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Articles

Implications of Spatially Variable Costs and Habitat Conversion Risk in Landscape-Scale Conservation Planning

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Abstract

"Strategic habitat conservation" refers to a process used by the U.S. Fish and Wildlife Service to develop cost-efficient strategies for conserving wildlife populations and their habitats. Strategic habitat conservation focuses on resolving uncertainties surrounding habitat conservation to meet specific wildlife population objectives (i.e., targets) and developing tools to guide where conservation actions should be focused on the landscape. Although there are examples of using optimization models to highlight where conservation should be delivered, such methods often do not explicitly account for spatial variation in the costs of conservation actions. Furthermore, many planning approaches assume that habitat protection is a preferred option, but they do not assess its value relative to other actions, such as restoration. We developed a case study to assess the implications of accounting for and ignoring spatial variation in conservation costs in optimizing conservation targets. We included assumptions about habitat loss to determine the extent to which protection or restoration would be necessary to meet an established population target. Our case study focused on optimal placement of grassland protection or restoration actions to influence bobolink Dolichonyx oryzivorus populations in the tallgrass prairie ecoregion of the north central United States. Our results show that not accounting for spatially variable costs doubled or tripled the cost of meeting the population target. Furthermore, our results suggest that one should not assume that protecting existing habitat is always a preferred option. Rather, our results show that the balance between protection and restoration can be influenced by a combination of desired targets, assumptions about habitat loss, and the relative cost of the two actions. Our analysis also points out how difficult it may be to reach targets, given the expense to meet them. We suggest that a full accounting of expected costs and benefits will help to guide development of viable management actions and meaningful conservation plans.

Keywords: landscape conservation planning; population objectives; landscape optimization

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Introduction

Strategic habitat conservation is a process used by the U.S. Fish and Wildlife Service (USFWS) to develop strategies for conserving wildlife populations and their habitats (USFWS 2008). This process can be thought of as an application of adaptive management (Walters 1986; Williams et al. 2009), in the sense that it is a cyclical learning process for making recurrent decisions under uncertainy. The strategic habitat conservation approach involves 1) establishing population objectives and apportioning them in space to guide conservation planning and management at scales relevant to decision makers (e.g., Adamcik et al. 2004; USFWS 2012), 2) developing spatially explicit models that estimate where those species occur on the landscape, and 3) developing tools to inform conservation planning and on-theground delivery. Managers then monitor the outcomes of management actions to test critical assumptions and address uncertainty.

Many optimization tools have been developed to guide land managers about how to best allocate effort to achieve objectives (e.g., Wilson et al. 2011). Similar approaches have been applied in ways that are consistent with the strategic habitat conservation framework (e.g., Thogmartin et al. 2014) and have relied on the use of readily available software tools such as Marxan (Ball et al. 2009) or Zonation (Moilanen et al. 2005). Such tools tend to acknowledge that species distributions and responses to management vary across the landscape. These tools also treat the issue of cost as a constraint, and in some cases that constraint is simply a limit on the number of management units or the amount of area that can be managed at any one time (e.g., Westphal et al. 2007; Thogmartin et al. 2014). Given that the costs of management likely vary across the landscape, not accounting for cost or for the variation in cost, may affect which management actions are selected as optimal.

This may have implications for the usefulness of planning tools that rely only on predictions of species or habitat distributions (e.g., Niemuth et al. 2009; Johnson et al. 2010). Including costs in such analyses can lead to more efficient strategies (e.g., Post van der Burg et al. 2014), but this may also depend on the range of actions considered. For example, some analyses focus only on the cost of protecting existing bird habitat (e.g., Walker et al. 2013), implying that habitat protection is the best action and may simply need to be done more efficiently. This may not be the case if the risk of losing existing habitat is fairly low or if restoration efforts are less expensive in some locations. In such cases, restoring habitat may be a more efficient option in meeting species population objectives.

