
0.630	0.490	1.0073	0.7476	3.2083	0.9911
0.630	0.580	1.0766	0.7692	3.2083	0.9063
0.630	0.650	1.1305	0.7860	3.2083	0.8403

P_A = adult survivorship; P_J = juvenile survivorship; λ_1 = growth rate of tallgrass prairie; λ_2 = growth rate of hayfield; $\beta_1 = 0.77$; $\beta_2 = 0.24$. The point of no return is the minimum fraction of high-quality sites that must remain to maintain the pristine population abundance.

et al. 1995*b*) is based only on data from sites that were of good enough quality that birds attempted to nest. Sites with no nest attempts (two of seven created marshes in our study; one of five hayfields in Vierling's [2000] study) cannot be counted toward the amount of mitigation if the goal is to preserve the pristine equilibrium abundance.

There have been many theoretical and empirical studies of the effect of habitat destruction without mitigation on population or species persistence. Since Pulliam's (1988) model of source–sink dynamics in an actively dispersing species, it has been recognized that destruction of source habitat can lead to local population extinction. Davis and Howe (1992) show that increasing the number of sink breeding sites beyond a threshold value will result in no further increase in metapopulation size. Like our point of no return, their threshold arises because the source cannot produce enough extra individuals to take advantage of additional sink breeding sites. Other theoretical and empirical studies have emphasized the importance of connectivity. In one typical empirical study, Radford and Bennett (2004) determined a critical "demographic isolation threshold" beyond which White-browed Treecreepers (*Climacteris affinis*), a threatened species, did not disperse. They also discussed a "habitat quality" threshold, which was dependent on cover by particular tree species. One of their conservation recommendations was the restoration of cleared habitat, but we have shown that simply restoring habitat is not sufficient to maintain population levels if habitat destruction is still taking place elsewhere and the restored habitat is not of high enough quality.

Our analysis has several limitations. We assume that the quality of breeding sites fall into two types, higher and lower quality. In reality, breeding site quality follows more of a continuous distribution ranging from high quality to unsuitable. Although incorporating this additional spatial complexity is unlikely to change the qualitative predictions of our models (i.e., if all created habitats are sinks, then there are still points of no return), it is likely to influence the quantitative predictions of how much and what quality of the pristine habitat can be destroyed before reaching a point of no return. This would, in turn, affect qualitative predictions about the rates of mitigation. We also assumed that the population exhibits an ideal preemptive distribution in which individuals move to sink habitats only when all source habitats are occupied (Pulliam 1988). This assumption does not account for site fidelity or costs of dispersing between sites. However, because the ideal preemptive distribution is evolutionarily stable, it serves as a good null hypothesis in the absence of evidence to the contrary.

An implicit assumption behind current wetland mitigation policy is that destroyed wetlands should be replaced at approximately the rate they are destroyed, to maintain the policy of no net loss. This policy has been followed closely in our region, where, over the past decade (1993–2002), local, state, and federal regulators have required the creation of 17.8 ha of salt marsh as compensation for the permitted destruction or alteration of 19.9 ha of similar wetland (ratio = 0.9:1; public communications, accessed 1 May 2004, http://www.vims.edu/rmap/wetlands/cgi-bin/index.htm, & H. Jackson, U.S. Army Corps of Engineers, personal communications, 2003). Our field data indicate that mitigation salt marshes are more likely to be population sinks than those that they replaced. Our model suggests that the equilibrium abundance of Red-winged Blackbirds is expected to decrease in the absence of further mitigation. Moreover, there is a point of no return when an insufficient amount of salt marshes are conserved. These predictions have dire implications for species of greater conservation importance than the Red-winged Blackbird, particularly those that have more specialized habitat requirements.

Acknowledgments

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Appendix

In this Appendix, we prove that if the created patches are sinks (i.e., $\beta_2 P_J + P_A < 1$), then there is a point of no return as defined in Eq. (7). Taking the derivative of $(\beta_1 \hat{n}_1 + \beta_2 \hat{n}_2 / \hat{n}_1 + \hat{n}_2) P_J + P_A$ with respect to $\hat{n}_2$ yields $(\beta_2 - \beta_1) \hat{n}_1 / (\hat{n}_1 = \hat{n}_2)^2 P_J < 0$. Hence, $(\beta_1 \hat{n}_1 = \beta_2 \hat{n}_2 / \hat{n}_1 = \hat{n}_2) P_J = P_A$ is a decreasing function of $\hat{n}_2$. Because we have assumed that the created patches are sinks, we get that $\lim_{\hat{n}_2 \to \infty} (\beta_1 \hat{n}_1 = \beta_2 \hat{n}_2 / \hat{n}_1 = \hat{n}_2) P_J = P_A = \beta_2 \quad P_J = P_A < 1$.

From these observations and the definition of z^*, it follows that z^* is an increasing function of $\hat{n}_2$ and $\lim_{\hat{n}_2 \to \infty} z* = P_J \hat{n}_1 (\beta_1 - \beta_2) / 1 - P_A - P_J \beta_2$. Hence, if there only remain $\hat{n}_1$ of the original N source patches, then the creation of sinks can only return the population abundance to pristine levels if $\lim_{\hat{n}_2 \to \infty} z* = P_J \hat{n}_1 (\beta_1 - \beta_2) / 1 - P_A - P_J \beta_2 \geq (N \beta_1 P_J / 1 - P_A)$. This latter inequality is equivalent to Eq. (7).