Here, we describe a case study using an optimization approach to design a landscape in the tallgrass prairie ecoregion of the United States that meets a grassland bird species population objective, while accounting for spatial variability in the cost of conservation actions. Note that although we based the analysis in this paper on a real population objective, we did not intend for this analysis to provide a comprehensive guide for conserving grassland bird species. Instead, we simplified a grassland bird conservation problem to provide insight into the implications of including or ignoring the spatial variation in cost efficiency of conservation actions in achieving a population objective. We expected, based on previous work (e.g., Post van der Burg et al. 2014), that not including cost would affect where actions were applied on the landscape and would lead to more expensive conservation portfolios. In addition, we assessed whether a conservation portfolio that meets the objective requires more protection of existing habitat vs. restoration of habitat. Our assumption was that protection of existing habitat would make up a large portion of the optimal solution but that portion would be dependent on assumptions about the probability of habitat conversion. Based on these analyses, we discuss how our approach could be used to refine and expand an assessment that will provide a comprehensive analysis of landscape scale habitat conservation for grassland bird species.

Methods

Study area

Our case study focused on the tallgrass prairie ecoregion in the U.S. portion of Bird Conservation Region 11 (BCR 11; North American Bird Conservation Initiative 2000; Figure 1); this region includes Iowa, Nebraska, South Dakota, North Dakota, and Minnesota. The temperate grasslands composing much of the native grasslands in this region are among the most threatened and least protected habitat types in the world (Hoekstra et al. 2005). For BCR 11, conversion of native grasslands to agriculture tends to be due to the region's productive soils, combined with policy and economic drivers. These conditions seem to have contributed to a long-term decline in grassland bird populations (Brennan and Kuvlesky 2005).

Case study

Our case study simulated a management scenario in which a manager invested in grassland conservation actions that increased or decreased a grassland bird population. We chose to work with the bobolink Dolichonyx oryzivorus because Partners in Flight (Rosenberg et al. 2016) identifies it as a species of concern and a model is available to predict the effects of changing grassland distributions on its abundance (Drum et al. 2015). We assumed the management objective in this scenario was to meet a population target for bobolinks for the smallest budget possible. Because our case study used a grassland-dependent species, we assumed that grassland habitat was the major limiting factor on bobolink abundance. We assumed that there were only two conservation actions that could be invested in: "protection" (i.e., purchase of land) of existing grassland or "restoration" (i.e., replacement of cropland with restored grassland and protection). We further assumed



Figure 1. Map based on the North American Bird Conservation Initiative map of the tallgrass ecoregion portion of Bird Conservation Region 11 (North American Bird Conservation Initiative. 2000, see Supplemental Material Reference S3). The region includes Iowa, Nebraska, South Dakota, North Dakota, and Minnesota. This map summarizes land use in terms of existing protected and unprotected grassland (green), cropland (yellow), and other land cover types (white). We developed land cover categories from a modified version of the 2011 National Land Cover Dataset (Drum et al. 2015). The resolution of this this map is 16.19 ha.

that each action was applied to 16.19-ha (40-acre) management units, which closely approximated the scale of USFWS management activities in this region (D. Hertel, USFWS, personal communication). A management unit of this size is often the basis of decisions for the purchase of land or conservation easements. We assumed that if a management unit was cropland, a restoration and protection action could be applied; when the management unit was grassland, only a protection action could be applied.

Bobolink population objective and response to management

Aside from identifying species of concern, Rosenberg et al. (2016) also specified short- and long-term population objectives for the bobolink. They based these objectives on analyses of population trend data and a desire to maintain or alter the trends. For bobolinks, their objective is to increase the continental population by 5–15%. For our case study, we evaluated this range of increase within BCR 11. To predict the impact of conservation actions on bobolink abundance, we used a zero-inflated Poisson regression statistical model that predicts abundance of bird pairs in response to land cover by using a modified version of the National Land Cover Dataset at a 0.09-ha resolution (Drum et al. 2015). Drum et al. (2015) developed a series of candidate models for a range of grassland bird species and used a model selection approach to select the models for making predictions. These models contained combinations of climate and land cover variables. In the case of bobolinks, the zero-inflation portion of the model included the following land use variables: the proportion of seasonal wetlands within 800 m and the proportion of trees, grasslands, and cropland within 400 m. The abundance portion of the model included the proportion of seasonal wetlands within 1,600 m; the proportion of trees within 3,200 m; and the proportion of temporary wetlands and undisturbed grasslands within 400 m. Parameter estimates in the bobolink model showed that

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abundance was positively correlated with the proportion of grass and negatively correlated with the proportion cropland. Drum et al. (2015) cross-validated their bobolink abundance predictions against BBS data from the tallgrass portion of BCR 11 and found a high correlation between the two ($R^2 = 0.86$), which indicates the model may be useful for making predictions.

We modified the land cover dataset used in Drum et al. (2015) using multiple sources of information to identify grassland as accurately as possible (e.g., by incorporating spatial data from the U.S. Department of Agriculture's Conservation Reserve Program and from the USFWS). We reclassified grasslands as protected grasslands if they were under federal or state easements, federal or state ownership, or managed by a nongovernmental organization. We classified grasslands that were not under public management as unprotected. We then aggregated this dataset to the 16.19-ha scale, to match the scale of primary management units described above, by using a majority rule. The rule assigned the land cover state to each management unit based on the dominant land cover type in each unit. We scaled predictions using the zero-inflated model so that they estimated the number of birds per hectare. Because we rescaled the land cover dataset described above, we also had to rescale abundance predictions from the model by multiplying predictions by 16.19.

We assumed that only unprotected grasslands could be protected. We considered as candidates for a combination of restoration and protection the sites that were classified as cropland. We simulated the effect of protection actions by removing the risk of conversion. But because we did not know the risk of conversion, we created 11 different scenarios in which the probability of converting all existing unprotected grasslands ranged between 0 and 1 in steps of 0.1. Under each scenario, we multiplied the predicted abundance on unprotected grasslands by the probability of conversion. This represented expected abundance without protection. When the protection action was applied to a given location, we simulated the effect of protection by setting the probability of conversion to zero. For cropland units we simulated the effect of restoration actions by assuming the unit was immediately converted to grassland. Because we based our predictive model on the effect of land use in neighboring units, each change in a unit required updating the current prediction and recalculating bobolink abundance in neighboring units. We assessed these changes in terms of the local effect of grassland restoration on the immediate neighbors around the unit under management (i.e., units within 400 m).

Assessing the cost of conservation actions

For simplicity, we assumed that the cost of protecting existing grassland in a management unit would be proportional to the real estate value of cropped land in that unit. We used land values from 2009 to 2013 for Minnesota (University of Minnesota 2013) and Iowa (Duffy 2013) at the county level. We assumed that management units that fell in these counties all had the same dollar value. We were not able to obtain land values for the other states in our study. To estimate land values in these states, we developed a model that predicted county land values as a function of average county rental rates. We developed the model using average county rental rates over a 5-y period for counties in Iowa and Minnesota from 2009 to 2013 (U.S. Department of Agriculture 2015). We fit a linear model to our known land value estimates for the two states, with rental rates as the independent variable. We then used the model to predict county-level land values in the states where we had rental rate data, but not land values. We recognize that actual protection costs may be more or less depending on market changes, policy changes, and special agreements with private land owners, such as existing easements. In cropland management units, we assumed that the cost of grassland "restoration" was \$2,000 per unit, plus the cost of protection (i.e., the estimated land value); we estimated restoration costs based on conversations with USFWS personnel.

Optimization model

We used a marginal gain heuristic optimization method (van Teeffelen and Moilanen 2008; van Teeffelen et al. 2008) because of the dynamic aspect of the model (i.e., the effect of actions on neighboring units) and because there were more than 1 million management units to consider. Although such an approach is not guaranteed to find a truly optimal solution, as would linear or dynamic programming approaches (Loehle 2000), heuristic approaches have been shown to find reasonable solutions to large, complex, or otherwise intractable numerical problems (Moilanen 2008). We applied an algorithm to iteratively search through all possible combinations of management units and actions and then choose the combination that maximized an objective function. The algorithm builds the optimal solution by iteratively adding the next best decision to assemble the overall solution portfolio. Because the effect of any individual action (protection or restoration) can affect bird abundance estimates on neighboring units, and vice versa, we ran the models iteratively for each decision to evaluate the potential outcome for the landscape. The algorithm keeps selecting sites and actions until a conservation target or budget cap is reached. For this case study, we looked at choosing the set of units that met the population target for bobolinks for the least cost. So, given a set of units (x), the algorithm chooses a new unit and action (x_{kl}^*) that maximizes

$$\frac{V\left(\sum(x^*c) + x^*_{kl}\right) - V(\sum x^*c)}{\cot(x^*_{kl})}$$

where k represents the kth unit, l represents the lth action, c represents a conversion probability, and V represents



Figure 2. Map based on the North American Bird Conservation Initiative map of predicted average number of bobolink *Dolichonyx oryzivorus* pairs inside the tallgrass ecoregion portion of Bird Conservation Region 11 (North American Bird Conservation Initiative. 2000, see *Supplemental Material* Reference S3). The region includes Iowa, Nebraska, South Dakota, North Dakota, and Minnesota. We based the predictions on land cover variables developed from the 2011 National Land Cover Dataset (Drum et al. 2015). The scale on the right measures the number of bobolink pairs. The resolution for the map is 16.19 ha.

the value derived from applying the given action on the unit. There are numerous ways to define value; in this case, the value function was simply the total number of bobolink pairs that could be expected from a set of management actions. For our analysis, we considered 11 different conservation targets ranging from a 5% to a 15% increase (in steps of 1%) over the estimate of the total number of bobolinks in the tallgrass portion of BCR 11.

We developed our optimization algorithm in the C++programming language and implemented the preprocessing of model predictions and making final visualizations of the solution in the R programming environment (Code S1; Code S2; R Core Team 2017). We used the R package Rcpp (Eddelbuettel and François 2011) for the actual execution of the optimization algorithms. We ran 121 different scenarios: one for each unique combination of conservation target and conversion probability. To further assess the effect of cost, we also ran all 121 scenarios without cost in the objective function. Given the large volume of scenarios, we executed each run of the algorithm in parallel on the YETI high throughput computing system maintained by the U.S. Geological Survey.

Results

The portion of BCR 11 we used in our case study contained 3,016,611 16.19-ha parcels. Only 1,255,231 parcels were classified as cropland or grassland (i.e., units that could be managed). Cropland units made up 91% of the management units and unprotected grasslands made up the remaining 9% (Figure 1). Nonmanagement units were classified as protected grasslands, hay, seasonal wetlands, or trees, which were needed to apply the bobolink abundance model. Other land cover classes such as urban development or open water were removed from this analysis. Our estimate of bobolink pair abundance, using the current state of all parcels (Figure 2), was 6.43 million pairs, a value that is close to what Drum et al. (2015) predicted for the same region.

Our model for estimating land values suggested that crop rental rates were positively correlated with actual market land values (intercept: estimate = -788.04 [SE = 150.99]; slope = 37.06 [SE = 0.83]) and served to predict land values with reasonable accuracy ($R^2 = 0.88$). Our predictions of land values per management unit ranged from low (~US\$27,000) in states such as Minnesota to relatively high (>US\$300,000) in states such as lowa (Figure 3). This spatial variation in cost drove the



Figure 3. Map based on the North American Bird Conservation Initiative map summarizing predicted average market land values by county and per hectare for the period 2009–2013 inside the tallgrass ecoregion portion of Bird Conservation Region 11 (North American Bird Conservation Initiative. 2000, see Supplemental Material Reference S3). The region includes Iowa, Nebraska, South Dakota, North Dakota, and Minnesota. The scale on the right is in thousands of U.S. dollars and ranged from a minimum of \$27,160 to a maximum of \$386,480.

optimization algorithm to select less expensive actions in the northern part of BCR 11 (Figures 4a–d). Ignoring cost variation drove the algorithm to select actions in the southern and central parts of BCR 11 (Figures 4e–h) and led to an increase in the total cost of those portfolios (Figure 5). Increasing conservation targets also increased the relative cost of the portfolios, because more actions were needed to meet the target. But simply ignoring cost seemed to have a much stronger effect on the cost of conservation portfolios. In fact, a portfolio built without considering cost tended to be two to three times higher than a cost-efficient portfolio built to meet the same conservation target.

Changes in conversion probabilities also drove changes in both the selection of actions (Figure 4) and the costs of conservation portfolios (Figure 5). For a given level of conservation target, increasing the level of conversion probability increased the number of actions needed to meet the target (e.g., Figures 4a and b). Increasing the level of conversion probability seemed to have a larger effect on increasing conservation portfolio cost than did increasing the conservation target level (Figure 5). Increasing conversion probability led to an increase in the number of protected grasslands needed to meet the target (Figure 6). Increasing the target tended to decrease the relative percentage of protected grasslands in the portfolio because more restorations were needed to meet higher targets. It also seemed that there was a threshold in terms of when protecting grasslands became part of the portfolio. When cost was included in the objective function, the threshold conversion probability was around 0.2. Without cost, the threshold was around 0.6 (Figure 6).

Discussion

Our case study demonstrates the implications of accounting for spatial variability in conservation costs and the role that conversion probabilities play in optimizing landscape decisions about whether to protect existing habitat or restore habitat. Our results show that ignoring spatially variable costs will produce conservation portfolios that are two to three times more expensive than more cost-efficient portfolios. Furthermore, our results suggest that one should not assume that protecting existing habitat is always a preferred option. Rather, the balance between protection and restoration should be determined by a combination of desired targets, assumptions about conversion risk, and relative cost. We have demonstrated how one can account for



Figure 4. Maps based on the North American Bird Conservation Initiative map of optimal conservation investments to benefit bobolink *Dolichonyx oryzivorus* populations in the tallgrass ecoregion portion of Bird Conservation Region 11 (North American Bird Conservation Initiative. 2000, see Supplemental Material Reference S3). The region includes Iowa, Nebraska, South Dakota, North Dakota, and Minnesota. We based the initial state of these maps on the 2011 National Land Cover Dataset (Drum et al. 2015). These investments include restoring grassland habitat (red) on cropland (yellow) or changing existing unprotected grassland habitat



Figure 5. Total cost of conservation portfolios optimized to meet bobolink *Dolichonyx oryzivorus* population targets in the tallgrass ecoregion portion of Bird Conservation Region 11. The region includes Iowa, Nebraska, South Dakota, North Dakota, and Minnesota. We based the solutions on the 2011 National Land Cover Dataset (Drum et al. 2015). The plot on the left represents the cost of an optimal conservation portfolio under a cost-efficient objective function assuming various levels of a population target and probability of habitat conversion. The plot on the right measures the same as the left, but under a no-cost maximizing objective function. The scale on the far right is measured in billions of U.S. dollars.

these issues and meet a specific goal or target most efficiently by solving for the optimal combination of habitat protection and restoration at a large spatial scale. Such landscape planning approaches have been promoted by the USFWS, as well as some landscape conservation cooperatives (Millard et al. 2012), but technical guidance has been limited regarding how to rigorously create large scale plans. We suggest that optimization tools that link conservation delivery decisions with management objectives and costs are an important set of tools to guide conservation planning over large areas.

The spatial configuration of decisions modeled in our case study was influenced by the cost of land across BCR 11, which was also broadly correlated with the amount of protected and unprotected grassland currently remaining. In turn, the cost of land likely reflects the value of that land for agricultural production. Our results suggest that focusing on areas where land is less productive may provide more potential for the successful delivery of conservation. However, to make this statement more meaningful, one would need to understand the success rate of conservation actions on less productive lands. Although we did not consider the likelihood of management success, the distribution of conservation effort from our model suggests that setting goals based on administrative units (e.g., wetland management districts) may not be as cost efficient when

considered in a broader context. That is, setting targets for administrative units within the larger BCR may lead to less cost-efficient outcomes if one is forced to meet conservation targets in portions of the landscape where costs are higher and likelihood of success is lower.

However, this also suggests that one may need to consider landscape-scale population targets more broadly in terms of agency management goals (i.e., spreading effort among administrative units) and larger societal goals. Targets are a useful tool for decision makers because they are easily communicated, promote transparency and accountability, and can integrate biological assumptions about sustainability and social values (Carwardine et al. 2009). For the bobolink, the conservation targets we used were developed based on subjective values about desired future continental bobolink populations (Rosenberg et al. 2016). In our case study, we focused only on this species, but certainly conservation is a multi-objective affair that combines biological and societal objectives. Thus, much like cost and conversion risk, we expect that a more comprehensive inclusion of additional objectives would change the optimal solution for bobolink conservation, as well as other grassland bird species.

For example, Klein et al. (2008) demonstrated the use of Marxan for designing marine reserves for preserving biological features while trying to minimize negative

⁽green) to protected grassland (blue). Maps a-d represent solutions developed under a cost-efficient objective function, and maps e-h represent solutions developed under a no-cost maximizing objective function: maps a and e, 5% population target, 0.0 conversion risk; maps b and f, 5% population target, 1.0 conversion risk; maps c and g, 15% population target, 0.0 conversion risk; and maps d and h, 15% population target, 1.0 conversion risk. The inset in the lower right corner shows the relative location of Bird Conservation Region 11.



Figure 6. Optimal proportion of grassland protection actions in conservation portfolios optimized to meet bobolink *Dolichonyx oryzivorus* population targets in the tallgrass ecoregion portion of Bird Conservation Region 11. The region includes Iowa, Nebraska, South Dakota, North Dakota, and Minnesota. We based the solutions were based on the 2011 National Land Cover Dataset (Drum et al. 2015). The plot on the left represents the optimal proportion under a cost-efficient objective function assuming various levels of a population target and probability of habitat conversion. The plot on the right measures the same as the left, but under a no-cost maximizing objective function. The scale on the far right is measured as the proportion of total actions invested in grassland protection.

effects on the commercial and recreational fishing industry. They showed that inclusion of other stakeholder objectives changed the optimal solution but resulted in a solution that met their biodiversity objectives with less of an impact to socioeconomic objectives. They argued that such an approach would be more acceptable to the fishing industry, because that industry's concerns were included in the analysis. A more comprehensive approach to multi-objective conservation in BCR 11 would likely include land owner values (e.g., increasing agricultural production) because, as our results suggest, land value plays such an important role in driving optimal habitat conservation decisions. An optimization approach such as the approach presented here could then be used to assess the trade-offs between these objectives and ultimately to find an efficient solution that balances these values.

Such an analysis could be used to construct a solution that is more reflective of multiple stakeholder values and maybe more acceptable to a broader constituency. However, this does not necessarily guarantee that the solution would be easy to implement or be financially feasible. In our analysis, the high cost of conservation portfolios is driven by the fact that our function requires meeting a target. This all-or-nothing approach may be unrealistic. A more effective way to represent conservation objectives may be to develop functions that measure the relative preferences of smaller changes in objectives in a continuous way. Numerous examples of approaches like this exist in the literature (e.g., Arponen et al. 2005; Gregory et al. 2012) that may allow for analyses of trade-offs under realistic budget conditions. In addition, using such functions along with a temporally explicit optimization framework (e.g., Moilanen and Cabeza 2007) may allow for analyses that account for diminishing returns in the future.

Our case study also made fairly simplistic assumptions about conversion risk, namely, that conversion risk was uncertain but spatially and temporally static. The reality is that the risks to wildlife populations, especially changes in land use and habitat conversion, are dynamic over both space and time (Rashford et al. 2011; Lipsey et al. 2015). In the region we chose for our analysis, much of the landscape is already altered. So, the importance of remaining unprotected habitat is potentially higher than in a landscape with a higher proportion of remaining habitat. But the relative importance of remaining habitat is also likely influenced by the probability that it will remain on the landscape. In fact, our results show that a higher conversion probability drove the optimization algorithm to choose more unprotected grassland. This happens because a higher conversion probability reduces the amount of contribution each unit provides to the objective function, effectively increasing the marginal gain from protecting grasslands. Depending on which objective function one uses, the point at which conversion probability starts to drive the algorithm to select protection actions changes. For our case study, this seemed to be driven by the relative costs of these actions. Under the no-cost objective function and low conversion probability, only restoration actions are chosen because they produce the highest abundances. Once the conversion probability reaches about 0.60, the marginal gain of protection increases enough to make protection valuable. Under the cost-effective objective function, the lower cost of protection actions makes the marginal gain of protection more valuable under lower conversion probabilities. Clearly, this is because the marginal gain of protection is higher on cheaper units. We were not able to incorporate variable estimates for conversion risk in our model within the timeframe of this project. However, approaches have been developed that could be used in future development of this approach (e.g., Stephens et al. 2008; Rashford et al. 2011). There have been numerous approaches suggested that can accommodate these dynamic changes and effectively order conservation actions temporally (Nicol and Chades 2011; Lipsey et al. 2015), and some could be incorporated into the marginal gain heuristic approach that we used in our case study (Moilanen and Cabeza 2007).

The static nature of the solution we found for bobolinks also makes an implicit assumption that all management units were available for conservation at any given time. This may be unrealistic if at least some conservation is focused on unplanned opportunities to implement certain actions (e.g., a land owner decides to enroll in a conservation program). Our results suggest that although these types of opportunities should not be ignored, they must be evaluated in the context of a larger conservation picture to ensure efficiency. Our approach did not evaluate the willingness of land owners to sell land for bobolink habitat conservation, but Knight et al. (2011) showed that ignoring the probability of this willingness reduced the ability to meet conservation targets. Incorporating the likelihood of adopting a conservation program would be an additional improvement in our modeling approach. Efficient solutions could result from incorporating private land conservation programs that result in habitat but may not require the full cost of acquisition. The relative importance of such programs may also vary depending on how much remaining habitat is still in the landscape. The area in our case study has already been largely modified, but meeting conservation objectives in other regions that have large portions of remnant habitat may be less expensive and may require less land be put into conservation programs.

Despite the limitations we point out, our model shows what the optimal combination of restoration and protection actions looks like when considered together in a spatial context. Whether cost was included or not, the optimal solutions for bobolink populations resulted in clusters of connected grassland habitat, which was a function of how the statistical model predicted species response to landscape configurations as well as the clustered relative costs of conservation actions. This is an important feature to mention because some landscape planning approaches focus on connectivity as a management objective. This focus may be potentially misleading since species populations likely respond to the amount and quality of habitat, rather than connectivity per se (Hodgson et al. 2009). In our analysis, we let the optimization algorithm choose how connected resulting habitat needed to be to meet an expected population size, rather than make connectivity the objective.

In summary, our results suggest that meeting grassland bird population targets in intensively farmed landscapes may require large budgets and extensive land bases, in large part because of losses of habitat that have occurred over the past century. Furthermore, our results show the implications of not considering the expense of meeting targets or how to most efficiently reach those targets. Our analysis points out how difficult it may be to reach targets, given the cost to meet them. This does not mean that optimizing over large landscapes is futile, but rather that accounting for expected costs and benefits allows planners to understand the full extent of resources needed to meet population objectives. Additional societal benefits could be incorporated iteratively over time as a form of adaptive management. Optimization techniques can serve to integrate multiple objectives and develop costefficient solutions for complex problems. Being able to accommodate such complexities will likely be important for more comprehensive conservation planning efforts in the future.

Supplemental Material

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Code S1. R code implementing a simple example of a marginal gain optimization algorithm. We derived the simple example from a larger analysis focused on optimizing the number of bobolink *Dolichonyx oryzivorus* pairs inside the tallgrass ecoregion portion of Bird Conservation Region 11 located in the northern portion of the central United States. (The region includes lowa, Nebraska, South Dakota, North Dakota, and Minnesota). We based the predictions used in the example on land cover variables developed from the 2011 National Land Cover Dataset (Drum et al. 2015).

Found at DOI: https://doi.org/10.3996/102016-JFWM-080.S1 (4 KB TXT).

Code S2. C+++ code used in a simple example of a marginal gain optimization algorithm. We derived the simple example from a larger analysis focused on optimizing the average number of bobolink *Dolichonyx oryzivorus* pairs inside the tallgrass ecoregion portion of Bird Conservation Region 11 located in the northern portion of the central United States. (The region includes lowa, Nebraska, South Dakota, North Dakota, and Minnesota). We based the predictions used in the example on land cover variables developed from the 2011 National Land Cover Dataset (Drum et al. 2015).

Found at DOI: https://doi.org/10.3996/102016-JFWM-080.S2 (4 KB TXT).

Reference S1. Adamcik RS, Bella ES, DeLong DC Jr, Schomaker JH, Hamilton DB, Laubhan MK, Schroeder RL. 2004. Writing refuge management goals and objectives: a handbook. Washington, D.C.: U.S. Fish & Wildlife Service.

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